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Feeding ecology and predatory importance of wolf spiders (*Pardosa* spp.) (Araneae, Lycosidae) in winter wheat fields[1]

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Abstract

Predation by wolf spiders (*Pardosa* spp.) was studied for two years in two winter wheat fields in eastern Switzerland, one field being investigated each year. The following wolf spiders predominated in the investigated wheat fields: *Pardosa agrestis* (Westr.), *Pardosa amentata* (Clerck), and *Pardosa palustris* (L.). *P. agrestis* constituted ≥75 % of all *Pardosa* spp. observed in the field.

Wolf spiders must be characterized as generalist predators of small, soft-bodied arthropods of the classes Insecta and Arachnida. Fourty to 50 % of the spiders' prey items were strongly masticated (chewed down by the spiders' chelicerae to a meat ball) and could therefore not be identified. Diptera, Collembola, and aphids constituted the major components in the spiders' diet (combined ca. 80 % of the identified prey by numbers). Overall, only 4 % of ca. 2500 observed wolf spiders held a prey between their chelicerae. Based on the knowledge of feeding frequency and handling time data, it was estimated that an adult female of *P. agrestis*, not carrying an egg sac or young, captured an average of a little more than 1 prey per day; adult females carrying an egg sac or young, as well as adult males of *P. agrestis* were estimated to have killed <1 prey per spider daily. The wolf spiders were observed to be predaceous on harmful cereal aphids (*Metopolophium dirhodum* Walk., *Rhopalosiphum padi* L., and *Sitobion avenae* F. constituted an essential portion in their diet), suggesting that they are beneficial. Our results are compared with data on wolf spiders' feeding ecology and predatory importance from literature.

1 Introduction

Wolf spiders (Lycosidae) are vagrant predators that capture their prey without a web and in which the females carry on a well developed brood care. The spiders of this family are characterized by the specific arrangement of their 8 eyes: They form three rows, with the front row consisting of four small eyes and the two back rows consisting each of two larger eyes. In crop fields in Europe, North America, and Asia, wolf spiders have frequently been found to belong to the dominant members of ground surface-dwelling spider communities. For instance, in alfalfa fields in northern California, one species of *Pardosa* comprised 60 % of all spiders sampled with the D-Vac (Yeargan and Dondale 1974), while in Texas cotton fields wolf spiders (*Pardosa* spp.) constituted ca. 40 % of all spiders captured in pitfall traps (Dean et al. 1982). In different parts of Asia, wolf spiders of the genus *Lycosa* were found to be abundant – and apparently important – predators in rice fields not or little treated with pesticides (IRRI Annual Report 1974; Kiritani 1979). In central European cereal fields, wolf spiders of the genus *Pardosa* often constitute by numbers >30 % of the spiders sampled with pitfall traps (Geiler 1963; Luczak 1975; Thaler et al. 1977, a. o.).

Since in some crop fields spiders occur in quite high population densities, they are suspected to play a beneficial role as natural control agents of insect pests. However, currently little is known about the spiders' role as predators of insects in agroecosystems (Nyffeler and Benz 1979a, 1987). In this paper observational data on the feeding ecology

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of wolf spiders (*Pardosa* spp.) inhabiting central European winter wheat fields are presented.

2 Materials and methods

2.1 Study area

This project was conducted during a 2-years' study (21 observation days from May to July in year 1, and 34 observation days from May to August in year 2). In each year, 1 winter wheat field with an area of approximately 2 hectares was used. The investigated fields both are located on the grounds of the Swiss Agricultural Experiment Station at Zurich-Reckenholz. Air temperatures (half monthly means at 13.00 hours) ranged from ca. 17–23 °C according to data of the Swiss Meteorological Institute (Weather Station Zurich).

2.2 Evaluation of the spiders' prey spectrum

In both years the ground of the winter wheat field was thoroughly searched for feeding *Pardosa* spp. The observations were conducted only during the daytime hours (between 9 a.m. and 7 p.m.), as spiders of the genus *Pardosa* are known to be diurnal (GRANSTRÖM 1973; FORD 1978, a. o.), at least in the temperate and northern zones of Europe. Feeding spiders were caught by hand with a transparent plastic cup (7 cm upper diameter), killed, preserved in 70 % ethanol and later on identified in the laboratory under a dissecting microscope along with the prey. Due to strong mastication of prey by the spiders' chelicerae the identification was often very difficult and in numerous cases impossible. Of the dominating prey groups "Collembola", "Diptera", and "aphids", samples were sent to specialists for accurate identification. Wolf spiders were identified with the keys of LOCKET and MILLIDGE (1951/53), TONGIORGI (1966), and LOCKET et al. (1974). The identification of females of *Pardosa agrestis* (Westr.) presented difficulties. There is a danger of mistaking them for females of *Pardosa monticola* (Cl.) (K. THALER, pers. comm.). 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 in *P. agrestis*. However, in a sample of 23 females collected in a winter wheat field of the Swiss Agricultural Experiment Station, the posterior margin of the epigyne was 0.51–0.63 mm ($\bar{x} \pm SE = 0.56 \pm 0.04$ mm), showing that the species studied by us was *P. agrestis*. While sampling wolf spiders by hand, we recorded in each case the duration of a sampling period in minutes, which later on allowed us to calculate relative population density values (no. of spiders/hour).

2.3 Evaluation of the spiders' prey capture rates

EDGAR (1970) developed a method wereby the prey capture rate of wolf spiders can be estimated on the basis of observational data collected in the field combined with data assessed in the laboratory. The spiders' daily prey capture rate *(b)* may be estimated as follows (according to EDGAR's formula modified by us):

$$b = \frac{T_f \cdot 60 \cdot w}{T_h \cdot 100}, \qquad (1)$$

where T_f is the time (hours/day) available for prey capture and feeding in the field, w is the average percentage of spiders with prey, and T_h is the average handling time (sensu KREBS 1985, in minutes). The handling time was defined as the period between the initiation of an attack and the cessation of feeding.

The spiders' feeding frequency *(w)* was assessed by sampling wolf spiders in the winter wheat field during the daytime hours (see above, table 1). In the case of each sampled spider it was recorded whether it held a prey in the chelicerae or not. In order to measure the handling time (T_h), adult males and females of *P. agrestis* were collected in a winter wheat field of the Swiss Agricultural Experiment Station Zurich-Reckenholz at the end of July and taken to the laboratory, where they were confined singly in 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 small Heteroptera, Diptera, Aphidina, and Arachnida of the same size as those occurring in the spiders' natural diet, and the handling times were measured. Based on activity data from literature (EDGAR 1969; GRANSTRÖM 1973, a. o.), we put T_f = 10 h/day; it follows that one can use the simplified formula:

$$b = (6 \cdot w)/(T_h). \qquad (2)$$

Table 1. **Numbers of immature, adult male, and adult female wolf spiders (*Pardosa* spp.) observed with prey**

Studies in winter wheat fields near Zurich

Spider species	Date	Males		Females without eggs or young		Females with egg sac		Females with young		Total	
		A	N	A	N	A	N	A	N	A	N
					Field 1						
P. agrestis	15–31 May	0	(8)	0	(8)	0	(2)	0	(0)	0	(18)
	1–14 June	0	(18)	0	(7)	0	(73)	0	(8)	0	(106)
	15–30 June	4	(92)	15	(86)	1	(113)	2	(42)	22	(333)
	1–14 July	0	(11)	1	(32)	3	(95)	0	(4)	4	(142)
	15–31 July	1	(24)	1	(29)	1	(16)	0	(4)	3	(73)
	Total	5	(153)	17	(162)	5	(299)	2	(58)	29	(672)
P. amentata	15–31 May	0	(1)	0	(0)	0	(25)	0	(0)	0	(26)
	1–14 June	0	(0)	2	(6)	0	(10)	0	(5)	2	(21)
	15–30 June	0	(1)	7	(24)	0	(13)	0	(3)	7	(41)
	1–14 July	0	(0)	0	(6)	1	(20)	0	(0)	1	(26)
	15–31 July	0	(2)	0	(0)	0	(0)	0	(0)	0	(2)
	Total	0	(4)	9	(36)	1	(68)	0	(8)	10	(116)
P. palustris	Total	0	(4)	4	(10)	3	(12)	0	(2)	7	(28)
Pardosa spp. (imm)	Total									4	(165)
					Field 2						
P. agrestis	15–31 May	6	(108)	2	(67)	0	(29)	0	(0)	8	(204)
plus	1–14 June	0	(62)	2	(17)	2	(44)	0	(0)	4	(123)
P. palustris[1]	15–30 June	1	(49)	0	(5)	1	(45)	0	(4)	2	(103)
	1–14 July	1	(71)	10	(119)	2	(183)	1	(16)	14	(389)
	15–31 July	4	(133)	9	(177)	4	(207)	4	(14)	21	(531)
	1–14 Aug.	1	(28)	4	(35)	0	(3)	0	(4)	5	(70)
	Total	13	(451)	27	(420)	9	(511)	5	(38)	54	(1420)
Pardosa spp. (imm)	Total									2	(98)
Total (field 1 plus field 2)		18	(612)	57	(628)	18	(890)	7	(106)	106	(2499)

A = number of spiders with prey, N = number of observed spiders.
[1] In field 2, data for *P. agrestis* and *P. palustris* were pooled together; *P. agrestis* was the dominant wolf spider in this winter wheat field.

3 Results

3.1 Dominant species of wolf spiders in winter wheat

The structure of the wolf spider guild (*Pardosa* spp.) on the ground surface of a Swiss winter wheat field (field 1) is presented in table 2, together with the spiders' relative densities. In this field *Pardosa agrestis* (Westr.) and *Pardosa amentata* (Clerck) were dominating, while *Pardosa palustris* (L.) occurred in low numbers. Overall, the ratio *P. agrestis* : *P. amentata* : *P. palustris* was 78 % : 20 % : 2 %. In all three *Pardosa* species, more adult females than adult males were encountered in the field. Females carrying an egg sac were recorded from May to July, females carrying young on the abdomen in June and July. The proportion of immatures on the total of observed wolf spiders was low in May and

June (≤1 %, counting only immatures that had already left the mother's abdomen) and increased to up to 28 % by the second half of July. The relative density of *Pardosa* spp. was lowest from May to mid-June (<20 spiders observed/hour) and increased with the progressing growing season, reaching a maximum in the second half of July (>40 spiders observed/hour) (table 2).

Table 2. **Structure of the hunting spider guild (wolf spiders) on the ground surface in a winter wheat field near Zurich (May to July, field 1)**

Values in this table represent numbers of spiders observed per hour

Date	Spider species	Males (M)	Females (F)	Total (M+F)	% females of total	Females	
		No. spiders obs./hour				% with egg sac	% with young
15–31 May	*P. agrestis* (adt)	3.0	3.7	6.7	55	19	–
	P. amentata (adt)	.4	9.3	9.7	96	100	–
	P. palustris (adt)	–	.7	.7	100	100	–
	Pardosa spp. (imm)[1]			1.1			
				18.2			
1–14 June	*P. agrestis* (adt)	1.8	8.9	10.7	83	83	9
	P. amentata (adt)	–	2.1	2.1	100	48	24
	P. palustris (adt)	–	.2	.2	100	50	–
	Pardosa spp. (imm)[1]			–			
				13.0			
15–30 June	*P. agrestis* (adt)	5.5	14.4	19.9	72	47	17
	P. amentata (adt)	.06	2.4	2.5	96	33	8
	P. palustris (adt)	.2	1.0	1.2	83	40	10
	Pardosa spp. (imm)[1]			.06			
				23.7			
1–14 July	*P. agrestis* (adt)	1.6	19.3	20.9	92	73	3
	P. amentata (adt)	–	3.8	3.8	100	76	–
	P. palustris (adt)	–	.4	.4	100	100	–
	Pardosa spp. (imm)[1]			3.8			
				28.9			
15–31 July	*P. agrestis* (adt)	5.0	10.1	15.1	67	33	8
	P. amentata (adt)	.4	–	.4	–	–	–
	P. palustris (adt)	–	.2	.2	100	–	–
	Pardosa spp. (imm)[1]			28.1			
				43.8			
Mean	*P. agrestis* (adt)	3.38	11.28	14.66	77	57	8
	P. amentata (adt)	.17	3.52	3.70	95	80	4
	P. palustris (adt)	.04	.50	.54	93	64	4
	Pardosa spp. (imm)[1]			6.61			
				25.51			

[1] Here only those immature wolf spiders were counted which had already left the mother's abdomen and were foraging individually.

Similar seasonal and age structure patterns were observed in the wolf spider guild of the other winter wheat field (field 2). However, the species composition of the wolf spider guild differed somewhat in field 2, with *P. agrestis* and *P. palustris* dominating, and with *P. amentata* occurring in low numbers. Overall, the ratio *P. agrestis* : *P. palustris* : *P. amentata* was 75 % : 24 % : 1 %.

P. agrestis and *P. palustris* reach average adult body lengths of ca. 7 mm in females, and of ca. 5 mm in males. *P. amentata* is slightly larger.

3.2 Natural diet

The natural diets of *Pardosa* spp. in two winter wheat fields near Zurich are represented in table 3. A considerable portion (ca. 40–50 %) of the prey items were strongly masticated by the spiders' chelicerae and thus not identifiable (wolf spiders have the habit of chewing down a killed prey organism to a meat ball with their chelicerae; see Discussion). In both fields the spiders' prey consisted exclusively of arthropods of the classes Insecta and Arachnida.

In field 1, Diptera (26 % by numbers) and aphids (20 %) constituted the major components in the wolf spiders' diet (table 3).

In field 2, Collembola (25 %) and aphids (11 %) constituted the wolf spiders' primary diet; other essential components were Diptera and spiders (table 3).

The Collembola found in the spiders' natural diet mostly belonged to the suborder Arthropleona [e.g. family Isotomidae, and *Orchesella villosa* (Geoffroy) of the family Entomobryidae].

The Diptera identified as wolf spiders' diet belonged to the following families: Dolichopodidae (*Dolichopus longicornis* Stann), Opomyzidae (*Opomyza florum* Fabr.), Drosophilidae, Scatophagidae, Anthomyzidae, and Muscidae.

The aphids captured by the spiders were identified to be so-called cereal aphids (apterous and winged *Metopolophium dirhodum* Walk., apterous *Rhopalosiphum padi* L., and apterous *Sitobion avenae* F.). Adult Carabidae, which were abundant on the ground surface of these winter wheat fields – as assessed with pitfall traps (NYFFELER and BENZ, unpubl. data) – were missing in the wolf spiders' food.

In nine observed cases of predation, the size of the wolf spider and its prey was measured. These spiders had killed prey of a size between 0.25- and 0.8-fold their own size. The nine prey items had an average body length of 3.8 mm (range: 1.5–5 mm).

3.3 Prey capture rates

Data on numbers of immature, adult male, and adult female wolf spiders (*Pardosa* spp.) found with a prey between the chelicerae are compiled in table 1. Of about 2500 wolf spiders observed in both fields, only 106 (= 4.2 %) held a prey between the chelicerae.

In adult *P. agrestis*, the proportion of feeding spiders was significantly higher for females (without egg sac/young) than for males ($p < 0.05$, χ^2-test for 2 × 2 contingency tables). Furthermore, in adult *P. agrestis* the proportion of spiders with prey was significantly lower in females carrying an egg sac than in females without eggs or young ($p < 0.01$). The percentages of all adult females combined (pooled data of females with/without eggs or young) did not differ significantly in the two species *P. agrestis* and *P. amentata* ($p > 0.05$).

The spiders' prey capture rates *(b)* were estimated with formula 2, using the following values: $T_b = 49.4$ and 47.5 for respectively adult male and female *P. agrestis* (based on data of table 4), *w*-values caculated from data given in table 1. We came to the following estimates of spiders' prey capture rates in winter wheat fields (table 5): Adult female *P. agrestis*, not carrying an egg sac or young, may capture an average of a little more than 1 prey per day ($b = 1.33$). Adult male *P. agrestis* or females carrying young on the abdomen may capture an average of 1 prey about every second to third day ($b = 0.40$ and 0.44 respectively). An adult female *P. agrestis*, carrying an egg sac, may capture an average of 1 prey about every fifth day ($b = 0.21$). Calculating the prey capture rate for all adult female *P. agrestis* combined (pooled data for females with/without egg sac or young) leads to a value of $b < 1$.

Table 3. **Diets of wolf spiders (*Pardosa* spp.) in winter wheat fields near Zurich**

Prey type	Field 1				Field 1		Field 2		Mean
	Pardosa agrestis	*Pardosa amentata*	*Pardosa palustris*	*Pardosa* (immature)	Total *Pardosa* spp.		Total *Pardosa* spp.[1]		
Aphidina									
Metopolophium dirhodum (u)	1	0	1	0	2		0		
Metopolophium dirhodum (w)	0	1	1	0	2		0		
Sitobion avenae (u)	0	1	0	0	1	(20.0 %)	0	(10.7 %)	(15.4 %)
Rhopalosiphum padi (u)	1	0	0	0	1		0		
Undt. aphids	4	0	0	0	4		6		
Diptera (small/medium)									
Dolichopodidae									
Dolichopus longicornis	0	0	1	0	1		0		
Opomyzidae									
Opomyza florum	1	0	0	0	1		0		
Drosophilidae	1	0	0	0	1		0		
Scatophagidae	0	1	0	0	1	(26.0 %)	0	(5.4 %)	(15.7 %)
Anthomyzidae	1	0	0	0	1		0		
Muscidae	1	1	0	0	2		0		
Undt. Diptera (adult)	3	1	1	0	5		3		
Undt. Diptera (larva)	1	0	0	0	1		0		
Collembola	1	0	0	0	1	(2.0 %)	14	(25.0 %)	(13.5 %)
Staphylinidae (small)	0	1	0	0	1	(2.0 %)	0	(0 %)	(1.0 %)
Carabidae larvae (small)	1	1	0	0	2	(4.0 %)	0	(0 %)	(2.0 %)
Hymenoptera (small)	1	0	0	0	1	(2.0 %)	1	(1.8 %)	(1.9 %)
Lepidoptera larvae	0	0	0	0	0	(0 %)	1	(1.8 %)	(0.9 %)
Araneae	0	0	0	1	1	(2.0 %)	3	(5.4 %)	(3.7 %)
Acari	0	1	0	0	1	(2.0 %)	1	(1.8 %)	(1.9 %)
Undt. prey[2]	12	2	3	3	20	(40.0 %)	27	(48.2 %)	(44.1 %)
Total prey	29	10	7	4	50	(100 %)	56	(100 %)	(100 %)

[1] In field 2, predominantly *Pardosa agrestis*. – [2] Among them were possibly several Collembola which were strongly masticated and therefore could not be identified unmistakebly.
u = unwinged, w = winged.

Table 4. **Average time (T_h, in min) spent for the processing of one prey item by adult males and females of *Pardosa agrestis* at room temperature in the laboratory**

Prey	Males $\bar{x} \pm SE$	Females $\bar{x} \pm SE$
Aphidina	68.86 ± 15.94 (N = 7)	55.71 ± 15.66 (N = 7)
Diptera (small)	30.05 ± 9.43 (N = 11)	57.75 ± 37.73 (N = 4)
Heteroptera (small)	66.81 ± 12.68 (N = 8)	47.50 ± 13.74 (N = 8)
Thomisidae (imm)	64.00 ± 24.70 (N = 5)	68.13 ± 15.43 (N = 4)
Lycosidae (imm)	17.30 ± 0.61 (N = 15)	8.31 ± 1.03 (N = 11)
Mean value	49.40	47.48

N = number of feedings.

Table 5. **Estimates of the daily prey capture rates of adult *Pardosa agrestis* (females and males) in a winter wheat field (field 1)**

Sex and condition of spider	% spiders feeding[1] (w)	Handling time[2] (T_h)	Prey/spider/day $b = (6w)/(T_h)$
♀ (without eggs/young)	10.5 AB	47.5	1.33
♀ (with egg sac)	1.7 A	47.5	.21
♀ (with young)	3.5	47.5	.44
♀ (all)[3]	4.6	47.5	.58
♂	3.3 B	49.4	.40

[1] Assessed in the winter wheat field (see table 1). Same letter in a column indicates statistically significant differences ($p < 0.05$, χ^2). – [2] Assessed in the laboratory (see table 4). – [3] Pooled data for all adult females (with and without egg sac or young).

4 Discussion

4.1 Dominant species of wolf spiders in winter wheat and other crop fields

In our study in winter wheat fields *P. agrestis* amounted to ≥75 % of all *Pardosa* spp. It also constituted ≥ 75 % of all *Pardosa* spp. sampled with pitfall traps in the same site (NYFFELER and BENZ, unpubl. data). Moreover, *P. agrestis* was found to be the dominating wolf spider in crop fields in Austria (THALER et al. 1977), the German Democratic Republic (GEILER 1963; BEYER 1981), and Poland (CZAJKA and GOOS 1976; LUCZAK 1979). It can be characterized as an "agrobiont" species (LUCZAK 1979).

4.2 Prey spectrum of wolf spiders

The diets of wolf spiders (*Pardosa* spp.) in Swiss winter wheat fields were found to be composed primarily of small, soft-bodied arthropods, which confirms our previous studies on wolf spiders' diets in meadow and forest habitats in eastern Switzerland (NYFFELER and BENZ 1979b, 1981; NYFFELER 1982).

By comparing our data on wolf spiders' natural diets with those from literature (table 6), the following general pattern is emerging: wolf spiders' natural diets are diverse, characterizing these spiders as non-specific feeders (generalist predators). The four arthropod groups Diptera, Hemiptera, Collembola, and Araneae evidently represent worldwide the major components in the diets of small and medium-sized wolf spiders, as already stated by YEARGAN (1975) and NYFFELER and BENZ (1981). Small Diptera, Collembola, and Homoptera have been found to occur in high numbers in wolf spiders' preferred

(%)

Table 6. **Natural diets of various wolf spiders (A–K: *Pardosa*, L–M: *Pirata*, N: *Lycosa*). A review based on literature data**

Spider species	*P. agrestis* *P. palustris* *P. amentata*	*P. palustris* *P. hortensis*	*P. lugubris*	*P. lugubris*	*P. lugubris*	*P. amentata*	*P. pullata*	*P. purbeck-ensis*	*P. ramulosa*	*P. hokkaido*	*P. piraticus*	*P. piraticus*	*L. pseudo-annulata*	Mean value
	A[1] N=106	B[1] N=35	C N=31	D N=119	E N=210	F N=46	G N=76	H N=114	I N=331	K N=124	L N=264	M N=64	N N=1553	
Diptera	16	6	26	33	17	67	25	20	22	36	12	13		22.5
Homoptera	15	23		20	3	} 2	5	3	24	} 20	7		78	} 18.8
Heteroptera				8				2	11		4	19		
Araneae	4	3	3	24	34	11	38	23	20	12	22	28	9	17.8
Collembola	13	11	39	2	6	13	3	39	2	9	43	25		15.8
Lepidoptera	1	3		7	4				1	14				2.3
Hymenoptera	2	3	3	4	< 1				< 1	4				1.3
Coleoptera	3								6	2				.8
Orthoptera					< 1		4		6					.8
Others	3		3	2	4	7		13 }	7	3	12 }	15	13	} 19.8
Unident.	43	51	26		30		25	}			}			
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100

[1] Sample size of each spider species small, thus, data for *Pardosa* spp. pooled together.
A = Swiss cereal fields (this paper), B = Swiss hay meadows (NYFFELER and BENZ 1979b), C = Swiss forest (NYFFELER and BENZ 1981), D = forest in Scotland (EDGAR 1969), E = forest in Sweden (HALLANDER 1970), F = habitat not mentioned, in Netherlands (EDGAR 1970), G = meadows in Sweden (HALLANDER 1970), H = salt meadow in West Germany (SCHAEFER 1986), I = California alfalfa fields (YEARGAN 1975, K = forest in Japan (SUWA 1986), L = salt meadow in West Germany (SCHAEFER 1974), M = river bank in West Germany (GETTMANN 1977, 1978), N = rice fields in Japan (KIRITANI et al. 1972).

Table 7. **Proportion of feeding specimens within wolf spider populations in various habitats. Review based on literature data**

Spider species	Country	Habitat	Authors	Percent spiders feeding
Pardosa agrestis (Westr.)[1]	Switzerland	wheat field	this paper	4.3 (N=672)
Pardosa amentata (Clerck)[1]	Switzerland	wheat field	this paper	8.6 (N=116)
Pardosa amentata (Clerck)	Netherlands	+	EDGAR (1970)	7.8 (N=520)
Pardosa lugubris (Walck.)	Switzerland	forest	NYFFELER and BENZ (1981)	6.0 (N=513)
Pardosa spp.	Switzerland	hay meadow	NYFFELER (1982)	5.0 (N=765)
Pardosa pauxilla Montgomeri	USA	cotton field	DEAN et al. (1987)	8.2 (N=73)
Pirata piraticus (Clerck)	West Germany	salt marsh	SCHAEFER (1974)	8.0 (N=large)
Lycosa rabida Walckenaer	USA	farmland	NYFFELER et al. (1986)	4.0 (N=50)
Lycosa carolinensis Walckenaer	USA	desert	SHOOK (1978)	.4 (N=674)
Mean value				5.8

[1] Field 1.
+ Habitat not mentioned, N = sample size (= 100 %).

habitats, as assessed with pitfall traps (NYFFELER and BENZ, unpubl. data). Hence, there is a high probability of predator/prey encounters between wolf spiders and these three insect groups, and since those insects fit ideally into the wolf spiders' prey preference range, as evidenced by laboratory feeding experiments (NYFFELER and BENZ, unpubl. data), such encounters often result in predation. Besides, wolf spiders frequently collide with conspecifics, which may lead to considerable levels of cannibalism (EDGAR 1969; FELTON 1969; HALLANDER 1970; SCHAEFER 1974).

The observed feeding patterns (table 6) seem to be restricted to small and medium-sized wolf spiders. In contrast to this, large-sized wolf spiders were observed feeding on large (including hard-bodied) insects, e.g. of the orders Lepidoptera, Coleoptera, and Orthoptera as well as on Araneae (KUENZLER 1958; FITCH 1963; WHITCOMB et al. 1963, 1967; NYFFELER et al. 1986).

4.3 Prey capture rates of wolf spiders

In various field studies (table 7) it was observed that the proportion of wolf spiders holding a prey between the chelicerae was $<10\,\%$.

In our study in winter wheat fields the prey capture rates for adult wolf spiders were estimated to be a little less or more than 1 small-sized prey item/spider/day. Studies in other habitats gave estimated values of the same magnitude (≤ 1 prey/spider/day) for medium-sized wolf spiders of the genera *Pardosa* and *Pirata* (EDGAR 1969, 1970; SCHAEFER 1974; NYFFELER and BENZ 1979b, 1981).

The wolf spiders' prey capture rates in the field appear to be low (only 106 feeding events observed during 104.5 hours). Comparatively, much higher prey capture rates of wolf spiders were observed in the laboratory if food was offered ad libitum. At artificially high prey densities, up to ≥ 20 small-sized prey were killed per adult *Pardosa* per day (KESSLER 1971; HARDMAN and TURNBULL 1974).

Thus, wolf spiders evidently consume less food in the field than they take in the laboratory when prey is offered ad libitum. Several authors stated that in the field wolf spiders were observed in a condition of underfeeding (MIYASHITA 1968a; HAGSTRUM 1970; KESSLER 1973; BREYMEYER and JOZWIK 1975). For instance, MIYASHITA (1968b) found in a species of wolf spider that the carapace width distribution of field specimens was somewhat similar to that of every fourth day feeding in the laboratory, suggesting poor feeding condition in the field. Regarding the malnourishment of wolf spiders in the field, BREYMEYER and JOZWIK (1975) assume that insufficient food would be a condition often observed among those predators which are characterized by great resistance to hunger, but that such animals would compensate their low food consumption by high food assimilation. The wolf spiders' habit of chewing down a killed arthropod to a meat ball with their chelicerae appears to be such a compensating mechanism, maximizing food assimilation by enabling the spiders to extract a maximum amount of energy from a prey organism. EDGAR (1971) found food assimilation values of ca. 80 % for *Pardosa*. Besides, other feeding mechanisms operate to maximize food utilization by wolf spiders, e.g. the ability to capture multiple prey (ROVNER and KNOST 1974), to scavenge (KNOST and ROVNER 1975), and to starve for a considerable time (ANDERSON 1974).

In this study the prey capture rates of adult spiders were lower in males than in females (without egg sac or young). In hunting spiders of other families, the prey capture rates of adults were also found to be lower in males than in females (HAYNES and SISOJEVIC 1966; MUNIAPPAN and CHADA 1970; HORNER 1972; FURUTA 1977; JACKSON 1977). The sex specific prey capture rates of adults may be explained by sexual dimorphism, the larger sized females being expected to capture more prey in order to satisfy their higher energy demand.

4.4 Importance of wolf spiders as natural control agents of pest insects

Since prey capture rates of adult wolf spiders were estimated to be ≤1.3 prey/spider/day and since aphids constituted ca. 10–20 % of the total prey, we assume that on the average less than 2 aphids per week are killed by one wolf spider. LUCZAK (1975) estimated the numbers of *Pardosa* spp. in Polish cereal fields at ca. 1 individual/m^2. If this density estimate is solid, one can expect only less than 2 aphids/m^2/week to be killed by wolf spiders in such a situation.

All identified aphids found a wolf spiders' prey in winter wheat fields belonged to three species of cereal aphids (*M. dirhodum, R. padi,* and *S. avenae*) which are considered to be pests of the cereal fields (VICKERMAN and WRATTEN 1979). Hence, as predators of cereal aphids wolf spiders can be considered beneficials. Beside wolf spiders, spiders of other families were observed to be predaceous on cereal aphids (NYFFELER and BENZ 1982). For instance, aphids (including cereal aphids) constituted almost 40 % by numbers of the prey captured by micryphantid spiders on the soil surface of winter wheat fields near Zurich (NYFFELER and BENZ 1988). Further investigations will be necessary to quantify the impact of wolf spiders and other spiders as predators of cereal aphids.

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Zusammenfassung

Zur Nahrungsökologie und Prädatorenbedeutung der Wolfsspinnen (Pardosa spp.) (Araneae, Lycosidae) in Winterweizenfeldern

Die Prädatorenaktivität von Wolfsspinnen (*Pardosa* spp.) wurde in schweizerischen Winterweizenfeldern studiert. In den untersuchten Weizenfeldern dominierten die folgenden Wolfsspinnenarten: *Pardosa agrestis* (Westr.), *Pardosa amentata* (Clerck) und *Pardosa palustris* (L.), wobei *P. agrestis* ≥75 % aller beobachteten *Pardosa* spp. stellte.

Auf Grund dieser Studie müssen Wolfsspinnen als unspezialisierte Prädatoren (Nahrungsgeneralisten) von kleinen, weichhäutigen Arthropoden der Klassen Insecta und Arachnida charakterisiert werden. Vierzig bis 50 % der Beutetiere waren stark deformiert und deshalb unidentifizierbar (mittels der Cheliceren zu einem Fleischballen zusammengekaut). Diptera, Collembola und Blattläuse waren die vorherrschenden Komponenten der Spinnennahrung (zusammen ca. 80 % der identifizierbaren Beutetiere). Nur 4 % der ca. 2500 beobachteten Wolfsspinnen trugen eine Beute zwischen den Cheliceren. Basierend auf der im Freiland beobachteten Freßhäufigkeit und der im Labor gemessenen „Handlungszeit" wurde geschätzt, daß ein adultes Weibchen von *P. agrestis* (ohne Kokon oder Jungtiere auf dem Abdomen) im Durchschnitt etwas mehr als 1 Beutetier pro Tag fing; die Beutefangrate von adulten Männchen und kokontragenden (bzw. Jungtiere tragenden) Weibchen von *P. agrestis* wurde auf < 1 Beutetier pro Spinne pro Tag geschätzt. Die Wolfsspinnen wurden beim Erbeuten von schädlichen Getreideblattläusen (*Metopolophium dirhodum* Walk., *Rhopalosiphum padi* L. und *Sitobion avenae* F.) beobachtet, was darauf hinweist, daß diese Spinnen Nützlinge sind. Die Resultate wurden mit Daten aus der Literatur verglichen.

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