Diss. ETH Nr. 7097

FIELD STUDIES ON THE ECOLOGICAL ROLE OF THE SPIDERS AS INSECT PREDATORS IN AGROECOSYSTEMS (ABANDONED GRASSLAND, MEADOWS, AND CEREAL FIELDS)

THESIS
submitted to the
SWISS FEDERAL INSTITUTE OF TECHNOLOGY
ZURICH

for the degree of Doctor of Natural Sciences

presented by
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aku-Fotodruck Zürich
1982

To my parents

ACKNOWLEDGEMENTS

Professor Dr. G. Benz, Head of the Dept. of Entomology, Swiss Federal Institute of Technology, Zurich, proposed the interesting theme of this thesis and supervised it very critically and helpfully.

Professor Dr. M. Schaefer, Dept. of Zoology II, University of Göttingen, Federal Republic of Germany, served as a co-referee.

Professor Dr. W.H. Whitcomb, Dept. of Entomology and Nematology, University of Florida, Gainesville, also served as a co-referee.

Lecturer Dr. K. Thaler, Dept. of Zoology, University of Innsbruck, Austria, checked my spider identifications and determined a few "difficult species".

Professor Dr. W. Sauter, Dept. of Entomology, Swiss Federal Institute of Technology, Zurich, gave me the permission to deposite specimens of all spider species, described in this thesis, in the Entomological Collection.

Professor Dr. H.U. Thiele, Dept. of Zoology, University of Köln, Federal Republic of Germany, determined Carabidae.

Professor Dr. H.J. Müller, Dept. of Biology, University of Jena, German Democratic Republic, identified cicadas.

Lecturer Dr. W. Dunger, State Museum of Natural Science, Görlitz, German Democratic Republic, carried out the determinations of Collembola.

Dr. W. Eglin, Natural History Museum Basel, Switzerland, identified Chrysopidae.

Dr. W. Meier, Swiss Federal Research Station for Agronomy Zurich-Reckenholz, determined aphids.

Dr. L. Gerig, Bee section, Swiss Federal Dairy Research Institute Liebefeld-Bern, identified bees.

Dr. A. Nadig, Chur, Switzerland, carried out determinations of grasshoppers.

Mr. A. Fraser, School of Biological Sciences, University of East Anglia, Great Britain, gave to me informations on the ecology of spiders in English cereal fields.

Professor Dr. F. Klötzli and Lecturer Dr. A. Gigon, Geobotanical Institute, The Rübel Foundation, Swiss Federal Institute of Technology, Zurich, gave to me informations on grasslands near Zurich.

Dr. F. Weilenmann, Swiss Federal Research Station for Agronomy Zurich-Reckenholz, allowed me to undertake studies in cereal fields of the research station.

Miss C. Vernazza was very helpful in translating this thesis, and Mrs. H. Müller and Mrs. S. Lauber were typing it.

The author is very grateful to all these persons.

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

CONTENTS

ABSTRACT

From 1976-1979, the ecology of spiders was investigated in abandoned grasslands, cultivated meadows and cereal fields near Zurich (Switzerland). The spiders of such ecosystems live in two strata, (1) on the ground surface, (2) in the vegetation zone. Different spider communities are found in the two strata.

In abandoned grasslands, the spiders live undisturbed all year round. They can therefore build up relatively large populations in these biotopes (near Zurich about 10 spiders/m^2; significantly higher values are reported in literature). Cultivated fields, on the other hand, are periodically mown, whereby the living space and the egg sacs of many spiders are destroyed. Only relatively small spider populations live therefore in the vegetation zone of cultivated fields (about 1 spider/m^2 in cultivated meadows and 0.1-0.6 spiders/m^2 in cereal fields). The ground surface of cultivated fields is rather densely populated (15-42 spiders/m^2 in cultivated meadows and 10-50 spiders/m^2 in cereal fields).

The spiders in the vegetation zone of cultivated meadows and cereal fields are primarily predators of Diptera and Homoptera. In the vegetation zone of abandoned grasslands, in addition honey bees and/or grasshoppers can form an essential part of the prey biomass of large web-building spiders. On the ground surface of cultivated meadows and cereal fields, the predominant spiders are mainly predators of small, soft-bodied insects (Collembola, Diptera, aphids etc.). From the food analyses it follows that the spiders are predators of pest insects (e.g. cereal aphids), indifferent species (most Diptera), and of beneficial arthropods as well (honey bees, Chrysopidae, Coccinellidae etc.).

The energy flow (prey killed) through the spider communities of the vegetation zone of abandoned grasslands can be high, e.g. >900 MJ/ha/year in a megaphorbe meadow. In comparison, the energy flow through the spider communities of cultivated fields is significantly lower, e.g. 1.1-6.5 MJ/ha/year in cereal fields, and ≤ 0.5 MJ/ha/year in maize fields. The energy flow through the ground-dwelling spider communities of cultivated fields should amount to about 10-50 MJ/ha/year.

Abandoned grasslands often are veritable spider paradises. In these ecosystems, the spiders of the vegetation zone represent an important predator group. In the vegetation zone of cereal fields, on the contrary, spiders do not seem to play a significant ecological role. Further studies will show, to what extent the ground-dwelling spiders in cultivated meadows and cereal fields are of ecological importance.

1. INTRODUCTION

Spiders are among the most dominant insect predators of terrestrial ecosystems (TISCHLER, 1965; VAN HOOK, 1971; MOULDER & REICHLE, 1972; SCHAEFER, 1974a; EDWARDS et al., 1976, a.o.). Under favorable conditions they can reach maximal densities of up to 1000 individuals/m^2 approximately (PEARSE, 1946; DUFFEY, 1962; WEIDEMANN, 1978). It has therefore been supposed for some time that spiders play an important role as stabilizing agents and/or regulators of insect populations in agroecosystems, forest ecosystems and other terrestrial ecosystems.

During the last 20 years, numerous studies on the spider fauna in agricultural biotopes have been published all over the world. Tables 1-4 give a review classified according to continents and countries: Table 1 for Europe, including the U.S.S.R., Table 2 for America, Table 3 for Asia and Table 4 for Africa and the Oceanic-Australian region.

In spite of the large number of existing studies the significance of the spiders as insect predators in agroecosystems is still largely unknown. This could be attributed to the fact that up to the present most stuies were limited either to the investigation of the species composition and the seasonal occurrence of spiders in the field (sweep net and pitfall trap collections) or to measurements of respiration, food consumption tests, and prey preference trials in the laboratory. However, the results of investigations on the nutrition of spiders in the laboratory cannot readily be transferred to field conditions, because to some extent spiders behave differently in the laboratory than in the field. In the laboratory, spiders consume considerably more prey than would be available under natural conditions (MIYASHITA, 1968a, b; HAGSTRUM, 1970; KESSLER, 1973; BREYMEYER & JÓŹWIK, 1975). Moreover, the prey composition established by means of prey preference tests often does not correspond to the prey composition realized in the field. Pest insects which are regularly preyed on by a spider species in the laboratory may be entirely missing in the prey composition of the field (temporal and/or spatial isolation of predator and prey). Therefore the results of faunistic field studies and of nutritional analyses in the laboratory cannot be combined to a genuine whole. There is a great danger that speculations disregarding this ambiguity lead to wrong results. Correspondingly, the opinions on the ecological relevance of spiders differ widely. BRISTOWE (1958) for instance estimates for Great Britain: "Even if we were so cautious as to attribute a hundred victims in the year to each spider, I calculate with a very conservative estimate of the spider population for the country as a whole that the weight of insects consumed annually in Britain exceeds that of the human inhabitants". The Canadian ecologist TURNBULL (1973) gives an even higher estimate: "I have calculated from 37 published censuses of spider populations that the mean density of spiders in a large variety of environments was 130.8 spiders/square meter, or 1 308 000/hectare. If the food consumption of A. argentata were representative of that of all spiders (which it is not), the average total weight of food consumed per year by spiders would be ..... 42 490 kg/hectare". Referring to these computations FOELIX (1979) wrote: "However impressing these

Table 1. List of literature on the spider faunas in agroecosystems in Europe, including the U.S.S.R.

Country	Agroecosystem	Authors
Austria	meadows	LUHAN (1979) THALER et al. (1977, 1978)
	arable land	THALER & STEINER (1975) THALER et al. (1977)
	orchards	PÜHRINGER (1982)
Belgium	cereals	DE CLERCQ (1979) COTTENIE & DE CLERCQ (1977)
	diverse crops	BOSMANS & COTTENIE (1977)
Bulgaria	pasture	DELCHEV & KAJAK (1974)
Czechoslovakia	pasture	POLENEC (1968)
	alfalfa	MILLER (cit. LUCZAK, 1979)
	sugar-beet	MILLER (1974)
Federal Republic of Germany	meadows	BONESS (1953) SCHAEFER & HAAS (1979)
	clover	BONESS (1958)
	alfalfa	BONESS (1958)
	cereals	BASEDOW (1973) BASEDOW & MIELKE (1977) BRASSE (1975)
	asparagus	DINGLER (1935)
	vineyard	KIRN (1978)
	orchards	KRAEMER (1961) NATON (1976)
	diverse crops	HEYDEMANN (1953) TISCHLER (1958)
Finland	leys	HUHTA & RAATIKAINEN (1974)
	cereals	HUHTA & RAATIKAINEN (1974) RAATIKAINEN & HUHTA (1968)
France	alfalfa	CHAUVIN (1960, 1967)
German Democratic Republic	meadows	BEYER (1981) MÜLLER et al. (1978)
	grass-clover mixture	BEYER (1981)
	alfalfa	GEILER (1963)
	cereals	BEYER (1981) DIETRICH & GÖTZE (1974)

Table 1 (contin.). List of literature on the spider faunas in agroecosystems in Europe, including the U.S.S.R.

Country	Agroecosystem	Authors
German Democratic Republic	rape	BEYER (1981)
	sugar-beet	BEYER (1981)
	kohlrabi	BEYER (1981)
	marrowstem kale	BEYER (1981)
Great Britain	pasture	CHERRETT (1964) DUFFEY (1962)
	meadows	DUFFEY (1974)
	cereals	FRASER (1982) LOCKET (1978) VICKERMAN & SUNDERLAND (1975)
	potato	DUNN (1949)
	orchards	CHANT (1956)
Hungary	alfalfa	BALOGH & LOKSA (1956)
Norway	strawberry	TAKSDAL (1973)
Poland	pasture	DELCHEV & KAJAK (1974)
	meadows	BREYMEYER (1967) KAJAK (1960, 1962, 1971, 1978, 1980) KAJAK & JAKUBCZYK (1975) KAJAK et al. (1968, 1971)
	alfalfa	LUCZAK (1975)
	cereals	LUCZAK (1974, 1975, 1976, 1979)
	potato	CZAJKA & KANIA (1976) GALECKA (1966) LUCZAK (1974, 1975, 1976, 1979)
	sugar-beet	CZAJKA & GOOS (1976) GOOS (1973)
Sweden	strawberry	ALMQUIST (1981)
Switzerland	meadows	BENZ & NYFFELER (1980) MAURER (1974, 1975) NYFFELER & BENZ (1979b, 1981e)
	cereals	NYFFELER & BENZ (1979a) NYFFELER & BENZ (1980a) NYFFELER & BENZ (1981e)
	rape	NYFFELER & BENZ (1979a)
U.S.S.R.	meadows	VILBASTE (1965)
	cereals	ASHIKBAYEV (1973)
	potato	KOVAL (1976)

Table 2. List of literature on the spider faunas in agroecosystems in America.

Country	Agroecosystem	Authors
Brazil	sugarcane	BARBOSA et al. (1979)
Canada	overgrazed pasture	TURNBULL (1966)
	meadows	DONDALE (1971, 1977) DONDALE & BINNS (1977) DONDALE et al. (1970, 1972) FOX & DONDALE (1972)
	wheat	DOANE & DONDALE (1979)
	orchards	DONDALE (1956, 1958) DONDALE et al. (1979) PUTMAN (1967) PUTMAN & HERNE (1966)
Panama	seed reservation	BREYMEYER (1978)
	pasture	BREYMEYER (1978)
	banana plants	HARRISON (1968)
Peru	cultivated fields	AGUILAR (1965)
	cotton	AGUILAR (1974)
U.S.A.	pasture	HOWARD & OLIVER (1978) PECK & WHITCOMB (1978) WHITCOMB et al. (1963a) WOLCOTT (1937)
	maedows	WOLCOTT (1937)
	alfalfa	HOWELL & PIENKOWSKI (1971) MUNIAPPAN & CHADA (1970b) SCHLINGER & DIETRICK (1960) WHEELER (1973) YEARGAN (1975a,b) YEARGAN & COTHRAN (1974a,b) YEARGAN & DONDALE (1974)
	cereals	HORNER (1972) MUNIAPPAN & CHADA (1970a)
	grain sorghum	BAILEY & CHADA (1968)
	sweet corn	EVERLY (1938)
	rice	WOODS & HARREL (1976)
	soybeans	BLICKENSTAFF & HUGGANS (1962) CULIN & RUST (1980) DEITZ et al. (1976) LESAR & UNZICKER (1978a,b) TURNIPSEED (1975) WHITCOMB (1980)

Table 2 (contin.). List of literature on the spider faunas in agroecosystems in America.

Country	Agroecosystem	Authors
U.S.A.	cole	PIMENTEL (1961)
	guar	ROGERS & HORNER (1977)
	sugarcane	HENSLEY et al. (1961) NEGM & HENSLEY (1969)
	cotton	BURLEIGH et al. (1973) CLARK & GLICK (1961) DORRIS (1970) JOHNSON et al. (1976) KAGAN (1943) LEIGH & HUNTER (1969) LOCKLEY et al. (1979) McDANIEL & STERLING (1979) PFRIMMER (1964) PIETERS & STERLING (1974) SHEPARD & STERLING (1972) STAM et al. (1978) WHITCOMB & BELL (1964) WHITCOMB & TADIC (1963) WHITCOMB et al. (1963a,b)
	citrus	CARROLL (1980) MUMA (1973, 1975)
	orchards	LEGNER & OATMAN (1964) McCAFFREY & HORSBURGH (1978, 1980) SPECHT & DONDALE (1960)
	diverse crops	BILSING (1920) WHITCOMB (1974, 1975)

Table 3. List of literature on the spider faunas in agroecosystems in Asia.

Country	Agroecosystem	Authors
India	maize	SHARMA & SARUP (1979) SINGH & SANDHU (1976)
	rice	KALODE (1976) SAMAL & MISRA (1975)
	cotton	BATTU & SINGH (1975)
	citrus	SADANA & KAUR (1974)
	grapevines	SADANA & SANDHU (1977)
Israel	citrus	SHULOV (1938)
	apple orchards	MANSOUR et al. (1980a,b,c) MANSOUR et al. (1981)
Japan	rice	HAMAMURA (1969, 1971) HASHIMOTO (1974) HIRANO & KIRITANI (1976) ITÔ et al. (1962) KAKIYA & KIRITANI (1976) KANG & KIRITANI (1978) KAWAHARA (1975) KAWAHARA & KIRITANI (1975) KAWAHARA et al. (1969, 1971) KIRITANI (1977, 1979) KIRITANI & KAKIYA (1975) KIRITANI & KAWAHARA (1973) KIRITANI et al. (1972) KOBAYASHI (1975, 1977) KOBAYASHI & SHIBATA (1973) KOYAMA (1972, 1975, 1976) MIYAI et al. (1978) OKUMA (1974, 1977) SASABA & KIRITANI (1974) SASABA et al. (1970) SASABA et al. (1973a,b) SUZUKI & KIRITANI (1974) TANAKA (1973, 1975) TANAKA & HAMAMURA (1968) TOYODA & YOSHIMURA (1966) YAGINUMA (1965) YAMANO (1977)
	cabbage	KAYASHIMA (1960) SUZUKI & OKUMA (1975)
	taro	NAKASUJI (1976)

Table 3 (contin.). List of literature on the spider faunas in agroecosystems in Asia.

Country	Agroecosystem	Authors
Japan	tea	KAIHOTSU (1979) TERADA (1977) TERADA et al. (1978)
	mulberry	KAYASHIMA (1967, 1972)
	citrus	KAIHOTSU (1979) NOHARA & YASUMATSU (1965)
	orchards	HUKUSIMA (1961) HUKUSIMA & KONDO (1962) OKUMA (1973)
Korea	rice	CHOI et al. (1978) HOKYO et al. (1976) OKUMA et al. (1978) PAIK & KIM (1973) PAIK et al. (1974)
	mulberry	PAIK et al. (1973)
People's Republic of China	rice	ANONYMOUS (1979)
Philippines	rice	GAVARRA & RAROS (1975) IRRI Ann. Report (1973, 1974) IRRI Ann. Report (1976, 1977) IRRI Ann. Report (1978) LUCERO & RAROS (1975) SALINAS & RAROS (1975)
Taiwan	rice	CHIU et al. (1974) CHU & OKUMA (1970) CHU & WANG (1972, 1973) CHU et al. (1975, 1976a,b,c) CHU et al. (1977)
Thailand	rice	OKUMA (1968) OKUMA & WONGSIRI (1973)

Table 4. List of literature on the spider faunas in agroecosystems in Africa and in the Oceanic-Australian region.

Country	Agroecosystem	Authors
Australia	cotton	BISHOP (1979, 1980, 1981) BISHOP & BLOOD (1980) ROOM (1979)
	orchards	DONDALE (1966) MacLELLAN (1973)
Egypt	clover	NEGM et al. (1975)
	cotton	WIESMANN (1955)
	granati trees	TEMERAK (1981)
Fiji Islands	coconut	TOTHILL et al. (1930)
New Guinea	coffee	ROBINSON & ROBINSON (1974)
South Africa	strawberry	DIPPENAAR-SCHOEMAN (1976, 1979a,b)

estimates may be, it would certainly be misleading to deduce from them that spiders play a significant role in pest control".

In order to understand the effectiveness of spiders on the population dynamics of insects, the species composition and the seasonal abundance of the spiders as well as their prey must be known. In every ecosystem there are diverse spider species and numerous prey species. According to the rules of combinatorics an enormous number of potential predator-prey interactions results from this fact, and a considerable part of them is realized. To evaluate the ecological importance of the spiders as insect predators, the predator-prey relations should be known. For this purpose, the prey compositions and the feeding rates of the different spiders should be determined in the field. Finally, the ecological significance of spiders could only be entirely appreciated, if the ecological importance of the prey insects were known as well. However, only a few studies give quantitative information on the spiders' prey in the field (e.g. BILSING, 1920; TURNBULL, 1960; KAJAK, 1965a, b; ROBINSON & ROBINSON, 1970, 1974; SCHAEFER, 1974a; TURNER, 1979). The lack of such studies on the feeding ecology of the majority of the spider species of whole ecosystems is probably due to the fact that up to now only few arachnologists have taken the trouble of observing several spider species in the field while they are feeding, as such observations require much time and patience.

The present study on the ecology of spiders in cereal fields, cultivated meadows and abandoned grasslands near Zurich should at least in part fill this gap. In the course of the investigations the following questions have been asked:

(1) Which spider species feed in meadows and cereal fields (species composition)?

(2) How many spiders per unit area feed in meadows and cereal fields (abundance of spiders)?

(3) Does the abundance of spiders change in the course of the year (seasonal abundance)?

(4) Where within the meadows and cereal fields do the spiders feed (horizontal and vertical distribution)?

(5) At which time of day do the spiders feed (diurnal rhythms)?

(6) Which strategies use the spiders to catch their prey (hunting strategy)?

(7) What is the prey composition?

(8) How much prey per time unit do the spiders catch (prey capture rate)?

From points 1-5 and 8 can be deduced to what extent the spider populations exert a predatory pressure on the insect populations, as these points supply information on the temporal and spatial distribution of the predatory pressure and on the energy flow through the spider communities. From points 6 and 7 can be gathered on which insect groups (pest species, beneficial species, indifferent species) the spiders act as predators.

As mentioned before, numerous different spider-prey interactions are possible in an agroecosystem. Therefore, since even the gathering of the data necessary for the evaluation of the interaction of just one spider species with one prey species needs much time, the investigation of all predator-prey interrelations within an ecosystem would far exceed the scope of a doctoral thesis.

The investigation of the population biology and feeding ecology of the diverse spider species varies in difficulty. For the vagrant hunting spiders (e.g. Lycosidae, Salticidae) the stationary population densities and the feeding ecology can be established only with great difficulty. Because of their extraintestinal digestion it is not possible, for instance, to carry out stomach content analyses as for birds, reptiles, amphibians and fishes. Hunting spiders must therefore be observed in the field during long periods of time. On the other hand, the population densities and feeding ecology of most web-building spiders can be determined relatively easily, as many ecological processes take place in the easily observable webs. For this reason, mostly web-building spiders have been observed.

2. MATERIALS AND METHODS

2.1. Study area

The investigations were conducted in meadows and cereal fields on the outskirts of the city of Zurich in the years 1976-1979. The study area covers approximately 40 km^2 of agricultural farmland at 395-600 metres above sea level (Fig. 1), 41% of it being arable land and 53% meadows. On the cultivated area the following crops were grown: Wheat, barley, rye, oats, maize, rape, sugar beet, field beans and vegetables. In 1975, the cereals (excluding maize) occupied about 54%, maize (grain, silage and green maize) about 13% of the tilled area.

The study area is located in the transition zone between the Western European oceanic climate and the Eastern European continental climate. Zurich (47.2° northern latitude) has a mean annual temperature of 8.8°C and an annual variation of temperature of 17.8°C. Table 5 gives informations on the temperature and precipitation conditions during the four years of the study. All climatic values were furnished by the Swiss Meteorological Institute (Weather station Zurich).

2.2. Biotopes studied

From 1976 to 1979, studies were made in abandoned grassland biotopes, cultivated meadows and cereal fields on the outskirts of the city of Zurich. The term "cultivated meadow" was used to express a contrast to the "uncultivated meadow-land" (megaphorbe meadow A1, dry meadow A2). "Abandoned grasslands" means formerly cultivated land which for any reason has not been tilled, fertilized or mown for some time or is altogether abandoned. The biotopes are described in Tables 6-7.

The locations of the cultivated meadows where the studies were carried out are described in Table 8. Most cultivated meadows in the region of Zurich are fertilized and mechanically mown several times a year.

The wheat, barley, rye, oat, and maize fields investigated are briefly characterized in Table 9. The areas of the cereal fields ranged from 0.5 to 3 ha. They are not treated with insecticides in the region of Zurich. However, herbicides are used in the maize fields. Pitfall trap studies were made in winter wheat fields on the territory of the Swiss Federal Research Station for Agronomy at Zurich-Reckenholz.

2.3. Methods of investigation

2.3.1. The family and species composition of the spiders

2.3.1.1. Direct observations in the vegetation zone of cereal fields

The cereal fields were visited periodically. The composition of the foliage-dwelling spider fauna was investigated by direct observations. All observation data were recorded. Of some species, only the genus could be ascertained by this procedure.

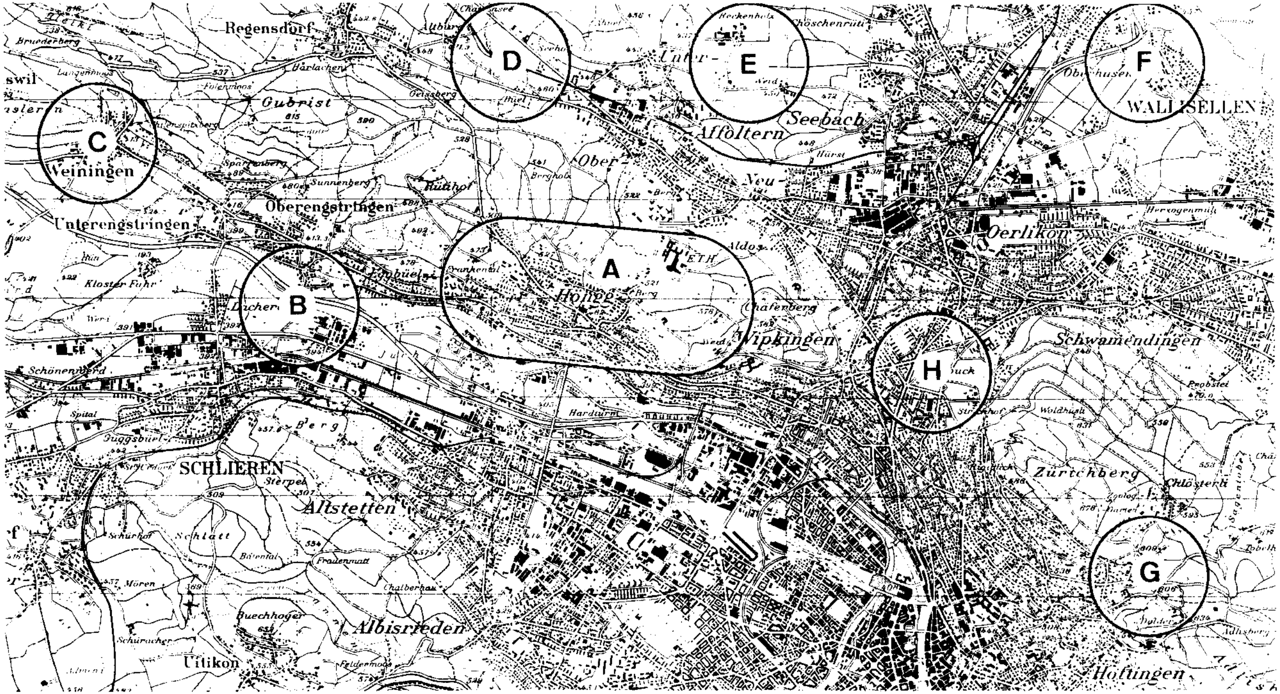

Fig. 1. View of the study area (scale 1:75'000): A = Höngg, B = Oberengstringen/Schlieren, C = Weiningen, D = Regensdorf/Affoltern, E = Swiss Fed. Res. Stat. Reckenholz, F = Opfikon, G = Fluntern, H = Unterstrass.

Table 5. Mean values of the air temperatures and precipitations measured at the Weather Station Zurich from January 1976 to December 1979 as well as the climatological normals for the region of Zurich.

Month		J	F	M	A	M	J	J	A	S	O	N	D
Temperature	(°C)												
Monthly mean	1976	1.3	1.1	3.7	8.1	13.4	18.2	19.0	15.7	12.6	10.5	4.5	-1.6
Monthly mean	1977	0.7	4.8	7.6	6.4	11.7	15.2	17.1	15.9	12.6	10.8	5.2	1.6
Monthly mean	1978	0.1	-0.4	4.9	7.3	10.9	14.3	16.3	15.6	13.3	8.3	3.3	1.8
Monthly mean	1979	-2.9	2.0	5.1	6.1	12.4	16.1	17.2	15.6	13.8	9.7	3.7	3.8
Mean	1931-1960	-1.1	0.3	4.5	8.6	12.7	15.9	17.6	17.0	14.0	8.6	3.7	0.1
Precipitation	(mm)												
Monthly totals	1976	54.0	42.0	12.9	56.7	80.8	34.1	228.4	118.3	103.5	61.9	58.9	110.7
Monthly totals	1977	80.9	139.4	71.8	165.7	75.5	122.4	122.2	104.1	57.3	74.0	89.5	67.5
Monthly totals	1978	65.9	127.5	145.8	47.9	135.7	136.2	100.0	179.4	51.6	102.8	16.5	95.3
Monthly totals	1979	74.3	88.2	137.6	100.8	48.4	124.9	70.6	108.3	95.6	87.5	148.2	99.8
Mean	1931-1960	74	70	66	80	107	136	143	131	108	80	76	65

Table 6. Two locations of abandoned grasslands (A1, A2), where studies were carried out in 1979 (comp. Fig. 1).

Location & national grid coordinates[1]	Year	Characterization of the biotope
A1 : Opfikon (685.65/253.65)	1979	The area is located in the south-west of Opfikon near the river Glatt. It refers to a megaphorbe meadow (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).
A2 : Altburg near Regensdorf (678.70/253.57)	1979	Uncultivated *Bromus* meadow (dry meadow) on the hillside of the castle Altregensberg. At the foot of the hill this dry meadow passes into a small wet grassland.

[1] In the following Tables = NGC

Table 7. Six locations of abandoned lands (A3 to A8), where studies were carried out from 1976 to 1978 (comp. Fig. 1).

Location & NGC	Year	Characterization of the biotope
A3 : Höngg (678.63/250.99)	1976	Abandoned land infested strongly with weeds (mainly Cirsium arvense (L.) Scop.). Today public parc.
A4 : Höngg (680.93/251.50)	1976	Building land overgrown with tall grasses on the Hönggerberg campus of the Swiss Federal Institute of Technology. Today public parc.
A5 : Höngg (679.67/251.77)	1977	Plot overgrown with tall grasses and herbs on the territory of the shooting-grounds Allmend.
A6 : Schlieren (676.70/250.65)	1976	Stripe of abandoned land between a street and cultivated fields. In certain parts strongly infested with weeds (Rubus sp.).
A7 : Oberengstringen (677.15/250.95)	1976	Stripe of grassland between superhighway and river bank.
A8 : Oberengstringen (677.25/250.95)	1978	Grassland infested with shrubs and bushes between superhighway and river bank. Today initial stage of a riparian forest.

Table 8. Locations of the cultivated meadows (C1 to C10) studied (comp. Fig. 1).

Location & NGC	Year	Characterization of the biotope
C1 : Höngg (681.00/251.40)(681.04/251.57)	1979	outskirts of Zurich, near a forest
C2 : Höngg (680.48/251.73)(680.30/251.49)	1977-1978	outskirts of Zurich, near a forest
C3 : Höngg (680.71/251.01)	1979	outskirts of Zurich, agricultural area
C4 : Höngg (681.03/250.33)	1977-1979	outskirts of Zurich, district with many small gardens
C5 : Affoltern (679.70/253.18)	1979	outskirts of Zurich, near a forest
C6 : Regensdorf (678.63/253.48)	1979	swampy and woody area
C7 : Opfikon (685.55/253.70	1979	area between streets and streamside
C8 : Fluntern (685.70/248.22)	1977	outskirts of Zurich on a hill, near a forest
C9 : Schlieren (676.93/250.93)	1979	outskirts of Zurich in the river valley, near streamside
C10: Schlieren (676.87/250.67)	1977	outskirts of Zurich in the river valley

Table 9. Locations, where studies in cereal fields were conducted from 1976 to 1979 (comp. Fig. 1).

Location	Year	C r o p					Characterization of the biotope
		Wheat	Barley	Rye	Oats	Maize	
Höngg	1976		X	X	X	X	outskirts of Zurich, close to forest
	1977		X	X	X	X	
Schlieren	1976					X	outskirts of Zurich, close to river
	1977	X			X	X	
	1981	X					
Weiningen	1976			X	X	X	agricultural area
	1977	X	X			X	
	1978					X	
Affoltern	1976	X			X	X	swampy and woody area
	1977	X	X				
Regensdorf	1979	X			X		swampy and woody area
Swiss Federal Research Station for Agronomy Reckenholz	1977	X		X	X	X	agricultural area, close to forest
	1978	X				X	
	1979	X					
Unterstrass	1978					X	within the city

2.3.1.2. Sweep net samples in the vegetation zone of abandoned grasslands and cultivated meadows

The foliage-dwelling spiders of abandoned grasslands and cultivated meadows 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 in June, July, August, and September of 1979. The single sweeps were counted. The collected spiders were carefully taken out of the net with the help of tweezers, killed and preserved in 70% ethanol. For every sample, the time of day and the number of sweeps were recorded. In order to have comparable data, the data were later converted into "number of spiders/ 100 single sweeps".

2.3.1.3. Pitfall trap studies in cultivated meadows and cereal fields

The spider fauna on the ground surface of cultivated meadows and cereal fields was studied by means of pitfall traps. Transparent plastic beakers (upper diameter 7 cm, height 7.5 cm) were used as traps; they were completely sunk into the ground until the upper rim was level with the ground surface. Each beaker was filled with 70 ml of 4% formalin, and a touch of a detergent was added to reduce the surface tension. The traps were not protected by a rain shelter. They were emptied at intervals of 1-2 weeks. In the laboratory, the spiders were washed in water and then preserved in 70% ethanol.

In 1977, the pitfall trap studies were made in a winter wheat field on the territory of the Swiss Federal Research Station for Agronomy Zurich-Reckenholz. The experimental field had an area of 2 ha approximately. Thereon, a screen of 45 pitfall traps was set up (Fig. 2). The shortest distance between two traps was 20 m.

In 1978 and 1979 respectively, 6 more pitfall traps were set up in the same field. In addition to this, 6 other traps were set up in a cultivated meadow in Zurich-Höngg.

2.3.1.4. Determination of the spiders

The spiders collected were identified in the laboratory under a stereomicroscope. Genital preparations were made of female spiders which could not definitely be determined 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 books. The following publications served as keys: BLANKE (1976), DAHL (1931), DAHL & DAHL (1927), HARM (1971), LOCKET & MILLIDGE (1951/53), LOCKET *et al.* (1974), REIMOSER (1937), ROEWER (1928), TONGIORGI (1966), and WIEHLE (1931, 1937, 1953, 1956, 1963).

The determination of ♀♀ of *Pardosa agrestis* (Westr.) presented difficulties. There is a danger of mistaking them for ♀♀ of *Pardosa monticola* (Cl.). According to LOCKET *et al.* (1974), the width of the epigyne (posterior margin) is 0.36-0.48 mm in *P. monticola*, and 0.48-0.78 mm for *P. agrestis*. However, in a sample of 23 ♀♀ from a winter wheat field, measured by myself, the posterior margin of the epigyne was 0.51-0.63 mm (Ø = 0.56 ± 0.04 mm), indicating that the species is *P. agrestis.*

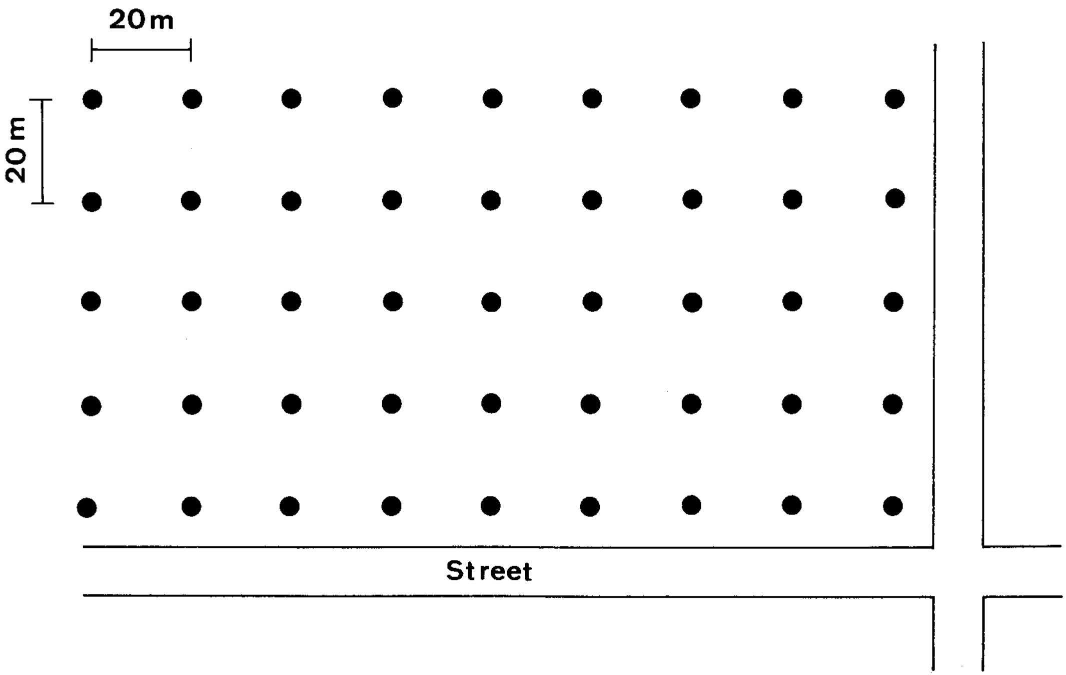

Fig. 2. Distribution of 45 pitfall traps in a winter wheat field on the territory of the Swiss Federal Research Station for Agronomy Zurich-Reckenholz (year 1977). The field has an area of 2 ha approximately.

The nomenclature according to MAURER (1978) was used. Samples of each spider species determined by myself were verified by Dr. K. Thaler, University of Innsbruck, Austria. A few species difficult to identify were determined by Dr. K. Thaler. At least one specimen of each spider species was deposited in the Entomological Collection of the Swiss Federal Institute of Technology Zurich (Curator: Prof. Dr. W. Sauter).

2.3.2. Investigation of the spider densities

2.3.2.1. Estimate of the relative density

Relative densities permit the comparison of different biotopes and different seasons (MÜHLENBERG, 1976). Relative densities were found by means of the sweeping technique (number of spiders/100 sweeps) and pitfall traps (number of spiders/week/trap).

2.3.2.2. Estimate of the absolute density

The spider density in abandoned grassland, cultivated meadows and cereal fields was investigated by means of the "square method". For this purpose, the spiders were counted within squares in several places of the field. In the vegetation zone, a square frame of 1 m x 1 m was used. On the ground surface square frames of 0.2 m x 0.2 m, 0.33 m x 0.33 m, and of 0.4 m x 0.4 m were used.

The square method could not be applied to wolf spiders, as their locomotory activity is very high. The density of adult wolf spiders was therefore estimated by direct observation.

2.3.3. Investigation of the seasonal change of abundance of spiders

The seasonal occurrence of the spider species in the vegetation zone of cereal fields was recorded by simple observations in the fields. The foliage dwelling spiders of abandoned grassland and cultivated meadows, on the other hand, were captured by sweeping with the net in different seasons. Information on the seasonal occurrence of the spiders and their numbers was derived from these sweeps.

The spiders caught in pitfall traps furnished informations on the seasonal occurrence of ground-dwelling spiders.

2.3.4. Investigation of the daily activity of spiders

The locomotory and feeding activity of the various spider species in the field was recorded at different times around the clock. At night, a flashlight was used.

2.3.5. Investigation of the spatial distribution of spiders

2.3.5.1. Investigation of the horizontal distribution of spiders

The dispersion index was calculated from the data collected by the square method (see 2.3.2.). The horizontal distribution of the spiders in the vegetation zone and on the ground was established in this way.

The distribution of the spiders in space has been estimated using MORISITA's index of aggregation (I_δ) independent of the size of the sampling unit (POOLE, 1974). The index of MORISITA has been calculated from the following equation:

$$I_\delta = \frac{n \sum_{i=1}^{n} x_i (x_i - 1)}{\sum_{i=1}^{n} x_i \; (\sum_{i=1}^{n} x_i - 1)} ,$$

where n is the number of samples, x_i is the number of individuals in the i^{th} sample, and $\sum_{i=1}^{n} x_i$ is the total number of individuals in all the samples.

The following relations are valid:

$I_\delta < 1$ uniform distribution,

$I_\delta = 1$ random distribution (Poisson distribution),

$I_\delta > 1$ aggregated distribution

After POOLE (1974) the significance of the deviation of I_δ from 1, is tested by calculating F as follows:

$$F = \frac{I_\delta (\sum_{i=1}^{n} x_i - 1) + n - \sum_{i=1}^{n} x_i}{n - 1} .$$

The value of F is compared to a table of the F distribution (with $\nu_1 = \infty$, $\nu_2 = n - 1$).

2.3.5.2. Investigation of the vertical distribution of orb-weaving spiders in the vegetation zone of abandoned grassland

For each of the different orb-weaving spider species the vertical distance from the ground to the orb hub was measured.

2.3.6. Analysis of diversity

For the calculation of the diversity index (H') the SHANNON-WIENER formula (also called Shannon-Weaver formula) of the information theory was used:

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

where S = number of species, p_i = relative frequency of the i^{th} species, measured from 0.0 to 1.0.

To test the significance of the difference between two H'-values, the t-Test was used as indicated by POOLE (1974).

The diversity index (H') does not show if its value is caused by a high number of species with irregular distribution or by a low number of species with regular distribution. Therefore, a supplementary measure, the evenness (E) after PIELOU (1966) is calculated:

$$E = \frac{H'}{H_{max}} = \frac{H'}{\ln S} \,.$$

The value of E ranges from 0 to +1. The higher the value the greater the evenness (i.e. the more regular the distribution).

2.3.7. Investigation of the prey composition of spiders

2.3.7.1. Investigation of the prey composition of web-building spiders in the vegetation zone of abandoned grassland, cultivated meadows, and cereal fields

Which insect groups were caught in the spiders' webs at different times of day and night was determined by means of continuous observations in the field.

During the night, the webs were observed in the light of a dimmed electric torch. Care was taken not to influence thereby the behaviour of the spiders and their prey. To some extent the prey items were determined and counted in the field, and the observation data recorded. In some cases the prey items were collected from the webs with tweezers, and preserved in 70% ethyl alcohol. They were counted under the stereo-microscope. Of some important prey groups samples were sent to specialists for exact determination.

2.3.7.2. Investigation of the prey composition of hunting spiders (crab spiders) in the vegetation zone of abandoned grassland, cultivated meadows, and cereal fields

During both day and night the vegetation zone was thouroughly searched for hunting spiders that were feeding. The prey items were determined either directly in the field or later on in the laboratory.

2.3.7.3. Investigation of the prey composition of web-spiders on the ground surface of cultivated meadows and cereal fields

The ground surface was searched for ground-dwelling spiders that were feeding. Because of the small size of these spiders and their prey, such studies could be made only during daytime. As before, the prey items were determined either directly in the field or later on in the laboratory. Samples of some important prey groups were sent to specialists for identification.

2.3.7.4. Investigation of the prey composition of diurnal hunting spiders (wolf spiders) on the ground surface of cultivated meadows and cereal fields

Wolf spiders were caught in the field by hand collections with a transparent plastic beaker (7 cm upper diameter). Spiders with prey were killed, preserved in alcohol and later determined in the laboratory under a stereo-microscope along with the prey. Wolf spiders were only observed in the daytime, as the dominant species (Pardosa spp.) are diurnal (see 3.2.3.2. and 3.3.3.2.). Of some important prey groups, samples were sent to specialists for accurate determination.

2.3.8. Investigation of the prey capture rate of spiders

2.3.8.1. Orb-weaving spiders

Two methods were used to study the prey capture rate:

Method 1: Direct observation in the field. The number of insects caught in the webs per day was counted round the clock. This method has the advantage of furnishing accurate data on how many insects a spider captures per day. It is, however, very time-consuming.

Method 2: Many orb-weaving spiders rebuild their web every day. For such spider species, the number of prey/web was counted at a time of the day when the webs were filled with prey. This number gives an estimate of the real capture rate which may be slightly higher, however, as sometimes single small insects are already consumed during the day and others get caught only after the prey has been counted. This method, though less accurate than direct observation, is far less time-consuming.

2.3.8.2. Wolf spiders

EDGAR (1969, 1970) developed a method by means of which the prey capture rate of wolf spiders can be calculated, if the feeding frequency in the field and the duration of feeding measured in the laboratory are known.

To determine the feeding frequency of the spiders, wolf spiders were caught in cultivated meadows and cereal fields on different days. In the case of each captured spider it was recorded whether it had a prey or not.

In order to measure the duration of feeding of wolf spiders, adult males and females of P. agrestis were caught in a winter wheat field and brought into the laboratory. There, they were confined singly to circular petri-dishes (Ø 9 cm, height 1.5 cm) with a moist filter paper on the bottom. At room temperature, the spiders were fed with aphids, small bugs, Diptera, and spiders of about the same size as those captured by the spiders in the field. The time spent on the consumption of one prey item was measured.

This method is suitable for the evaluation of prey capture rates of crab spiders, too.

2.3.9. Calculation of the niche breadth and niche overlap concerning food of the spiders

In order to examine to what extent the coexisting spider species use the available food resources in common, the overlap and breadth of the food compositions was determined. For this purpose, a resource matrix was set up (MÜHLENBERG, 1976). In our niche system, the compared spider groups 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 (1959), modified by HORN (1966):

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

where S is the total number of food items, x_i and y_i are proportions of the i^{th} item in the prey compositions of spider species x and y. The values of $\hat{C}\lambda$ range from zero to 1.0 (from entirely different to identical prey composition). According to ZARET & RAND (1971) one assumes that $\hat{C}\lambda$ values >0.60 indicate a considerable overlap. In the present study, the niche overlap could not be calculated at species level, as only the order or family of most prey items were determined. Therefore, the overlap values calculated in this thesis are probably overestimated compared with the overlap determined at species level.

This overlap index has been applied for the comparison of predators' prey compositions by other authors, too (ZARET & RAND, 1971; OBRTEL & HOLISOVA, 1976).

The niche breadth B_i was calculated after LEVINS (1968), applying the following formula derived from Simpson's index:

$$B_i = \frac{1}{\sum_{i=1}^{n} p_i^2} .$$

In this formula p_i is the proportion of the i^{th} of n resource categories used by a spider species. ~~Niche breadth values range from 0 to 1.~~

2.3.10. Comparison of spider communities of different locations

For the comparison of two spider communities the "overlap index" (C_{jk}) after SCHOENER (1970) was used. The formula is as follows:

$$1 - 0.5 \sum |p_{ij} - p_{ik}|$$

where p_{ij} and p_{ik} are the proportions of species i of the species communities in the locations j and k. This index ranges from 0 (no overlap) to 1 (total overlap). This index, too, was used for the comparison of spider communities of different locations by CURTIS (1978) and by SCHAEFER & KOCK (1979).

2.3.11. Estimate of the energy flow through spider communities

The different pathways in a spider's energy budget are as follows: Of the "prey killed" only a part reaches the alimentary canal (= "prey consumed"); the rest is not fed by the spider (= "prey not consumed"). Of the prey consumed a part is absorbed by the gut and assimilated in the body (= "prey assimilated"); the rest is eliminated as "faeces". Of the assimilated prey a part is lost by "respiration" and "secretions"; the rest remains for "production". Of these six components of the energy flow, only the energy-input into a spider community ("prey killed" and/or "prey consumed") could be determined or calculated within the framework of this thesis.

In the vegetation zone the "prey killed" by the large web-building spiders can be studied easily by direct observation. Therefore, in the vegetation zone the energy flow was calculated on the basis of "prey killed". On the ground surface the "prey killed" by the small web-building spiders could not be studied easily. For that reason, in the determination of the energy flow through the spider communities the "prey consumed" C was calculated theoretically (C calculated as a function of the weight of a spider, see below).

2.3.11.1. Vegetation zone

From the knowledge of the prey capture rates and population densities, the prey killing rate (number of prey items/ha/time unit) of the spiders could be calculated (see 3.1.11. and 3.3.9.). From the prey killing rate the energy flow through the foliage-dwelling spider communities was calculated by conversing the number of prey items into weight of prey (kg prey/ha/time unit) and weight of prey into Joule or Megajoule (MJ/ha/time unit).

The caloric value of soft-bodied insects (small Diptera, aphids) amounts to approximately 5.44 J/mg fresh weight (VAN HOOK, 1971, BREYMEYER & JOZWIK, 1975).

2.3.11.2. Ground surface

Following LUCZAK (1975) the daily consumption (C) of one spider was calculated after the equation of EDWARDS *et al.* (1972), generally applicable to invertebrates:

$$\underline{\log C = \log 0.071 + 0.725 \log X} \text{ ,}$$

where C is expressed as cal/spider/day and X is the caloric content of the body of a spider (1 mg dry weight = 5.8 cal = 24.3 J).

The daily energy flow E_c (= "prey consumed") through the ground-dwelling web-building spider community was estimated after the formula:

$$\underline{E_c = C \cdot D} \text{ ,}$$

in which D is the density of the spiders (N/m^2).

The mean fresh weight of a ground-dwelling web-building spider was assumed to be 2.5 mg. This is the fresh weight of one micryphantid spider with a body length of 2-2.5 mm (HEYDEMANN, 1962). In application of this equation the average consumption of one micryphantid spider was calculated to be 5.22 cal/day.

Approximately 80% of the killed prey is consumed by spiders (EDGAR, 1971; MOULDER & REICHLE, 1972; WORKMAN, 1978).
Hence follows the energy flow E_{pk} ("prey killed"):

$$\underline{E_{pk} = 1.25\ E_c} \text{ .}$$

2.3.12. Statistical analysis of data

In most cases the data collected in the field refer to frequencies. Such data have an assymmetric distribution. If data have a symmetric distribution one gives the arithmetic mean $\bar{x}$ (± SE) as characteristic values of the random samples. On the contrary, for assymmetric distributions one should give the median $\tilde{x}$ (± confidence interval) as characteristic values of the random samples (SACHS, 1974). However, a perusal of the renowned journals "Ecology", "Oecologia", "Oikos", "J. Anim. Ecol.", "Nature" and "Science" has shown, that in most field studies the mean value $\bar{x}$ and not the median $\tilde{x}$ was calculated. In the literature mainly the following characteristic values of random samples are given: $\bar{x}$ ± SD, $\bar{x}$ ± SE, $\bar{x}$ ± 95% C.L.

Therefore, in order to make the results of this thesis comparable with those of the literature, $\bar{x}$ ± SE was given as characteristic value of random samples.

For the comparison of two mean values nonparametric tests were applied (SACHS, 1974).

3. RESULTS

3.1. The role of spiders as insect predators in abandoned grasslands

3.1.1. Characterization of the biotopes and colonization by spiders

In biotopes with plants the spiders live in two zones: in the vegetation zone (= foliage-dwelling spiders) and on the ground surface (= ground-dwelling spiders). In the two zones different spider families are found. In abandoned grasslands, only the foliage-dwelling spiders were studied within the framework of this thesis.

The abandoned grassland biotopes studied were mostly uncultivated meadowland, shooting-grounds and future building sites overgrown with high grass, unmown stripes of grassland along field borders and river banks (see Tables 6-7). The vegetation zone of these grassland biotopes is heterogenous. It is composed of grasses on the one hand and of herbs and weeds (Cirsium arvense (L.) Scop., Rubus sp.) on the other hand. Some of these grasslands are interspersed with single shrubs.

Abandoned grassland is only little influenced by men. As spiders live more or less undisturbed in such biotopes, they are found in relatively high densities in the vegetation zone.

The result of the investigation of the spiders' density in the vegetation zone of two abandoned grassland biotopes (megaphorbe meadow A1 and dry meadow A2) was 8.8 and 9.6 spiders/m^2 respectively between mid-May and the end of May, and 10.6 spiders/m^2 in A2 at the beginning of July. The estimate in A1 in the beginning of September resulted in 9.4 spiders/m^2 as well. This means that in 1979 the spider density in the vegetation zone of both abandoned grassland biotopes was relatively constant from May til September and amounted to about 10 individuals/m^2.

3.1.2. Spider communities of abandoned grasslands

3.1.2.1. Spider community of biotope A1

The family composition of the foliage-dwelling spider community of the megaphorbe meadow A1 was investigated by means of the sweeping method and is summarized in Tables 10-11, together with the relative densities and the age structure of the spiders. If we consider the total (June to September), we find the following results: spiders belonging to the six families Tetragnathidae, Pisauridae, Micryphantidae, Araneidae, Salticidae, and Agelenidae prevailed in the sweep net samples (89% of all spiders, 90% of the adult spiders). Tetragnathidae were found most frequently. What the tables do not show is the fact that more than two thirds of the captured spiders were females.

In Table 12, the species composition of the foliage-dwelling spiders occurring in location A1 is represented. The table shows that the five species Tetragnatha extensa (L.), Hylyphantes nigritus (Simon), Evarcha arcuata (Cl.), Neottiura bimaculata (L.), and Pisaura mirabilis (Cl.) prevailed in the sweep net samples (>80% of the total). T. extensa and H. nigritus were the two species most frequently captured.

The spider community of location A1 consisted to a considerable degree of species of medium to large size. Argiope bruennichi (Scop.), Araneus

Table 10. Family composition in % of the spider fauna in the vegetation zone of the megaphorbe meadow A1 at different dates in summer 1979. The composition was investigated by means of sweep net collections. Immature and adult spiders were counted.

Spider family	12.6.	28.6.	17.7.	14.8.	20.9.	Total
	N=434	N=817	N=950	N=906	N=649	N=3756
	%	%	%	%	%	%
Tetragnathidae	30.65	42.23	57.16	61.48	51.31	50.88
Pisauridae	2.07	15.06	10.95	9.38	7.24	9.80
Micryphantidae	13.59	5.75	2.63	10.49	21.73	9.77
Araneidae	26.27	13.71	8.42	3.42	4.31	9.72
Salticidae	8.29	8.45	4.32	8.94	4.78	6.87
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
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
Theridiidae	5.99	1.96	2.00	0.33	0.15	1.73
Dictynidae	0	0	0.32	0.55	0.46	0.29
Philodromidae	0	0	0	0.22	0.15	0.08
Unident. spiders	4.38	0.98	3.47	0.99	3.85	2.50
Total	100.0	100.0	100.0	100.0	100.0	100.0

Table 11. Relative density of immature and adult spiders in the vegetation zone of the megaphorbe meadow A1 from June to September 1979. i = immature stages, a = adult stages, t = total

Spider family		Number of spiders/100 sweeps			
		June	July	August	September
1 - Araneidae	i	22.4	16.0	9.6	5.0
	a	0.4	0	2.3	9.0
	t	22.8	16.0	11.9	14.0
2 - Tetragnathidae	i	2.8	96.6	212.7	*
	a	23.8	12.0	1.5	
	t	26.6	108.6	214.2	166.5
3 - Linyphiidae	i	2.6	6.6	0.4	0
	a	0	0	0.8	5.5
	t	2.6	6.6	1.2	5.5
4 - Micryphantidae	i	0.2	0.6	36.2	70.0
	a	11.6	4.4	0.4	0.5
	t	11.8	5.0	36.6	70.5
5 - Theridiidae	i	2.4	1.6	0	0.5
	a	2.8	2.2	1.2	0
	t	5.2	3.8	1.2	0.5
6 - Agelenidae	i	2.6	8.0	0.8	0
	a	0	0	2.7	3.0
	t	2.6	8.0	3.5	3.0
7 - Dictynidae	i	0	0.6	1.9	1.5
8 - Salticidae	i	5.0	6.2	24.2	11.0
	a	2.2	2.0	6.9	4.5
	t	7.2	8.2	31.1	15.5
9 - Thomisidae	i	0.8	3.0	6.5	2.0
	a	0.8	0.6	0.4	0.5
	t	1.6	3.6	6.9	2.5
10 - Philodromidae	i	0	0	0.8	0.5
11 - Pisauridae	i	0.4	20.4	31.5	23.5
	a	1.4	0.4	1.2	0
	t	1.8	20.8	32.7	23.5
12 - Clubionidae	i	0.8	2.2	3.1	8.0
	a	0	0	0	0.5
	t	0.8	2.2	3.1	8.5
Unidentified spiders	i	3.8	6.6	3.5	12.5
Total	i	43.8	168.4	331.2	301.0
	a	43.0	21.6	17.4	23.5*
	t	86.8	190.0	348.6	324.5

* Developmental stage of T. extensa not distinguished in September

Table 12. Species composition of the spider fauna in the vegetation zone of the megaphorbe meadow A1 in summer 1979. Species investigated by means of sweep net collections. Only adult spiders are listed in the table. The numbers in parentheses behind the names correspond with the family-numbers in Table 11.

Spider species	12.6.	28.6.	17.7.	14.8.	20.9.	Total	%
Araneus diadematus[a] (1)	0	0	0	0	0	0	0
Araneus quadratus (1)	0	1	0	4	3	8	1.27
Nuctenea cornuta (1)	2	0	0	1	0	3	0.47
Argiope bruennichi (1)	0	0	0	1	1	2	0.32
Meta segmentata (1)	0	0	0	0	14	14	2.22
Tetragnatha extensa (2)	109	80	58	2	52	301	47.63
Tetragnatha pinicola (2)	1	0	0	0	0	1	0.16
Tetragnatha spec.[b] (2)	9	1	2	2	0	14	2.22
Pachygnatha clercki (2)	0	0	0	0	1	1	0.16
Linyphia triangularis (3)	0	0	0	2	9	11	1.74
Floronia bucculenta (3)	0	0	0	0	2	2	0.32
Dismodicus bifrons (4)	1	2	0	0	0	3	0.47
Hylyphantes nigritus (4)	57	44	21	1	1	124	19.62
Erigone dentipalpis (4)	0	0	1	0	0	1	0.16
Enoplognatha ovata (5)	0	2	11	3	0	16	2.53
Neottiura bimaculata (5)	14	6	0	0	0	20	3.16
Agelena gracilens (6)	0	0	0	7	6	13	2.06
Evarcha arcuata (8)	11	13	9	18	9	60	9.49
Heliophanus flavipes (8)	0	6	1	0	0	7	1.11
Xysticus cristatus (9)	2	0	3	0	1	6	0.95
Xysticus kochi (9)	2	0	0	1	0	3	0.47
Pisaura mirabilis (11)	7	6	2	3	0	18	2.85
Clubiona reclusa (12)	0	2	0	0	1	3	0.47
Clubiona neglecta (12)	0	1	0	0	0	1	0.16
Total	215	164	108	45	100	632	100.0

[a] Species not rare, often observed but never caught with the sweep net

[b] Sternum without median light patch

quadratus Cl., Araneus diadematus Cl., Agelena gracilens C.L. Koch, and P. mirabilis were the largest spiders found in A1 (see Table 13). The large web-building spiders A. bruennichi, A. quadratus and A. gracilens were only rarely and A. diadematus never caught with the sweep net (Table 12). These four species were however rather frequent in location A1 (see also Table 22). This probably signifies that large web-building spiders are underproportionately represented in sweep net samples.

3.1.2.2. Spider community of biotope A2

In the dry meadow A2, also, more than two thirds of the adult spiders caught in the vegetation zone were females. Tables 14-15 show the family composition of the spiders found in this location. From the totals of Table 14 (right column) results that spiders belonging to the seven families Thomisidae, Salticidae, Micryphantidae, Tetragnathidae, Pisauridae, Theridiidae and Araneidae predominated in the sweep net samples (89% of all spiders, 96% of the adult spiders). The two spider families Thomisidae and Salticidae, whose members hunt their prey without webs, were caught most frequently.

Table 16 represents the species composition of the foliage-dwelling spiders occurring in location A2. The table shows that in the sweep net samples the six species Tetragnatha pinicola L. Koch, H. nigritus, Enoplognatha ovata (Cl.), E. arcuata, Heliophanus flavipes (Hahn), and Xysticus cristatus (Cl.) predominated (>80% of the total). Most frequent were the two species E. arcuata and X. cristatus.

The spider community was thus mainly composed of species of medium size (see Table 13). A. bruennichi, Aculepeira ceropegia (Walck.), and P. mirabilis were the largest spiders in A2, but reached only relatively low densities.

3.1.2.3. Comparison of the spider communities of the two abandoned grassland biotopes

The distance between the two locations A1 and A2 is 7 km. In accordance with the differing levels of humidity, the moisture-loving T. extensa is more frequent in A1, while in A2 the dryness-loving T. pinicola is more often found. In both locations, however, the same spider families were encountered, only in different percentages. In both locations, the adult stages of more than 20 species could be caught by means of the sweep net and identified. Twelve species, namely A. bruennichi, Meta segmentata Cl., T. pinicola, Linyphia triangularis Cl., H. nigritus, E. ovata, N. bimaculata, E. arcuata, H. flavipes, Xysticus cristatus, Xysticus kochi Thorell, and P. mirabilis occurred in both biotopes (Tables 12 and 16). Only one immature specimen of the interesting jumping spider Myrmarachne formicaria (Deg.) was found in each location.

Diversity (H') and evenness (E) were lower in A1 than in A2 (Table 17). The difference between the diversity indices H'_{A1} and H'_{A2} is statistically significant (t-test, $p<0.05$). The lower diversity in the more humid A1 can be explained by the fact that only two species were highly predominant in A1, namely T. extensa and H. nigritus.

To establish the similarity of the spider communities of the two locations A1 and A2, SCHOENER's "overlap index" C_{jk} was calculated.

Table 13. Body length (mm) of the adult spiders, which have been observed in abandoned lands, cultivated meadows and cereal fields near Zurich. Informations compiled from literature (mainly after LOCKET & MILLIDGE, 1951/53).

Spider species	♀	♂	Spider species	♀	♂
D. fimbriatus	13 -20	9 -13	*L. hortensis*	4 -5	3 -4
P. mirabilis	12 -15	12	*M. mengei*	3.5-5	3.5-5
A. gracilens	10 -15	7.5-12.5	*F. bucculenta*	4	4
A. ceropegia	11.5-14	6.5	*T. impressum*	4 -4.5	2.5-3.5
A. bruennichi	11 -14	4	*E. angulatus*	4 -4.5	4
A. quadratus	9 -15	6 - 8	*M. pusilla*	3.5-5	3
A. diadematus	10 -12	4.5- 8	*P. rufus*	3.5-4	3
A. labyrinthica	8 -12	8 - 9	*A. sturmi*	3 -5	3.5
T. extensa	8 -11	6 - 9	*M. acalypha*	4	2.5
T. montana	6.5-10	6.5- 8	*A. riparia*	3.5	3 -3.3
A. alsine	8.5	6	*H. sanguinea*	3 -3.8	3
N. cornuta	6 - 8.5	5 - 8	*T. varians*	2.5-3.5	2.3-2.8
C. reclusa	6 - 8.5	5 - 6	*N. bimaculata*	2.5-3.3	2.5-3
E. arcuata	7	5 - 6	*H. nigritus*	3	2.3
X. kochi	6 - 8	4 - 5	*P. degeeri*	2.5-3	2.5-3
C. neglecta	6 - 8	4.5	*D. puella*	2.5-3	2 -2.8
P. amentata	5.5- 8	6 - 6.5	*D. uncinata*	2.5-2.8	2 -2.5
M. segmentata	5 - 8	5 - 6	*O. apicatus*	2.5	2.3
P. clercki	6	5 - 6	*O. tuberosus*	2.5	2 -2.3
X. cristatus	6 - 7	4 - 5	*O. fuscus*	2.5	2
P. agrestis	6 - 6.5	4.5	*P. convexum*	2.3-2.5	2.3-2.5
T. obtusa	5 - 7	3.5- 5.5	*E. atra*	2 -2.5	2 -2.5
L. triangularis	5 - 6	5 - 6	*L. humilis*	2 -2.5	1.8-2
T. pinicola	5 - 6	4.5- 5	*B. gracilis*	2 -2.5	1.5-1.8
P. cespitum	5 - 6	4	*D. bifrons*	2 -2.3	1.8-2
H. flavipes	5 - 6	3.5- 4	*T. vagans*	2 -2.2	1.5-2
P. palustris	4.5- 6	4.5- 5.5	*E. dentipalpis*	1.8-2.5	1.8-2.5
E. ovata	5 - 5.5	3 - 4	*D. pusilla*	1.8-2.5	2
H. auratus	4.5-6.5	3 - 4	*M. rurestris*	1.8-2.2	1.8-2.2
P. pullata	4 - 6	4 - 4.5	*T. boesenbergi*	2	1.8
A. cucurbitina	4 - 6	3.5- 4	*P. oblitum*	1.5	1.5
A. opisthographa	4 - 6	3.5- 4			

Table 14. Family composition in % of the spider fauna in the vegetation zone of the dry meadow A2 at different dates in summer 1979. The composition was investigated by means of sweep net collections. Immature and adult spiders were counted.

Spider family	10.6. 11.6.	26.6.	16.7. 18.7.	9.8. 13.8.	17.9.	Total
	N=236	N=115	N=296	N=368	N=281	N=1296
	%	%	%	%	%	%
Thomisidae	27.54	20.87	51.86	22.83	7.83	26.85
Salticidae	27.12	46.96	12.54	18.21	32.03	24.07
Micryphantidae	5.51	4.35	2.71	14.95	25.27	11.73
Tetragnathidae	8.05	3.48	8.14	15.49	3.56	8.80
Pisauridae	4.24	6.96	10.85	8.97	5.69	7.64
Theridiidae	16.95	9.57	5.08	1.63	1.07	5.71
Araneidae	7.63	2.61	2.03	1.90	7.83	4.32
Dictynidae	0	0	0.34	2.99	4.63	1.93
Linyphiidae	0.42	2.61	1.36	1.63	0.36	1.16
Clubionidae	0.85	0	0.34	1.36	0.36	0.69
Lycosidae	0.85	0.87	0.34	0	0.71	0.46
Agelenidae	0	0	0.34	0.27	0	0.15
Philodromidae	0.42	0	0	0	0	0.08
Unident. spiders	0.42	1.74	4.07	9.78	10.68	6.33
Total	100.0	100.0	100.0	100.0	100.0	100.0

Table 15. Relative density of immature (i) and adult (a) spiders in the vegetation zone of the dry meadow A2 from June to August 1979. t = total number of spiders.

Spider family		Number of spiders/100 sweeps June	July	August
1 - Araneidae	i	0.7	1.2	1.2
	a	0.7	0	0.2
	t	1.4	1.2	1.4
2 - Tetragnathidae	i	0.3	4.8	11.4
	a	1.1	0	0
	t	1.4	4.8	11.4
3 - Linyphiidae	i	0.1	0.4	0.8
	a	0	0.4	0.4
	t	0.1	0.8	1.2
4 - Micryphantidae	i	0	0.8	10.8
	a	1.0	0.8	0.2
	t	1.0	1.6	11.0
5 - Theridiidae	i	2.6	0.2	0
	a	0.5	2.8	1.2
	t	3.1	3.0	1.2
6 - Agelenidae	i	0	0.2	0.2
7 - Dictynidae	i	0	0.2	2.2
8 - Salticidae	i	2.4	5.8	10.4
	a	2.4	1.6	3.0
	t	4.8	7.4	13.4
9 - Thomisidae*	i	3.0	30.2	16.6
	a	2.0	0.4	0.2
	t	5.0	30.6	16.8
11 - Pisauridae	i	0.6	6.2	6.6
	a	0.2	0.2	0
	t	0.8	6.4	6.6
12 - Clubionidae	i	0.2	0.2	1.0
13 - Lycosidae	i	0	0.2	0
Unidentified spiders	i	0.1	2.4	7.2
Total	i	10.0	52.8	68.4
	a	8.2	6.2	5.2
	t	18.2	59.0	73.6

* + 1 adult specimen of Philodromidae (10) in June

Table 16. Species composition of the spider fauna in the vegetation zone of the dry meadow A2 in summer 1979. The numbers in parentheses behind the names correspond with the family-numbers in Table 15. The composition was investigated by means of sweep net collections. Only the adult spiders are listed in the table.

Spider species	10.6. 11.6.	26.6.	16.7. 18.7.	9.8. 13.8.	17.9.	Total	%
Aculepeira ceropegia (1)	6	0	0	0	0	6	2.56
Araniella cucurbitina (1)	0	0	0	1	0	1	0.43
Argiope bruennichi (1)	0	0	0	0	1	1	0.43
Mangora acalypha (1)	3	0	0	0	0	3	1.28
Meta segmentata (1)	0	0	0	0	1	1	0.43
Tetragnatha pinicola (2)	15	4	0	0	0	19	8.12
Linyphia triangularis (3)	0	0	0	2	1	3	1.28
Linyphia spec. (3)	0	0	1	0	0	1	0.43
Meioneta rurestris (3)	0	0	1	0	0	1	0.43
Hylyphantes nigritus (4)	13	5	4	1	0	23	9.83
Theridion boesenbergi (5)	1	0	0	0	0	1	0.43
Theridion impressum (5)	0	1	0	0	0	1	0.43
Enoplognatha ovata (5)	1	0	14	5	1	21	8.97
Neottiura bimaculata (5)	4	2	0	1	0	7	2.99
Evarcha arcuata (8)	23	22	8	13	18	84	35.90
Heliophanus flavipes (8)	9	6	0	2	0	17	7.26
Xysticus cristatus (9)	25	3	2	1	0	31	13.25
Xysticus kochi (9)	1	0	0	0	0	1	0.43
Philodromus rufus (10)	1	0	0	0	0	1	0.43
Pisaura mirabilis (11)	2	5	1	0	0	8	3.42
Pardosa pullata (13)	1	1	0	0	0	2	0.85
Pardosa amentata (13)	1	0	0	0	0	1	0.43
Total	106	49	31	26	22	234	100.0

Table 17. Number of families, number of species, diversity, and evenness (see Methods, 2.3.6.) of the adult spiders in the vegetation zone of two abandoned grassland biotopes (investigated by means of the sweep net data of Tables 12 and 16). The two diversity values are significantly different (t-test, $P < 0.05$).

	Megaphorbe meadow A1	Dry meadow A2
Number of families	10	10
Number of species S	23	22
Diversity H'	1.85	2.14
Evenness $E = H'/\ln S$	0.59	0.69

The comparison of the total of spiders captured in A1 and A2 results in an "overlap index" C_{jk} of 0.32 (see 2.3.10). Thus, the spider communities in the two abandoned grassland biotopes differ widely.

More extensive studies in other abandoned grassland locations in the surroundings of Zurich resulted in the additional species Agelena labyrinthica (Cl.), Hyposinga sanguinea (C.L. Koch), Meta mengei (Blackw.), Dolomedes fimbriatus L. and Heliophanus auratus C.L. Koch.

3.1.3. Seasonal change of abundance and daily activity

3.1.3.1. Seasonal change of abundance

Tables 11 and 15 show the spiders' seasonal trends. Adult stages of T. extensa, T. pinicola, H. nigritus, N. bimaculata, E. ovata, H. flavipes, P. mirabilis, and X. cristatus were found mainly in June, immature stages mostly between July and September. Of E. arcuata adult stages could be found relatively often from June to September and immature stages in August/September. The contrary was true for L. triangularis, A. gracilens, M. segmentata, A. quadratus, and A. bruennichi: immature stages were caught by sweeping in June/July, adult stages not before August/September.

Table 18 represents the relative density of the spiders (= number of spiders/100 sweeps) as a function of the season. The table shows similar trends for the two locations A1 and A2. In all the seasons, more immature than adult spiders were captured. Considering the total spider density (immature + adult stages), a strong increase in the spider density from spring to late summer can be noticed. The adult spiders reached their maximal density in June, the minimal density in August. On the contrary, the minimal density of the immature spiders occurred in June, the maximal density in August. The females of several spider species of the locations studied probably laid their egg sacs in spring and died soon thereafter. The spiderlings then hatched in the course of the summer. Since abandoned grasslands are spared to a large extent from human influences all year long, the spiders can live there undisturbed and catch their prey from spring to autumn (about 6-7 months/year).

3.1.3.2. Daily activity

Table 19 gives informations on the daily activity of the spiders living in abandoned grasslands.

Most orb-weaving spiders were observed feeding by day and by night (e.g. A. bruennichi, Table 20). They are both diurnal and nocturnal. Of the orb-weaving spider Nuctenea cornuta (Cl.), only the immature stages are occasionally active during the day, whereas the adult stages of this species are nocturnal* (NYFFELER & BENZ, 1980b; NYFFELER, 1981).

The web-building spiders studied in abandoned grasslands belonging to the families Agelenidae, Linyphiidae, Micryphantidae, Theridiidae, and Dictynidae were observed feeding during daytimes in most cases. In the webs, however, the remains of nocturnal prey species were found, too. These spiders are therefore both diurnal and nocturnal.

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*It happens very rarely that an adult specimen of N. cornuta can be observed in its orb-web during the daylight hours.

Table 18. Relative density (number of spiders/100 sweeps) of the spiders in the vegetation zone of two abandoned grassland biotopes near Zurich (spring/summer 1979). N = number of sweeps.

Season	A1				A2			
	N	No. spiders/100 sweeps			N	No. spiders/100 sweeps		
		immature +	adult =	total		immature +	adult =	total
10-12.6.1979	500	43.8	43.0	86.8	1310	10.0	8.2	18.2
26-28.6.1979	500	130.6	32.8	163.4	800	8.3	6.1	14.4
16-18.7.1979	500	168.4	21.6	190.0	500	52.8	6.2	59.0
9-14.8.1979	260	331.2	17.4	348.6	500	68.4	5.2	73.6
17-20.9.1979	200	301.0[a]	23.5[a]	324.5	?[b]	51-130	4- 12	55-142

[a] Specimens of _T. extensa_ of doubtful age were counted as immature individuals

[b] Protocol lost

Table 19. Daily rhythm of activity of the spiders in abandoned lands and in cultivated meadows (direct observations in the field and supplementary informations from literature).

Spider group		Type of activity
Orb-weaving spiders:		
Araneidae	A. ceropegia	diurnal and nocturnal
	A. diadematus	diurnal and nocturnal
	A. cucurbitina	diurnal and nocturnal
	A. bruennichi	diurnal and nocturnal
	M. acalypha	diurnal and nocturnal
	M. segmentata	diurnal and nocturnal
	A. quadratus	(diurnal) and nocturnal
	N. cornuta	mainly nocturnal
Tetragnathidae	Tetragnatha spp.	diurnal and nocturnal
	Pachygnatha spp.	diurnal and nocturnal[a]
Space web spiders:		
Agelenidae	Agelena spp.	diurnal and nocturnal
Linyphiidae	L. triangularis	diurnal and nocturnal
Micryphantidae	div. species	diurnal and nocturnal
Theridiidae	E. ovata	diurnal and nocturnal
	T. impressum	diurnal and nocturnal
	N. bimaculata	diurnal and nocturnal
Dictynidae	div. species	diurnal and nocturnal
Hunting spiders:		
Salticidae	E. arcuata	diurnal
	H. flavipes	diurnal
Thomisidae	Xysticus spp.	diurnal[b] and nocturnal
Philodromidae	Philodromus spp.	diurnal[c]
Pisauridae	P. mirabilis	diurnal[c]
Lycosidae	Pardosa spp.	diurnal
Clubionidae	Clubiona spp.	nocturnal[a]

[a] After informations from literature, adult stages are hunters

[b] Mainly diurnal

[c] It has not been observed if also nocturnal

Table 20. Daily rhythm of feeding activity in *Argiope bruennichi* in the vegetation zone of the abandoned land biotope A3 in summer 1976.

Daytime	Date		
	4.8.1976	5.8.1976	6.8.1976
	N = 10	N = 13	N = 17
	% spiders feeding:		
9.00	10.00	15.38	41.18
10.00	50.00	-	-
11.00	40.00	-	41.18
12.00	50.00	30.77	47.06
13.00	-	38.46	-
14.00	60.00	30.77	35.29
15.00	-	38.46	-
16.00	60.00	38.46	35.29
17.00	-	15.38	-
18.00	60.00	23.08	-
20.00	-	-	29.41
24.00	-	-	35.29

Hunting spiders of the families Salticidae, Philodromidae, Pisauridae and Lycosidae (genus Pardosa) were observed hunting during the day. Whether they hunt also at night, could not be ascertained. Thomisidae (genus Xysticus) could be observed feeding mostly during the day, less often at night. The Clubionidae (genus Clubiona) are hiding in a silken tube within a leaf during the daytime and hunt at night.

The observations show that in both abandoned grassland biotopes diurnal as well as nocturnal spiders are present, indicating that the predatory pressure of the spiders on the insects of these biotopes is exerted day and night.

3.1.4. Spatial distribution of spiders

3.1.4.1. Vertical distribution of spiders

In Table 21, the vertical distribution of five species of orb-weaving spiders in location A1 is represented for September 1979. The table shows that orb-webs are found from directly above the ground (A. bruennichi, M. segmentata) up to the top of the vegetation zone (A. diadematus, N. cornuta).

The weighted average ($\bar{x}^*$) is an estimate of the vertical distribution of the web sites of the whole orb-weaving spider guild in the open grass area of biotope A1. The population densities of Table 22 were used as weighing factors for the calculation of $\bar{x}^*$. The distribution of $\bar{x}^*$ shows that in 71% of all orb-weaving spiders the orb hub was placed at a height of 50-100 cm above ground. This means that in the open grass area the orb-weaving spiders exert the strongest predatory pressure on insect populations at a height of 50-100 cm. At heights of less than 25 cm and more than 125 cm above ground, the predatory pressure exerted by orb-weaving spiders was negligible.

In Fig. 3, the vertical distribution of the orb-weaving spiders A. bruennichi, A. quadratus and N. cornuta in location A1 in the summer of 1979 is represented graphically. A statistical analysis of the data shown in the figure produced significant differences in the mean values of A. bruennichi, A. quadratus, and N. cornuta from July to September (Mann-Whitney U-test, $p < 0.01$). The mean values of A. quadratus and N. cornuta showed significant differences only in July and August ($p < 0.01$), but not in September ($p > 0.05$). These values indicate that different spider species exert their predatory pressure on insect populations at different heights above ground.

The vertical segregation of the prey catching areas of spiders can have prey selection as a consequence. This could be observed in orb-weaving spiders mainly: A. bruennichi builds its webs near the ground (orb hub at about 0.3 m above ground). For this reason, A. bruennichi captures many grasshoppers in grasslands abounding in grasshoppers. A. quadratus and A. diadematus build their webs at more than 0.5 m above ground on the average. Thus, even in grasslands abounding in grasshoppers, only a few grasshoppers are caught by A. quadratus and A. diadematus (<0.5% of their food).

3.1.4.2. Horizontal distribution of spiders

Horizontal distribution among different habitats

Table 22 shows the horizontal distribution of six orb-weaving spider

Table 21. Vertical distribution of the spiders in the vegetation zone of the megaphorbe meadow A1 at the beginning of September 1979.

Height of orb hub above the ground (cm)	Argiope bruennichi N = 40 %	Araneus quadratus N = 52 %	Araneus diadematus N = 68 %	Nuctenea cornuta N = 40 %	Meta segmentata N = 50 %	$\bar{x}$ %	$\bar{x}^*$ %
225 - 250	0	0	1.47	0	0	0.29	0.02
200 - 225	0	0	0	0	0	0	0
175 - 200	0	0	0	5.00	0	1.00	1.66
150 - 175	0	0	8.82	7.50	0	3.26	0.93
125 - 150	0	0	6.62	15.00	4.00	5.12	2.29
100 - 125	0	8.65	25.00	16.25	7.00	11.38	8.46
75 - 100	0	45.19	29.41	16.25	15.00	21.17	32.33
50 - 75	25.00	43.27	22.06	35.00	34.00	31.87	38.69
25 - 50	62.50	2.88	6.62	5.00	35.00	22.40	14.60
0 - 25	12.50	0	0	0	5.00	3.50	2.15

$\bar{x}$ = mean value

$\bar{x}^*$ = weighted average. The population densities for the "open grass area" of Table 22 were used as weighing factors

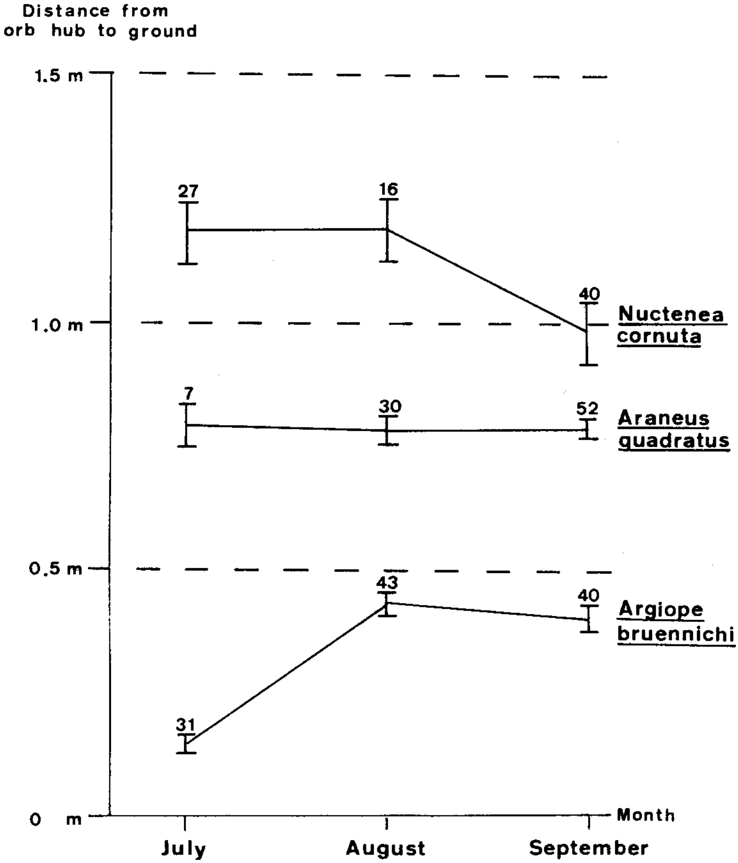

Fig. 3. Vertical distribution of three orb-weaving spiders in the megaphorbe meadow A1 in Opfikon near Zurich (July to September 1979). Mean value ± 1 SE, numbers in the graphic indicate the no. of webs observed.

Table 22. Population densities (N/m^2) of six orb-weaving spider species in five different habitats in the megaphorbe meadow A1 (September 2, 1979). The population densities were investigated by means of the "square method". Every number represents a mean value ($\bar{x}$) of 30 square samples (each square had an area of 1 m^2).

Spider species	Open grass area (above)	Open grass area (below)	Wayside (above)	Wayside (below)	Shrubs at periphery of grass area
	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
Argiope bruennichi	0.37 ± 0.12	0	0.73 ± 0.18	0.83 ± 0.17	0
Araneus quadratus	1.00 ± 0.16	0.73 ± 0.17	1.27 ± 0.20	0.23 ± 0.09	0.03 ± 0.03
Araneus diadematus	0	0.03 ± 0.03	0.07 ± 0.05	0	0.93 ± 0.26
Nuctenea cornuta	0.17 ± 0.07	0.13 ± 0.08	0.33 ± 0.10	0.07 ± 0.05	0
Meta segmentata	0.10 ± 0.06	0.27 ± 0.11	0.23 ± 0.09	0.47 ± 0.11	2.17 ± 0.40
Tetragnatha extensa	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

species among different habitats within location A1 (September 1979). The table shows a heterogenous horizontal distribution of the six spider species.

Of the spiders of the open grass area, A. quadratus, and to some extent N. cornuta and T. extensa are the most important insect predators; on the waysides, on the other hand, A. bruennichi and to some extent A. quadratus are important, whereas in the shrubs around the open grassland, M. segmentata and A. diadematus predominate.

Horizontal distribution within a habitat

Tables 23-24 show the index of Morisita of the spiders in the locations A1 and A2 for two observation data. The values indicate that within the vegetation zone of the two abandoned grassland biotopes, the horizontal distribution of the spiders represented a random distribution (I_δ not significantly different from 1; $p > 0.05$) or a slightly aggregated distribution (I_δ significantly larger than 1; $p < 0.05$). From these spider distributions, a corresponding distribution of the spiders' predatory pressure on the insect populations can be derived.

3.1.5. Prey capture of spiders

3.1.5.1. Hunting strategies

The hunting strategies which the spiders living in abandoned grasslands are equipped with are manifold. In Table 25, the quantitative composition of the hunting strategies used by the foliage-dwelling spiders of both locations A1 and A2 are represented. The table shows that in the relatively moist location A1 the greater part of the spiders catch their prey with orb-webs, while in the dry grassland of location A2 most spiders hunt their prey without webs. The average web areas of the orb-weaving spiders living in location A1 amounted to 160-640 cm^2 in August/September (Table 26).

3.1.5.2. Prey composition

Orb-weaving spiders

Observations in 1976 - Table 27 represents a comparative compilation of the prey compositions of adult females of A. bruennichi and A. quadratus in the four locations A3, A4, A6, and A7. Considering the number of captured prey, the food of A. bruennichi and A. quadratus consisted essentially of small Diptera. Regarding the biomass, the prey of A. bruennichi was mainly composed of grasshoppers in two locations and predominantly of honey-bees in two other locations. In the biomass of A. quadratus, the bees predominated, too.

Observations in 1978 - During the summer of 1978, an A. bruennichi population was observed in location A8. Grasshoppers (about 20%, chiefly Chorthippus parallelus (Zett.)), cicadas (about 20%, mainly Cicadella viridis (L.) and Diptera (about 40%) were predominant in the prey composition of this A. bruennichi population.

Observations in 1979 - Tables 28-31 give a compilation of the prey compositions of the orb-weaving spider guild on the megaphorbe meadow A1. Diptera and Homoptera (cicadas, aphids) were the most important food components of this orb-weaving spider guild. Relatively often A. bruennichi, A. quadratus, and

Table 23. Horizontal distribution of spiders in the vegetation zone of two abandoned grassland biotopes near Zurich. The data were collected with the "square method". Values with * deviate significantly from $I_\delta = 1$ (F-test, $P < 0.05$).

Location	Date	No. squares	Morisita index I_δ					
			Araneus quadratus	*Tetragnatha extensa*	*Agelena gracilens*	Linyphiidae	Total web spiders	Total spiders incl. hunting spiders
A1	17.5.1979	16[a]	-	1.19	-	1.21	1.10	1.11
A1	1.9.1979	21[a]	0.90	-	1.27*	1.78	1.10	-
A2	30.5.1979	100[b]	-	-	-	-	1.10	1.10
A2	6.7.1979	40[b]	-	-	-	1.38	2.07*	1.11

[a] Square of 1.0 m x 1.0 m

[b] Square of 0.4 m x 0.4 m

Table 24. Horizontal distribution of orb-weaving spiders in the vegetation zone of five habitats of the megaphorbe meadow A1 (September 2, 1979). The data were collected with the "square method". Values with * deviate significantly from $I_{\delta} = 1$ (F-test, $P < 0.05$).

Habitat	No. squares	Morisita index I_{δ}					
		Argiope bruennichi	*Araneus quadratus*	*Araneus diadematus*	*Meta segmentata*	*Tetragnatha extensa*	Total orb web-building spiders
Open grass area (above)	30[a]	-	0.76	-	-	-	0.95
Open grass area (below)	30[a]	-	1.17	-	-	1.27*	1.22*
Wayside (above)	30[a]	1.43	0.98	-	-	1.24	1.08
Wayside (below)	30[a]	1.10	-	-	-	-	1.33
Shrubs at the border of the open grass area	30[a]	-	-	1.35	1.53*	-	1.02

[a] Square of 1.0 m x 1.0 m

Table 25. Composition of the spider fauna in the vegetation zone of the locations A1 and A2 according to hunting strategies (June to September 1979). The composition has been investigated by means of sweep net collections (immature + adult stages, calculated with the data of Tables 10 and 14).

Location	Hunting strategy[a]	Season June 10-12 %	 June 26-28 %	 July 16-18 %	 August 9-14 %	 September 17-20 %	 Total %
A1	Orb-weaving spiders (Fam. 1 - 2[b])	56.92	55.94	65.58	64.90	55.62	60.60
	Space web spiders[c] (Fam. 3 - 7)	25.58	13.34	12.63	12.69	24.95	16.42
	Hunting spiders (Fam. 2[d] and 8 - 13)	13.12	29.75	18.32	21.41	15.56	20.47
	Unidentified spiders	4.38	0.98	3.47	0.99	3.85	2.50
A2	Orb-weaving spiders	15.68	6.09	10.14	17.39	11.39	13.12
	Space web spiders	22.46	16.53	10.14	21.47	31.33	20.76
	Hunting spiders	61.02	75.66	75.68	51.37	46.62	59.79
	Unidentified spiders	0.85	1.74	4.05	9.78	10.68	6.33

[a] The family numbers correspond with the numbers used in Tables 11 and 15

[b] Including immature *Pachygnatha* spp.

[c] "Space web spiders" refers to all web-building spiders which do not construct orb-webs

[d] Adult *Pachygnatha* spp.

Table 26. Web diameters and web areas of six species of orb-weaving spiders in the megaphorbe meadow A1 (summer 1979). The web areas have been calculated as approximately circular areas.

Month	Spider species	N	Web diameter	Web area
			$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
August	*Argiope bruennichi*	43	24.26 ± 0.91 cm	489.49 ± 36.38 cm^2
	Araneus quadratus	33	22.76 ± 1.23 cm	444.98 ± 47.62 cm^2
	Araneus diadematus	13	22.85 ± 1.27 cm	425.02 ± 48.99 cm^2
	Nuctenea cornuta[a]	19	15.49 ± 1.81 cm	234.90 ± 51.98 cm^2
	Meta segmentata	18	14.24 ± 0.99 cm	172.15 ± 22.61 cm^2
	Tetragnatha extensa	7	15.71 ± 2.81 cm	231.13 ± 84.79 cm^2
September	*Argiope bruennichi*	40	25.05 ± 0.92 cm	518.68 ± 36.14 cm^2
	Araneus quadratus	41	24.37 ± 0.88 cm	490.34 ± 35.59 cm^2
	Araneus diadematus	40	28.61 ± 1.01 cm	673.72 ± 47.27 cm^2
	Nuctenea cornuta[a]	14	15.45 ± 1.82 cm	221.19 ± 44.50 cm^2
	Meta segmentata	44	15.06 ± 0.75 cm	197.18 ± 20.77 cm^2
	Tetragnatha extensa	-	-	-

[a] Immature + adult stages, therefore large variance

Table 27. Prey composition of adult females of *Araneus quadratus* and *Argiope bruennichi* in four different abandoned grassland biotopes in the region of Zurich (August/September 1976).

Grassland type		Bee-rich grassland			Grasshopper-rich grassland	
Location		A6	A3	A6	A4	A7
Spider species		*Araneus quadratus*	*Argiope bruennichi*	*Argiope bruennichi*	*Argiope bruennichi*	*Argiope bruennichi*
No. prey items		N=194 %	N=215 %	N=224 %	N=90 %	N=377 %
Prey composition relating the no. of prey captured	Diptera[a]	79.4	69.2	80.4	77.8	79.5
	Apidae	6.7	15.5	8.0	4.4	0
	Aphidae	7.2	11.1	4.0	0	4.4
	Orthoptera	0	0.1	0.9	12.2	3.5
	Others	6.7	4.1	7.6	5.6	12.6
	Total	100.0	100.0	100.0	100.0	100.0
Prey composition relating the biomass of prey captured	Diptera[a]	17.6	7.9	13.5	5.6	17.6
	Apidae	74.2	88.2	67.4	15.9	0
	Aphidae	0.8	0.6	0.3	0	0.5
	Orthoptera	0	1.0	13.1	76.5	67.9
	Others	7.4	2.3	5.6	2.0	14.0
	Total	100.0	100.0	100.0	100.0	100.0

[a] Mainly small individuals

Table 28. Prey compositions of three araneid species in the megaphorbe meadow A1 in summer 1979. s = small, m/l = medium to large species.

	Araneus quadratus			*A. diadematus*		*Arg. bruennichi*	
Prey	July	Aug.	Sept.	Aug.	Sept.	Aug.	Sept.
	%	%	%	%	%	%	%
Diptera s	88.24	75.42	70.00	57.06	60.58	44.67	68.25
Diptera m/l	0	1.84	0.88	1.80	2.19	5.27	0.40
Apterous ants	0	0.14	0	0.28	0	0.54	0.40
Bees	0	0.99	1.32	0.69	0.73	4.63	0
Other Hymenopt. s[a]	0.65	7.49	8.25	13.71	18.25	5.06	7.94
Other Hymenopt. m/l	0	0.42	0.35	1.52	0	3.55	0.79
Winged aphids	4.58	1.84	6.23	13.02	0	4.52	11.51
Apterous aphids	0	0	0	0	0	0.32	0
Cicadas	0	9.04	9.47	6.51	6.57	24.76	6.35
Thysanoptera	0	0.42	0.61	0.14	0	2.05	0.40
Heteroptera	0	0.14	0.09	1.25	0.73	0.11	0
Grasshoppers[b]	0	0	0	0	0	0.22	0
Lepidoptera	1.31	0	0.09	0.55	0	0	0.40
Trichoptera	0	0	0	0.14	0	0	0
Chrysopidae	0.65	0	0	0	0	0	0
Scorpionflies	0	0	0	0.28	0	0.11	0
Coleoptera	1.31	0.99	0.61	1.25	0.73	0.97	1.59
Ephemeroptera	0	0.28	0.09	0	0	0.32	0
Salticidae	0	0	0	0	0	0.11	0
Other spiders	0	0.14	0	0.14	0	0.22	0.40
Unidentified prey	3.27	0.85	2.02	1.66	2.92	2.58	1.59
No. prey items	153	708	1140	722	137	929	252
No. webs	7	47	59	129	11	95	24
No. observation days	1	3	4	6	1	5	2

[a] Winged individuals

[b] One adult specimen of *Roeseliana roeseli* (Hgb.)

Table 29. Prey composition of *Nuctenea cornuta* in the megaphorbe meadow A1 (spring/summer 1979).

Prey	May %	June %	July %	August %
Small Diptera	82.98	75.40	80.78	85.05
Medium/large Diptera	2.84	0	0.17	0
Small winged Hymenoptera	0	0.49	0.17	1.87
Bees	0	0	0.09	0
Winged aphids	10.64	4.21	12.17	8.41
Cicadas	0.71	0.16	0.09	0
Thysanoptera	0.71	0.65	0.70	3.74
Lepidoptera	0	0.16	0.35	0
Trichoptera	0	12.46	1.91	0.93
Ephemeroptera	0	0	0.96	0
Coleoptera	0.71	4.05	1.13	0
Tetragnatha spec.	0	0	0.09	0
Unidentified prey	1.42	2.43	1.39	0
No. prey items	141	618	1150	107
No. webs	26	47	64	11
No. observation days	3	5	6	2

Table 30. Prey composition of *Meta segmentata* in the megaphorbe meadow A1 (summer 1979).

Prey	August %	September %
Small Diptera	27.39	39.34
Medium/large Diptera	14.23	5.46
Small winged Hymenoptera	4.25	2.73
Medium/large Hymenoptera	0.64	0
Apterous ants	1.27	0
Winged aphids	15.92	18.58
Apterous aphids	0.42	0
Cicadas	31.21	31.15
Thysanoptera	0.42	0
Trichoptera	0.42	0
Ephemeroptera	1.49	0.55
Unidentified prey	2.34	2.19
No. prey items	471	183
No. webs	309	75
No. observation days	7	3

Table 31. Prey composition of _Tetragnatha_ _extensa_ in the megaphorbe meadow A1 (spring/summer 1979).

Prey	May %	June %	July %
Small Diptera	_88.77_	_82.18_	_57.50_
Medium/large Diptera	1.09	0	0.83
Small winged Hymenoptera	0	1.21	0.83
Winged aphids	3.62	4.53	_15.83_
Cicadas	3.62	1.51	0
Thysanoptera	0	0.60	0
Trichoptera	0	4.83	_24.17_
Ephemeroptera	0.36	0	0
Chrysopidae	0	0.30	0
Coleoptera	0.72	1.81	0
Tetragnatha spec.	0.36	0	0.83
Unidentified prey	1.45	3.02	0
No. prey items	276	331	120
No. webs	138	156	53
No. observation days	3	5	5

A. diadematus captured Hymenoptera as well. Temporarily, N. cornuta and T. extensa captured Trichoptera quite often. In this location, the A. bruennichi population captured almost no grasshoppers (only in one web one adult female of Roeseliana roeseli (Hgb.) was found). The captured Homoptera were cicadas (95% Stenocranus major (Kbm.)) and winged aphids (mostly Anoecia corni) (Tables 32-33).

Space web spiders

The prey compositions of funnel web spiders are compiled in Table 34 (locations A3 and A5; observation years 1976-1977) and Table 35 (location A1, June/July 1979). Table 34 indicates that the prey composition of A. labyrinthica varies. In location A3, the prey composition of the funnel web spiders consisted mainly of ants, Apidae, Trichoptera, Lepidoptera and Diptera; in location A5, the food of the funnel web spiders was largely composed of Orthoptera, Lepidoptera and Diptera. In the prey composition of A. gracilens in location A1 beetles and cicadas predominated in June, whereas Trichoptera (75%) prevailed in July (Table 35). In other locations, remains of cicadas and beetles in quite large numbers have been found in the webs of funnel web spiders.

Spiders with space webs belonging to other families were only cursorily observed. Linyphiidae (L. triangularis) were often observed capturing Diptera and Homoptera (aphids, cicadas) in abandoned grasslands. Of Theridiidae (Theridion impressum L. Koch, E. ovata), only a few data on the prey compositions could be gathered in abandoned grasslands. Their prey compositions seem to be quite heterogenous (from small to large insects, and flying and running insects as well). In abandoned grasslands, Dictynidae could mostly be observed as predators of Diptera.

Hunting spiders

With regard to hunting spiders in abandoned grasslands, quantitative analyses were made only for crab spiders. In 1976, it was observed that they captured mainly Diptera (about 80% of their food). In 1977-1979, Xysticus sp. were also observed consuming Diptera, but ants and bees as well.

3.1.5.3. Prey capture rates

Estimate of the prey capture rate of an A. bruennichi population

Table 36 shows how many insects of medium to large size were captured on the average by females of A. bruennichi in location A3 on three observation days at the beginning of August 1976. As the table indicates, a female of A. bruennichi caught on the average one larger insect/day, 61% being bees and 10% grasshoppers. Small flying insects (dipterans, aphids) have not been taken into consideration in this census. If the small flying insects had been counted, too, the capture rate would be several times as high (see Table 37).

Estimate of the prey capture rate of an orb-weaving spider guild

Table 37 shows, how many insects on the average were counted per web of three orb-weaving spider species in location A1. These figures do not represent the exact capture rate, but are a slight underestimate of it (see 2.3.8.1., method 2). However, the values impart an impression of how many insects are filtered out of the aerial plankton by one web per day on the average. The table shows that the average capture rate of N. cornuta equalled more than 18 prey organisms/web/day. This means that from 200 up to over 400 insects were caught per m^2 of web area per day.

Table 32. Cicada species in the food of orb-weaving spiders in the vegetation zone of the megaphorbe meadow A1 near Opfikon (August/September 1979).

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

Table 33. Winged aphids in the food of orb-weaving spiders in the vegetation zone of the megaphorbe meadow A1 (summer 1979).

Aphid species	*A. bruennichi*	*A. quadratus*	*A. diadematus*	*M. segmentata*
Anoecia corni[a]	many	many	many	many
Rhopalosiphum padi	+	+	+	
Sitobion avenae		+		
Sitobion sp.?	+			
Aphis fabae		+	+	+
Aphis sp.			+	
Myzus persicae		+		
Hyalopterus pruni	+			
Rhopalomyzus lonicerae			+	
Linosiphon galiophagum				+
Dysaphis spp.		+		

[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 34. Prey composition of Agelena labyrinthica in the abandoned land biotopes A3 (summers 1976/77) and A5 (summer 1977).

Prey	A3 %	A5 %
Diptera	11.7	15.1
Ants	13.3	5.7
Bees	23.3	1.9
Other Hymenoptera	8.3	1.9
Aphids	1.7	0
Heteroptera	5.0	0
Orthoptera	0	26.4
Lepidoptera	18.3	37.7
Trichoptera	10.0	0
Coleoptera	5.0	7.5
Other orders	3.4	3.8
No. prey items	60	53
No. webs	26	29

Table 35. Prey composition of Agelena gracilens in the megaphorbe meadow A1 (summer 1979).
+ (about 5 %), ++ (about 10 %), +++ (about 20 %), ++++ (about 50 %)

Prey	June 23 %	July 1 %
Small Diptera	0	4.81
Medium/large Diptera	+	4.33
Medium/large Hymenoptera	+	0.48
Apterous ants	0	1.44
Bees	0	1.92
Winged aphids	+	4.81
Cicadas	++	0.96
Heteroptera	0	0.48
Trichoptera	0	75.00
Ephemeroptera	0	0.96
Coleoptera	++++	3.37
Tetragnatha spec.	0	0.48
Unidentified prey	+++	0.96
No. prey items	> 30	> 208
No. webs	12	35
No. observation days	1	1

Table 36. Number of medium to large sized prey items, which were captured day and night by *Argiope bruennichi* in the abandoned land biotope A3 during three subsequent days in August 1976. Small insects (Diptera + Aphidae) were not taken into consideration in this census. The population density of the females of *A. bruennichi* amounted to about 0.3 individuals/m^2. Accordingly the value 0.3$\bar{x}$ in the last column gives an estimate for the number of medium to large sized prey items/m^2 killed daily by this *A. bruennichi* population at the beginning of August.

Date	4.8.1976	5.8.1976	6.8.1976		
Observation time	9.00-20.30	9.00-18.00	9.00-23.30	$\bar{x}$	0.3$\bar{x}$
No. webs	10	13	17		
Prey	No. prey items/spider/day:				
Bees	0.80 ± 0.20	0.69 ± 0.26	0.35 ± 0.12	0.61	0.18
Grasshoppers	0.30 ± 0.15	0	0	0.10	0.03
Syrphidae	0	0.08 ± 0.08	0.06 ± 0.06	0.05	0.02
Heteroptera	0	0	0.06 ± 0.06	0.02	0.01
Cicadas	0	0.08 ± 0.08	0	0.03	0.01
Coleoptera	0	0	0.06 ± 0.06	0.02	0.01
Lepidoptera	0	0	0.06 ± 0.06	0.02	0.01
A. bruennichi-♂	0.10 ± 0.10	0	0	0.03	0.01
Unidentified prey	0.40 ± 0.16	0.23 ± 0.12	0	0.21	0.07
Total	1.60 ± 0.27	1.08 ± 0.24	0.59 ± 0.17	1.09	0.33

Table 37. Prey capture rate (no. prey items/web/day) of three orb-weaving spider species in the megaphorbe meadow A1 (study year 1979). When not otherwise stated three days of observation; exceptions as numbers in parentheses.

	Saison	Nuctenea cornuta	Araneus quadratus	Argiope bruennichi
Prey/web/day	May	> 5		
	June	>18		
	July	>18	>21 (1d)	
	August		>14	>10 (5d)
	September		>20	>10 (1d)
Prey/m^2 web/day[a]	August		>315	>204 (5d)
	September		>408	>193 (1d)

[a] Calculated from the data of Table 26; from May to July the diameters of webs were not measured

Table 38. Niche breadth (B_i) concerning food. Observations in six orb-weaving spider species in the megaphorbe meadow A1 (spring/summer 1979). The values were calculated from the data of Tables 28-31.

	Niche breadth B_i				
	May	June	July	August	September
T. extensa	1.26	1.47	2.41	-	-
N. cornuta	0.72	1.70	1.50	1.37	-
A. quadratus	-	-	1.28	1.71	1.96
A. diadematus	-	-	-	2.73	2.46
A. bruennichi	-	-	-	3.66	2.04
M. segmentata	-	-	-	4.53	3.44

Maximum prey capture rates in orb-webs which were particularly well placed

The values of Tables 36 and 37 represent the average of well and badly placed webs. In a few particularly well exposed orb-webs, a much higher number of insects could be counted; in the web of an A. bruennichi, for instance, 7 grasshoppers at one time, in another web 44 cicadas. Occasionally, more than 100 Diptera could be counted per web of N. cornuta. These observations indicate that large orb-weaving spiders have a high killing potential.

3.1.6. Niche breadth and niche overlap concerning food of web-building spiders

The niche breadths concerning food of six orb-weaving spiders are compiled in Table 38. They were calculated on the basis of method 2.3.9., using the data of Tables 28-31. The niche breadth of N. cornuta proved to be the smallest ($B_i = 0.72-1.70$), the one of M. segmentata ($B_i = 3.44-4.53$) was the largest.

With the data of Tables 28-31 and 35, the overlaps of the prey compositions of web-building spiders in location A1 were also calculated. The overlap values $\hat{C}\lambda$ are shown in Table 39. Of the 23 tested pairs 20 (87%) have a $\hat{C}\lambda$ of more than 0.60. This indicates that the prey compositions of the various orb-weaving spiders overlap rather strongly.* On the other hand, the prey compositions of orb-weaving spiders and funnel web spiders show only small overlaps ($\hat{C}\lambda < 0.10$). Therefore, orb-weaving spiders and funnel web spiders complement each other in their function as insect predators.

3.1.7. Spiders as predators of pest insects

In abandoned grasslands, aphids form an important component in the food of web-building spiders. The species composition of the aphids captured by orb-weaving spiders in A1 is compiled in Table 33. The table shows that, among others, the spiders caught aphid species which can be agricultural pests, e.g. Rhopalosiphum padi L., Sitobion avenae F., Aphis fabae Scop., Hyalopterus pruni Geoffr., and Myzus persicae Sulz. This indicates that spiders destroy pest insects in abandoned grasslands.

3.1.8. Spiders as predators of beneficial insects

As the prey compositions (Tables 27-35) indicate, the spiders feed not only on pest and neutral insects, but also on beneficial insects as honey-bees, Coccinellidae, Chrysopidae, and Syrphidae. Whether one or the other group dominates, depends on the biotope and its biocenose. Therefore, the same spider species, which is a predator of neutral or pest insects in one biotope, can be a predator of beneficial insects in another biotope. This phenomenon could be observed especially in A. bruennichi and A. labyrinthica. In the biotope A3 in 1976, an A. bruennichi population fed for the most part on honey-bees, another

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*If the overlap had been calculated at species level of the prey instead of order level, lower overlap values would possibly have resulted.

Table 39. Overlap of prey composition of six orb-weaving spider species and one funnel web spider species (niche overlap $\hat{C}\lambda$) in the megaphorbe meadow A1 in spring/summer 1979. The values were calculated from the data of Tables 28-31 and 35.

Species pairs	Niche overlap $\hat{C}\lambda$				
	May	June	July	August	September
T. extensa N. cornuta	0.99	0.99	0.90		
T. extensa A. quadratus			0.86		
N. cornuta A. quadratus			0.99	0.98	
A. bruennichi N. cornuta				0.77	
A. bruennichi A. quadratus				0.85	1.00
A. bruennichi A. diadematus				0.89	0.97
A. bruennichi M. segmentata				0.88	0.80
A. quadratus A. diadematus				0.95	0.97
N. cornuta A. diadematus				0.91	
N. cornuta M. segmentata				0.52	
A. quadratus M. segmentata				0.61	0.80
A. diadematus M. segmentata				0.70	0.76
A. gracilens N. cornuta			0.10		
A. gracilens A. quadratus			0.07		

one in the biotope A4, at a distance of 2 km, mainly on grasshoppers (Table 27). Likewise, an A. labyrinthica population in location A3 fed largely on bees, but in location A5, at a distance of 1 km, mainly on grasshoppers (Table 34).

3.1.9. Predator-prey relations between spiders and adult lepidopterans

EISNER et al. (1964) state that: "Moths, by virtue of the loose scales that cover their wings and bodies, are admirably adapted to elude capture by orb-weaving spiders. Rather than sticking to the web, they may simply lose some of their scales to the viscid threads, and then fly on". In the course of the present investigations one could actually observe rather often that Lepidoptera, having flown into spider webs, tear themselves away from the webs, thereby losing some scales, and fly on (NYFFELER & BENZ, 1981b). That the anti-predator mechanism found by EISNER et al. plays an important role for Lepidoptera in the field, is corroborated by the fact that Lepidoptera form only a small component of the total food of the orb-weaving spider species studied (<1%, see Tables 28-31). A possible connection between EISNER's anti-predator mechanism and the predatory behaviour of A. bruennichi has been reported by NYFFELER & BENZ (1982a).

3.1.10. Prey killing rate (estimate) and energy flow through the spider communities of abandoned grasslands

3.1.10.1. Prey killing rate of an A. bruennichi population

Table 36 shows that in the beginning of August 1976 about 0.18 bees/m^2/day (= 1800 bees/ha/day) and about 0.03 grasshoppers/m^2/day (= 300 grasshoppers/ha/day) were killed by this A. bruennichi population. Assuming constant weather conditions during 30 days, this would amount to a capture rate of 54'000 bees (about 5 bee colonies) and 9'000 grasshoppers/ha/month.

3.1.10.2. Prey killing rate of an orb-weaving spider guild

The question of the spiders' importance within an ecosystem is closely related to the question of their prey killing rate. This rate can be estimated most easily for web-building spiders and among those most easily for orb-weaving spiders. The quantity of insects which is daily filtered out of the aerial plankton by orb-weaving spiders in the vegetation zone of abandoned grassland biotopes necessarily depends on the total area A_p of the webs of all spiders living in a biotope, i.e.

$$A_p = \sum_{i=1}^{n} A_i$$

where A_i is the web area of spider i.

This web area is built on each fair-weather day and filters the aerial plankton in the vegetation zone. For the sake of simplicity, this model was limited to the orb-weaving spider guild of the biotope A1. In order to have a plain area relation, the number of insects caught by the spiders per ha and day was estimated. For this purpose, two preliminary questions had to be answered:

Table 40. a) Web area/ground area of orb-weaving spiders in five habitats of location A1 (September 1979), calculated from the data of Tables 22 and 26.

b) Minimum estimate of number of prey items/m^2 ground area/day killed by orb-weaving spiders at the beginning of September 1979 in location A1. Calculated from the data of Tables 37 and 40a after the method described in 2.3.7.1.

Spider species	Open grass area (above)	Open grass area (below)	Wayside (above)	Wayside (below)	Shrubs
a)	cm^2 web area / m^2 ground area:				
Argiope bruennichi	191.91	0	378.64	430.50	0
Araneus quadratus	490.34	357.95	622.73	112.78	14.71
Araneus diadematus	0	20.21	47.16	0	626.56
Nuctenea cornuta	37.60	28.75	72.99	15.48	0
Meta segmentata	19.72	53.24	45.35	92.67	427.88
Tetragnatha extensa	23.11	723.44	293.54	30.05	39.29
Total	762.68	1183.59	1460.41	681.48	1108.44
b)	number of prey / m^2 ground area / day:				
Argiope bruennichi	3.70	0	7.31	8.31	0
Araneus quadratus	20.00	14.60	25.41	4.60	0.60
Araneus diadematus	0	0.82	1.92	0	25.56
Nuctenea cornuta	1.53	1.17	2.98	0.63	0
Meta segmentata	0.80	2.17	1.85	3.78	17.46
Tetragnatha extensa	0.94	29.52	11.98	1.23	1.60
Total	26.97	48.28	51.45	18.55	45.22

(1) How large is the web area built by orb-weaving spiders per unit ground area (cm^2 web area/m^2 ground area)? - Knowing the web densities (Table 22) and web areas (Table 26), the average web area/ground area was calculated. The values for September 1979 are compiled in Table 40a.

(2) How many insects in the vegetation zone fly on the average through one m^2 of web area and are entangled in it per day? - Table 37 shows that in September 1979, more than 408 insects/m^2 web area of A. quadratus webs and more than 193 insects/m^2 area of A. bruennichi webs were filtered out of the aerial plankton.

From the data established in points 1 and 2, the prey killing rate P, i.e. the number of prey insects/m^2 ground area/day, was calculated by means of the formula

$$\underline{P = A \cdot N}$$

where A is the web area in cm^2/m^2 ground area and N the number of captured insects/m^2 web area/day. The capture rate established for A. quadratus (>408 insects/m^2 web area) was also used for the species A. diadematus, N. cornuta, M. segmentata, and T. extensa.

The P-values compiled in Table 40b show how many insects, at least, were destroyed by orb-weaving spiders per m^2 per day in the biotope A1 in September 1979. They amounted to respectively 27 or 48 insects/m^2/day in the open grass area and respectively 19 or 51 insects/m^2/day on its borders (wayside). In the shrubbery, at least 45 insects/m^2/day were killed by orb-weaving spiders. The prey killing rate thus varied between at least 19 insects/m^2/day and 51 insects/m^2/day (mean value: >38 insects/m^2/day). Supposing that this orb-weaving spider guild is active during 100 days per year, it would destroy more than 38 million insects/ha/year. If, on the basis of the prey compositions (Tables 28-31), an average fresh weight of 4 mg/insect is assumed, a biomass of more than 150 kg/ha of insect fresh weight would be killed each year. This is merely the prey killing rate of the orb-weaving spider guild. The spider community of the biotope A1 contained however various space web spiders and hunting spiders as well. The prey killing rate of the whole spider community is therefore significantly higher than 150 kg fresh weight/ha/year.

3.1.10.3. Energy flow through spider communities

A conversion (2.3.11.1.) of the prey biomass values of section 3.1.10.2. results in an energy flow (= prey killed) through the orb-weaving spider guild of the biotope A1 in the order of more than 900 MJ/ha/year.

3.2. The role of spiders as insect predators in cultivated meadows

Cultivated meadows are characterized by the fact, that their vegetation zone is mown 3-4 times per year. The cultivated grasslands investigated in this study are permanent meadows. They represent a mixture of numerous flowering plants (grasses, legumes, herbs). As lignified plants are largely absent, the vegetation in cultivated meadows is more elastic than in abandoned grasslands and thus facilitates the sweeping method. Through mowing the vegetation zone is removed, i.e. the living space of many spiders is destroyed; it regrows in the following weeks. The locations of the cultivated meadows studied are compiled in Table 8. In contrast to the investigations in abandoned grasslands, the studies in cultivated meadows included also the spiders on the ground surface. The spider communities of the vegetation zone (= foliage-dwelling spiders) and of the ground surface (= ground dwelling spiders) distinctly differed in their composition.

3.2.1. The influence of mowing

The periodic destruction of the living space and the egg sacs through mowing is an extreme stress for the spider populations of the vegetation zone. The total spider density in the vegetation zone diminishes drastically after mowing. The example listed in Table 41 shows that after mowing, the total spider density of the vegetation zone of a meadow had decreased by 50%. Similar effects could be observed in other cultivated meadows. As a consequence of these periodic stress situations, the densities of the foliage-dwelling spiders in cultivated meadows are extremely low (1.5 spiders/m^2, in Table 41).

As the values in Table 42 indicate, mowing has a negative effect on ground-dwelling spiders, too. Compared to the vegetation zone, the spider densities on the ground surface are nevertheless relatively high (16-42 spiders/m^2, Table 43).

3.2.2. Spider communities of cultivated meadows

3.2.2.1. Spiders of the vegetation zone

The family and species composition of the foliage-dwelling spiders in five cultivated meadows were investigated by means of sweep net samples. Tables 44-48 show the family composition of the immature and adult spiders in these meadows. Spiders of the eight families Araneidae, Tetragnathidae, Linyphiidae, Micryphantidae, Theridiidae, Salticidae, Thomisidae, and Lycosidae predominated in the sweep-net samples (>85% of the immature and adult spiders). More than 50% of the captured adult spiders were females.

The species composition of the adult spiders in the five meadows is represented in Tables 49-51. Adult stages of the families Thomisidae (X. cristatus, X. kochi), Tetragnathidae (T. pinicola, Pachygnatha degeeri Sundevall), Theridiidae (E. ovata primarily) and Araneidae (mostly Mangora acalypha (Walck.)) were the ones most frequently captured with the sweep net.

In cultivated meadows, adult Salticidae were found only in very low densities. Also A. bruennichi and A. quadratus, the orb-weaving spider species rather frequent in abandoned grasslands, were seldom located in cultivated meadows (as immature stages).

The foliage-dwelling spiders in cultivated meadows were for the most part species whose adult stages are medium-sized (see Table 13).

A. ceropegia is the largest spider found in cultivated meadows around Zurich.

3.2.2.2. Spiders of the ground surface

The family and species composition of the ground-dwelling spiders living in the cultivated meadow C3 was investigated by means of pitfall traps.

Table 41. Comparison of the densities of foliage-dwelling spiders in the cultivated meadow C4 before and after mowing (spring 1979). The square method was used.
N = number of squares of 0.4 m x 0.4 m.

Spider group	Before mowing 15.5.1979 N=96	After mowing 22.5.1979 N=100	
	Spiders/0.16 m^2 $\bar{x}$ ± SE	Spiders/0.16 m^2 $\bar{x}$ ± SE	Diff.
Xysticus spec.	0.07 ± 0.03	0.03 ± 0.02	- 57 %
Lycosidae	0.01 ± 0.01	0	
Tetragnatha spec. (immature)	0.01 ± 0.01	0	
Mangora acalypha (immature)	0.02 ± 0.02	0	
Very small orb-weavers[a]	0.10 ± 0.03	0.09 ± 0.04	- 10 %
Unidentified spiders	0.03 ± 0.02	0	
Total	0.24 ± 0.05 (1.56 spiders/m^2)	0.12 ± 0.04 (0.75 spiders/m^2)	- 50 %

[a] Probably immature *Pachygnatha* spec., web diameter about 2.5 cm

Table 42. Influence of mowing on the "activity density" of the ground-dwelling spiders in the cultivated meadow C3 (study year 1979). The investigations were carried out with pitfall traps. The significance was examined with a two-tailed Mann-Whitney U-test.

Spider group		Before mowing $\bar{x} \pm SE$	After mowing $\bar{x} \pm SE$	Difference	Signif.
		spiders/week/trap			
Pardosa palustris	adult	1.56 ± 0.49	0.39 ± 0.39	- 75 %	$P > 0.05$
Pardosa pullata	adult	0.20 ± 0.19	0	- 100 %	$P > 0.05$
Trochosa ruricola	adult	0.39 ± 0.25	0.20 ± 0.20	- 49 %	$P > 0.05$
Tarentula spec.	adult	0.39 ± 0.25	0	- 100 %	$P > 0.05$
Lycosidae gen. spec.	immature	1.56 ± 1.11	0.59 ± 0.26	- 62 %	$P > 0.05$
Total Lycosidae		4.08 ± 1.53	1.17 ± 0.52	- 71 %	$P < 0.05$
Pachygnatha degeeri	adult	0.58 ± 0.40	1.17 ± 0.52	+ 102 %	$P > 0.05$
Pachygnatha clercki	adult	0	0.39 ± 0.39	-	$P > 0.05$
Pachygnatha spec.	immature	0.59 ± 0.26	0	- 100 %	$P > 0.05$
Total Tetragnathidae		1.17 ± 0.43	1.56 ± 0.65	+ 33 %	$P > 0.05$
Erigone atra	adult	27.81 ± 2.26	11.67 ± 1.88	- 58 %	$P < 0.01$
Erigone dentipalpis	adult	17.31 ± 3.49	7.19 ± 1.66	- 58 %	$P < 0.05$
Oedothorax fuscus	adult	33.05 ± 3.81	29.56 ± 3.61	- 11 %	$P > 0.05$
Oedothorax apicatus	adult	4.28 ± 1.80	1.56 ± 0.58	- 64 %	$P > 0.05$
Total Micryphantidae		82.45 ± 5.38	49.97 ± 5.11	- 39 %	$P < 0.01$
TOTAL		87.69 ± 6.75	52.70 ± 5.26	- 40 %	$P < 0.01$

Table 43. Density of the ground-dwelling web-building spiders in two cultivated meadows near Zurich (June/July 1979).

Meadow	Date	Number of squares	Vegetation height	Spiders/m^2	
				unmown	mown
C1	13.6.1979	80[a]	15-18 cm	-	21.88
C1	26.7.1979	40[a]	4- 8 cm	-	42.50
C5	27.6.1979	20[b]	very short	-	15.94
C5	26.7.1979	40[a]	50 cm	18.13	-

[a] Square of 0.2 m x 0.2 m [b] Square of 0.4 m x 0.4 m

Table 44. Family composition of the spider fauna in the vegetation zone of the cultivated meadow C1 (spring 1979). The composition was investigated by means of sweep net collections. Immature and adult spiders were counted.

Spider family	23.5.	5.6.	Total
	N=122	N= 46	N=168
Composition in %:			
Araneidae	28.69	34.78	30.36
Tetragnathidae	30.33	17.39	26.79
Thomisidae	17.47	15.22	19.64
Theridiidae	8.20	19.57	11.31
Micryphantidae	2.46	10.87	4.76
Philodromidae	4.10	0	2.98
Linyphiidae	0	2.17	0.60
Dictynidae	2.46	0	1.79
Unidentified spiders	2.46	0	1.79
Total	100.0	100.0	100.0

Table 45. Family composition of the spider fauna in the vegetation zone of the cultivated meadow C4 (summer 1979)(otherwise as Table 44).

Spider family	29.6.	12.7.	6.8. 7.8.	Total
	N=115	N=272	N=416	N=803
Composition in %:				
Thomisidae	65.22	92.28	67.79	75.72
Tetragnathidae	7.83	3.68	15.38	10.34
Salticidae	0	3.31	11.30	6.97
Theridiidae	12.17	0	1.68	2.62
Lycosidae	1.74	0	2.16	1.37
Linyphiidae	5.22	0.37	0.48	0.87
Micryphantidae	3.48	0	0	0.50
Araneidae	1.74	0	0.24	0.37
Philodromidae	1.74	0	0.24	0.37
Pisauridae	0	0	0.24	0.12
Dictynidae	0.87	0	0	0.12
Unident. spiders	0	0.37	0.48	0.37
Total	100.0	100.0	100.0	100.0

Table 46. Family composition of the spider fauna in the vegetation zone of the cultivated meadow C5 (June/July 1979)(otherwise as Table 44).

Spider family	11.6.	23.7.	Total
	N= 39	N= 30	N= 69
Composition in %:			
Tetragnathidae	41.03	26.66	34.78
Thomisidae	0	33.33	14.49
Micryphantidae	15.38	6.67	11.59
Araneidae	10.26	10.00	10.14
Linyphiidae	15.38	0	8.70
Lycosidae	0	16.67	7.25
Theridiidae	10.26	0	5.80
Clubionidae	2.56	3.33	2.90
Dictynidae	2.56	0	1.45
Philodromidae	2.56	0	1.45
Unident. spiders	0	3.33	1.45
Total	100.0	100.0	100.0

Table 47. Family composition of the spider fauna in the vegetation zone of the cultivated meadow C6 (summer 1979)(otherwise as Table 44).

Spider family	26.6.	16.7. 18.7.	13.8.	Total
	N= 14	N= 63	N= 67	N=144
Composition in %:				
Lycosidae	0	9.52	40.30	22.92
Tetragnathidae	7.14	12.70	28.36	19.44
Thomisidae	14.29	23.81	4.48	13.89
Linyphiidae	21.43	14.29	11.94	13.89
Theridiidae	7.14	14.29	0	6.94
Araneidae	21.43	4.76	4.48	6.25
Pisauridae	0	9.52	2.99	5.56
Micryphantidae	14.29	1.59	1.49	2.78
Salticidae	7.14	1.59	0	1.39
Dictynidae	7.14	0	0	0.69
Philodromidae	0	1.59	0	0.69
Unident. spiders	0	6.35	5.97	5.56
Total	100.0	100.0	100.0	100.0

Table 48. Family composition of the spider fauna in the vegetation zone of the cultivated meadow C7 (June/July 1979)(otherwise as Table 44).

Spider family	12.6.	19.7.	Total
	N= 53	N=266	N=319
Composition in %:			
Thomisidae	50.94	74.44	70.53
Tetragnathidae	32.08	15.04	17.87
Araneidae	7.55	3.01	3.76
Salticidae	1.89	3.76	3.45
Theridiidae	3.77	1.88	2.19
Linyphiidae	0	1.13	0.94
Micryphantidae	3.77	0	0.63
Lycosidae	0	0.38	0.31
Unident. spiders	0	0.38	0.31
Total	100.0	100.0	100.0

Table 49. Species composition of the spider fauna in the vegetation zone of the cultivated meadow C1 (spring 1979). The composition was investigated by means of sweep net collections. Only the adult spiders were counted.

Spider species	23.5.	5.6.	Total	%
Aculepeira ceropegia	2	0	2	4.76
Mangora acalypha	1	7	8	19.05
Tetragnatha montana	0	1	1	2.38
Tetragnatha obtusa	0	1	1	2.38
Bathyphantes gracilis	0	1	1	2.38
Erigone dentipalpis	1	0	1	2.38
Tiso vagans	2	3	5	11.90
Neottiura bimaculata	0	1	1	2.38
Theridion spec.[a]	0	1	1	2.38
Dictyna uncinata	1	0	1	2.38
Lathys humilis	2	0	2	4.76
Xysticus cristatus	10	6	16	38.10
Xysticus kochi	1	1	2	4.76
Total	20	22	42	100.0

[a] Palpus was lost

Table 50. Species composition of the spider fauna in the vegetation zone of the cultivated meadow C4 (summer 1979)(otherwise as Table 49).

Spider species	29.6.	12.7.	6.8. 7.8.	Total	%
Araniella opisthographa	1	0	0	1	1.59
Tetragnatha pinicola	2	1	0	3	4.76
Pachygnatha degeeri	1	0	32	33	52.38
Microlinyphia pusilla	0	0	1	1	1.59
Meioneta rurestris	0	0	1	1	1.59
Oedothorax fuscus	1	0	0	1	1.59
Theridion impressum	2	0	0	2	3.17
Enoplognatha ovata	2	0	6	8	12.70
Neottiura bimaculata	1	0	1	2	3.17
Dictyna puella[a]	1	0	0	1	1.59
Heliophanus flavipes	0	1	0	1	1.59
Xysticus cristatus	5	0	0	5	7.94
Xysticus kochi	1	0	0	1	1.59
Philodromus cespitum	1	0	0	1	1.59
Philodromus rufus	1	0	0	1	1.59
Pardosa palustris	0	0	1	1	1.59
Total	19	2	42	63	100.0

[a] This species is new for the Swiss fauna

Table 51. Species composition of the spider fauna in the vegetation zone of the cultivated meadows C5, C6 and C7 in summer 1979. Otherwise as Table 49.

Spider species	Cultivated meadow C5				Cultivated meadow C6					Cultivated meadow C7			
	11.6.	23.7.	Total	%	26.6.	16/18.7.	13.8.	Total	%	12.6.	19.7.	Total	%
Araniella cucurbitina	-	-	-	-	1	0	0	1	3.70	-	-	-	-
Atea sturmi	-	-	-	-	0	1	0	1	3.70	-	-	-	-
Mangora acalypha	3	0	3	11.54	1	0	0	1	3.70	1	0	1	2.17
Tetragnatha extensa	-	-	-	-	-	-	-	-	-	5	2	7	15.22
Tetragnatha pinicola	11	1	12	46.15	1	0	0	1	3.70	2	0	2	4.35
Linyphia triangularis	-	-	-	-	0	0	5	5	18.52	-	-	-	-
Linyphia hortensis	-	-	-	-	0	2	0	2	7.41	-	-	-	-
Microlinyphia pusilla	-	-	-	-	0	0	1	1	3.70	0	1	1	2.17
Bathyphantes gracilis	-	-	-	-	-	-	-	-	-	0	1	1	2.17
Meioneta rurestris	-	-	-	-	-	-	-	-	-	0	1	1	2.17
Porrhomma convexum	-	-	-	-	1	0	0	1	3.70	-	-	-	-
Porrhomma oblitum	1	0	1	3.85	-	-	-	-	-	-	-	-	-
Erigone atra	2	0	2	7.69	1	0	0	1	3.70	-	-	-	-
Erigone dentipalpis	2	0	2	7.69	-	-	-	-	-	-	-	-	-
Hylyphantes nigritus	-	-	-	-	-	-	-	-	-	2	0	2	4.35
Tiso vagans	2	0	2	7.69	-	-	-	-	-	-	-	-	-
Theridion impressum	1	0	1	3.85	0	2	0	2	7.41	-	-	-	-
Theridion varians	1	0	1	3.85	0	1	0	1	3.70	-	-	-	-
Enoplognatha ovata	-	-	-	-	0	6	0	6	22.22	0	3	3	6.52
Neottiura bimaculata	1	0	1	3.85	1	0	0	1	3.70	-	-	-	-
Episinus angulatus	1	0	1	3.85	-	-	-	-	-	-	-	-	-
Dictyna pusilla	-	-	-	-	1	0	0	1	3.70	-	-	-	-
Evarcha arcuata	-	-	-	-	0	1	0	1	3.70	-	-	-	-
Heliophanus flavipes	-	-	-	-	-	-	-	-	-	1	1	2	4.35
Xysticus cristatus	-	-	-	-	-	-	-	-	-	17	2	19	41.30
Xysticus kochi	-	-	-	-	-	-	-	-	-	5	2	7	15.22
Pardosa amentata	-	-	-	-	0	1	0	1	3.70	-	-	-	-
Total	25	1	26	100.0	7	14	6	27	100.0	33	13	46	100.0

Table 52 shows the family composition of the spiders in this meadow. Spiders of the families Lycosidae and Micryphantidae predominated. Moreover, spiders of the family Tetragnathidae (genus Pachygnatha) repeatedly fell into the pitfall traps.

Table 53 shows the composition of the spider species frequently found on the ground of the cultivated meadow C3. The wolf spider species Pardosa palustris (L.) and P. agrestis as well as the Micryphantidae Erigone atra (Blackw.), Erigone dentipalpis (Wider) and Oedothorax fuscus (Blackw.) were the ones most frequently found in pitfall traps. Similar observations were made in other cultivated meadows.

Most spiders living on the soil surface of cultivated meadows are of small body size (Micryphantidae, see Table 13). The wolf spiders, and among these the genus Trochosa, are the largest spiders found on the ground surface of cultivated meadows.

3.2.3. Seasonal change of abundance

The following seasonal trends for the predominant species can be derived from Tables 54-55: Adult stages of T. pinicola, M. acalypha, X. cristatus and X. kochi were for the most part found in June and immature stages mostly between July and August. Adult stages of N. bimaculata and T. impressum could be collected in July mainly. In E. ovata, immature stages were captured in June, adult stages in July/August. No trends could be established for the rest of the predominant spiders, as the number of captured spiders was too low.

In Table 56, the spiders' relative densities (= number of spiders/100 sweeps) is recorded for different dates from May to August. It shows therefore the spider density as a function of the season.

The total density (immature + adult stages) in the vegetation zone of cultivated meadows is far lower than in abandoned grasslands; it increases from June to July/August. This can probably be explained by the fact that the number of immature spiders greatly increased during that period of time (see 3.1.3.1.). With a few exceptions, however, by June most samples already contained more immature than adult spiders.

Ground-dwelling spiders were found in cultivated meadows from spring to autumn (about 6-7 months/year).

3.2.4. Spatial distribution of spiders

3.2.4.1. Vertical distribution of spiders

As can be derived from section 3.2.1.2., most spiders in cultivated meadows live near the ground (>90%). A predatory pressure on insect populations exists therefore primarily near the ground of such meadows.

3.2.4.2. Horizontal distribution of spiders

For all the spiders present in the unmown vegetation zone of the cultivated meadow C4, the index of Morisita was calculated (Table 57). A distribution, which did not significantly differ from a random distribution (F-test, $p > 0.05$), was found in this meadow in mid-May.

In two cultivated meadows (C1 and C5), the index of Morisita was calculated for all the spiders of the ground surface (Table 57). The values

Table 52. Family composition of the spiders on the ground surface of the cultivated meadow C3 (traps emptied nine times in the study year 1979).

Sex	Family	T r a p s e m p t i e d 1 June	2	3 July	4	5	6	7 August	8	9	Total
		%	%	%	%	%	%	%	%	%	%
Males	Lycosidae	12.3	12.2	2.7	1.0	2.4	8.5	17.3	17.1	8.5	8.2
	Tetragnathidae[a]	5.5	2.2	0.8	1.9	0.8	3.4	1.3	0.9	3.4	2.1
	"Web-builders"[b]	82.2	85.6	96.5	97.1	96.8	88.1	81.4	82.0	88.1	89.7
Females	Lycosidae	3.6	15.6	4.9	1.2	0.9	2.4	3.2	4.7	2.4	3.2
	Tetragnathidae[a]	7.1	0	0	4.6	0	0.8	0.8	0	0.8	1.2
	"Web-builders"[b]	89.3	84.4	95.1	94.2	99.1	96.8	96.0	95.3	96.8	95.6
Total	Lycosidae	9.9	12.7	2.9	1.0	1.6	6.7	12.4	12.7	6.7	6.7
	Tetragnathidae[a]	5.9	1.9	0.7	2.8	0.4	2.6	1.1	0.6	2.6	1.8
	"Web-builders"[b]	84.2	85.4	96.4	96.2	98.0	90.7	86.5	86.7	90.7	91.5

[a] Tetragnathidae refers to species of the genus *Pachygnatha*. The immature stages are orb-weavers, the adult stages hunt without a web

[b] "Web-builders" refers to small sheet web spiders (mainly Micryphantidae)

Table 53. Dominant spider species on the ground surface of the cultivated meadow C3 (traps emptied nine times in the year 1979). a = adult males, b = adult females

		T r a p s e m p t i e d								
		1 June	2	3 July	4	5	6	7 August	8	9
Composition in %:										
a) Males	Pardosa agrestis	5.5	1.7	0	0	0.8	5.9	10.8	10.3	5.9
	Pardosa palustris	6.8	6.1	1.3	0.5	0	0.7	6.5	6.8	0.7
	Trochosa ruricola	0	4.4	0.5	0.5	1.6	1.9	0	0	1.9
	Pachygnatha degeeri	5.5	2.2	0.8	1.9	0	3.0	0.9	0.9	3.0
	Erigone atra	32.9	32.8	35.4	24.8	31.5	27.1	37.5	46.2	27.1
	Erigone dentipalpis	45.2	31.1	22.2	17.0	32.3	39.4	32.3	29.1	39.4
	Oedothorax fuscus	0	17.2	34.0	47.6	29.9	18.6	8.6	3.4	18.6
	Oedothorax apicatus	0	0	3.2	3.9	1.6	1.9	1.7	0	1.9
b) Females	Pardosa agrestis	0	0	0	0	0	1.6	1.6	3.1	1.6
	Pardosa palustris	3.6	12.5	3.7	1.2	0.9	0.8	1.6	1.6	0.8
	Trochosa ruricola	0	3.1	0	0	0	0	0	0	0
	Pachygnatha degeeri	7.1	0	0	2.3	0	0.8	0.8	0	0.8
	Erigone atra	14.3	0	11.0	10.5	6.3	9.5	4.8	7.8	9.5
	Erigone dentipalpis	10.7	9.4	6.1	2.3	6.3	3.2	2.4	4.7	3.2
	Oedothorax fuscus	60.7	46.9	50.0	62.8	79.3	77.0	83.1	75.0	77.0
	Oedothorax apicatus	0	0	12.2	0	0.9	2.4	3.2	1.6	2.4
Males + females	Pardosa agrestis	4.0	1.4	0	0	0.4	4.6	7.6	7.7	4.6
	Pardosa palustris	5.9	7.1	1.7	0.7	0.4	0.8	4.8	5.0	0.8
	Trochosa ruricola	0	4.2	0.4	0.3	0.8	1.3	0	0	1.3
	Pachygnatha degeeri	5.9	1.9	0.7	2.1	0	2.3	0.8	0.6	2.3
	Erigone atra	27.7	27.8	31.0	20.5	19.7	21.5	26.1	32.6	21.5
	Erigone dentipalpis	35.6	27.8	19.3	12.7	20.1	27.8	21.9	20.4	27.8
	Oedothorax fuscus	16.8	21.7	36.9	52.1	52.7	37.2	34.6	28.7	37.2
	Oedothorax apicatus	0	0	4.8	2.7	1.3	2.0	2.2	0.6	2.0

Table 54. Relative density of the immature and adult spiders (no. of spiders/100 sweeps) in the vegetation zone of the cultivated meadows C1 (spring 1979) and C4 (summer 1979).
i = immature stages, a = adult stages

Spider family		Meadow C1		Meadow C4		
		23.5.	5.6.	29.6.	12.7.	6./7.8.
Agelenidae	t	0	0	0	0	0
Araneidae	i	2.6	1.1	0.2	0	0.2
	a	0.2	0.9	0.2	0	0
	t	2.8	2.0	0.4	0	0.2
Tetragnathidae	i	3.0	0.8	1.2	4.5	6.2
	a	0	0.2	0.6	0.5	6.4
	t	3.0	1.0	1.8	5.0	12.6
Linyphiidae	i	0	0	1.2	0.5	0
	a	0	0.1	0	0	0.4
	t	0	0.1	1.2	0.5	0.4
Micryphantidae	i	0	0.2	0.6	0	0
	a	0.2	0.4	0.2	0	0
	t	0.2	0.6	0.8	0	0
Theridiidae	i	0.8	0.9	1.8	0	0
	a	0	0.2	1.0	0	1.4
	t	0.8	1.1	2.8	0	1.4
Dictynidae	a	0.2	0	0.2	0	0.2
Salticidae	i	0	0	0	4.0	9.4
	a	0	0	0	0.5	0
	t	0	0	0	4.5	9.4
Thomisidae	i	1.2	0	14.0	125.5	56.4
	a	0.9	0.9	1.2	0	0
	t	2.1	0.9	15.2	125.5	56.4
Philodromidae	i	0.4	0	0	0	0.2
	a	0	0	0.4	0	0
	t	0.4	0	0.4	0	0.2
Pisauridae	i	0	0	0	0	0.2
Lycosidae	i	0	0	0.4	0	1.6
	a	0	0	0	0	0.2
	t	0	0	0.4	0	1.8
Clubionidae	t	0	0	0	0	0
Unident. spiders	i	0.2	0	0	0.5	0.4
Total	i	8.2	3.0	19.4	135.0	74.6
	a	1.5	2.7	3.8	1.0	8.6
	t	9.7	5.7	23.2	136.0	83.2

Table 55. Relative density of the immature and adult spiders (no. spiders/100 sweeps) in the vegetation zone of the cultivated meadows C5, C6 and C7 in summer 1979. i = immature stages, a = adult stages

Spider family		Meadow C5		Meadow C6			Meadow C7	
		11.6.	23.7.	26.6.	16.7. 18.7.	13.8.	12.6.	19.7.
Agelenidae	t	0	0	0	0	0	0	0
Araneidae	i	0.1	0.6	0.1	0.4	0.6	0.6	1.6
	a	0.3	0	0.3	0.2	0	0.2	0
	t	0.4	0.6	0.4	0.6	0.6	0.8	1.6
Tetragnathidae	i	1.6	1.4	0	1.6	3.8	2.0	7.6
	a		0.2	0.1	0	0	1.4	0.4
	t	1.6	1.6	0.1	1.6	3.8	3.4	8.0
Linyphiidae	i	0.3	0	0.3	1.4	0.4	0	0
	a	0.3	0	0.1	0.4	1.2	0	0.6
	t	0.6	0	0.4	1.8	1.6	0	0.6
Micryphantidae	i	0	0.4	0.1	0.2	0.2	0	0
	a	0.6	0	0.1	0	0	0.4	0
	t	0.6	0.4	0.2	0.2	0.2	0.4	0
Theridiidae	i	0.1	0	0	0	0	0.4	0.4
	a	0.3	0	0.1	1.8	0	0	0.6
	t	0.4	0	0.1	1.8	0	0.4	1.0
Dictynidae	i	0.1	0	0	0	0	0	0
	a	0	0	0.1	0	0	0	0
	t	0.1	0	0.1	0	0	0	0
Salticidae	i	0	0	0.1	0	0	0	1.8
	a	0	0	0	0.2	0	0.2	0.2
	t	0	0	0.1	0.2	0	0.2	2.0
Thomisidae	i	0	2.0	0.3	3.0	0.6	1.0	38.8
	a	0	0	0	0	0	4.4	0.8
	t	0	2.0	0.3	3.0	0.6	5.4	39.6
Philodromidae	i	0.1	0	0	0.2	0	0	0
Pisauridae	i	0	0	0	1.2	0.4	0	0
Lycosidae	i	0	1.0	0	1.0	5.4	0	0.2
	a	0	0	0	0.2	0	0	0
	t	0	1.0	0	1.2	5.4	0	0.2
Clubionidae	i	0.1	0.2	0	0	0	0	0
Unid. spiders	i	0	0.2	0	0.8	0.8	0	0.2
Total	i	1.5	5.8	0.9	9.8	12.2	4.0	50.6
	a	2.4	0.2	0.8	2.8	1.2	6.6	2.6
	t	3.9	6.0	1.7	12.6	13.4	10.6	53.2

Table 56. Relative density of the spiders (no. of spiders/100 sweeps) in the vegetation zone of five cultivated meadows near Zurich (spring/summer 1979). N = number of sweeps

Location Meadow	Season	N	No. spiders/100 sweeps				
			immature	+	adult	=	total
C1	23.5.1979	1250	8.2		1.5		9.7
C1	5.6.1979	800	3.0		2.7		5.7
C4	29.6.1979	500	19.4		3.6		23.0
C4	12.7.1979	200	135.0		1.0		136.0
C4	6-7.8.1979	500	74.6		8.6		83.2
C5	11.6.1979	1000	1.5		2.4		3.9
C5	23.7.1979	500	5.8		0.2		6.0
C6	26.6.1979	800	0.9		0.8		1.7
C6	16-18.7.1979	500	9.8		2.8		12.6
C6	13.8.1979	500	12.2		1.2		13.4
C7	12.6.1979	500	4.0		6.6		10.6
C7	19.7.1979	500	50.6		2.6		53.2

Table 57. Horizontal distribution of the spiders in the vegetation zone (A) and on the ground surface (B) of cultivated meadows near Zurich. The data were investigated with the square method. Values with * deviate significantly from $I_\delta = 1$ (F-test, $P < 0.05$).

Stratum	Location	Mown	Date	Squares	Morisita index I_δ
A)	C4	-	15.5.1979	96[a]	0.70
B)	C1	+	13.6.1979	80[b]	1.03
	C1	+	26.7.1979	40[b]	1.76*
	C5	+	27.6.1979	20[a]	1.05
	C5	-	26.7.1979	40[b]	1.18

[a] Square of 0.4 m x 0.4 m

[b] Square of 0.2 m x 0.2 m

show that the horizontal distribution of the spiders of the two meadows represented a random distribution as well (F-test, $p > 0.05$) or, at the most, a slightly aggregated distribution (C1, July: F-test, $p < 0.05$).

From these spider distributions, a corresponding distribution can be derived for the predatory pressure which the spiders exert on insect populations.

3.2.5. Prey capture of spiders

3.2.5.1. Hunting strategies

The quantitative composition of the spiders, grouped according to their hunting strategies, is compiled in Table 58. It shows that the spectrum of hunting strategies used by the foliage-dwelling spiders differs from meadow to meadow. In certain cultivated meadows the web-building spiders predominated, in others the hunting spiders were more prevalent, even though no qualitative differences could be detected between the types of meadows.

From the fact that far more web-building spiders (mainly Micryphantidae) were caught in pitfall traps than cursorial spiders (Lycosidae) - Micryphantidae having a lower "activity density" than the Lycosidae (HEYDEMANN, 1962) - one can gather that the former hunting strategy is the most frequently adopted on the ground surface.

3.2.5.2. Prey composition

Vegetation zone

Orb-weaving spiders and space web spiders - The prey compositions of the orb-weaving spiders in cultivated meadows consisted for the most part of small flying insects (Diptera). This is shown in Table 59 for *N. cornuta*. The prey of the Dictynidae, Linyphiidae and Theridiidae, too, was mainly composed of small flying insects (Diptera, aphids).

Hunting spiders - The prey composition of foliage-dwelling crab spiders in cultivated meadows is represnted in Table 60. The table indicates that they prey mostly on Diptera (about 60% of their food). The prey group second in importance are the Hymenoptera (about 16%). Among these, even large and well-armed prey insects as bees and bumble-bees are found.

Ground surface

Web-building spiders - The prey composition of the Micryphantidae living in cultivated meadows is represented in Table 61. The table shows that the food of the Micryphantidae consisted exclusively of small, soft-bodied prey organisms. Aphids, Diptera, and Collembola (predominantly Sminthuridae) were the most important prey components. Table 62 shows which Collembola and aphid species were captured by the Micryphantidae. The cereal aphids *Rhopalosiphum padi* L. and *Sitobion avenae* F. were also found among the captured aphids.

Hunting spiders - The prey composition of the Lycosidae living in cultivated meadows is represented in Table 63. The table indicates that the prey of the Lycosidae in meadows consists for the most part of small,

Table 58. Frequencies in percent of the hunting strategies used by the spiders in the vegetation zone of five cultivated meadows near Zurich at different seasons in 1979. The frequencies were calculated from the data of the Tables 44-48.

Location Meadow	Hunting strategy	Season				
		May %	June %	July %	August %	Total %
C1	Orb-weaving spiders	59.02	52.17			57.15
	Space web spiders[a]	10.66	32.61			16.67
	Hunting spiders	21.57	15.22			22.62
	Unident. spiders	4.92	0			3.57
C4	Orb-weaving spiders		8.70	4.05	8.17	6.47
	Space web spiders		21.74	0.37	2.16	4.36
	Hunting spiders		69.57	95.59	89.18	88.66
	Unident. spiders		0	0.37	0.48	0.37
C5	Orb-weaving spiders		51.29	36.66		44.92
	Space web spiders		43.58	6.67		27.54
	Hunting spiders		5.12	53.33		26.09
	Unident. spiders		0	3.33		1.45
C6	Orb-weaving spiders		28.57	17.46	32.84	25.69
	Space web spiders		50.00	30.17	11.94	23.60
	Hunting spiders		21.43	46.03	47.77	44.45
	Unident. spiders		0	6.35	7.46	6.25
C7	Orb-weaving spiders		39.63	18.05		21.63
	Space web spiders		7.54	3.01		3.76
	Hunting spiders		52.83	78.58		74.29
	Unident. spiders		0	0.38		0.31

[a] The expression "space web spiders" refers to all web-building spiders not constructing an orb-web

Table 59. Prey composition of *Nuctenea cornuta* in the cultivated meadow C9 (spring 1979).

Prey type	May %	June %
Diptera	95.95	83.48
Small Hymenoptera	0	0.87
Winged aphids	2.39	0.87
Lepidoptera	0	0.87
Trichoptera	0	2.61
Ephemeroptera	0.18	0
Coleoptera	0	2.61
Unidentified prey	1.47	8.70
No. prey items	543	115
No. webs	55	27
No. observation days	2	2

Table 60. Prey composition of foliage-dwelling and of ground-dwelling crab spiders in cultivated meadows near Zurich (data from several meadows combined, study years 1976-1978).

Spider group	Foliage-dwelling crab spiders (*Xysticus* spp.) N = 134	Ground-dwelling crab spiders (*Xysticus* spp.) N = 37
Prey composition in %:		
Collembola	0	5.7
Orthoptera	0	2.9
Thysanoptera	4.0	0
Heteroptera	0.8	2.9
Cicadas	0.8	2.9
Aphidae	0	11.4
Carabidae	0	5.7
Other Coleoptera	4.8	2.9
Diptera	64.8	0
Lepidoptera	1.6	0
Apidae	4.0	0
Ants	4.8	34.3
Other Hymenoptera	8.0	2.9
Spiders	6.4	25.7
Lumbricide worms	0	2.9

Table 61. Prey composition of small ground-dwelling web-building spiders (mainly Micryphantidae) in cultivated meadows near Zurich (study year 1977).

Prey	C2 + C4 N	C8 N	C10 N	Total N	%
Collembola	53	12	10	75	45.45
Apterous aphids	15	24	0	39	23.64
Winged aphids	2	2	0	4	2.42
Small Diptera	7	4	1	12	7.27
Small Hymenoptera	3	1	2	6	3.64
Thysanoptera	3	1	1	5	3.03
Mites	2	3	0	5	3.03
Small cicadas	4	0	0	4	2.42
Small Heteroptera	1	0	0	1	0.61
Small Orthoptera	1	0	0	1	0.61
Larvae of insects	0	2	0	2	1.21
Unidentified prey	8	1	2	11	6.67
Total	99	50	16	165	100.0

Table 62. Species of Collembola and aphids in the food of small ground-dwelling web-building spiders. Observations in cultivated meadows near Zurich (year 1977).

Group Family	Species		Meadow C2 + C4	Meadow C8	Meadow C10
Collembola					
Sminthuridae	*Sminthurus viridis*		+	+	+
	Heterosminthurus bilineatus		+	+	
	Deuterosminthurus flavus				+
	Dicyrtomina minuta		+		
Entomobryidae	*Orchesella villosa*		+		
	Lepidocyrtus lanuginosus-group		+		
	gen. spec. immature		+		
Isotomidae	*Isotomurus palustris*		+		
Aphids					
	Rhopalosiphum padi	a[1]	+		
	Rhopalosiphum padi?	l		+	
	Sitobion avenae	l	+		
	Anoecia corni	ω		+	
	Pemphigidae	ω	+		

[1] l = larva, a = apterous, ω = winged

Table 63. Prey composition of wolf spiders (*Pardosa* spp.) in cultivated meadows near Zurich (study years 1977 and 1978).

Location	Date	Collembola	Aphidae	Diptera	Small cicadas	Small lepidopteran larvae	Ants	Small spiders	Unidentified arthropods
C2	6. 9.	-	-	-	-	-	-	-	1
C4	8. 9.	2	1	-	-	-	-	-	-
C4	8. 9.	-	-	-	-	-	-	-	1
C4	10. 9.	-	-	1[a]	-	-	-	-	1
C4	15. 9.	-	-	-	-	-	-	-	-
C4	17. 9.	-	-	-	1	-	-	-	-
C4	21. 9.	-	-	-	-	-	-	-	1
C4	22. 9.	-	1	-	-	-	-	1	-
C4	24. 9.	-	1	-	-	-	-	-	1
C4	26. 9.	-	-	-	-	-	-	-	5
C4	4.10.	-	1	-	-	-	-	-	3
C4	5.10.	-	2	-	-	-	-	-	2
C4	7.10.	-	-	-	-	-	-	-	1
C[b]		1	-	-	-	-	-	-	-
C4	6. 6.	-	-	-	-	-	1	-	-
C2	12. 6.	-	-	-	-	1	-	-	-
C4	12. 6.	1	-	-	-	-	-	-	1
C4	30. 6.	-	1	-	-	-	-	-	-
C2	3. 7.	-	-	1	-	-	-	-	-
C2	15. 7.	-	-	1	-	-	-	-	-
TOTAL		4	7	(3)	1	1	1	1	17

[a] Possibly a small hymenopteran

[b] Meadow near Zurich-Weiningen

soft-bodied prey organisms. Aphids, Collembola (e.g. Orchesella villosa (Geoffroy)), and Diptera seem to form the most important food components of the Lycosidae.

Occasionally, crab spiders (X. cristatus) were also seen on the ground surface of cultivated meadows. Especially after mowing, ground-dwelling X. cristatus were rather frequent. Table 60 (right column) gives information on the food composition of such crab spiders. They fed mainly on ants and spiders (e.g. wolf spiders). In addition, they captured aphids, Carabidae, and Collembola (e.g. Orchesella villosa (Geoffroy)). Even small lumbricide worms were present in the food of ground-dwelling crab spiders.

As the prey compositions (Tables 59-63) indicate, the spiders living in cultivated meadows catch neutral insects (e.g. Diptera), pest insects (e.g. cereal aphids), and beneficial insects (e.g. bees).

3.2.5.3. Prey size

Most spiders living in cultivated meadows captured mainly small, soft-bodied prey of merely 1-3 mm body-length. Such prey organisms have a fresh weight of only 1-2 mg.

3.2.5.4. Prey capture rates

About 10 insects/web/day on the average were counted in webs of N. cornuta in the cultivated meadow C9 in May 1979.

Of the hunting spiders, less than 10% of a population were found feeding at any given time (Tables 64-66). Adult wolf spiders (P. agrestis) spend about 45-60 min for the consumption of a small prey (Table 67). These data being known, the prey capture rate was calculated by means of the method of EDGAR (1969, 1970) (see 2.3.8.2.). It amounts to about 1 prey item/spider/day.

3.2.6. Niche overlap of spiders concerning food

The prey compositions of Araneidae and Thomisidae show a large overlap at order level. Both spider families feed on small Diptera for the most part (see 3.2.5.2.).

The prey compositions of Micryphantidae and Lycosidae had relatively large overlaps at order level, too. Both spider families lived mostly on small, soft-bodied prey organisms (aphids, Collembola, Diptera).

3.2.7. Predator-prey relations between crab spiders and wolf spiders

In cultivated meadows, crab spiders come occasionally into collision with wolf spiders, especially after mowing. If one looks at the chelicerae of the two spider families, it should seem that the highly active Pardosa species, which have significantly larger fangs than the clumsier Xysticus species equipped with only moderately developed mouthparts, would dominate over the Xysticus species (Fig. 4).

If one compares the four pairs of legs of the two spider families however, it is evident that the two pairs of forelegs of the crab spiders are much stronger than those of the wolf spiders (Fig. 5). By taking advantage of the element of surprise, the crab spiders can defeat well-armed

Table 64. Feeding activity of crab spiders (*Xysticus* spp.). Numbers of crab spiders captured in the cultivated meadow C4 and percentage of spiders feeding (years 1977 and 1978).

Date	Hours of observation	Number of spiders captured	Number of spiders feeding
6.5.1977	10-12	10	2
14.5.1977	14-16	18	0
12.7.1977	18-20	14	5
16.7.1977	10-12	90	5
22.7.1977	16-18	194	14
Total (1977)		326 (= 100 %)	26 (= 7.98 %)
24.4.1978	12-16	7	0
26.4.1978	12-16	19	4
3.5.1978	12-16	11	2
10.5.1978	14-16	4	0
17.5.1978	14-16	17	0
30.5.1978	16-18	1	0
1.6.1978	10-12	3	0
6.6.1978	10-12	2	0
12.6.1978	10-12	5	0
Total (1978)		69 (= 100 %)	6 (= 8.70 %)
Total (1977 + 1978)		395 (= 100 %)	32 (= 8.10 %)

Table 65. Feeding activity of wolf spiders (*Pardosa* spp.). Numbers of wolf spiders captured in the cultivated meadow C4 and percentage of spiders feeding (study year 1977).

Date	Hours of observation	Number of spiders captured	Number of spiders feeding	Percentage of spiders feeding
6. 9.1977	14-16	9	0	0
7. 9.1977	14-18	22	0	0
8. 9.1977	10-12	14	3	10.0
	16-18	26	1	
10. 9.1977	10-12	20	0	5.1
	14-16	17	1	
	14-18	27	1	
14. 9.1977	14-16	21	0	0
15. 9.1977	16-18	23	1	4.3
17. 9.1977	14-16	24	1	4.2
21. 9.1977	14-16	20	1	5.0
22. 9.1977	12-16	53	2	3.8
23. 9.1977	14-16	22	0	0
24. 9.1977	12-16	36	2	5.6
26. 9.1977	10-14	23	1	9.8
	14-18	28	4	
4.10.1977	14-16	43	4	9.3
5.10.1977	10-12	10	0	8.0
	14-16	40	4	
7.10.1977	10-12	20	1	5.0
18.10.1977	16-18	8	0	0
TOTAL		506	27	5.3

Table 66. Feeding activity of wolf spiders (Pardosa spp.). Numbers of wolf spiders captured in two cultivated meadows and percentage of spiders feeding (study year 1978).

Location and date	Hours of observation	Number of spiders captured	Number of spiders feeding	Percentage of spiders feeding
Meadow C2:				
12.6.1978	12-14	10	1	(10.0)
3.7.1978	14-18	20[a]	1	5.0
15.7.1978	14-16	15	1	(6.7)
3.8.1978	?	10	0	(0)
Total Meadow C2		55	3	5.5
Meadow C4:				
20.4.1978	14-16	21	0	0
24.4.1978	12-16	25	1	4.0
26.4.1978	12-16	40	0	0
3.5.1978	12-16	24	1	4.2
10.5.1978	14-16	20	1	5.0
17.5.1978	14-16	20	1	5.0
1.6.1978	10-12	10	0	(0)
6.6.1978	10-12	14	1	(7.1)
12.6.1978	10-12	12	2	(16.7)
30.6.1978	10-14	18	1	5.6
Total Meadow C4		204	8	3.9
Total Meadows C2 + C4		259	11	4.3

[a] Incl. Pirata spec.

Table 67. Time (in minutes) spent for the consumption of one prey item by adult males and females of _Pardosa agrestis_ at room temperature in the laboratory.

Prey	males			females		
	N	$\bar{x} \pm$ SD	Range	N	$\bar{x} \pm$ SD	Range
Small Heteroptera	8	66.81 ± 35.87	16.5-135*	8	47.50 ± 38.87	21 -130
Aphidae	7	68.86 ± 42.18	15 -122*	7	55.71 ± 41.43	10 -128
Small Diptera	11	30.05 ± 31.29	8 -120	4	57.75 ± 75.46	7 -170*
Thomisidae (imm.)	5	64.00 ± 55.23	22 -160*	4	68.13 ± 30.85	29.5- 94
Lycosidae (imm.)	15	17.30 ± 2.36	11.5- 26	11	8.32 ± 3.42	5 - 15
Mean value		49.40			47.48	

* Observations terminated; the upper limit of the range would therefore be larger

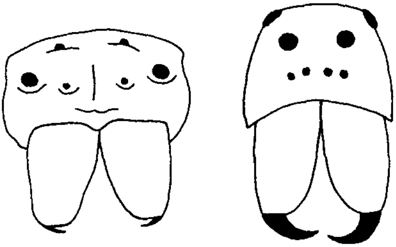

Fig. 4. Comparison of the mouthparts of crab spiders (Xysticus spp.) and wolf spiders (Pardosa spp.). The different formation of the chelicerae of the two spider families is an expression of different feeding behaviours.

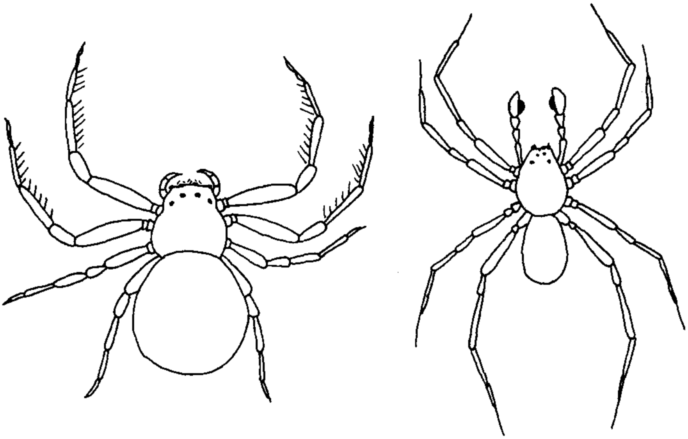

Fig. 5. Comparison of the habits of a crab spider (Xysticus sp.) and of a wolf spider (Pardosa sp.).

arthropods (e.g. wolf spiders) with the help of these legs. In all confrontations observed between individuals of the two spider families, the wolf spiders were always killed by the crab spiders. Crab spiders are potential predators of wolf spiders. It has been observed also in Great Britain and Japan that crab spiders killed wolf spiders (ORI, 1974; O'NEILL, pers. comm.).

3.2.8. Energy flow through the ground-dwelling spider communities

The prey killing rate of ground-dwelling spiders was not investigated. But the energy flow (= food consumed) through the ground-dwelling web-building spider guild could be estimated by means of the method described in section 2.3.10.2. It was calculated to be about 155-419 kJ/ha/day. Supposing 100 activity days per year, this would amount to 15-40 MJ/ha/year.

3.3. The role of spiders as insect predators in cereal fields

3.3.1. Immigration into cereal fields

Data on the time of immigration, the time of harvest and the spiders' duration of stay in the fields are compiled in Table 68. The values in the table indicate that spiders can live in cereal fields only for a limited length of time, from the time of immigration to the time when the fields are harvested. The harvest is a severe stress for the spiders of the vegetation zone (destruction of the living space and the spiders' egg sacs). For this reason, a recolonization of the fields from the surrounding land is necessary every year. As a consequence of the periodic disturbance of the spider population through mowing, the spider densities in the vegetation zone of cereal fields are very low (Table 68).

To what extent the soil cultivation influences the ground-dwelling spider populations, was not examined within the framework of this thesis. Compared to the vegetation zone, the spider densities on the ground surface of cereal fields are relatively high (Table 69).

3.3.2. Spider communities of cereal fields

3.3.2.1. Vegetation zone

The family and species composition of the foliage-dwelling spiders in cereal fields was investigated by direct observations. The data of 1976-1977 are compiled in Table 70. Further observations in the years 1978-1981 were not made quantitatively.

Web-building spiders of the families Araneidae (Araniella cucurbitina/opisthographa*, A. ceropegia, N. cornuta, M. acalypha), Tetragnathidae (T. extensa, T. pinicola), Theridiidae (T. impressum a.o.) and Linyphiidae (L. triangularis a.o.) prevailed in the vegetation zone of cereal fields.

Hunting spiders of the family Thomisidae (Xysticus spp.) were only rarely observed.

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*Araniella cucurbitina (Cl.) and Araniella opisthographa (Kulcz.) are two species which could not be visually distinguished in the field.

Table 68. Time of immigration, time of harvest, duration of colonization, as well as density of the spiders in the vegetation zone of cereal fields near Zurich.

Crop	Time of harvest	Duration of vegetation of the crop (days)	Time of immigration of spiders into the fields	Duration of colonization of fields (days/year)	Population density as spiders/m^2 in 1976/77
Summer cereal fields	July	120 - 160	May to June	about 60	0.1 - 0.6
Winter cereal fields	July	300	April to June	" 70	
Maize fields	October	140 - 180	June	" 130	≤ 0.1

Table 69. Density of the ground-dwelling web-building spiders in three maize fields and in two winter wheat fields near Zurich (study years 1978 and 1979).

Location	Crop	Date	No. squares	Spiders/m^2
Weiningen	maize	6.6.1978	65[a]	13.38
Milchbuck	maize	12.6.1978	20[a]	19.00
Reckenholz	maize	14.7.1978	20[a]	35.00
Reckenholz	winter wheat	7.6.1978	40[b]	53.13
Reckenholz	winter wheat	16.5.1979	50[c]	11.88

[a] Square of 0.33 m x 0.33 m

[b] Square of 0.20 m x 0.20 m

[c] Square of 0.40 m x 0.40 m

Table 70. Composition of the spider fauna in the vegetation zone of cereal fields near Zurich in 1976/77. Adult and immature spiders counted by direct observation.

Crop	Oats	Maize	Wheat	Wheat	Barley	Barley	Rye	
Location	Höngg	diverse	Schlieren	Reckenholz	Weiningen	Katzensee	Höngg	Total
Season or month(s)	summer	summer/ autumn	VI-VII	V-VII	V-VI	V	V-VII	
Araniella cucurbitina[a] *Araniella opisthographa*[a]	53	-	25	8	3	6	10	105
Aculepeira ceropegia	50	6	-	4	2	1	8	71
Araneus diadematus	129	1	-	-	-	-	1	131
Nuctenea cornuta	-	16	19	2	66	-	-	103
Nuctenea sp.	-	4	-	-	-	-	-	4
Mangora acalypha	7	-	3	6	-	-	-	16
Meta sp.	-	3	-	-	-	1	-	4
Zygiella sp.	18	1	-	-	-	-	-	19
Cyclosa sp.	-	-	-	-	-	-	1	1
Araneidae gen. sp.	25	291[b]	15	8	-	-	1	340
Tetragnatha sp.	3	12	6	20	1	50	-	92
Theridiidae	43	36	24	12	-	1	1	117
Linyphiidae Micryphantidae	28	2	5	-	-	2	9	46
Thomisidae Philodromidae	6	6	1	1	4	3	11	32
Salticidae	-	-	1	-	-	-	2	3
Unidentified spiders	31	35	1	1	-	-	6	74
Total	393	413	100	62	76	64	50	1158

[a] Two species which could not be visually distinguished in the field, [b] Immature orb-weaving spiders

In contrast to abandoned grasslands, jumping spiders and large funnel web spiders were only seldom encountered in cereal fields. The same is true for A. bruennichi and A. quadratus, which predominate in abandoned grasslands.

It is conspicuous that the spider fauna in the vegetation zone of cereal fields consists to a large extent of orb-weaving spiders (Araneidae, Tetragnathidae). The Araneidae found in maize fields show a significantly higher percentage of immature stages than in the rest of the cereal crops (χ^2 2 x 2 contingency table, $p < 0.01$). The almost complete absence of adult orb-weaving spiders in maize fields might be explained by the fact that maize develops a dense plant stand much later than the other cereals.

The composition of the spider fauna differs from field to field. In each case, however, it depends on the surroundings of the field. Predominantly medium-sized species (see Table 13) are found among the adult foliage-dwelling spiders, A. ceropegia being the largest species in cereal fields.

3.3.2.2. Ground surface

The family and species compositions of spiders established by means of pitfall traps on the ground of winter wheat fields are compiled in Tables 71-73. Spiders belonging to the families Micryphantidae and Lycosidae predominated.

In Tables 72-73, the composition of spider species captured frequently on the ground surface of winter wheat fields is listed for the years 1977-78. P. agrestis, P. palustris, E. atra, E. dentipalpis, and Oedothorax apicatus (Blackw.) were the most frequent species found in pitfall traps. Similar results have been obtained in 1979. Comparable data were also collected in other cereal fields.

Most spiders living on the ground surface of cereal fields are of small body size (Micryphantidae, see Table 13). Wolf spiders of the genus Trochosa are the largest spiders on the ground of cereal fields.

3.3.3. Seasonal change of abundance and daily activity

3.3.3.1. Seasonal change of abundance

In Table 74, the seasonal occurrence of the predominant spiders in the fields is compared to the seasonal development of the cereal vegetation. As the table indicates, most spiders migrate into the vegetation zone of the fields in spring only after the stem elongation has occurred. The colonizing spiders come from small, intact marginal biotopes, such as stripes of meadows, and forest fringes. From the time of immigration up to the harvest, the spiders spend only 60-70 days in cereal fields and about 130 days in maize fields (Table 68).

The ground-dwelling spiders show statistically significant differences of abundance in different seasons (analysis of variance, $p < 0.01$).

3.3.3.2. Daily activity

The orb-weaving spider N. cornuta is prevalently nocturnal. Fig. 6

Table 71. Family composition in % of the ground-dwelling spiders in a winter wheat field near Zurich-Reckenholz (year 1978; traps dug into the ground on May 21).

Spider family	Traps emptied on:				
	1.6.	19.6.	4.7.	31.7.	Total
	N= 89	N=432	N=118	N=235	N=874
Micryphantidae	87.6	52.6	88.1	94.5	72.4
Lycosidae	11.2	44.0	8.4	0.4	24.1
Tetragnathidae	0	0.9	0.8	0	0.6
Linyphiidae	0	1.2	0	0	0.6
Thomisidae	0	0.2	0	0	0.1
Unidentified spiders	1.1	1.2	2.5	4.3	2.1
Total	100.0	100.0	100.0	100.0	100.0

Table 72. The dominant ground-dwelling spider species in a winter wheat field near Zurich-Reckenholz (year 1977, traps dug into the ground on May 17).

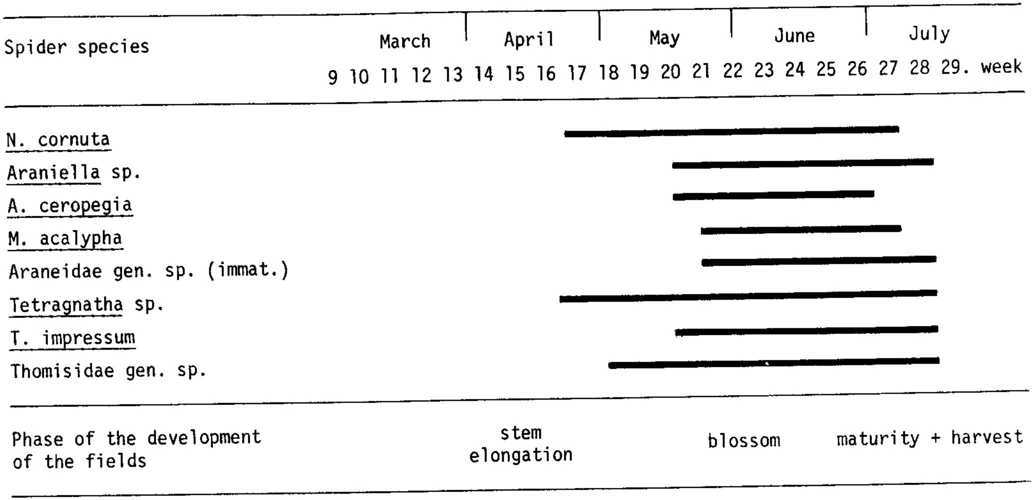
Spider species		Traps emptied on:					
		26.5. N= 502	3.6. N= 373	18.6. N=1490	5.7. N=1647	20.7. N=4289	3.8. N=4572
		%	%	%	%	%	%
Erigone atra	♂	33	20	44	50	36	19
Erigone dentipalpis	♂						
Erigone atra	♀	0	0	0.3	0.5	0.8	0.7
Erigone dentipalpis	♀	0	0	0.3	0.9	0.4	0.7
Oedothorax apicatus	♂	9	3	6	17	23	20
Oedothorax fuscus	♂	0	0.3	0.3	0.5	1	1.5
Oedothorax apicatus	♀	29	16	9	6	29	36
Oedothorax fuscus	♀						
Pardosa agrestis	♂	16	35	13	4	0.2	4
Pardosa palustris	♂	3	13	2	0.2	0	0.1
Pardosa agrestis	♀	7	4	2	1	0.3	2
Pardosa palustris	♀	< 0.5	< 0.5	0	0.1	0	0.04

Table 73. The dominant ground-dwelling spider species in a winter wheat field near Zurich-Reckenholz (year 1978, traps dug into the ground on May 21).

Spider species		Traps emptied on:				
		1.6. N= 89	19.6. N=432	4.7. N=118	31.7. N=235	Total N=874
		%	%	%	%	%
Erigone atra	♂	34	21	31	26	25
Erigone atra	♀	0	0.7	2.5	0	0.7
Erigone dentipalpis	♂	24	18	30	18	20
Erigone dentipalpis	♀	0	0.7	2	0.9	0.8
Oedothorax apicatus	♂	6	3	9	19	8
Oedothorax apicatus	♀	24	8	3	28	14
Pardosa agrestis	♂	8	29	2.5	0	16
Pardosa agrestis	♀	1	3	4	0	2
Pardosa palustris	♂	2	11	0	0	6
Pardosa palustris	♀	0	0	0	0	0
Other spiders	♂/♀	2	6	15[a]	8	7

[a] Among them 7.6% males of *Erigone* spp. with destroied pedipalps

Table 74. Comparison of the seasonal occurrence of dominant spiders in the vegetation zone of winter cereal fields near Zurich with the seasonal development of the fields (years 1976-1977).



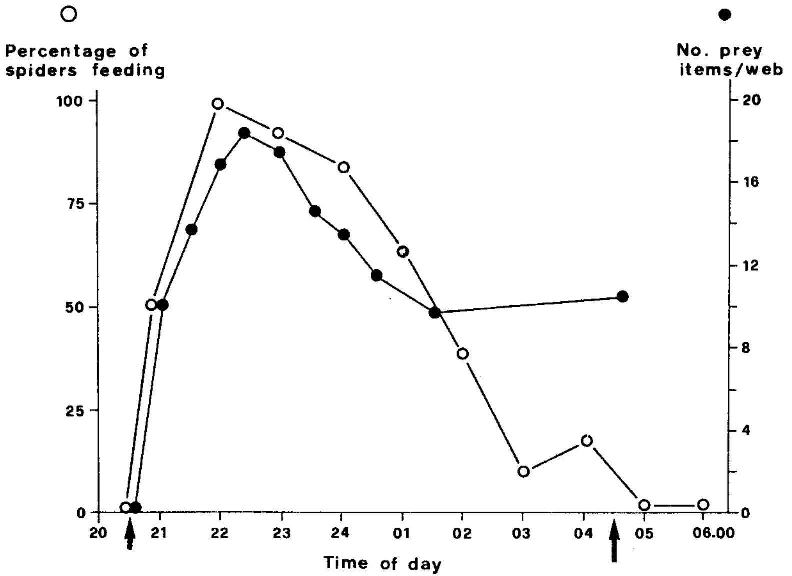


Fig. 6. Daily rhythm of feeding activity of Nuctenea cornuta in a rye field in Weiningen near Zurich in summer 1976. The arrows indicate the times of sunset and sunrise.

represents the feeding activity and number of prey/web of N. cornuta at different daytimes. This spider species captures its prey at night in the following manner: The web-building activity is induced in the evening twilight, when the intensity of the light drops below a critical intensity. The building of an orb-web requires 30-60 minutes. At about the same time, the flying activity of many cereal insects active at night or in the twilight begins. Tipulidae, Noctuidae, Pyralidae, and Chrysopidae begin to fly about, and many small Nematocerae swarm in the flowering zone of the field, where the orb-webs, about 25 cm in diameter, have been built. These now continuously filter the swarms of nocturnal flying insects. Most of the prey gets caught in the webs between 20.30 and 22.30; during these two hours, the spiders captured 10-20 prey items/web on the average. The hungry spider starts feeding immediately after having built the web. The highest feeding activity lies between 22.00 and 24.00. Since only occasionally prey organisms fly into the webs after 22.00, the webs are gradually emptied through the spiders' feeding activity. The spiders' feeding activity diminishes after midnight and ends towards daybreak. The spiders then retire into their retreats where they hide during the day.

Most of the other orb-weaving spiders were observed feeding during the day and at night (e.g. A. diadematus and A. ceropegia, Table 75). Space web spiders of the families Theridiidae, Linyphiidae and Micryphantidae are also diurnal and nocturnal, whereas wolf spiders of the genus Pardosa are prevalently diurnal.

3.3.4. Spatial distribution of spiders

3.3.4.1. Vertical distribution of spiders

In cereal fields, we find spiders from the ground surface up to the flowering zone (Table 76). As can be derived from section 3.3.1.2., most spiders live near the ground (>90%).

3.3.4.2. Horizontal distribution

In 1977 and 1979, the horizontal distribution of the spiders of the vegetation zone and the ground surface in winter wheat fields was studied by means of the square method, and the index of Morisita was calculated (Table 77). The observed distributions of the foliage-dwelling spiders did not statistically deviate significantly from a random distribution (F-test, $p > 0.05$). The same is true for the distribution of the ground-dwelling web-building spiders (Micryphantidae) in the winter wheat fields as well as in other wheat fields and in two maize fields (F-test, $p > 0.05$). However, a slightly aggregated distribution was noted in another maize field (F-test, $p < 0.05$).

The horizontal distribution of the ground-dwelling spiders was also studied by means of pitfall traps in a winter wheat field at different seasons. Although the Figs. 7-18 give only the activity-densities of the ground-dwelling spiders, the figures may be regarded as graphical representations of the horizontal distribution of these spiders. The Figs. 7-12 show the horizontal distribution of the Micryphantidae at different times of the year. A comparison of the capture rates of the traps on the border of the field with those in the centre did not show

Table 75. Feeding activity in % of two orb-weaving spider species (% f) at different times of day in an oat field near Zurich-Höngg in summer 1976 (N = no. spiders observed). Activity values followed by the same letter differ significantly (χ^2 test 2 x 2 contingency table, $P < 0.05$).

Hours of observation	*A. diadematus*		*A. ceropegia*	
	N	% f	N	% f
00-04	33	21.2 d	-	-
04-08	60	10.0 ac	-	-
08-12	112	25.0 a	22	18.2
12-16	25	20.0 b	12	25.0
16-20	11	63.6 abcd	11	45.5
20-24	48	27.1 c	9	22.2

Table 76. Vertical distribution of the orb-weaving spiders and of *Achaearanea riparia* in the vegetation zone of a winter wheat field near Zurich-Reckenholz in June 1979; the vegetation was 1.2 m high.

Height of orb hub above ground (cm)	*Mangora acalypha*	Other orb-weavers	All orb-weavers	*Achaearanea riparia*
100 - 125	3	0	3 (3 %)	0 (0 %)
75 - 100	6	19	25 (25 %)	0 (0 %)
50 - 75	42	16	58 (59 %)	0 (0 %)
25 - 50	12	1	13 (13 %)	0 (0 %)
0 - 25	0	0	0 (0 %)	38 (100 %)
Total	63	36	99 (100 %)	38 (100 %)

Table 77. Horizontal distribution of the web-building spiders in the vegetation of winter wheat fields and on the ground surface of maize and winter wheat fields near Zurich. The data were investigated by means of the square method. Values with * deviate significantly from $I_\delta = 1$ (F-test, $P < 0.05$).

Stratum	Crop	Location	Date	No. squares	Morisita index I_δ
Vegetation	Winter wheat	Reckenholz	16.7.1977	35[a]	1.11
	Winter wheat	Reckenholz	22.5.1979	100[b]	0.67
Ground surface	Maize	Weiningen	6.6.1978	65[c]	1.29*
	Maize	Milchbuck	12.6.1978	20[c]	1.34
	Maize	Reckenholz	14.7.1978	20[c]	1.03
	Winter wheat	Reckenholz	7.6.1978	40[d]	0.96
	Winter wheat	Reckenholz	16.5.1979	50[b]	0.75

[a] Square of 1.00 m x 1.00 m

[b] Square of 0.40 m x 0.40 m

[c] Square of 0.33 m x 0.33 m

[d] Square of 0.20 m x 0.20 m

Figs. 7-12. Horizontal distribution of the ground-dwelling sheet-web spiders (mainly Micryphantidae) captured by pitfall traps in a winter wheat field near Zurich-Reckenholz in the year 1977. Each square represents a pitfall trap. The number of points per square represents the number of spiders captured per trap and per time unit. A horizontal bar instead of a number means that the pitfall trap was destroied. The distribution of the squares corresponds with the distribution of the pitfall traps in the field (comp. Fig. 2). Traps emptied on May 26 (Fig. 7), June 3 (Fig. 8), June 18 (Fig. 9), July 5 (Fig. 10), July 20 (Fig. 11), and August 3 (Fig. 12).

Figs. 13-18. Horizontal distribution of the wolf spiders (mainly *Pardosa agrestis* and *P. palustris*) captured by pitfall traps in a winter wheat field near Zurich-Reckenholz (otherwise as Figs. 7-12, see above). Traps emptied on May 26 (Fig. 13), June 3 (Fig. 14), June 18 (Fig. 15), July 5 (Fig. 16), July 20 (Fig. 17), and August 3 (Fig. 18).

Fig. 7

1	13	0	16	13	14	18	12	10
3	13	0	8	11	4	10	10	8
7	5	14	4	6	7	6	9	10
13	1	0	17	12	13	—	8	16
8	0	4	8	6	1	7	7	7

Fig. 8

8	6	12	8	4	6	6	6	4
4	1	6	8	4	4	2	4	4
2	4	0	10	4	1	13	2	1
2	0	6	2	1	2	2	5	5
1	0	0	0	2	1	2	5	2

Fig. 9

57	20	24	54	51	52	15	28	—
24	27	33	27	39	22	16	24	6
26	38	24	29	34	41	32	46	11
—	30	17	25	38	36	—	16	21
16	9	15	11	7	11	14	23	16

Fig. 10

52	18	23	35	51	44	25	14	20
66	24	22	35	46	18	29	54	13
45	27	6	23	69	31	31	33	40
50	43	40	37	75	39	30	45	52
68	63	31	11	20	21	25	0	30

Fig. 11

74	50	58	70	13	73	61	76	108
89	122	70	129	159	81	125	190	—
96	67	108	57	115	57	76	136	—
—	90	100	129	144	166	132	143	254
102	49	86	63	117	68	65	65	76

Fig. 12

—	125	88	79	—	105	94	109	—
50	163	75	38	75	120	77	118	102
0	83	103	117	104	126	140	117	166
90	—	109	33	70	62	123	68	164
81	—	82	43	84	96	104	73	—

Fig. 13

1	1	0	2	0	1	1	7	4
2	15	0	0	0	2	1	7	1
3	0	3	3	0	1	7	1	2
4	0	0	5	6	6	—	13	4
8	0	2	0	0	4	4	3	1

Fig. 14

11	8	3	3	1	8	6	17	12
4	14	2	2	3	1	2	2	1
7	1	0	3	—	1	8	3	1
4	5	2	5	6	11	0	2	2
15	0	4	0	2	7	4	6	1

Fig. 15

6	6	9	3	3	11	9	6	—
5	9	10	2	14	11	2	2	0
20	4	4	3	0	16	5	6	3
—	1	2	5	8	29	—	11	0
26	5	3	4	8	4	4	4	3

Fig. 16

4	0	2	1	0	0	0	4	—
1	2	0	1	8	12	0	0	0
2	0	0	4	0	8	3	1	—
—	0	1	2	5	3	—	3	1
7	6	0	1	2	4	2	0	—

Fig. 17

1	0	1	0	0	0	0	1	1
0	2	0	0	1	1	1	1	—
0	1	0	1	0	0	1	0	—
—	0	0	0	0	4	1	2	5
1	1	1	1	0	2	0	1	1

Fig. 18

—	2	0	4	—	0	2	6	—
1	12	1	0	18	4	5	7	2
0	1	2	0	2	4	4	7	6
18	—	0	1	1	34	4	8	112
6	—	0	0	1	0	1	3	—

statistically significant differences (t-test*, $p > 0.05$). Thus no noteworthy edge effect could be detected.

The same is true for the hunting spiders living on the ground. A graphical representation of the horizontal distribution of the Lycosidae in the winter wheat field at different seasons is given in the Figs. 13-18.

3.3.5. Prey capture of spiders

3.3.5.1. Hunting strategies

Table 78 gives a view over the hunting strategies of the spiders living in cereal fields. In the vegetation zone of cereal fields, 95-98% of all spiders capture their prey by means of webs, and only 2-5% catch their food as hunting spiders without webs. The proportion of orb-weaving spiders (families Araneidae and Tetragnathidae) of the total of all web-building spiders of cereal fields was 75-88%.

In the pitfall traps, 75% were web-building spiders and 25% hunting spiders. This indicates that most ground-dwelling spiders in cereal fields capture their prey by means of webs.

3.3.5.2. Prey composition

Vegetation zone

Orb-weaving spiders - The prey compositions of orb-weaving spiders of wheat, barley, rye, oat and maize fields are represented in Table 79. The table indicates that Diptera (68.8-92.1%), and winged aphids (4.0-17.5%) prevail in the prey compositions of orb-weaving spiders in cereal fields. Detailed information on the prey compositions of orb-weaving spiders in cereal fields are given by NYFFELER & BENZ (1979a).

Space web spiders - Table 80 shows the prey compositions of *T. impressum* in wheat and oat fields. Diptera and aphids are the most important components of the food of *T. impressum*. The prey of the foliage-dwelling Linyphiidae in cereal fields also consisted mostly of small Diptera and Homoptera.

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*The asymmetric distribution of the data was corrected, in order to permit the use of the t-test.

Table 78. The hunting strategies of the spiders living in cereal fields.

Spider species, and/or genus	Hunting manner	Mesh width (mm)	Web Ø cm	Web area cm^2
Nuctenea cornuta	orb-web	3-4	20-30	500
Araniella cucurbitina	"	2-3	6- 8	40
Aculepeira ceropegia	"	1-3	20-30	500
Araneus diadematus	"	3	15-25	300
Mangora acalypha	"	1	14	150
Araneidae gen. sp. (imm.)	"	1-2	2- 8	20
Tetragnatha spp.	"	3	8-15	100
Pachygnatha degeeri (imm.)	"		2.5	5
Theridion impressum	irregular web	-	-	-
Achaearanea riparia	tangled web	-	-	-
Linyphia spp.	sheet-web	-	-	-
Erigone spp.	"	-	-	-
Oedothorax spp.	"	-	-	-
Xysticus spp.	ambusher	-	-	-
Pardosa spp.[a]	runner	-	-	-

[a] In the literature the *Pardosa* spp. are usually described as runners. However, FORD (1978) found that *Pardosa amentata* adopts a "sit-and-wait" strategy with periodic changes of site.

Table 79. Prey composition of orb-weaving spiders in the vegetation zone of cereal fields near Zurich (years 1976-1977).

Prey	1976			1977	
	Rye	Oats	Maize	Wheat	Barley
	%	%	%	%	%
Heteroptera	0.2	0.4	1.7	0	0
Thysanoptera	0	0.9	5.8	10.2	0.8
Aphidae	17.5	5.6	12.7	14.8	4.0
Coleoptera	0.3	1.7	1.2	0.2	0.8
Hymenoptera	0	1.3	0	1.0	0.4
Chrysopidae	3.9	1.3	0.6	0	0.8
Diptera	77.6	71.5	68.8	68.4	92.1
Number of prey items	375	231	144	412	529

Table 80. Prey composition of *Theridion impressum* in the vegetation zone of wheat and oat fields near Zurich (years 1976-1977).

Prey	Wheat %	Oats %
Ephemeroptera	7.6	7.9
Thysanoptera	9.0	1.6
Aphidae	42.6	33.3
Coleoptera	3.1	11.1
Hymenoptera	0.4	9.5
Trichoptera	0	7.9
Diptera	27.8	20.6
Number of prey items	223	76

Hunting spiders - Thomisidae and other hunting spiders were only rarely observed feeding in the vegetation zone of cereal fields. Since foliage-dwelling hunting spiders (Thomisidae, Philodromidae, Salticidae, Clubionidae, Pisauridae) appear to live in low densities in cereal fields and since only a small percentage of a hunting spider population is feeding at a given observation time, the probability of surprising a hunting spider with a prey is exceedingly low. Thomisidae could be observed capturing Diptera, spiders, and one aphid in cereal fields.

Ground surface

Web-building spiders - The prey composition of the Micryphantidae of wheat and maize fields is represented in Table 81. The table indicates that the food of the Micryphantidae exclusively consisted of small soft-bodied prey, aphids, Collembola, and Diptera being the most important components. The Collembola captured by the Micryphantidae, generally belong to the Sminthuridae.

Hunting spiders - The prey composition of the Lycosidae of wheat fields is represented in Tables 82-84. It also includes mainly small, soft-bodied prey organisms, especially aphids, Collembola, and Diptera. The Collembola for the most part belong to the Arthropleona-group (e.g. Isotomidae and Orchesella villosa (Geoffroy) of the family Entomobryidae).

The captured aphids were exclusively cereal aphids (Metopolophium dirhodum Walk., Rhopalosiphum padi L., Sitobion avenae F., as listed in Table 85.

Spiders with special hunting strategies - Adult Carabidae and Staphylinidae were missing in the food of the Lycosidae and Micryphantidae, as both, the Lycosidae and the Micryphantidae, are not capable of killing hard-bodied beetles. There is, however, a spider species belonging to the family Theridiidae, Achaearanea riparia (Blackw.), which often captures adult Carabidae and Staphylinidae by means of tangled webs (Table 86). As Table 87 shows, several Carabidae-species (mainly of the genus Amara) were captured by A. riparia. It captured a rather typical selection of medium-sized Carabidae living in cereal fields of Western Europe (comp. THIELE, 1977, p. 27). (A. riparia has been observed killing Carabidae also in meadows, with slopes, where this spider lives, too).

3.3.5.3. Prey size

More than 90% of the food of spiders in cereal fields consisted of small, soft-bodied prey organisms of only 1-3 mm body length. Such prey organisms have a fresh weight of merely 1-2 mg.

3.3.5.4. Prey capture rates

Vegetation zone

In order to determine how many insects per day are killed by one web, continuous observations of orb-webs were conducted on a total of 7 days. The results of these observations are compiled in Table 88. The table

Table 81. Prey composition of the Micryphantidae in cereal fields near Zurich (years 1977 and 1978).

Prey	Winter wheat 1977	Winter wheat 1978	Maize 1978	Total	
Collembola	11	31	9	51	37.2 %
Aphidae	18	25	13	56	40.9 %
Small Diptera	6	9	2	17	12.4 %
Other small arthropods	1	3	1	5	3.6 %
Unidentified prey	2	5	1	8	5.8 %
Total of prey items	38	73	26	137	100 %

Table 82. Prey composition of wolf spiders (P. agrestis and P. palustris) in a winter wheat field near Zurich (year 1978). Index: + = ≲ 10%; ++ = 10-20%; +++ = 20-35%; ++++ = > 35%.

	May	June	July/August	Total
No. observation days	6	7	21	34
No. spiders captured	263	242	1013	1518
Spiders with prey	9	10	40	59
Prey composition:				
Collembola	++++	+++	++	40 %
Aphidae	++	+++	+++	24 %
Diptera		++	+	12 %
Lepidoptera (larvae)			+	4 %
Mites			+	4 %
Spiders		++	+++	16 %

Table 83. Prey composition of wolf spiders (*Pardosa* spp.) in a winter wheat field near Zurich-Reckenholz (June/July 1979).

Prey	Immature	Adult males	Adult females			Total
				with egg sac	with young	
Diptera (small/medium-sized)	0	2	6	2	1	11
Diptera?	0	0	1	0	0	1
Diptera larvae	0	0	1	0	0	1
Aphidae (winged)	0	1	2	0	0	3
Aphidae (apterous)	0	1	4	1	1	7
Hymenoptera (small)	0	0	1	0	0	1
Ephemeroptera?	0	0	1	0	0	1
Staphylinidae (small)	0	0	1	0	0	1
Carabidae larvae (small)	0	0	2	0	0	2
Collembola (Arthropleona)	0	0	1	0	0	1
Spiders (small)	1	0	0	0	0	1
Mites	0	0	1	0	0	1
Unidentified prey[a]	3	1	8	7	0	19
Total	4	5	29	10	2	50

[a] Among them were possibly several Collembola; they were so strongly deformed that they could not be determined unmistakably.

Table 84. Prey composition of three wolf spider species in a winter wheat field near Zurich-Reckenholz (June/July 1979) (same data as in Table 83 but other representation).

Prey	*Pardosa agrestis*	*Pardosa palustris*	*Pardosa amentata*	*Pardosa* sp. (immature)	Total	
					N	%
Diptera	7 + (1?)	2	3	0	13	26.0
Aphidae	6	2	2	0	10	20.0
Hymenoptera	1	0	0	0	1	2.0
Collembola	1	0	0	0	1	2.0
Ephemeroptera?	0	0	1	0	1	2.0
Staphylinidae	0	0	1	0	1	2.0
Carabidae larvae	1	0	1	0	2	4.0
Spiders	0	0	0	1	1	2.0
Mites	0	0	1	0	1	2.0
Unidentified prey[a]	12	2	1	3	19	38.0
Total	29	6	10	4	50	100.0

[a] Among them here are possibly several collembolans, which were strongly deformed and therefore could not be determined unmistakably

Table 85. Aphid species in the food of wolf spiders. Observations in a winter wheat field near Zurich-Reckenholz (June/July 1979).
a = apterous, w = winged, + = prey of wolf spiders.

Aphid species		Wolf spiders		
		P. agrestis	*P. palustris*	*P. amentata*
Metopolophium dirhodum	a	+ (June)	+ (June)	
Metopolophium dirhodum	w		+ (June)	+ (June)
Rhopalosiphum padi	a	+ (July)		
Sitobion avenae	a			+ (June)

Table 86. Prey composition of *Achaearanea riparia* in winter wheat fields near Zurich (years 1977-1979).

Prey	1977 %		1978 %		1979 %	
Dermaptera	0		2.1		0	
Orthoptera	1.3		0		0	
Heteroptera	0		0		2.1	
Cicadas	0		1.1		0.7	
Aphidae	0		3.2		27.0	
Carabidae (see Table 87)	26.7	50.6	2.1	6.4	5.7	14.2
Staphylinidae	13.3		3.2		5.0	
Other Coleoptera	10.6		1.1		3.5	
Diptera	2.6		8.4		7.1	
Apterous ants	22.7	24.0	23.2	59.0	17.0	26.2
Winged Hymenoptera	1.3		35.8		9.2	
Spiders	0		5.4		0.7	
Mites	0		7.4		4.3	
Unidentified prey	22.7		7.4		17.7	
No. prey items	76		95		141	

Table 87. Carabidae species in the prey of *Achaearanea riparia* in a winter wheat field near Zurich (years 1977 and 1979).

Carabidae species	1977	1979	Total	
	N	N	N	%
Loricera pilicornis	3	1	4	16.67
Clivina fossor	1	1	2	8.33
Acupalpus teutonus	1	-	1	4.17
Agonum dorsale	1	-	1	4.17
Agonum muelleri	-	1	1	4.17
Amara spec.	11	0	11	45.83
Amara spec. ?[a]	2	0	2	8.33
Carabidae gen. spec.[a]	2	0	2	8.33
Total	21	3	24	100.0

[a] Only fragments found

Table 88. Number of prey items captured by *Nuctenea cornuta* per web and per day in a rye field near Zurich-Weiningen (summer 1976).

Date	No. webs	Prey/web/day
25.6.	7	12.6
26.6.	8	15.0
28.6.	5	9.2
1.7.	7	20.0
2.7.	8	8.1
5.7.	4	25.0
6.7.	4	10.3
$\bar{x} \pm$ SE	-	14.3 ± 2.3

shows that on days without rain, 14.3 ± 2.3* prey items/day on the average got caught in a web of about 500 cm^2 of N. cornuta. In a cereal field, more than 200 Diptera were found in a single web of N. cornuta. This indicates that spiders have a high killing potential.

Ground surface

As can be seen in Table 89, about 4% of the wolf spiders, observed in winter wheat fields in 1978 and 1979, held a prey between their chelicerae. Of the ground-dwelling web-building spiders also, only about 4% were actually feeding. Adult wolf spiders (P. agrestis) need about 45-60 min for the consumption of a small prey (Table 67). These data being known, the prey capture rate was calculated by means of the method of EDGAR (1969, 1970), and was found to be less than 1 prey item/spider/day for the Micryphantidae and Lycosidae.

3.3.5.5. Number of prey capture days per year

Vegetation zone

As rain destroys the spiders' webs and impairs the flying abilities of the prey insects, only days without rainfall offer optimal conditions for the spiders to catch prey. The spider webs not destroyed by wind and rain capture significantly less prey on rainy days than on rainless days, even when precipitations are restricted to part of the day (Mann-Whitney U-test, $p < 0.01$). In the year 1976, only 45 days of the period which the spiders stayed in the cereal fields were without rainfall, and in 1977 only 36 days. In maize fields, however, 78 and 64 days resp. were rainless during the time the spiders stayed there in 1976 and 1977. Spiders can thus actively capture prey on 40 days/year on the average under most favorable and on 30 days/year under less favorable conditions in cereal fields, but on 71 days/year or 59 days/year resp. in maize fields.

Ground surface

The ground-dwelling spider community is less influenced by combine harvesting. The ground surface can therefore be colonized by spiders during a longer period of time than the vegetation zone.

3.3.6. Niche breadth and niche overlap concerning the food of spiders

3.3.6.1. Vegetation zone

The coefficients $\hat{C}\lambda$ of the food overlaps of the web-building spiders coexisting in the vegetation zone of cereal fields are compiled in Table 90. The values show that 12 of the 21 tested overlap pairs are significant ($\hat{C}\lambda \geq 0.60$)**. The food compositions of the Araneidae show a total overlap, although each species has a different web pattern ($\hat{C}\lambda > 0.95 \therefore$ prey compositions identical). Between the food compositions of Araneidae and Tetragnathidae there is also a significant overlap in every case ($\hat{C}\lambda = 0.68$-0.76). The overlaps between Theridion impressum with a space web, on the one hand, and the orb-weaving spiders, on the other hand, are

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*Mean ± standard error ($\bar{x} \pm SE$)

**If the overlap had been calculated at species level of the prey instead of order level, lower overlap values would possibly have resulted.

Table 89. Percentage of feeding (f) wolf spiders (Pardosa spp.) captured in two winter wheat fields near Zurich-Reckenholz.

1978	May			June			July/August			Total			
No. observation days	6			7			21			34			
Air temperature ^oC (monthly mean)	10.9°C			14.3°C			16.0°C			-			
	$\sum$	f	%f	$\sum$	f	%f	$\sum$	f	%f	$\sum$	f	%f	
Pardosa ♂	108	6	5.56	111	1	0.90	232	6	2.59	451	13	2.88	
Pardosa ♀	67	3	4.48	22	2	9.09	331	23	6.95	420	28	6.67	4.13
Pardosa ♀ with egg sac	29	1	3.45	89	3	3.37	393	6	1.53	511	7	1.37	
Pardosa ♀ with young	0	0	0	4	0	0	34	5	14.71	38	5	13.16	
Pardosa immature	59	0	0	16	1	6.25	23	1	4.35	98	2	2.04	
Total	263	10	3.80	242	7	2.89	1013	41	4.05	1518	55	3.62	

1979	May			June			July			Total			
No. observation days	1			12			8			21			
Air temperature ^oC (monthly mean)	12.4°C			16.1°C			17.2°C			-			
	$\sum$	f	%f	$\sum$	f	%f	$\sum$	f	%f	$\sum$	f	%f	
Pardosa ♂	9	0	0	116	4	3.45	61	1	1.64	186	5	2.69	
Pardosa ♀	9	0	0	133	24	18.05	69	3	4.35	211	27	12.80	5.14
Pardosa ♀ with egg sac	29	0	0	219	1	0.46	135	4	2.96	383	5	1.31	
Pardosa ♀ with young	0	0	0	60	2	3.33	8	0	0	68	2	2.94	
Pardosa immature	3	0	0	1	0	0	161	4	2.48	165	4	2.42	
Total	50	0	0	529	31	5.86	434	12	2.76	1013	43	4.24	

Table 90. Niche breadth (B_i) and niche overlap ($\hat{C}\lambda$) concerning food in coexisting web-building spiders in the vegetation zone of the cereal fields (calculated from the data of 1976-1977).

	Prey overlap $\hat{C}\lambda$							Niche breadth
	Araneus diadematus	Aculepeira ceropegia	Nuctenea cornuta	Mangora acalypha	Tetragnatha sp.	Theridion impressum	$\bar{x}$	B_i
Araneus diadematus	—							1.40
Aculepeira ceropegia	1.0	—					1.0	1.61
Nuctenea cornuta	1.0	1.0	—				1.0	1.41
Mangora acalypha	1.0	1.0	1.0	—			1.0	2.03
Tetragnatha sp.	0.8	0.7	0.8	0.7	—		0.75	1.14
Theridion impressum	0.5	0.6	0.6	0.7	0.4	—	0.56	3.50
Achaearanea riparia	0.04	0.05	0.04	0.04	0.03	0.1	0.05	2.81

not significant for the most part ($\hat{C}\lambda$ = 0.35-0.72) because, although *T. impressum* with its space web filters flying insects out of the aerial plankton, just as the orb-weaving spiders, it often happens that jumping insects and insects running on plants get caught in the space webs. The prey composition of *T. impressum* shows therefore a considerably wider range of prey types than the one of the orb-weaving spiders (niche breadth, see Table 80). A verification by means of the Mann-Whitney U-test confirms that the niche breadth (concerning food) of the Theridiidae is significantly larger than that of the orb-weaving spiders ($p < 0.05$). It is interesting to note that also the food compositions of the two Theridiidae *T. impressum* and *A. riparia* overlap only little ($\hat{C}\lambda$ = 0.1). This can be explained by the vertical isolation of the catching areas of the two species. Whereas *T. impressum* builds its webs mostly in the upper part of the vegetation zone of cereal fields and therefore capture only insects of the vegetation zone, *A. riparia* builds its species-characteristic retreats near the ground (about 15.7 ± 0.9 cm above ground) and constructs a tangle web down to the ground, in which mostly ground-dwelling arthropods get caught (Carabidae, Staphylinidae, ants, etc.).

As a consequence of the isolation of the catching areas, there are practically no overlaps between the food compositions of *A. riparia* and those of the orb-weaving spiders ($\hat{C}\lambda < 0.10$).

3.3.6.2. Ground surface

The wolf spiders and the ground-dwelling web-building spiders show large prey size overlaps, since both spider groups prey primarily on small, soft-bodied prey organisms.

3.3.7. Spiders as predators of pest insects and beneficial insects

As mentioned before, cereal aphids, which can be pests in cereal crops, have been recorded in the food of ground-dwelling spiders. Unfortunately, the aphids captured by foliage-dwelling spiders were not determined at species level. But doubtless there were cereal aphids, too, among the aphids captured by foliage-dwelling spiders.

On the other hand, as spiders are polyphagous predators who, to a certain extent, capture their prey at random out of the existing insect supply, they kill beneficial as well as neutral arthropods along with economically harmful insects.

Foremost of all, beneficial aphidivore insects are occasionally captured by spiders in cereal fields.

Adult stages of *Chrysopa carnea* Steph., whose larvae are well-known aphid predators, got often caught in the orb-webs of *N. cornuta* in cereal fields. In a rye field, for instance, a population of *N. cornuta* captured 1.0 ± 0.2 *C. carnea*/web/night in the summer of 1976. The locally sometimes high proportion of Chrysopidae in the food of *N. cornuta* can probably be explained by the temporal as well as vertical coincidence between the flying space of *C. carnea* and the living space of *N. cornuta*, for both species are active at night or in twilight, and the flying height of *C. carnea* lies in the catching range of *N. cornuta* webs.

Other aphid predators such as Coccinellidae, Cantharidae and Syrphidae are also occasionally preyed upon by web-building spiders in cereal fields. On the average, the spiders caught one aphid predator per 6.6 aphids.

3.3.8. Prey killing rate

3.3.8.1. Prey killing rate in the vegetation zone

The prey killing rate of the foliage-dwelling spiders in cereal fields was calculated similarly as for the spiders in abandoned grasslands (see 3.1.11.1.), on the basis of the estimated total web area (A_p). This web area exists on at least all air-weather days, from the date of immigration into the field until harvest, and filters the aerial plankton in the vegetation zone. Hunting spiders, which amount to merely 2-5% of the total spider fauna, were not included in the calculation.

The yearly prey killing rate P can be calculated by means of the equation

$$\underline{P = A \left[(N_f \cdot T_f) + (N_r \cdot T_r)\right]}$$

where A is the area of the spider's webs in m^2/ha ground area ($A = 10$-$100\ m^2$ web area/ha ground area in wheat, rye, and oat fields; $A < 5\ m^2$ web area/ha ground area in maize fields); N_f and N_r are the numbers of captured insects/m^2 web area/day in respectively fair and rainy weather and T_f and T_r = time as numbers of prey capture days/year in respectively fair and rainy weather. N_f amounts to about 290 insects/m^2 web area/day in cereal fields (see 3.5.4.1.). Only a fraction of N_f was used for N_r, as less prey is captured on rainy days. The values for T_f and T_r were chosen on the basis of sections 2.1. (Table 5) and 3.3.5.5.

The computations produced the following values: A yearly number of insects in the order of 0.2-1.2×10^6 insects/ha (insect biomass: 0.2-1.2 kg fresh weight/ha/year) is filtered out of the aerial plankton by the foliage-dwelling spider community of wheat, rye, and oat fields.

The foliage-dwelling spider community of maize fields filters a yearly number of insects in the order of $<0.1 \times 10^6$ insects/ha out of the aerial plankton (insect biomass <0.1 kg fresh weight/ha/year).

It is probable that these values for cereal and maize fields range far lower in rainy summers.

3.3.8.2. Prey killing rate on the ground surface

In the wolf spiders, the prey killing rate P_w in a winter weat field was calculated after the following formula:

$$\underline{P_w = 10^4\ D \cdot C \cdot T}$$

where the parameters are: D = density (number of wolf spiders/m^2), C = prey capture rate (number of prey items/spider/day), T = time (number of activity days/year). The following estimate values were used in the formula: $D = 0.5$ (see 2.3.2.2., below), $C = 1$ (see 3.3.5.4.), and $T = 100$. Thus P_W amounted to 10^6 D.

On this basis it could be calculated, that approximately 0.5×10^6 prey organisms/ha/year are killed by wolf spiders in a winter wheat field. On the assumption that the prey items of the wolf spiders have an average fresh weight of about 1 mg, the biomass of the prey amounts to 0.5 kg fresh weight/ha/year. This is, however, a rough estimate, without consideration of the seasonal variations of density and age structure of the wolf spider populations.

The prey killing rate of the ground-dwelling web-building spiders in cereal fields was not investigated. However, since in cereal fields the density of the Micryphantidae is about 100 times higher than that of wolf spiders, the former will probably kill a far larger number of prey items/ha/year.

3.3.9. Energy flow through the spider communities

3.3.9.1. Energy flow through the spider communities in the vegetation zone of cereal fields

A conversion of the prey biomass values (kg fresh weight/ha/year) of section 3.3.8.1. into energy flow values (MJ/ha/year) gave the following results: The energy flow (= prey killed) through the foliage-dwelling spider community ranges in the dimension of 1.1-6.5 MJ/ha/year in cereal fields and <0.5 MJ/ha/year in maize fields.

3.3.9.2. Energy flow through the spider communities on the ground surface of cereal fields

The daily energy flow (= food consumed) through the ground-dwelling web-building spider guild was estimated by means of the method described in section 2.3.10.2.

The energy flow through the ground-dwelling web-building spider guild of winter wheat fields was calculated to be approximately 117-524 kJ/ha/day. This corresponds to 12-52 MJ/ha/100 days.

The computation of the energy flow through the ground-dwelling web-building spider guild of maize fields resulted in approximately 130-344 kJ/ha/day. This corresponds to 13-34 MJ/ha/100 days.

The energy flow through the wolf spider guild of a winter wheat field was calculated to be approximately 2.4 MJ/ha/100 days.

3.4. New records of remarkable spider species in the region of Zurich

Within the frame of this thesis more than 15'000 spiders were collected. Because of lack of time, not all of these spiders could be identified. Among the determined spiders, some species were found which, so far, had exceedingly seldom been recorded in Switzerland (comp. MAURER, 1978; MAURER & WALTER, 1980)* The following are the most important discoveries:

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*Compare also NYFFELER & BENZ (1982b)

One adult ♂ of Theridion boesenbergi Strand was found in an abandoned grassland biotope (A2), (det. THALER, Table 16). This species had previously very seldom been recorded in Switzerland (DE LESSERT, 1910; HOLZAPFEL, 1937; MAURER, 1978). T. boesenbergi is a rare species in general (WIEHLE, 1937; BRAUN, 1960; THALER, pers. comm.).

One adult ♂ of Dictyna puella Simon was found in cultivated meadow C4 (det. THALER, Table 50). As far as is known, this record of the species in Switzerland is the only for Central Europe (see also NYFFELER & BENZ, 1981d). It is a typically Mediterranean species (BONNET, 1956). D. puella is reported to have been found also in Western Europe as well as Southeastern Europe (LOCKET & MILLIDGE, 1951/53; BONNET, 1956).

One adult ♀ of Porrhomma oblitum (O.P.-Cambr.) was found in cultivated meadow C5 (det. THALER, Table 51). This species had been recorded only once before in Switzerland (MÜLLER & SCHENKEL, 1895).

Adult specimen of Oedothorax fuscus (Blackw.) were collected in the cultivated meadows C3 and C4 (det. NYFFELER, Tables 50, 53). Adult ♂♂ of O. fuscus were also captured in winter wheat fields of the Swiss Federal Research Station for Agronomy Zurich-Reckenholz. O. fuscus had, so far, only very seldom been recorded in Switzerland (MAURER, 1980). This species is not rare, however, in Europe (LOCKET & MILLIDGE, 1951/53; WIEHLE, 1960). It has probably escaped notice in Switzerland before, because only few pitfall trap studies have been made in this country.

Adult ♂♂ of Oedothorax tuberosus (Blackw.) were collected in a winter wheat field of the Swiss Federal Research Station for Agronomy, Zurich-Reckenholz (det. NYFFELER). This species was captured by means of pitfall traps. The species had seldom been found in Switzerland before (MAURER, 1980). It is not rare, however, in Europe (LOCKET & MILLIDGE, 1951/53; WIEHLE, 1960).

One adult ♂ of Araneus alsine Walck. was found in a wheat field near Regensdorf (det. NYFFELER). It was captured with the sweep net in mid-August. This spider species had not been recorded in Switzerland in the last 40 years (MAURER, 1978).

Four juvenile Heriaeus spec. were collected in the "Chrähenriet" near Regensdorf (coordinates 679.05/254.35) (det. NYFFELER). The location is a moorland ecosystem complex in a nature preserve. As only immature stages were found, it was not possible to determine the species. Up to the present, only the species Heriaeus oblongus Simon had been found before in Switzerland (MAURER, 1978). North of the Alpes only one specimen of H. oblongus had been found so far on Swiss territory (VOGELSANGER, 1939). Heriaeus species are rare in Central Europe.

4. DISCUSSION

4.1. Colonization of grassland and cereal fields by spiders

The knowledge of population densities is one of the most important basic informations needed for the evaluation of the ecological importance of animals in ecosystems. It was therefore of great interest to compare the spider densities determined within the frame of this thesis near Zurich with the observations from other places stated in the literature.
Table 91 is a comparative representation of the population densities of foliage-dwelling spiders in arable land and grassland ecosystems on the one hand and forest ecosystems on the other hand. The table can be interpreted in the following manner: Spiders living undisturbed in the vegetation zone of abandoned grasslands all year long can reproduce in accordance with their prey supply and can therefore build up rather large populations. Abandoned grasslands often constitute veritable "spider paradises".

Cultivated meadows, on the other hand, are periodically mown, whereby the living spaces and the egg sacs of many spiders are destroyed. For that reason, only small spider populations (about 1 spider/m^2) live in the vegetation zone of cultivated meadows. Although there is a controversy in the literature still today, as to whether or not mowing is an ecological disaster for the foliage-dwelling fauna (see BONESS, 1953; KAJAK, 1962; CHAUVIN, 1967; SOUTHWOOD & VAN EMDEN, 1967; MORRIS, 1968; SCHAEFER, 1973; SCHAEFER & HAAS, 1979; NYFFELER & BENZ, 1979b), our data show that mowing, at least in the region of Zurich, is an "ecological disaster" for the spiders of the vegetation zone of meadows.

Also for the foliage-dwelling spiders of cereal fields, the harvest is an extreme stress (destruction of the living space and the egg sacs of many spiders). Therefore, a recolonization of the fields from the surroundings is necessary every year (see also TISCHLER, 1958; GEILER, 1963; LUCZAK, 1979). As cereal fields are annual monocultures, which allow only few different ecological niches, they can probably be colonized only by a few species, whose ecological demands are adapted to the microclimatic conditions and the vertical structure of cereal fields. The species composition of the spiders of cereal fields represents therefore a selection of the spiders living in the neighbouring undisturbed biotopes. The colonization of the fields, on the one hand, is dependent on the relation of the area of undisturbed biotopes (the so called ecological cells or "ökologische Zellen" of the German literature) to the area of cultivated land in the landscape and, on the other hand, on the species compositions, population densities, and reproduction rates of the spiders living in these ecological cells (i.e. less disturbed habitats and biotopes, like unmown stripes of grassland, woods, hedges, reeds, gardens, etc.). On the outskirts of Zurich, the fields are mostly surrounded by only few small undisturbed biotopes (unmown stripes of grassland, forest fringes, hedges), wherefrom the spiders can colonize the vegetation zone of the fields. As the area of these biotopes, untouched by agriculture, is probably too small to produce cereal-dwelling spiders in numbers so large that hundreds of thousands of them could emigrate, many fields are only thinly colonized. The colonization of annual crops

Table 91. Comparison of the densities of the foliage-dwelling spiders as reported in literature for agroecosystems, grassland ecosystems and forest ecosystems. The different data have been collected by means of different methods and under different circumstances. The table therefore can give only a rough comparison.

Crop	Country	Density N/m^2	Author
Intensively cultivated:			
Cereals	Switzerland	0.1- 0.6	NYFFELER & BENZ (1979a)
Rye	Poland	0.6- 7.0	LUCZAK (1975)
Barley	Poland	2.2	LUCZAK (1975)
Oats	Finland	small	RAATIKAINEN & HUHTA (1968)
Maize	Switzerland	<0.1- 0.1	NYFFELER & BENZ (1979a)
Potato	Switzerland	<1.0- 5.0	NYFFELER & BENZ (1979a)
Potato	Poland	0.6-29.6	LUCZAK (1975)
Rape	Switzerland	0.1- 0.5	NYFFELER & BENZ (1979a)
Cotton	U.S.A.	0.8	WHITCOMB et al. (1963b)
Coffee[a]	New Guinea	6.6	ROBINSON & ROBINSON (1974)
Alfalfa	Poland	2.2- 3.6	LUCZAK (1975)
Cultivated meadow	Poland	0.6- 4.4	KAJAK et al. (1971)
Extensively cultivated/ uncultivated:			
Grassland[b]	Great Britain	842.0	DUFFEY (1962)
Grassland[b]	Great Britain	559.6	BRISTOWE (1939)
Grassland	Poland	52.0	KAJAK et al. (1971)
Overgrazed pasture[b]	Canada	44.0	TURNBULL (1966)
Grassland[b]	U.S.A.	56.0	VAN HOOK (1971)
Tulip poplar forest	U.S.A.	25.0	REICHLE & CROSSLEY (1967)
Deciduous forest	U.S.A.	51.0	PECK (1966)
Pine forest	Poland	18.8-33.0	LUCZAK (1975)
Mixed forest	Poland	22.0-31.2	LUCZAK (1975)

[a] Only web-building spiders

[b] All strata including ground surface; in some grassland types a clear separation of the spider fauna of the vegetation zone and of the ground surface is not possible, as in such grasslands many ground-dwelling spiders hunt also in the vegetation zone

Table 92. Comparison of the densities of ground-dwelling spiders as reported in literature for agroecosystems, uncultivated grassland ecosystems and forest ecosystems. Otherways as Table 91.

Ecosystem	Country	Spiders/m^2	Author
Agroecosystems:			
Winter wheat field[a]	Switzerland	12- 53	NYFFELER & BENZ (1979a)
Maize field[b]	Switzerland	13- 35	NYFFELER & BENZ (1979a)
Winter wheat field[c]	Germany	19	BASEDOW (1973)
Cereal and beet fields[d]	Germany	250	HEYDEMANN (1962)
Cereal field	Great Britain	20- 30	FRASER (1982)
Cultivated meadow	Austria	54	THALER et al. (1978)
Cultivated meadow[e]	Great Britain	35	DUFFEY (1974)
Cultivated meadow	Poland	10- 14	KAJAK et al. (1971)
Cultivated meadow	Poland	74	KAJAK & JAKUBCZYK (1975)
Pasture[f]	Panama	37	BREYMEYER (1978)
Undisturbed grassland ecosystems:			
Uncult. grassland	Austria	37	THALER et al. (1978)
Uncult. grassland[g]	Great Britain	53- 62	DUFFEY (1974)
Uncult. grassland	Poland	45	KAJAK et al. (1971)
Overgrazed pasture[h]	Canada	44	TURNBULL (1966)
Forest ecosystems:			
Spruce forest	Germany	61	PFETTEN (1925)
Alder forest	Austria	51	THALER et al. (1978)
Chestnut forest	France	75	CHRISTOPHE & BLANDIN (1977)
Oak-beech forest	Great Britain	15-110	GABBUTT (1956)
Beech forest	Netherland	163-231	VAN DER DRIFT (1951)
Oak forest	Denmark	60	BORNEBUSCH (1930)
Pine-spruce forest	Sweden	240	FORSSLUND (1943, 1945)
Pine forest	Finland	183	HUHTA (1971)
Tulip poplar forest	U.S.A.	126	MOULDER & REICHLE (1972)

[a] In May/June, without Lycosidae. [b] June/July, without Lycosidae. [c] In July.
[d] Only Oedothorax apicatus. [e] Including spiders of the 12 cm high vegetation.
[f] In August/September. [g] Including spiders of the 25 cm high vegetation.
[h] Including spiders of the vegetation zone (comp. Table 91).

never trespasses the initial stage of a succession. According to RAATIKAINEN & HUHTA (1968), in Finland, too, only low spider densities were observed in the vegetation zone of oat fields.

If we consider the ground surface, however, we notice that there the spiders live in rather large populations, not only in natural ecosystems but also in agroecosystems (Table 92). In cultivated fields near Zurich, densities of up to 53 ground-dwelling spiders/m^2 were observed, and this number includes merely the spiders found on the ground surface. But in cultivated fields, there are also spiders which live in cracks of the soil. If soil extractions had been examined by means of Berlese funnels, even more ground-dwelling spiders/m^2 might have been found. In the German Democratic Republic, too, GEILER (1963) observed that the greater part of the spiders in crop fields lived near the ground. The relatively high spider density near the ground can be explained by the fact that crop fields never get beyond the initial stage of a succession and that, therefore, the area near the ground is for the most part colonized by pioneer species which have a high reproductive potential (r-strategists, e.g. Erigone atra).

The influence of soil cultivation (e.g. tilling, fertilizing) on the ground-dwelling spider populations of agroecosystems could not be investigated within the framework of this thesis. Informations from literature indicate, however, that soil cultivations does influence the composition of ground-dwelling spider communities (TISCHLER, 1965; LUCZAK, 1975; KAJAK, 1978, 1980).

4.2. Family and species composition of the spiders

A multitude of spider species of the families Araneidae, Tetragnathidae, Theridiidae, Linyphiidae, Micryphantidae, Agelenidae, Dictynidae, Salticidae, Thomisidae, Pisauridae, and Clubionidae can be found in the vegetation zone of abandoned grasslands.

In contrast to this, only a limited number of predominant species of the first four families and the Thomisidae can be observed regularly in the vegetation zone of cultivated meadows and cereal fields.

Large orb-weaving spiders (Argiope bruennichi, Araneus quadratus) and funnel web spiders (Agelena labyrinthica, Agelena similis), which are found in high densities in abandoned grasslands, are almost entirely missing in cultivated fields. Also, jumping spiders (Evarcha arcuata, Heliophanus flavipes) and pisaurid spiders (Pisaura mirabilis), which predominate in the vegetation of abandoned grasslands, are found in exceedingly low densities in cultivated fields. These differences between the spider faunas of undisturbed and cultivated biotopes can be explained by the fact that by cultivating the land (tilling, mowing, single-crop farming, pesticides etc.) biotopes are created, wherein only those spiders can exist whose demands are met even in these "artificial environments".

Also the spider fauna of the vegetation zone of cereal fields in the region of Zurich is composed of mainly web-building spiders (95-98%) of the families Araneidae, Tetragnathidae, Theridiidae, and Linyphiidae. In contrast to meadows, however, hunting spiders of the family Thomisidae were only seldom observed in the fields. Similar observations were made by LUCZAK (1974) for potato and rye fields in Poland.

A comparison of the species composition of the spiders in the vegetation zone of cultivated fields in Switzerland, the Federal Republic of Germany, Finland, The German Democratic Republic, Norway, and Poland shows a certain conformity (DINGLER, 1935; GEILER, 1963; TISCHLER, 1965; GALECKA, 1966; RAATIKAINEN & HUHTA, 1968; TAKSDAL, 1973; HUHTA & RAATIKAINEN, 1974; LUCZAK, 1974, 1975, 1976; CZAJKA & GOOS, 1976; CZAJKA & KANIA, 1976; NYFFELER & BENZ, 1979a). Theridiidae (Theridion impressum, Enoplognatha ovata), Linyphiidae (several species), Tetragnathidae (Tetragnatha extensa, Tetragnatha pinicola), Araneidae (Araniella spp., Aculepeira ceropegia, Nuctenea cornuta, Mangora acalypha) as well as Thomisidae (Xysticus spp.) predominated.

The ground-dwelling spider fauna of the investigated fields near Zurich was uniform and was dominated in 1977-1979 by the Lycosidae Pardosa palustris and Pardosa agrestis, as well as the Micryphantidae (Erigone atra, Erigone dentipalpis, and Oedothorax spp.). A little less frequent were the Tetragnathidae (Pachygnatha spp.) and Linyphiidae (several species). This species composition in the investigated fields largely corresponds with the situation in field crops of Austria, England, the Federal Republic of Germany, the German Democratic Republic, and Poland (see TISCHLER, 1965; LUCZAK, 1974; VICKERMAN & SUNDERLAND, 1975, CZAJKA & GOOS, 1976; THALER et al., 1977).

With the exception of Dictyna puella, the spider species described in this study have all been previously recorded in Switzerland (see MAURER, 1978; MAURER & WALTER, 1980). Although agroecosystems are very monotonous systems with few different ecological niches, some rare spider species were discovered in them (e.g. Porrhomma oblitum). The term "rare spider species" is however relative, as, up to the present, only few arachnologists have conducted faunistic studies in Switzerland. These rare species probably are not true components of the spider communities of agroecosystems, but rather inhabitants by mistake.

4.3. Spatial distribution of spiders

4.3.1. Vertical distribution of spiders

In the vegetation zone of abandoned grassland near Zurich a vertical stratification in orb web-building spiders could be ascertained (see also NYFFELER & BENZ, 1978). Similar observations were reported by PASQUET & KRAFFT (1980) in an old prairie in France. American investigations in uncultivated grassland also have shown vertical stratification in orb web-building spiders (ENDERS, 1974; UETZ et al., 1978; OLIVE, 1980; BROWN, 1981).

In cereal fields near Zurich spiders were found from the ground surface up to the ear zone, whereby some spider species life more near ground, other ones more in the middle or higher stratums of the vegetation. In other countries, too, it could be noticed that spiders in cultivated fields are present from the ground surface up to the ear zone, whereby in some cases vertical stratification of the spiders was observed (WHITCOMB et al., 1963b; BAILEY & CHADA, 1968; OKUMA & WONGSIRI, 1973; LESAR & UNZICKER, 1978a).

4.3.2. Horizontal distribution of spiders

In cultivated meadows and cereal fields near Zurich the horizontal distribution of the foliage-dwelling spiders corresponded with a random distribution, in abandoned grassland with a random or slightly aggregated distribution. The same is true for the horizontal distribution of the ground-dwelling spiders in cultivated meadows and cereal fields near Zurich.

A comparison with the data of literature shows, that also in other ecosystems the spiders are distributed at random and/or aggregated, whereby the aggregated distribution seems to dominate (see CHERRETT, 1964; TURNBULL, 1966; HUHTA, 1971; PIETERS & STERLING, 1974; SCHAEFER, 1974b; DIPPENAAR-SCHOEMANN, 1976; CHRISTOPHE & BLANDIN, 1977; BISHOP, 1981). Reports on a nearly regular distribution of spiders are rare (RIECHERT et al., 1973; SUZUKI & OKUMA, 1975; ES'KOV, 1981).

4.3.3. Distribution of spiders among the outer, middle and inner parts of a cultivated field (edge effect?)

In a winter wheatfield near Zurich the ground-dwelling spiders were equally distributed in the outer, middle and inner parts. The same has been reported from an Australian cotton field, where dominant spider species were equally distributed, too (BISHOP, 1981). On the other hand, an investigation of DOANE & DONDALE (1979) in Canada showed that significant fewer spiders were captured per pitfall trap in a wheat field than in its grassy borders.

4.4. Prey compositions

If we consider the food composition of the spiders relating to the number of captured prey items in the vegetation zone of grassland, cereal fields and other biotopes, it is evident that small Diptera form the main part in the food of orb-weaving spiders (Table 93). Moreover, winged aphids are also an important component of the food of these spiders. Diptera and aphids also predominate in the food of many space web spiders in the vegetation of grasslands and cereal fields.

Numerous other authors have also observed that Diptera predominate in number in the prey of most foliage-dwelling web spiders of cultivated and uncultivated areas (DINGLER, 1935; TURNBULL, 1960; WHITCOMB et al., 1963b; RUPPERTSHOFEN, 1964; PUTMAN, 1967; HARRISON, 1968; WHEELER, 1973; MUMA, 1975; SUZUKI & OKUMA, 1975; ROGERS & HORNER, 1977; NENTWIG, 1980, 1981). That small Diptera constitute such an essential part in the food of the foliage-dwelling spiders, is due to the fact that - in number - Diptera form the main part of the insects in the vegetation zone of grasslands (BONESS, 1953; PERTERER & THALER, 1976), field crops (DINGLER, 1935; PRILOP, 1957; KARG & DABROWSKA, 1974), and the aerial plankton in general (GEILER, 1975). As the web-building spiders, to a certain extent, filter their prey out of the aerial plankton, the small Diptera which are the first in frequency fall victims first. The same is true for winged aphids at certain times of the year (see KAJAK, 1965a, b; NYFFELER & BENZ, 1979a).

If one considers the spiders' prey composition with respect to biomass, one sees that here, too, the food of the spiders living in the vegetation

Table 93. Comparison of the percentage of dipterans and aphids in the food of orb-weaving spiders (Araneidae and Tetragnathidae) in different biotopes.

Biotope	Author	Country	Species	Percentage Diptera	Percentage Aphidae
Wheat field	NYFFELER & BENZ (1979a)	Switzerland	diverse	71.0	13.7
Barley field	"	"	"	91.1	4.0
Rye field	"	"	"	76.5	16.0
Oat field	"	"	"	70.6	5.6
Maize field	"	"	"	68.8	9.4
Rape field	"	"	"	82.2	1.9
Cultivated meadow	"	"	*N. cornuta*	84.3	6.0
Cultivated meadow	"	"	*A. diadematus*	85.9	3.1
Uncult. grassland	NYFFELER & BENZ (1978)	Switzerland	*A. quadratus*	76.8	8.1
Uncult. grassland	"	"	*A. bruennichi*	76.7	4.9
Forest meadow	KAJAK (1965a,b)	Poland	*N. cornuta* *A. quadratus*	69-79	7-14
Vineyard	NYFFELER & BENZ (1979a)	Switzerland	diverse	79.0	9.1
House garden	"	"	*N. umbratica*	74.7	17.1
House garden	BILSING (1920)	U.S.A.	*N. foliata*	85.0	5.0
Forest	DABROWSKA & LUCZAK (1968)	Poland	*T. montana*	79-88	0-2
Mean value				78.7	7.7

zone of cultivated meadows and cereal fields consists of Diptera mainly.

For the large web-building spiders of abandoned grasslands, on the other hand, the situation is different. The food of A. bruennichi, for instance, consists mostly of large, heavy honey-bees and grasshoppers. Up to the present, this spider species was considered to be primarily a predator of grasshoppers in Europe (WIEHLE, 1931; MARPLES, 1935; FISCHER, 1943; CROME & CROME, 1961; PÖTZSCH, 1963; CANARD & CHAUVIN, 1979; LOHMEYER & PRETSCHER, 1979; GILLANDT & MARTENS, 1980). In the region of Zurich, this feeding behaviour was observed mainly in abandoned grasslands with a high percentage of grasses and few flowering plants (NYFFELER & BENZ, 1978). Besides grasshoppers, also dragonflies, Megaloptera, Lepidoptera and ants were described in the literature as primary prey of A. bruennichi (FISCHER, 1943; CROME & CROME, 1961; PÖTZSCH, 1963). In contrast to these former studies, several locations near Zurich were found, where grasshoppers were almost entirely missing in the food of A. bruennichi (Tables 27-28). In abandoned grasslands with a high percentage of Cirsium arvense and/or Rubus sp., A. bruennichi was observed to perform as an outright bee-killer (NYFFELER & BENZ, 1978).

The prey composition of this spider species seems to be largely genus-specific; for, in abandoned grasslands, grasshoppers (Acrididae) and also bees are mentioned as main food of the mediterranean Argiope lobata (Pallas) and the American A. trifasciata (Forskal), A. aurantia Lucas, and A. argentata (Fab.) (BILSING, 1920; RICHTER, 1960; ROBINSON & ROBINSON, 1970).

With respect to biomass, the prey of A. quadratus of abandoned grassland biotopes near Zurich also consisted mostly of bees (NYFFELER & BENZ, 1978). The same was noticed by BILSING (1920) in abandoned grasslands in Ohio for the closely related species Araneus trifolium (Hentz).

The food of the funnel web spider A. labyrinthica in abandoned grasslands near Zurich is very rich and mainly composed of grasshoppers, honey-bees, ants, Lepidoptera, Coleoptera, and Diptera, both with regard to the number of captured prey as well as biomass. According to BILSING (1920) and RIECHERT & TRACY (1975), the same is true for the American funnel web spiders Agelena naevia Walckenaer and Agelenopsis aperta (Gertsch).

The quite different prey compositions of the three large web-building spiders A. bruennichi, A. quadratus, and A. labyrinthica even within the same biotope shows that the vertical isolation of the webs and their construction has a great influence on which insects are captured.
Fig. 19 shows the vertical distribution of the webs of the three spider species and the selection of prey types resulting from it (NYFFELER & BENZ, 1978). The two Araneidae A. bruennichi and A. quadratus build orb-webs, but are vertically isolated from each other. A. quadratus builds its webs in the higher strata of the vegetation (orb hub >0.5 m above ground, on the average) and captures almost exclusively flying insects, mostly Diptera and bees. A. bruennichi, on the other hand, builds its webs near the ground (orb hub on the average <0.35 m above ground) and captures for that reason also jumping insects such as grasshoppers. Its prey composition is therefore wider than the one of A. quadratus. The funnel web spider A. labyrinthica, uses an entirely different hunting strategy, since the funnel webs serve to catch both, flying insects as

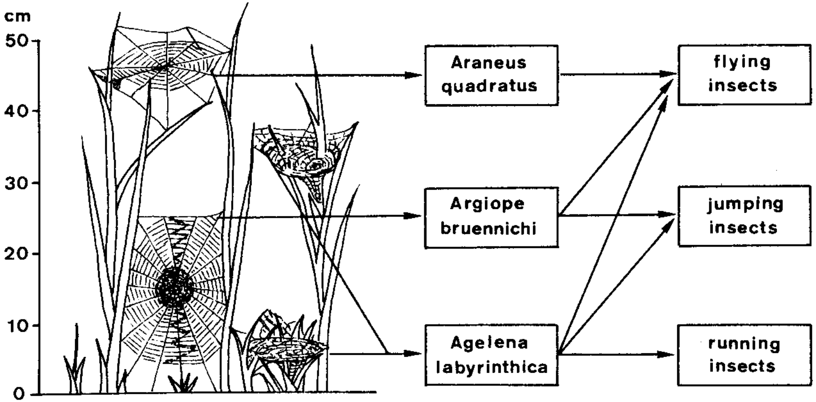

Fig. 20. Vertical distribution of the webs of the three spider species Argiope bruennichi, Araneus quadratus and Agelena labyrinthica and the selection of prey groups resulting from it. Observations in undisturbed grassland biotopes (see also NYFFELER & BENZ, 1978).

well as jumping and running arthropods. Its prey composition is therefore significantly wider than that of the two orb-weaving spiders.

The food of the ground-dwelling spiders in cultivated meadows and cereal fields near Zurich was primarily composed of small, soft-bodied insects (mostly Collembola, aphids, Diptera). Up to the present, ground-dwelling spiders have generally been known from literature to be predators of Collembola (BUCHE, 1966; SIMON, 1967; CLARKE & GRANT, 1968; EDGAR, 1970; HALLANDER, 1970; HÅGVAR, 1973; WINGERDEN, 1973; SCHAEFER, 1974a; SALINAS & RAROS, 1975; MANLEY *et al.*, 1976; GETTMANN, 1978; NYFFELER & BENZ, 1979b). However, their rôle as predators of Diptera and aphids has also been recognized earlier (BASEDOW, 1973; DE CLERCQ, 1977).

Further discussions of the feeding ecology of spiders in agroecosystems can be found in NYFFELER & BENZ (1978, 1979a, 1981a,c).

4.5. The spiders' effectiveness as predators of agricultural pests

Insects belonging to the agriculturally important families Pentatomidae (Heteroptera), Elateridae, Chrysomelidae, Scarabaeidae, Curculionidae, Nitidulidae (Coleoptera), Noctuidae, Pyralidae (Lepidoptera), and Tipulidae (Diptera) are also found in the prey of the spiders living in cereal fields, but amount to such a low percentage of the entire spider food (Tables 79-80) that the spiders are probably ineffective as predators of the cereal pests belonging to these families.

According to NYFFELER & BENZ (1979a), the populations of the nitidulid beetle *Meligethes aeneus* Fbr. were only little influenced by the spiders in the vegetation zone of rape fields.

The same conclusion has been drawn by the Polish ecologist KAJAK (1971) who found that spiders exert merely a negligible influence on the mortality of the insect populations in the vegetation zone of cultivated meadows.

Whether spiders are effective as predators of aphids on cultivated land in Europe cannot be answered conclusively yet; for in spite of repeated investigations on spiders as aphid predators, there are still no quantitative informations on the influence of the spiders on aphid mortality (DUNN, 1949; GALECKA, 1966; SUTER & KELLER, 1977).

Investigations in the U.S.A. have also shown that spiders are predators of pest insects in cultivated land (SCHLINGER & DIETRICK, 1960; CLARK & GLICK, 1961; WHITCOMB *et al.*, 1963b; DORRIS, 1970; McDANIEL & STERLING, 1979). WHITCOMB (1974) considers the spiders of North American agroecosystems as highly beneficial. In a personal communication he stresses especially the effectiveness of the cursorial spiders (oxyopids, salticids, gnaphosids, and lycosids). However, there are no quantitative data published as yet on how far spiders influence the population dynamics of pests in the U.S.A.

4.6. Spiders as predators of beneficial insects

A certain percentage of economically beneficial insects was regularly found in the prey compositions of the foliage-dwelling spiders of cereal fields. Aphidivore insects (Chrysopidae, Coccinellidae, Syrphidae), and pollinating insects (bees) are rather frequently captured by spiders.

Spiders have been repeatedly reported in literature to capture beneficial insects (LOVELL, 1915; BILSING, 1920; DINGLER, 1935; KIRCHNER, 1964; WHITCOMB, 1974; MORSE, 1978, 1979; TEMERAK, 1981).

DINGLER (1935) observed in a German asparagus field that the most important asparagus-dwelling spider species, Theridion impressum, captured mainly economically beneficial insects (Asilidae, Tachinidae, Apidae, Ichneumonidae, Sphegidae, Coccinellidae, Chrysopidae). He therefore assumed that the most frequent spider of the asparagus field was not at all useful, but rather harmful.

As mentioned before WHITCOMB (1974) discussing the importance of spiders as regulators of insect populations in American agroecosystems, considers spiders on the whole as highly beneficial, but came, among others, also to the conclusion: "Since spiders tend to be general feeders, they are natural enemies of most beneficial insects. The orb-weavers, theridiids, and other spiders destroy large numbers of parasitoids and predators".

To sum up, one can note that spiders as polyphagous predators destroy "pests", "neutral", and "beneficial" insects likewise. As with many other predators (e.g. birds), whose prey compositions are composed both of "beneficial" and "pest" species, it is sometimes very difficult with spiders to determine quantitatively whether in the end the beneficial effects (destruction of pest insects) or the detrimental effects (destruction of beneficial arthropods) prevail.

4.7. Energy flow through the spider communities

The energy flow through the foliage-dwelling spider communities of different ecosystems is compared in Table 94. The table shows the following: Because the fields are colonized only during a short period of time and because the spider densities are low, the energy flow through the foliage-dwelling spider communities of European cultivated land (cultivated meadows and cereal, rape, and potato fields) is very low (prey killing rate: 0.1-2.0 kg fresh weight/ha/year). In comparison the production of Diptera alone amounts to about 15 kg fresh weight/ha/year in rye fields, and to about 20 kg fresh weight/ha/year in potato fields in Poland (DABROWSKA-PROT & KARG, 1974).

In contrast to cultivated fields, spiders can colonize uncultivated grassland and forest ecosystems all year long in high densities. The energy flow through the foliage-dwelling spider communities of such ecosystems is therefore high. The prey killing rate is 50-200 kg fresh weight/ha/year. The energy flow reaches similar values in these biotopes as the energy flow through the foliage-dwelling web-building spider community of a tropical coffee plantation, where ROBINSON & ROBINSON (1974) have observed a prey killing rate of 160 kg fresh weight/ha/year.

An intermediate system between cultivated fields and uncultivated grassland may be represented by the Phragmites belt of some European lakes. Since these reeds are mown once in a year, their spider populations are reduced, though less than in cultivated fields. As Table 94 shows, the energy flow through the spider community in the reed belt of an European lake corresponded to 5 kg fresh weight/ha/year on the average, with a maximum of 12 kg/ha/year.

Table 94. Energy flow through the spider communities of the vegetation zone of different ecosystems.

Biotope	Country	Authors	Prey killing rate kg $ha^{-1}year^{-1}$	 MJ $ha^{-1}year^{-1}$
Intensively cultivated:				
Maize fields	Switzerland	NYFFELER & BENZ (1979a)	<0.1- 0.1	<0.5- 0.5
Cereal and rape fields	Switzerland	NYFFELER & BENZ (1979a)	0.1- 1.2	0.5- 6.5
Rye fields[a]	Poland	LUCZAK (1975)	0.2- 1.1	1.3- 5.7
Potato fields[a]	Poland	LUCZAK (1975)	0.5- 2.1	2.6-11.6
Cultivated meadow	Poland	KAJAK et al. (1971)	2	10.9
Extensively cultivated/ uncultivated:				
Reed belt of lake	Austria	PÜHRINGER (1979)	5 -12	26-65
Grassland[b]	U.S.A.	VAN HOOK (1971)	52	282.8
Grassland	Switzerland	this thesis	>150	>900
Grassland	Poland	KAJAK et al. (1971)	120	652.7
Forest[bc]	Germany	KIRCHNER (1964)	100	543.9
Spartina swamp[bc]	U.S.A.	TEAL (1962)	215	1170.0
Tropical crops:				
Coffee plantation	New Guinea	ROBINSON & ROBINSON (1974)	160-320	870.3-1740.6

[a] LUCZAK gives only the prey consumption values. Since spiders kill more prey than they consume, the prey killing rates in the Polish fields are a little higher than the values given in this table.

[b] All strata incl. ground surface. [c] Rough estimate.

Table 95. Energy flow (= food ingested) through the ground-dwelling spider communities of different ecosystems.

Ecosystem	Country	Energy flow $kJ \cdot ha^{-1} \cdot day^{-1}$	Authors
Winter wheat field[ab]	Switzerland	117- 524	this thesis
Maize field[a]	Switzerland	130- 344	this thesis
Winter wheat field[c]	Switzerland	24[d]	this thesis
Rye field[c]	Poland	40	LUCZAK (1975)
Cultivated meadow[b]	Switzerland	155- 419	this thesis
Cultivated meadow[e]	Poland	1070	KAJAK et al. (1971)
Uncult. grassland[e]	Poland	3360	KAJAK et al. (1971)
Tulip poplar forest[f]	U.S.A.	140- 330	MOULDER & REICHLE (1972)

[a] In June

[b] Without Lycosidae

[c] Only Lycosidae

[d] This value has been calculated by dividing the prey killing rate of section 3.3.9.2. by 1.25 (see method 2.3.11.2.)

[e] Mg/m^2/year were converted into approximate values of kJ/ha/day, by dividing the annual energy flow by 180 days

[f] Minimum in winter, maximum in spring

The energy flow through the ground-dwelling spider communities of different ecosystems is compared in Table 95. The table shows that the energy flow through the ground-dwelling spider communities of Central European wheat and maize fields corresponds, in the order of magnitude, to the energy flow through the spider community on the floor of an American tulip tree forest. In contrast to this, the energy flows through the ground-dwelling spider communities of Polish meadows showed significantly higher values.

4.8. Numerical and functional responses of the spiders to changes in prey density

To evaluate the role of spiders as regulators of insect populations in the agricultural biocenose, it is important to know whether spiders react to fluctuations in density of their prey populations (RIECHERT, 1974; LUCZAK, 1979). In our case, we have predator-prey systems with the spiders as predators. According to HOLLING (1961, 1966) there are two different possibilities for a predator to demonstrate a density-dependent response to changes in prey abundance:

(1) The predator reacts to an increase in the prey density by capturing more prey (functional response).

(2) The predator follows an increase in the prey density by increasing its own reproduction (numerical response).

Under laboratory conditions, both a "functional response" of spiders (HAYNES & SISOJEVIC, 1966; HARDMAN & TURNBULL, 1974; MANSOUR _et al_., 1980a; a.o.) as well as a "numerical response" of spiders (WISE, 1979; a.o.) has been demonstrated. Laboratory ecosystems, however, are greatly simplified systems. One cannot positively conclude from laboratory experiments that spiders will show the same behaviour in open-field ecosystems, which are essentially more complex in structure.

The question is, whether functional and numerical responses of the spiders to density changes of their prey populations are possible in abandoned grasslands. As these areas are not cultivated, the spider populations and their egg sacs are not destroyed by agricultural treatments, as is regularly the case in cultivated meadows and cereal fields. Functional and numerical responses of the spiders to density changes of the prey populations should therefore be possible in such biotopes. One can thus assume that the spiders in abandoned grasslands reproduce in accordance with the prey supply, i.e. that they adapt themselves to the prey density numerically. However, although a regulatory activity of the spiders in abandoned grasslands is conceivable, it has to be proven yet.

What about functional and numerical responses of the spiders to density changes of the prey populations in cultivated meadows and cereal fields? A functional response by the spiders in cultivated meadows and cereal fields is possible according to KAJAK (1965a) and NYFFELER & BENZ (1979a). A numerical response, however, is probably severely handicaped in cultivated meadows and cereal fields, because by the mowing and harvesting of the vegetation zone many egg sacs are destroyed. A regulatory activity by the spiders in the vegetation zone of such agro-ecosystems is therefore highly improbable. Whether or not a regulatory activity of spiders on the ground surface is taking place, has not yet been examined.

4.9. Ecological importance of the spiders in grassland and cereal ecosystems

Spiders can be of ecological importance in diverse respects. For example they can be food for other predators (WHITCOMB, 1974). Or the spider webs can be food sources for kleptoparasites (THORNHILL, 1975; NYFFELER & BENZ, 1980b). In this section, only the role of spiders as insect predators will be discussed.

An ecological importance of spiders is to be expected in abandoned grasslands foremost, where they can feed and reproduce in the vegetation without human interference. As already mentioned, such biotopes often represent veritable "spider paradises". Large funnel web spiders and orb-weaving spiders often live in high densities in abandoned grasslands. With their strong webs they capture large amounts of insects. A. bruennichi, e.g. may capture up to 7 grasshoppers/web/day. LOHMEYER & PRETSCHER (1979) found on the average 6 webs of A. bruennichi per m^2 in an abandoned grassland in the Federal Republic of Germany. This corresponds to a web area of 3000 m^2/ha ground area. It is evident that such a gigantic web area exerts an enormous predatory pressure on insect populations.

Polish studies have also shown that the orb-weaving spiders can exert a strong predatory pressure on the insect populations in the vegetation zone of abandoned grasslands (KAJAK et al., 1968; KAJAK & OLECHOWICZ, 1970; KAJAK, 1971). Thus web-building spiders eliminated 25-40% of the adult Diptera in undisturbed grasslands (KAJAK & OLECHOWICZ, 1970).

Funnel web spiders (A. labyrinthica) can also occur in high densities in undisturbed grasslands. Near Zurich, more than 3 funnel web spiders/m^2 on the average were counted in some abandoned grassland biotopes. At certain points of aggregation within such a biotope, up to 12 funnel web spiders/m^2 were found. The food of these spiders was composed of up to 23% of bees (NYFFELER & BENZ, 1978). In other countries, too, it has been observed that funnel web spiders can be predators of bees. OLBERG (1960) wrote on this subject: "Sometimes, 20 to 30 captured honey-bees on the average can be found in each web; thus with a spider that frequent, a considerable damage can result. This is why flocks of sheep are driven through the dangered areas. The fleecy animals destroy the webs, which cannot be replaced immediately, as is the case in orb weaving-spiders". This example demonstrates that spiders can have a noticeable effect on insect populations.

Hunting spiders, too, can play an important ecological role in abandoned grasslands (VAN HOOK, 1971; SCHAEFER, 1974a).

In contrast to the conditions in uncultivated biotopes, the present results show that the energy flow through the foliage-dwelling spider communities of cultivated meadows and annual crops is low (see also KAJAK, 1971; LUCZAK, 1975). Moreover, spiders are ineffective as predators of many agriculturally important pest insects (see also DINGLER, 1935; KAJAK, 1971). Therefore, the spiders of the vegetation zone of Central European cultivated fields probably play no important role as predators or regulators of pest insects.

The agroecosystems in Southern Europe are to some extent cultivated in a considerably more extensive way than in Central Europe. It is therefore conceivable that the spiders still have a greater ecological importance in cultivated fields of Southern Europe than in the region of Zurich. Thus, near Florence (Italy), rather high spider densities were found in the vegetation zone of a weedy cereal field (STREULI, pers. comm.).

In contrast to the vegetation zone, the spiders living on the ground surface of cultivated meadows and cereal fields showed relatively high population densities (r-strategists, see 4.1.). Together with the carnivorous beetles (Carabidae and Staphylinidae), they belong to the most frequent ground-dwelling predators of insects in cereal fields near Zurich. German studies had also established that spiders form an important component within the ground-dwelling predator-complex (TISCHLER, 1958, 1965, GEILER, 1963; BASEDOW, 1973; BRASSE, 1975; BASEDOW & MIELKE, 1977). In the German Democratič Republic, one has even recorded that spiders and harvestmen can form up to one third of all invertebrates captured in pitfall traps (GEILER, 1963). The prey compositions of the ground-dwelling spiders overlap to some extent with those of the predatory Carabidae and Staphylinidae, which also feed on Collembola, aphids, and Diptera. Further investigations will be necessary to establish whether this ground-dwelling predator-complex has a significant influence on pest insects (e.g. aphids). First studies already indicate that the ground-dwelling predator potential actually exerts a strong predatory pressure on insect populations (BASEDOW, 1973; KAJAK & JAKUBCZIK, 1975; DE CLERCQ, 1979). In any event, this ground-dwelling predator-complex probably has a stabilizing effect on insect populations, as assumed by the American ecologist RIECHERT (1974).

Studies from Japan, India, China, Taiwan, Korea, Thailand, and the Philippines indicate that such ground-dwelling spiders, because of their high density in rice fields*, have a damping influence on the population of pest insects, mainly cicadas (ITÔ et al., 1962; OKUMA, 1968; IRRI Annual Report, 1973; CHIU et al., 1974; GAVARRA & RAROS, 1975; KIRITANI & KAKIYA, 1975; SAMAL & MISRA, 1975; HOKYO et al., 1976; NAKASUJI, 1976; KANG & KIRITANI, 1978; KIRITANI, 1979). Rice fields are swamp ecosystems. In European swamp ecosystems, spiders can also be an important group of predators (MILLER & OBRTEL, 1975). The same is assumed concerning the ecological role of spiders in American swamp ecosystems (GARCIA & SCHLINGER, 1972).

4.10. Ecological importance of spiders in forest ecosystems and orchards

As a comparison to the studied gramineae biotopes, some tree ecosystems will be briefly discussed.** With regard to forest ecosystems, the German ecologist WEIDEMANN (1978) attributes an important role to the ground-dwelling spiders as insect predators, together with the other litter-dwelling predators. American scientists, too, concluded that the ground-dwelling spiders can be of great importance as insect predators in forests (CLARKE & GRANT, 1968; MOULDER & REICHLE, 1972; MANLEY et al., 1976). In contrast to this, the ecological importance of the foliage-dwelling spiders of forest ecosystems is still controversial (VITÉ, 1953;

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*This is valid for rice fields, which were not or little treated with pesticides.

**Compare also NYFFELER (1982).

KIRCHNER, 1964). Some field studies had shown that certain spider species in the vegetation were ineffective against lepidopteran pests (POINTING, 1966; KIRCHNER, 1967; FURUTA, 1977). According to data by the last mentioned authors, some spider species could reduce butterfly populations by 5% at the most. A slightly higher mortality was recorded by ENGEL (1942), who estimated that during a pine moth calamity, 12-23% of the moth population was destroyed by spiders; but at the same time he also observed that significantly less moths were killed by spiders than by bugs. The ineffectiveness of certain spider species as predators of butterflies might be connected with the butterflies' ability to escape from these spiders' webs (KIRCHNER, 1967; NYFFELER & BENZ, 1981b). However, this negative effect may not be very important, since other insects seem not to be killed at a higher rate by forest spiders. Thus, for a comparison, the mortality of chestnut gall wasp populations as a result of predation by spiders was of the same magnitude in normal years (7-20%) as that recorded by ENGEL for the pine moth (NAKAMURA & NAKAMURA, 1977). Contrary to what has been said so far, some other authors have assumed that spiders can be important predators of Lepidoptera, aphids, and mosquitos in the vegetation zone of forest ecosystems (SUBKLEW, 1939; JUILLET, 1961; DABROWSKA-PROT et al., 1968a, b; LUCZAK, 1968; FOX & GRIFFITH, 1976).

Like the forests, orchards are also tree ecosystems. Field studies have shown that spiders form a frequent predator group in pesticide-free orchards (HARRISON, 1968; MacLELLAN, 1973; CARROL, 1980). Several authors have therefore supposed that spiders play an important role as insect predators in pesticide-free orchards (CHANT, 1956; KAYASHIMA, 1972; MacLELLAN, 1973; MANSOUR et al., 1980a), though precise results do not exist. However, it has been demonstrated that the treatment of orchards with pesticides leads to a significant reduction of the density of spiders (CHANT, 1956; SPECHT & DONDALE, 1960; DONDALE et al., 1979; MANSOUR et al., 1980b; McCAFFREY & HORSBURGH, 1980). This indicates that pesticide treatments reduce the effectiveness of spiders as insect predators in orchards.

4.11. Using spiders in "biological pest control"

Ground-dwelling spiders, together with the ground-dwelling raptorial Carabidae and Staphylinidae, form an important predator potential in cereal fields. This predator potential can be utilized within "programs for integrated pest control" (BASEDOW & MIELKE, 1977; KIRITANI, 1979). Thus, attempts have been made in Japan to raise the spider density in rice fields artificially by releasing *Drosophila* flies. This additional food then caused an increased fertility in the spiders (KOBAYASHI, 1975). According to a report of the Chinese News Agency Xinhua of August 15, 1979, in the Peoples Republic of China spiders are introduced into rice fields as biological control agents of rice pests.

As most spiders are cannibals, it would probably be difficult to breed large numbers of spiders in the laboratory. RUPPERTSHOFEN (1976) and KAYASHIMA (1967) have looked for an alternative. They have proposed that egg sacs of spiders could be gathered somewhere and placed in forests or mulberry plantations respectively to raise the population density of spiders.

Another example on the use of spiders for biological pest control is reported from South Africa. There, spiders were settled in houses. STEYN (1959) recorded a reduction of the fly populations by 99% within 2½ months and, at the same time, a pronounced decrease of gastrointestinal infections of men in that region, because the vectors of disease were destroyed.

What about the possibility of utilizing spiders for biological pest control in Switzerland? Here, spiders could only become of greater importance, if it were possible to increase the spider density in cultivated fields. This would be possible if the area of the "ecological cells" (abandoned grasslands, hedges, wet areas, etc.), which serve as predator-reservoirs for agroecosystems, could be enlarged. However, uncultivated lands of that kind may serve as reservoirs for predators and pest organisms as well. The expansion of the area of the "ecological cells" could therefore also bring about an increase of pest incidence. With present day knowledge it is difficult to estimate, whether the useful effect (reservoirs of predators) or the detrimental effect (reservoirs of pests) would ultimately prevail. Intensive research on the complex functions of such "ecological cells" in the agricultural landscape would be necessary, before the expansion of their area with the intentions of increasing the predator density in the cultivated areas could be recommended.

5. ZUSAMMENFASSUNG

Von 1976-1979 wurde die Oekologie von Spinnen in unbewirtschafteten Graslandbiotopen, Mähwiesen und Getreidefeldern bei Zürich (Schweiz) untersucht. In solchen Oekosystemen leben Spinnen in zwei Straten, 1) auf der Bodenoberfläche, 2) in der Vegetationsschicht. Wir finden in den beiden Straten verschiedene Spinnengemeinschaften.

In unbewirtschaftetem Grasland leben die Spinnen während des ganzen Jahres ungestört. Sie können daher in solchen Biotopen in der Vegetationsschicht relativ grosse Populationen aufbauen (bei Zürich: ca. 10 Spinnen/m^2, in Literatur wesentlich höhere Werte). Demgegenüber werden Kulturfelder periodisch gemäht, wobei die Lebensräume und Eikokons vieler Spinnen zerstört werden. In der Vegetationsschicht von Kulturfeldern leben daher nur kleine Spinnenpopulationen (ca. 1 Spinne/m^2 in Mähwiesen, 0.1-0.6 Spinnen/m^2 in Getreidefeldern). Die Bodenoberfläche von Kulturfeldern ist relativ dicht besiedelt (15-42 Spinnen/m^2 in Mähwiesen, 10-50 Spinnen/m^2 in Getreidefeldern).

Die Spinnen in der Vegetationsschicht von Wiesen und Getreidefeldern sind primär Prädatoren von Dipteren und Homopteren. In der Vegetationsschicht unbewirtschafteter Wiesen können zusätzlich Bienen und/oder Heuschrecken einen essentiellen Anteil an der Beutebiomasse grosser Netzspinnen ausmachen. Auf der Bodenoberfläche von Mähwiesen und Getreidefeldern sind die dominanten Spinnen hauptsächlich Prädatoren von kleinen, weichhäutigen Insekten (Collembolen, Blattläuse, Dipteren etc.). Aus den Nahrungsanalysen geht hervor, dass die Spinnen Prädatoren sowohl von Schadinsekten (z.B. Getreideblattläuse) als auch von Nutzarthropoden (Honigbienen, Chrysopiden, Coccinelliden etc.) sind.

Der Energiefluss (= prey killed) durch die Spinnengemeinschaften der Vegetationsschicht von Brachlandbiotopen kann hoch sein (z.B. in einem Hochstaudenried: >900 MJ/ha/Jahr). Demgegenüber ist der Energiefluss durch die Spinnengemeinschaften von Kulturfeldern signifikant niedriger (in Getreidefeldern: 1.1-6.5 MJ/ha/Jahr, in Maisfeldern: ≤0.5 MJ/ha/Jahr). Der Energiefluss durch die bodenbewohnenden Spinnengemeinschaften der Kulturfelder dürfte in der Grössenordnung von 10-50 MJ/ha/Jahr liegen.

Unbewirtschaftete Grasland-Oekosysteme stellen oft wahre "Spinnenparadiese" dar. In solchen Oekosystemen stellen die Spinnen der Vegetationsschicht eine wichtige Prädatorengruppe dar. Im Gegensatz dazu scheinen Spinnen in der Vegetationsschicht von Getreidefeldern keine ökologische Rolle zu spielen. Inwieweit in den Mähwiesen und Getreidefeldern die epigäischen Spinnen eine ökologische Bedeutung haben, werden erst künftige Studien zeigen.

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Curriculum vitae

Educational Background:

March 25th, 1950	Born in Zurich, as son of Hans Nyffeler, teacher, and of Irma Nyffeler-Brunnhofer
1970-1976	Studies at the Faculty of Agronomy of the ETH Zurich. Specialisation in Crop Science and Entomology. During this time practical experience at the Natural History Museum Basel in winter 1971 (supervision: Prof. Dr. Stefan Graeser), the Swiss Federal Research Station for Agronomy Zurich-Reckenholz in summer 1972 (supervision: Dr. Ferdinand Weilenmann), and the Entomological Laboratory of the Swiss Federal Research Station Wadenswil in summer 1973 (supervision: Drs. Th. Wildbolz and E. Mani). Graduation with the Diploma degree of "Engineer in Agronomy"
1976-1982	Scientific assistant at the Department of Entomology where I prepared the present thesis under the supervision of Prof. Dr. Georg Benz. Teaching assistant in Biology-courses for undergraduate students.

Explorations in Natural Sciences:

1972-1973	In the Tessin Alpes I discovered an Ag-Pb-Bi-Sulfosalt, which was identified by Prof. Dr. Stefan Graeser, University of Basel, to be probably a new mineral (publication in prep.)

Prizes:

1968	Second prize at the 2nd Swiss Science Fair (Schweizer Jugend forscht) for a field study in Natural Sciences (Contest-President: Prof. Dr. Adolf Portmann)
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