

## Prey selection and prey capture strategies of linyphiid spiders in high-input agricultural fields

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### Summary

This study deals with the poorly-known feeding ecology of linyphiid spiders occurring abundantly in many habitat types, including crop fields, and concentrates mainly on *Bathypantes gracilis*, *Erigone atra*, *E. dentipalpis*, *Lepthyphantes tenuis*, *Linyphia clathrata*, *Meioneta rurestris*, *Oedothorax apicatus* and *O. fuscus*. It was confirmed that *B. gracilis* and *L. tenuis* are exclusively web-building spiders depending completely on their web for capturing prey, whereas adult *Oedothorax* no longer build webs but have a sit-and-wait predatory strategy. The prey capture strategy observed for *Erigone* species is remarkably versatile. Beside capturing prey in a small web, they can also feed actively on small prey items.

Web size and web placement of all these species is compared in field conditions. Detailed data are provided on the prey spectrum of 15 spider species in crop fields. Only 61.6% of the prey captured is consumed. Pest species, in this case Aphididae, comprise 55.1% of the total number of prey items captured, Collembola 29.8%. A striking difference was observed in the consumption rate of these two most abundant prey groups. Ivlev-indices were used to compare actual prey spectra with potential ones, indicating that Aphididae, Isotomidae, Delphacidae and some Diptera are consumed by spiders more often than expected from their respective average abundances. This was confirmed by laboratory feeding experiments. Other laboratory experiments demonstrated a preference of spiders for the most abundant springtail *Isotomurus palustris* over *Lepidocirtus*. There is a tendency towards a preference for larger springtails (1.6-2.1 mm total length) compared with smaller ones (0.45-0.95 mm). The results on the feeding ecology obtained here are useful in the framework of an evaluation of the influence of spiders as beneficial polyphagous predators on certain pest populations in crop fields.

### Introduction

Spiders have, for several decades, been recognised as potentially beneficial polyphagous predators on arable land. They can reach considerable densities in all kinds of crop fields and seem to be surprisingly flexible under conditions of high pressure from external agricultural management practices. For some species, it is known that they prey regularly on pest species which reduce crop yields (Chiverton, 1986; Edwards *et al.*, 1979; Sopp & Wratten, 1986; Sunderland *et al.*, 1980, 1986a, 1987; Vickerman & Sunderland, 1975).

However, there is no general consensus on their potential to prevent pest species from reaching economically important population levels (see discussions in Agnew & Smith, 1989; Brignoli, 1983; Kirchner, 1964; Nyffeler & Benz, 1980, 1982, 1987; Riechert, 1974; Riechert & Lockley, 1984; Sunderland & Chambers, 1982).

A thorough analysis of this important problem is hampered by the lack of information on the feeding ecology of most of the abundant species occurring in these habitat types. Although many studies dealing with spider feeding ecology exist, they mainly concentrate on prey selection, web-building behaviour and web orientation of larger, exclusively web-building species occurring in more natural or semi-natural habitats (e.g. Castillo & Eberhard, 1983; Greenstone, 1984; Nentwig, 1980, 1982, 1983, 1985; Nyffeler & Benz, 1989; Rypstra, 1982). This is partly a result of the possibilities offered by these species to collect a large number of prey items within a relatively short time period. Other publications concentrate on prey size in relation to prey capture strategy of larger web-building versus hunting spiders (e.g. Enders, 1975; Nentwig & Wissel, 1986; Rypstra, 1990). However, the dominant western European spider taxocoenosis occurring in high-input agricultural fields mainly consists of small linyphiid spider species. Although several of these species are among the commonest invertebrates in many different habitat types, surprisingly little is known of their prey capture strategies and prey selection. This is partly due to the methodological problems of collecting sufficient data for statistical analysis. It was generally thought that they all depend on small webs to capture prey (e.g. Bristowe, 1958). However, several authors have questioned the role of the web of certain Erigoninae (Heimer & Nentwig, 1982; Jocqué, 1984; Thornhill, 1983). Others have suggested that some species might also leave their webs and hunt for prey (Chant, 1956; Wheeler, 1973).

This contribution, based on field and laboratory observations, summarises new data on prey spectra, prey selection, prey capture strategies, web placement and web size observed in linyphiid spiders occurring abundantly on arable land.

### Material and methods

Spiders were observed and collected in several maize and Italian ryegrass fields and their edge zones situated at Melle (15 km south-east of Ghent, Belgium). The fields belong to the Experimental Farm of the University of Ghent (Faculty of Agronomy). Field size is approximately 4 ha. More general information on the study site can be found in Alderweireldt (1993).

Several different methods have previously been used in ecological studies on spider feeding (e.g. serological, electrophoretic, etc.), all having their specific assumptions and disadvantages (see discussion in Crook & Sunderland (1984), Greenstone (1977), Kiritani & Dempster (1973), Lövei (1986) and Sunderland (1988)). Direct observation, albeit very time consuming, was chosen here, because it permits easy and immediate interpretation of the results. Data were gathered between 1986 and 1988 at weekly intervals. Searching effort was kept as constant as possible throughout the year (one hour on each occasion). Despite several attempts during the night, spiders with prey were captured only during daytime. Predation during the night by night-active species may thus be underestimated. Spiders

carrying prey in the chelicerae were collected and stored in 70% ethanol. For certain species, prey remains were collected from webs, prepared and identified with a microscope.

It should be noted that the results are not presented here for males and females separately because this would needlessly reduce the number of observations on which interpretations are based. Moreover, males of several species were rarely seen with prey in field conditions. From laboratory rearing we know that males of several linyphiid species hardly consume any prey after having reached maturity (Alderweireldt & Lissens, 1988; De Keer & Maelfait, 1987, 1988).

Prey capture strategies and prey selection were observed in field and laboratory conditions. Animals for laboratory experiments, were reared at 20°C and L/D 16:8. All prey selection laboratory experiments were performed with adult females of *Bathyphantes gracilis* (Blackwall, 1841), *Erigone atra* Blackwall, 1833, *Oedothorax apicatus* (Blackwall, 1850) or *O. fuscus* (Blackwall, 1834). They were kept in small petri-dishes (3.5 cm diameter, 1.5 cm high). A small layer of plaster of Paris on the bottom of the dishes was moistened daily to maintain relative humidity close to 100%. All specimens received the same preparatory treatment in order to keep the experiments as comparable as possible. They were fed for two days *ad libitum* with wingless *Drosophila melanogaster*, and then kept for two days without prey before being used in the experiments.

In a first series of prey selection experiments the influence of prey size was tested by offering each time 10 Collembola (*Isotomurus palustris*) of two different sizes (5 of each size): large Collembola 1.60–2.10 mm total length, small Collembola 0.45–0.95 mm total length. The springtails were collected by a small vacuum cleaner in nearby grasslands where they reach very high densities.

In a second series of prey selection experiments, different types of prey items, of known size and collected in the crop fields or adjacent areas, were offered. The time between the prey item entering the petri-dish and its capture by the spider was measured. Refusal of certain prey items after a quick check by the spider, or other specific reactions, were noted.

In a final series of prey selection experiments, spiders were given the choice between two species of Collembola. Each time, they were presented with 10 individuals of the same size (0.6–0.9 mm), 5 of *Lepidocircus* sp. and 5 of *Isotomurus palustris*. After three days, the number of consumed collembolans of each species was counted.

Web placement was recorded in field conditions. When necessary, webs were made more visible by spraying with water. The exact position of the web was measured (height above soil level) and the attachment sites localised. Web area was then measured by digitising the web contours with a plotter. The spider in the web was collected, stored in 70% ethanol and identified. As a rule, web size of juvenile spiders is smaller than for adults. The web sizes provided in this paper are exclusively based on adult specimens.

Homogeneity of variances of the normally distributed results of web size measurements was observed. They could therefore be analysed by parametric multiple t-test comparisons (Bailey, 1981; Sokal & Rohlf, 1981).

Density estimates of all invertebrate groups present in the fields were obtained by quadrat sampling during 1986–1987. On each occasion, 30 quadrat samples (size 12.5 × 12.5 cm, depth *c.* 12 cm) were taken every month in two field centres and two field edges (120 quadrats per month). More details on the methods used can be found in Alderweireldt (1993).

All invertebrate groups found during one year by this quadrat sampling campaign (absolute abundances in number of individuals per m<sup>2</sup>) are considered to be potential prey. Comparisons between potential and actual prey spectra were made for each species, based on the results from maize fields only, by using a simple index designed by Ivlev (1955, 1961). The Ivlev-index (Iv) has already been used for comparing spider prey spectra by Kajak (1965) and Nentwig (1980). It varies between -1 and +1 and is defined as  $Iv = (A - P)/(A + P)$  where A is the proportion of a certain prey group in the actual prey spectrum and P is the proportion of the same prey item in the potential prey spectrum.

## Results and discussion

The most abundant spider species occurring in the crop fields studied belong to the Linyphiidae, a family which is subdivided into two groups, previously regarded as subfamilies: Erigoninae and Linyphiinae. As is characteristic in many types of arable land, a few species occur in very high numbers whereas most others occur only sporadically or are restricted to the field edges (Alderweireldt, 1989). Data were collected on the feeding ecology of eight abundant species of Linyphiidae: *Bathyphantes gracilis*, *Erigone atra*, *E. dentipalpis* (Wider, 1834), *Lepthyphantes tenuis* (Blackwall, 1852), *Linyphia clathrata* Sundevall, 1829, *Meioneta rurestris* (C. L. Koch, 1836), *Oedothorax apicatus* and *O. fuscus*.

### Prey capture strategies, web size and web placement

#### Exclusively web-building species

*Bathyphantes gracilis*, *Lepthyphantes tenuis* and *Linyphia clathrata* are exclusively web-building spiders of the family Linyphiidae (Linyphiinae). They build sheet webs with a central, horizontal, relatively dense part, typical of this group of spiders (cf. Bristowe, 1958; Ford, 1977). In field as well as in laboratory conditions, these species were always encountered in a web or during web-building activity. They are completely dependent on their web for capturing prey.

In field conditions, mean web size for *B. gracilis* was 42.54 ± 4.49 cm<sup>2</sup> (mean ± 95% confidence limits, *n* = 35). However, web size varied considerably in this species depending on its placement. The total range observed in crop fields was 19.60–70.89 cm<sup>2</sup>. The largest webs were observed in Italian ryegrass fields, the smallest in maize fields. Ryegrass offers more possibilities for attachment

of the web. The same is true for grasslands, in which De Keer (unpublished results) observed web sizes for *B. gracilis* of 40–80 cm<sup>2</sup>, i.e. generally higher than in maize fields. This is likely to be due to the clear structural similarities between intensively grazed pastures and Italian ryegrass fields. Sunderland *et al.* (1986b) found somewhat larger webs of *B. gracilis* (median area 74.2 cm<sup>2</sup>), but this might be due to their assumption of the rectangular shape of the webs (to facilitate measurements). Moreover, these authors demonstrated a significant increase in *B. gracilis* web size as the season progressed. We did not test for this.

The broad range of possible web sizes indicates considerable flexibility in this species. This could be very important for survival in highly disturbed areas where the number of suitable sites for web-building can be very limited, e.g. in maize fields. *B. gracilis* seems to be well adapted, as it can use different microhabitats for web construction. In Italian ryegrass fields, the webs are always found attached to grass leaves a few centimetres above soil level (cf. *L. tenuis*). In maize fields, the species almost exclusively uses the small "stilt roots" to construct its web. They were never found in a web above bare soil, in agreement with Thornhill (1983) who observed the species in sugar-beet fields. Vegetation seems indispensable for web attachment.

*Lepthyphantes tenuis* builds a web of average size 75.10 ± 4.28 cm<sup>2</sup> ( $n=23$ , range 60.02–95.03 cm<sup>2</sup>). It is significantly larger than that of *B. gracilis* (t-test:  $t=10.49$ ,  $p<0.001$ ). Thornhill (1983) records a mean of 61.7 cm<sup>2</sup> ( $n=12$ ). The species seems to be less flexible as far as web size and web placement is concerned. It usually constructs its web at about 10 cm above soil level, easily bridging the distance between two maize stems (c.10 cm). Like *B. gracilis*, it never constructs a web above bare soil without anchoring it to the vegetation.

*Linyphia clathrata* builds a much larger web (520 and 682 cm<sup>2</sup>,  $n=2$ ) situated high in the vegetation (54 and 75 cm above soil level,  $n=2$ ).

#### The Erigone strategy

*Erigone* species (*E. atra*, *E. dentipalpis*) build an untidy, small web with a mean size for adult spiders of 5.40 ± 0.45 cm<sup>2</sup> ( $n=42$ , range 2.2–7.8 cm<sup>2</sup>). The web size does not differ significantly between *E. atra* (5.33 ± 0.54 cm<sup>2</sup>,  $n=30$ ) and *E. dentipalpis* (5.48 ± 0.44 cm<sup>2</sup>,  $n=12$ ) (t-test:  $t=0.29$ ,  $p>0.05$ ). *Erigone* webs are, however, significantly smaller than those of *B. gracilis* (t-test:  $t=16.46$ ,  $p<0.001$ ) and *L. tenuis* (t-test:  $t=32.40$ ,  $p<0.001$ ). Sunderland *et al.* (1986b) observed a median

Species	<i>B. gracilis</i>		<i>E. atra</i>		<i>L. tenuis</i>		<i>L. clathrata</i>		Total	
	Items	%	Items	%	Items	%	Items	%	Items	%
Aphididae	48/31 (48/31)	33.8/28.7 (36.6/31.0)	16/8 (14/7)	39.0/26.7 (43.8/29.2)	104/40 (85/30)	82.5/66.7 (83.3/66.7)	44/6 (38/2)	65.7/23.1 (70.4/13.3)	212/85 (185/70)	56.3/37.9 (58.1/38.1)
Isotomidae	83/72 (77/66)	58.5/66.7 (58.8/66.0)	16/16 (16/16)	39.0/53.3 (50.0/66.7)	13/13 (13/13)	10.3/21.7 (12.7/28.9)			112/101 (106/95)	29.7/45.2 (33.3/51.7)
Sminthuridae	3/0 (3/0)	2.1/0.0 (2.3/0.0)	2/1 (2/1)	4.9/3.3 (6.3/4.2)			1/1 (0/0)	1.5/3.8 (0.0/0.0)	6/2 (5/1)	1.5/1.0 (1.6/0.5)
<i>Lepidocirtus</i> sp.							1/0 (1/0)	1.5/0.0 (1.9/0.0)	1/0 (1/0)	0.3/0.0 (0.3/0.0)
Sciaridae	2/2 (0/0)	1.4/1.9 (0.0/0.0)	4/3 (0/0)	9.8/10.0 (0.0/0.0)	4/4 (2/2)	3.2/6.7 (2.0/4.4)	4/4 (0/0)	6.0/15.4 (0.0/0.0)	14/13 (2/2)	3.7/5.9 (0.6/1.1)
Chloropidae			2/1 (0/0)	4.9/3.3 (0.0/0.0)	2/2 (0/0)	1.6/3.3 (0.0/0.0)	2/2 (2/2)	3.0/7.7 (3.7/13.3)	6/5 (2/2)	1.6/2.2 (0.6/1.1)
Dolichopodidae							1/1 (1/1)	1.5/3.8 (1.9/6.7)	1/1 (1/1)	0.3/0.4 (0.3/0.5)
Agromyzidae							1/1 (0/0)	1.5/3.8 (0.0/0.0)	1/1 (0/0)	0.3/0.4 (0.0/0.0)
Cecidomyiidae							2/1 (1/0)	3.0/3.8 (1.9/0.0)	2/1 (1/0)	0.5/0.4 (0.3/0.0)
Chironomidae					1/1 (0/0)	0.8/1.6 (0.0/0.0)			1/1 (0/0)	0.3/0.4 (0.0/0.0)
Delphacidae+ Cicadellidae	6/3 (3/3)	4.2/2.8 (2.3/3.0)	1/1 (0/0)	2.4/3.3 (0.0/0.0)			8/8 (8/8)	11.9/30.8 (14.8/53.3)	15/12 (11/11)	4.0/5.4 (3.4/6.0)
Hemiptera							1/1 (1/1)	1.5/3.8 (1.9/6.7)	1/1 (1/1)	0.3/0.4 (0.3/0.5)
Staphylinidae							1/1 (1/1)	1.5/3.8 (1.9/6.7)	1/1 (1/1)	0.3/0.4 (0.3/0.5)
Acari					2/0 (2/0)	1.6/0.0 (2.0/0.0)			2/0 (2/0)	0.5/0.0 (0.6/0.0)
Thysanoptera							1/0 (1/0)	1.5/0.0 (1.9/0.0)	1/0 (1/0)	0.3/0.0 (0.3/0.0)
<b>Total</b>	142/108 (131/100)	100/100 (100/100)	41/30 (32/24)	100/100 (100/100)	126/60 (102/45)	100/100 (100/100)	67/26 (54/15)	100/100 (100/100)	376/224 (319/184)	100/100 (100/100)

Table 1: Total number of prey items (total number/number consumed) collected during 1986/1987 for *Bathypantes gracilis*, *Erigone atra*, *Lepthyphantes tenuis* and *Linyphia clathrata* in all sampled sites (first line) and in maize fields separately (between brackets). The percentage of each prey group in the total diet of each species is also shown.

web size of 7.6 cm<sup>2</sup> for *E. atra* and 4.1 cm<sup>2</sup> for *E. dentipalpis* in cereal fields. Taking the amount of variation into account, this is also in agreement with the size of 4 cm<sup>2</sup> mentioned for Erigoninae in general by Nyffeler & Benz (1980).

*Erigone* webs are almost exclusively built above bare soil. Exceptionally, *E. atra* was found in a small web at the base of leaves of maize plants. Adult males were almost always found wandering around; only one out of 42 was found in a tiny web. This is in agreement with Thornhill (1983) who found only one male out of 11 in a small web.

Field and laboratory observations made it obvious that the small web of *Erigone* (both *atra* and *dentipalpis*) is used in different ways and that it is not vital for prey capture or feeding. Besides killing prey entangled in the threads in the same way as typical web-building spiders, the spider can use the web as a base from which prey is actively attacked and killed. However, *Erigone* individuals were seen with prey between the chelicerae without traces of a web in the vicinity, indicating that they can also kill without the aid of a web.

Our results thus indicate that the prey capture strategy of *Erigone* is diverse. *Erigone* species appear to use several methods of capturing suitable prey. This versatile prey capture strategy contributes to the survival and expansion of these spider species in all kinds of disturbed areas.

#### Non-web-building species in the adult stage

Adult females of *Oedothorax fuscus* and *O. apicatus* were never found in a web, either during laboratory rearing or during field observations. This is in agreement with the results of Thornhill (1983) who observed especially *O. apicatus* in sugar-beet fields. In the laboratory, adult males produced some irregular threads which are probably useless for capturing prey. From laboratory rearing experiments we know that juvenile *Oedothorax* build a small web in which they capture prey and which is apparently important for moulting. In the adult stage, these species capture their prey actively by using a sit-and-wait strategy.

#### Prey spectra of the most abundant species

In total 430 prey items were collected in field conditions during about three years (1986–1988). For *Bathypantes gracilis*, *Erigone atra*, *Lepthyphantes tenuis* and *Linyphia clathrata*, more than 40 observations on prey items were made and the results for these species are summarised in Table 1. Table 2 shows the prey spectrum of all other species of linyphiids. Finally, Table 3 summarises the results of the prey analyses for all Araneae.

It is important to differentiate between a prey item captured in the web of a spider but not consumed and a prey item which is consumed by the predator. When studying the impact of spiders on prey populations in agroecosystems, both groups of prey items should be considered together. However, when considering the prey spectra of the predator species, only the consumed part of the captured prey should be taken into consideration.

It is no coincidence that most data were obtained for web-building species. Indeed, the chance of finding a non-web-building spider consuming a prey item in the field is much lower than for web-builders. Moreover, the chance of finding prey differs between the different web-building species partly because of the differences in web size (see above). We found a mean number of prey items per web with prey (excluding webs without prey remains) of 7.44 for *L. clathrata* but only 2.80 for *L. tenuis*, 1.62 for *B. gracilis* and 1.11 for *E. atra*. Because *E. atra* is less dependent on a web for capturing prey we would expect a value close to one prey item per web with prey. This is confirmed by the similar value found for *E. dentipalpis*, despite a much lower number of observations.

The prey spectra of the different species studied here (Tables 1, 2) appear to be similar. Compared with the high diversity of invertebrates occurring in the fields (potential prey), the number of groups found as prey of linyphiid spiders is restricted. For all spider species (except *L. clathrata*), Aphididae and Collembola are the most frequent prey (Table 3) followed by Diptera, Hemiptera (especially nymphs) and Homoptera (adults or nymphs, mostly belonging to the family Delphacidae,

Species	<i>E. dentip.</i>	<i>P. vagans</i>	<i>O. fuscus</i>	<i>O. apicatus</i>	<i>O. spp.</i>	<i>M. rurestris</i>	<i>D. concolor</i>	<i>M. inerrans</i>	Total
Aphididae	1/1 (0/0)	10/3 (10/3)	2/2 (2/2)	1/1 (1/1)	7/2 (7/2)	1/1 (1/1)	1/1 (0/0)	1/1 (1/1)	24/12 (22/10)
Isotomidae		1/1 (1/1)		5/5 (5/5)			1/1 (0/0)	8/7 (8/7)	15/14 (14/13)
Sciaridae				2/2 (2/2)					2/2 (2/2)
Sminthuridae	1/1 (0/0)	1/0 (1/0)	1/1 (1/1)			1/1 (1/1)		1/1 (1/1)	5/4 (4/3)
Acari					1/1 (1/1)		1/1 (0/0)		2/2 (1/1)
Sphaeroceridae				1/1 (1/1)			1/1 (1/1)		2/2 (2/2)
Drosophilidae		1/0 (1/0)							1/0 (1/0)

Table 2: Total number of prey items (total number/number consumed) collected during 1986/1987 for *Erigone dentipalpis*, *Prinerigone vagans*, *Oedothorax fuscus*, *Oedothorax apicatus*, *Oedothorax spp.* (juveniles), *Meioneta rurestris*, *Diplostyla concolor* and *Mülleriana inerrans* in all sampled sites (first line) and in maize fields separately (between brackets).

rarely Cicadellidae). It should be noted that many webs contained exuviae of Aphididae which had fallen off the vegetation. These were of course not taken into consideration.

Adult Coleoptera (Staphylinidae) were found once as prey of *L. clathrata* (the largest species). During field experiments with *L. tenuis* and *B. gracilis* it was shown that small, adult Coleoptera (Carabidae or Staphylinidae) are systematically refused by the spiders, often after a quick check. These small spiders are probably unable to pierce through the hard cuticle of the beetles. Moreover, it was observed that the Coleoptera have a high chance of escape. Nentwig (1980) provided data on escape possibilities of different prey groups.

Within the Collembola, *Isotomurus palustris* was taken most frequently, together with, to a lesser extent, several species of Sminthuridae. *Isotoma viridis* was only sporadically found as prey.

There is a fundamental difference between the two most abundant prey items (Aphididae and *Isotomurus palustris*) when one considers the ratio between captured and consumed individuals. Aphididae comprise 55.1% of the total number of prey items captured, Isotomidae only 29.8%. However, this proportion is reversed when only consumed prey is considered: 37% Aphididae, 43.8% Isotomidae (Table 3). This shows that a large proportion of the captured Aphididae are not consumed by the spiders whereas almost 100% of the Isotomidae captured in a spider's web are also consumed. This discrepancy is (at least partly) due to behavioural differences between these insects when captured in a web. Field observations show that Aphididae remain almost motionless, whereas Isotomidae continuously struggle while trying to escape the spider's web. The latter are thus more easily detected by the spider. However, owing to this behaviour, Isotomidae have a considerably better chance of escape as compared with Aphididae, which

explains why unconsumed Isotomidae are rarely found in webs.

Besides these ethological differences between Isotomidae and Aphididae there may also be an element of active choice by the spiders resulting in an under-consumption of aphids. It is known that the aphid species occurring in arable land feed on plant juices containing high amounts of sugar (J. Prinsen, pers. comm.). In order to accumulate sufficient amounts of other necessary nutrients (e.g. amino acids), large amounts of sugar have to be digested, of which a large part is excreted after being transformed to some extent in the gut (J. Prinsen, pers. comm.; Taylor, 1981). Many insects and other organisms feed on this honeydew. Although detailed measurements and further research are necessary here, it is hypothesised that the relatively high concentration of sugars in aphids may contribute to the fact that spiders find aphids distasteful.

Collembola are also the most important prey item in cereal fields (Sunderland *et al.*, 1986b), and in some cases collembolan population density can regulate the density of certain spider species depending on them (*Erigone arctica*, Van Wingerden, 1978). In other habitats, aphids may be more important as linyphiid prey (38–63%, Nentwig, 1983). The composition of the prey spectrum of erigonines living on the soil surface in cereal fields in Switzerland is somewhat different (41% aphids, 37% Collembola, Nyffeler, 1982), which is similar to our results. For other spider families, Aphididae are also often important prey (20% for Lycosidae (Nyffeler, 1982); 8.2% for Araneidae (Nyffeler & Benz, 1989); 43% for *Theridion impressum* (Nyffeler & Benz, 1979, 1982).

#### Prey selection in field and laboratory conditions

Nentwig (1982) showed that webs inevitably select for certain prey groups as compared with the potential prey

Prey item	All observations				Observations in maize fields			
	Items captured	Items consumed	Captured %	Consumed %	Items captured	Items consumed	Captured %	Consumed %
Aphididae	237	98	55.1	37.0	208	81	56.7	37.0
Isotomidae	128	116	29.8	43.8	121	109	33.0	49.8
Sciaridae	16	15	3.7	5.7	4	4	1.1	1.8
Delph. + Cicad.	16	13	3.7	4.9	11	11	3.0	5.1
Sminthuridae	11	6	2.6	2.3	9	4	2.5	1.8
Chloropidae	6	5	1.4	1.9	2	2	0.5	0.9
Acari	4	4	0.9	1.5	3 *	3	0.8	1.4
Sphaeroceridae	2	2	0.5	0.8	2	2	0.5	0.9
Chironomidae	1	1	0.2	0.4	—	—	—	—
Dolichopodidae	1	1	0.2	0.4	1	1	0.3	0.5
Agromyzidae	1	1	0.2	0.4	—	—	—	—
Drosophilidae	1	—	0.2	—	1	—	0.3	—
<i>Lepidocirtus</i> sp.	1	—	0.2	—	1	—	0.3	—
Cecidomyiidae	2	1	0.5	0.4	1	—	0.3	—
Hemiptera	1	1	0.2	0.4	1	1	0.3	0.5
Staphylinidae	1	1	0.2	0.4	1	1	0.3	0.5
Thysanoptera	1	—	0.2	—	1	—	0.3	—
<b>Total</b>	<b>430</b>	<b>265</b>	<b>100.0</b>	<b>100.0</b>	<b>367</b>	<b>219</b>	<b>100.0</b>	<b>100.0</b>
<b>Collembola total</b>	<b>140</b>	<b>122</b>	<b>32.6</b>	<b>46.1</b>	<b>131</b>	<b>113</b>	<b>35.8</b>	<b>51.6</b>

Table 3: Summary of all prey items collected for all spider species in all sites sampled and in maize fields separately. In each case the numbers of individuals captured and consumed are indicated in absolute numbers and in percentages.

Prey item	Ivlev	% Captured	% Density	Mean density
Acari	-0.98	0.8	81.72	4844.00
<i>Lepidocirtus</i> sp.	-0.89	0.3	4.96	294.27
<i>Sminthurus</i> sp.	-0.31	0.3	0.57	33.96
Staphylinidae	-0.08	0.3	0.35	20.97
<i>Isotoma viridis</i>	-0.03	2.5	2.67	158.43
<i>Sphaeridia pumilis</i>	0.12	2.2	1.72	101.87
<i>Isotomurus palustris</i>	0.83	30.5	2.67	158.47
Cecidomyiidae	0.96	0.3	0.01	0.36
Aphididae	0.99	56.7	0.28	16.36
Delph. + Cicad.	0.99	3.0	0.01	0.36
Chloropidae	1.00	0.5	0.00	0.00
Dolichopodidae	1.00	0.3	0.00	0.00
Drosophilidae	1.00	0.3	0.00	0.00
Hemiptera	1.00	0.3	0.00	0.00
Sciaridae	1.00	1.1	0.00	0.00
Sphaeroceridae	1.00	0.5	0.00	0.00
Thysanoptera	1.00	0.3	0.00	0.00
Sminthuridae total	0.04	2.5	2.29	135.83
Isotomidae total	0.68	33.0	6.30	373.50
Collembola total	0.45	35.8	13.56	803.60

Table 4: Mean density (individuals/m<sup>2</sup>) from May to September, percentage of the potential prey (% Density), percentage in the actual prey (% Captured) and Ivlev-index (Ivlev) of all prey groups in maize fields. In order from low to high Ivlev-index. Further explanation in text.

spectrum present in the habitat. Prey capture strategy and spider size clearly influence prey size (Enders, 1975). Moreover, escape chances differ between prey groups and this influences the prey caught (Nentwig, 1980). It is also evident that relative abundances and differences of availability between prey groups for the spider (living on vegetation, at ground-level, in the soil, etc.) influence the observed prey spectra. Finally, the spider itself seems to prefer certain prey groups above others. Here prey selection by spiders is first assessed in field conditions; later some aspects of prey selection are tested in laboratory experiments.

#### Potential versus actual prey

Potential prey is considered here in its broadest sense, i.e. all invertebrate groups detected by means of quadrat sampling (absolute abundances in number of individuals per m<sup>2</sup>), allowing comparisons with the actual prey spectra by using the Ivlev index (Iv, see Material and methods). The results are summarised in Table 4.

Aphididae, *Isotomurus palustris*, Homoptera (usually nymphs) and Cecidomyiidae are captured more by spiders than would be predicted on the basis of their mean density (high positive Iv). This can be explained by the fact that they are not only highly available but also actively selected for by the spiders (see laboratory experiments described below).

The numbers of *Isotoma viridis* and Sminthuridae captured by spiders are comparable to those predicted by their mean densities in maize fields when no selection occurs (Iv around zero).

In contrast to this, Table 4 shows that some other prey groups, present abundantly in the habitat (high to very high mean abundances), are rarely captured by the

spider species under study (Acari, *Lepidocirtus* sp.). Although these occur in the close neighbourhood of the spiders, they are rarely captured because of their size, morphology, behaviour or chitinised exoskeleton (e.g. also Coleoptera). Some other groups are relatively unavailable to the spiders owing to a cryptic way of life (e.g. many soil-living Acari, Lumbricidae, etc.).

These results demonstrate that spiders select certain prey groups. This selection can be influenced by many different, interacting factors partly related to the characteristics of the prey, and partly related to the characteristics of the predator. An important conclusion is that Aphididae are positively selected whereas Aphididae-specific predators, such as larval Syrphidae, Coccinellidae, larval Chrysopidae, were never found as prey of the spider species investigated. This is important with regard to the study of the influence of polyphagous predators, such as spiders, on Aphididae pests.

#### Prey selection according to prey species

Field data suggest that *Isotomurus palustris* is highly preferred over *Lepidocirtus* sp. This finding is confirmed by a laboratory experiment conducted with 30 females of *Oedothorax apicatus*. One hundred and seventeen out of 150 individuals (78.0 ± 15.5%) of *Isotomurus palustris* were consumed by the spiders. However, only 42 out of 150 individuals (28.0 ± 16.8%) of *Lepidocirtus* were captured. The 95% confidence limits, given in Fig. 1, show that this difference is statistically significant.

The results of the laboratory experiments, performed to test the preferences for other prey groups (see Material and methods), are summarised in Table 5 and the following conclusions can be drawn:

(1) Field observations showing a high consumption of Isotomidae are confirmed. This prey group is easily captured ( $T=24.27 \pm 5.89$  min, mean ± standard error).

(2) In contrast to field observations, a higher proportion of Delphacidae nymphs was taken and consumed in

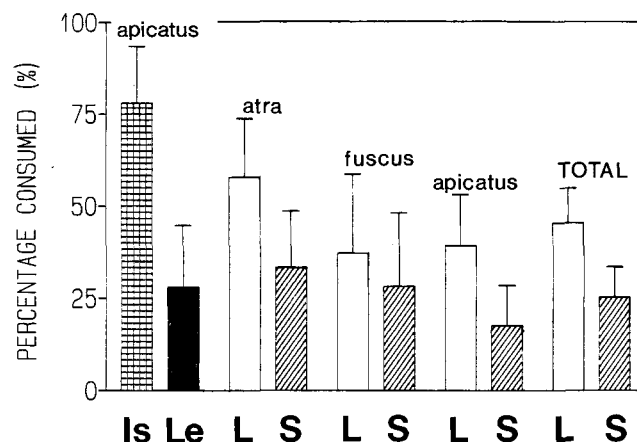


Fig. 1: Percentage of Collembola consumed (with 95% confidence limits) as observed in laboratory feeding experiments. Fractions calculated according to Wonnacott & Wonnacott (1972). Prey selection for species: *Isotomurus palustris* (Is, crossed bar) against *Lepidocirtus* sp. (Le, filled bar) for *Oedothorax apicatus*. Prey selection for size: large Collembola (L, open bars) against small Collembola (S, striped bars) for *Erigone atra*, *Oedothorax fuscus*, *O. apicatus* and the total respectively.

the laboratory experiments. This is probably due to the reduced chance of escape while being trapped in the petri-dish (reducing their chance of jumping away). The same applies to adult Diptera.

(3) No Acari were captured or consumed, in agreement with the field observations.

(4) No significant difference was found between the mean total length of the prey items offered and those consumed.

#### Prey selection according to prey size

The laboratory experiments with different size classes of the same prey item (cf. Material and methods) were performed with females of *Erigone atra* ( $n=39$ ), *Oedothorax fuscus* ( $n=22$ ) and *O. apicatus* ( $n=50$ ). The results are summarised in Table 6, and Fig. 1 shows the proportion of Collembola consumed according to size for each species.

*Erigone atra* females consumed 45.6% of all *Isotomurus palustris* Collembola offered, *O. fuscus* 32.7% and *O. apicatus* 28.4%. These proportions are relatively low owing to saturation effects (10 Collembola in three days).

All three species tested showed a tendency to prefer large Collembola over small ones (Table 6) but this difference was not significant when using 95% confidence limits calculated on the proportion as a statistical test (*E. atra*:  $P(L)=57.9 \pm 15.9\%$ ,  $P(S)=33.3 \pm 15.3\%$ ; *O. fuscus*:  $P(L)=37.2 \pm 21.4\%$ ,  $P(S)=28.2 \pm 19.9\%$ ; *O. apicatus*:  $P(L)=39.2 \pm 13.9\%$ ,  $P(S)=17.6 \pm 10.8\%$ ). However, when considering the total proportions consumed, a significant preference for the larger individuals was observed ( $P(L)=45.4 \pm 9.4\%$ ,  $P(S)=25.2 \pm 8.2\%$ ).

It is concluded here that, within the size ranges tested, only minor preferences for the larger collembolans are found. The smaller individuals are still regularly taken.

	# O	# C	SO (mm)	SC (mm)	T (min)
<i>Isotoma viridis</i>	36	15	1.12 ± 0.08	1.11 ± 0.06	24.3 ± 5.9
Aphididae	28	1	0.95 ± 0.04	0.84 ± 0.00	12.0 ± 0.0
Delphacidae nymphs	14	9	1.18 ± 0.03	1.19 ± 0.03	56.1 ± 14.1
<i>Isotomurus palustris</i>	7	3	0.96 ± 0.05	0.91 ± 0.03	58.3 ± 5.4
<i>Sminthurus viridis</i>	6	1	0.57 ± 0.06	0.90 ± 0.00	7.0 ± 0.0
Chloropidae	5	2	1.21 ± 0.08	1.13 ± 0.01	50.5 ± 8.3
Psychodidae	4	2	0.63 ± 0.04	0.55 ± 0.02	10.5 ± 4.5
Cecidomyiidae	1	1	0.50 ± 0.00	0.50 ± 0.00	2.0 ± 0.0
Sciaridae	1	1	1.10 ± 0.00	1.10 ± 0.00	78.0 ± 0.0
Hymenoptera	4	0	0.79 ± 0.06	—	—
Acari	2	0	0.55 ± 0.07	—	—
Araneae juveniles	1	0	0.44 ± 0.00	—	—
Bibionidae (♂)	1	0	3.10 ± 0.00	—	—
Formicidae	1	0	1.70 ± 0.00	—	—

Table 5: Results of laboratory experiments concerning selection of prey species. #O=number of individuals offered, #C=number of individuals taken by the spider, SO=average total length (mm) of prey items offered, SC=average total length (mm) of prey items taken, T=average time (min) between presenting the prey to the spider and capture. All averages include standard errors ( $s/\sqrt{n}$ ). Further explanation in text.

	<i>E. atra</i>	<i>O. fuscus</i>	<i>O. apicatus</i>	Total
Number of observations (n)	39	22	50	111
Offered large (L)	195	110	250	555
Offered small (S)	195	110	250	555
Total offered (L+S)	390	220	500	1110
Consumed large (L)	113	41	98	252
Consumed small (S)	65	31	44	140
Total consumed (L+S)	178	72	142	392
% consumed large (L)	57.9	37.2	39.2	45.4
% consumed small (S)	33.3	28.2	17.6	25.2
% total consumed (L+S)	45.6	32.7	28.4	35.3
Ratio L/S	1.74	1.32	2.23	1.80

Table 6: Results of laboratory experiments concerning selection for prey size by *Erigone atra*, *Oedothorax fuscus* and *O. apicatus*. (L)=large Collembola, (S)=small Collembola. Further explanation in text.

#### Conclusion

Many studies have tried to resolve the question of whether spiders in certain situations are able to limit numbers of crop pest species efficiently (see reviews in Kirchner (1964), Nyffeler (1982), Nyffeler & Benz (1987)). However, no consensus has been reached. Agnew & Smith (1989) listed a number of characteristics of spiders which suggest that they are well suited to control numbers of certain harmful insects. On the contrary, other authors conclude that spiders are not efficient enough in situations where pest species reach economically unacceptable levels, because they are too generalistic (Bristowe, 1941; Kajak, 1965; Riechert, 1974; Vite, 1953). However, many of the conclusions are still speculative and lack detailed supporting data.

Quantitative data on spider predation are very scarce (Kiritani *et al.*, 1972; Nyffeler, 1982). They can be calculated if the time taken to eat a prey item and the proportion of spiders feeding at any time are known (Edgar, 1970). However, this is almost impossible for nocturnal species (e.g. several erigonines) because, as stated above, observing predation of spiders at night was not feasible. The same constraint was encountered by Nyffeler (1982) and Sunderland *et al.* (1986b).

The results presented here show that the spider species occurring abundantly in arable land in western Europe are not as generalistic as generally thought and depend on the availability of relatively few prey groups. A clear preference for certain abundant prey items has been observed, this preference being influenced by many different factors (e.g. availability on a spatial and temporal basis, relative density).

In the crop fields studied here (especially maize fields), we believe that, considering the high proportion of aphids captured (although not so often consumed) and the extremely rapid colonisation of the fields by the spiders, the initial population growth of this pest is certainly retarded early in spring and summer (predation on winged fundatrix females). This suggests that temporal effects add to the complexity of the problem and should be taken into consideration when trying to evaluate the impact of spiders on pest populations in different agro-ecosystems.



Finally, it is shown that some species exhibit a diverse prey capture strategy which may partly explain their efficient survival and expansion in highly disturbed areas. This kind of new information is very important for our understanding of those spider species which might play an important role in biological control of certain pest species. It is suggested that further research should also take these kinds of behavioural aspects into account.

## References

- AGNEW, C. W. & SMITH, J. W. 1989: Ecology of spiders (Araneae) in a peanut agroecosystem. *Envir. Ent.* **18**(1): 30–42.
- ALDERWEIRELDT, M. 1989: An ecological analysis of the spider fauna (Araneae) occurring in maize fields, Italian ryegrass fields and their edge zones, by means of different multivariate techniques. *Agric. Ecosyst. Environ.* **27**: 293–306.
- ALDERWEIRELDT, M. 1993: A five year survey of the invertebrate fauna of crop fields and their edges. Part 1. Study area, crop history and methodology. *Bull. Anlms Soc. r. ent. Belg.* **129**: 41–52.
- ALDERWEIRELDT, M. & LISSENS, A. 1988: Laboratorium-waarnemingen van de ontwikkeling en reproductie bij *Oedothorax apicatus* (Blackwall, 1850) en *Oedothorax retusus* (Westring, 1851). *Nieuwsbr. belg. arachnol. Ver.* **9**: 19–26.
- BAILEY, N. T. J. 1981: *Statistical methods in biology* (2nd ed.). 1–216. Hodder & Stoughton, London.
- BRIGNOLI, P. M. 1983: Ragni quali predatori di insetti: il loro potenziale ruolo negli agroecosistemi (Araneae). *Atti Congresso naz. ital. Ent.* **13**: 591–597.
- BRISTOWE, W. S. 1941: *The comity of spiders* **2**: 229–560. Ray Society, London.
- BRISTOWE, W. S. 1958: *The world of spiders*. 1–304. Collins, London.
- CASTILLO, J. A. & EBERHARD, W. G. 1983: Use of artificial webs to determine prey available to orb-weaving spiders. *Ecology* **64**(6): 1655–1658.
- CHANT, D. A. 1956: Predacious spiders in orchards in south-eastern England. *J. hort. Sci.* **31**: 35–46.
- CHIVERTON, P. A. 1986: Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Homoptera: Aphididae) in spring barley. *Ann. appl. Biol.* **190**: 49–60.
- CROOK, N. E. & SUNDERLAND, K. D. 1984: Detection of aphid remains in predatory insects and spiders by ELISA. *Ann. appl. Biol.* **105**: 1–10.
- DE KEER, R. & MAELFAIT, J.-P. 1987: Laboratory observations on the development and reproduction of *Oedothorax fuscus* (Blackwall, 1834) under different conditions and food supply. *Revue Ecol. Biol. Sol* **24**(1): 63–73.
- DE KEER, R. & MAELFAIT, J.-P. 1988: Laboratory observations on the development and reproduction of *Erigone atra* (Araneae, Linyphiidae). *Bull. Br. arachnol. Soc.* **7**(8): 237–242.
- EDGAR, W. D. 1970: Prey and feeding behaviour of adult females of the wolf spider *Pardosa amentata* (Clerck). *Neth. J. Zool.* **20**: 487–491.
- EDWARDS, C. A., SUNDERLAND, K. D. & GEORGE, K. S. 1979: Studies on polyphagous predators of cereal aphids. *J. appl. Ecol.* **16**: 811–823.
- ENDERS, F. A. 1975: The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae and Salticidae). *Am. Nat.* **109**: 737–763.
- GREENSTONE, M. H. 1977: A passive haemagglutination inhibition assay for the identification of stomach contents of invertebrate predators. *J. appl. Ecol.* **14**: 457–464.
- GREENSTONE, M. H. 1984: Determinants of web spider species diversity: vegetational structural diversity vs. prey availability. *Oecologia* **62**: 299–304.
- HEIMER, S. & NENTWIG, W. 1982: Thoughts on the phylogeny of the Araneoidea Latreille, 1806 (Arachnida, Araneae). *Z. zool. Syst. Evol. Forsch.* **20**(4): 284–295.
- IVLEV, V. S. 1955: *Ekspiermental'naja ekologija pitanija ryb* [in Russian]. 1–252. Moscow.
- IVLEV, V. S. 1961: *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven.
- JOCQUÉ, R. 1984: Notes on the African Linyphiidae (Araneae). III. The genus *Tybaertiella*, with the description of a new species of *Pelecopsis*. *Bull. Br. arachnol. Soc.* **6**(3): 217–228.
- FORD, M. J. 1977: Energy costs of the predation strategy of the webspinning spider *Lepthyphantes zimmermanni* Bertkau (Linyphiidae). *Oecologia* **28**: 341–349.
- KAJAK, A. 1965: An analysis of food relations between the spiders *Araneus cornutus* and *A. quadratus* and their prey in meadows. *Ekol. pol. (A)* **13**: 717–768.
- KIRCHNER, W. 1964: Bisher bekanntes über die forstliche Bedeutung der Spinnen. Versuch einer Literaturanalyse. *Waldhygiene* **5**(6/7): 161–198.
- KIRITANI, K. & DEMPSTER, J. P. 1973: Different approaches to the quantitative evaluation of natural enemies. *J. appl. Ecol.* **10**: 323–330.
- KIRITANI, K., KAWAHARA, S., SASABA, T. & NAKASUJI, F. 1972: Quantitative evaluation of predation by spiders on the green rice leafhopper *Nephotettix cincticeps*, by a sight-count method. *Researches Popul. Ecol. Kyoto Univ.* **13**: 187–200.
- LÖVEI, G. L. 1986: *The use of biochemical methods in the study of carabid feeding: the potential of isoenzyme analysis and ELISA*. Meeting of the European Carabidologists at Stara Brda Pilska, Poland, September 13–15, 1982. Warsaw Agricultural University Press, Warsaw.
- NENTWIG, W. 1980: The selective prey of linyphiid-like spiders and of their space webs. *Oecologia* **45**: 236–243.
- NENTWIG, W. 1982: Why do only certain insects escape from a spider's web? *Oecologia* **53**: 412–417.
- NENTWIG, W. 1983: The prey of web-building spiders compared with feeding experiments (Araneae: Araneidae, Linyphiidae, Pholcidae, Agelenidae). *Oecologia* **56**: 132–139.
- NENTWIG, W. 1985: Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia* **66**: 580–594.
- NENTWIG, W. & WISSEL, C. 1986: A comparison of prey lengths among spiders. *Oecologia* **68**: 595–600.
- NYFFELER, M. 1982: *Field studies on the ecological role of spiders as insect predators in agroecosystems (abandoned grassland, meadows and cereal fields)*. 1–174. Doctoral thesis, Swiss Federal Institute of Technology, Zürich.
- NYFFELER, M. & BENZ, G. 1979: Studies on the ecological importance of spider populations of the field layer of cereal and rape fields near Zürich, Switzerland. *Z. angew. Ent.* **87**: 348–376.
- NYFFELER, M. & BENZ, G. 1980: The role of spiders as insect predators in cereal fields near Zürich (Switzerland). *Proc. 8th int. arachnol. Congr.* (Vienna): 127–131.
- NYFFELER, M. & BENZ, G. 1982: Spinnen als Prädatoren von landwirtschaftlich schädlichen Blattläusen. *Anz. Schädlingssk. Pfl.-Umweltschutz* **55**: 120–121.
- NYFFELER, M. & BENZ, G. 1987: Spiders in natural pest control: a review. *J. appl. Ent.* **103**: 321–339.
- NYFFELER, M. & BENZ, G. 1989: Foraging ecology and predatory importance of a guild of orb-weaving spiders in a grassland habitat. *J. appl. Ent.* **107**: 166–184.
- RIECHERT, S. E. 1974: Thoughts on the ecological significance of spiders. *Bioscience* **24**(6): 352–356.
- RIECHERT, S. E. & LOCKLEY, T. 1984: Spiders as biological control agents. *A. Rev. Ent.* **29**: 299–320.
- RYPSTRA, A. L. 1982: Building a better insect trap: an experimental investigation of prey capture in a variety of spider webs. *Oecologia* **52**: 31–36.
- RYPSTRA, A. L. 1990: Prey capture and feeding efficiency of social and solitary spiders: a comparison. *Acta zool. fenn.* **190**: 339–343.
- SOKAL, R. R. & ROHLF, F. J. 1981: *Biometry. The principles and practice of statistics in biological research*. 1–859. Freeman, San Francisco.



- SOPP, P. & WRATTEN, D. 1986: Rates of consumption of cereal aphids by some polyphagous predators in the laboratory. *Entomologia exp.appl.* **41**: 69–73.
- SUNDERLAND, K. D. 1988: Quantitative methods for detecting invertebrate predation occurring in the field. *Ann.appl.Biol.* **112**: 201–224.
- SUNDERLAND, K. D. & CHAMBERS, R. J. 1982: Invertebrate polyphagous predators as pest control agents: some criteria and methods. *Proceedings of the European Community Experts' Meeting*, Portici, Nov. 1982: 100–108.
- SUNDERLAND, K. D., CROOK, N. E., STACEY, D. L. & FULLER, B. J. 1987: A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *J.appl.Ecol.* **24**: 907–933.
- SUNDERLAND, K. D., FRASER, A. M. & DIXON, A. F. G. 1986a: Field and laboratory studies on money spiders (Linyphiidae) as predators of cereal aphids. *J.appl.Ecol.* **23**: 433–447.
- SUNDERLAND, K. D., FRASER, A. M. & DIXON, A. F. G. 1986b: Distribution of linyphiid spiders in relation to capture of prey in cereal fields. *Pedobiologia* **29**: 367–375.
- SUNDERLAND, K. D., STACEY, D. L. & EDWARDS, C. A. 1980: The role of polyphagous predators in limiting the increase of cereal aphids in winter wheat. *West Palaearctic Regional Section Bulletin* **III**(4): 85–91.
- TAYLOR, L. R. (ed.) 1981: *Aphid forecasting and pathogens*. 1–45. Rothamsted Experimental Station, Euraphid 1980, England.
- THORNHILL, W. A. 1983: The distribution and probable importance of linyphiid spiders living on the soil surface of sugar-beet fields. *Bull.Br.arachnol.Soc.* **6**(3): 127–136.
- VAN WINGERDEN, W. K. R. E. 1978: Population dynamics of *Erigone arctica* (White) (Araneae: Linyphiidea). II. *Symp.zool. Soc.Lond.* **42**: 195–202.
- VICKERMAN, G. P. & SUNDERLAND, K. D. 1975: Arthropods in cereal crops: nocturnal activity, vertical distribution and aphid predation. *J.appl.Ecol.* **12**: 755–766.
- VITE, J. P. 1953: Untersuchungen über die ökologischen und forstliche Bedeutung der Spinnen im Walde. *Z.angew.Ent.* **34**: 313–334.
- WHEELER, A. G. 1973: Studies on the arthropod fauna of alfalfa. V. Spiders (Araneida). *Can.Ent.* **105**: 425–432.
- WONNACOTT, T. H. & WONNACOTT, R. J. 1972: *Introductory Statistics*. 1–510. John Wiley, New York.