

Habitat preferences of *Enoplognatha latimana* Hippa et Oksala, 1982, and *Enoplognatha ovata* (Clerck, 1757) (Araneae: Theridiidae) in agricultural landscapes in Southern Bavaria (Germany)

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ABSTRACT

The distribution of *Enoplognatha ovata* and *Enoplognatha latimana* was studied on field margins, fallow land, abandoned grassland and cultivated grassland in agricultural landscapes of Southern Germany between 1993 and 1995. *E. ovata* was present on 54 and *E. latimana* on 50 of 97 investigated field margins. In fallow land, *E. latimana* occurred in a higher abundance than *E. ovata*. On abandoned grassland only *E. ovata* was found. On cultivated grassland, one specimen of *E. ovata* was recorded during the entire investigation period. Both species were significantly more abundant in study areas with a high margin density (between 230 and 300 m/ha) and on wider margins (more than 3 m in width). The population size of both species was reduced if man-made mechanical treatments affected the field margins. On south and south-western inclined margins, *E. latimana* was recorded with a high abundance. *E. ovata* preferred north and north-western exposure.

Occurrence and abundance of both species is highly correlated with the total species number of foliage-dwelling spiders at each study plot. Therefore, in combination with other spider species, they are suggested as indicator species for the evaluation of habitat quality of field margins for foliage-dwelling spiders.

INTRODUCTION

Enoplognatha latimana was recently described by Hippa and Oksala (1982). Before, specimens of *Enoplognatha latimana* were not separated from *Enoplognatha ovata* (Clerck, 1757). Some studies on these two closely related species deal with their morph-frequency variation (Oxford 1991;

Oxford & Reillo 1993) and slightly different phenology (Oxford 1992; Nährig 1991). So far, little is known about abundance and ecology of *E. latimana*. Oxford (1993) investigated the variation in population size in *E. ovata* for a period of 10 to 19 years. Nährig (1991) described abundance and vertical distribution of both species in hedges.

Both *Enoplognatha* species are distributed in middle Europe (Oxford & Reillo 1994).

Data presented in this paper are part of a research on foliage-dwelling spiders in agricultural landscapes from 1993 to 1995 (Barthel & Plachter 1995, 1996). Therefore, a relative abundance of both *Enoplognatha* species with respect to other foliage-dwelling spider species on field margins is given.

METHODS AND STUDY AREA

Enoplognatha specimens were recorded together with other foliage-dwelling spiders by standardized visual search in the herbaceous vegetation layer. Standardisation of the search was achieved by monitoring only foliage-dwelling spiders made conspicuous by their body size, characteristic webs, hiding places or cocoons and by using a constant study plot-size of 1 m x 50 m in uncultivated field margins, wood edges, fallow land (formerly used as arable land), abandoned grassland and cultivated grassland (Tab. 1). Adults of *Enoplognatha* were collected for species determination in the laboratory. Juveniles and adults of the other studied spiders were determined, if possible, to species level in the field or collected for determination in the laboratory. The mainly ground-dwelling wolf spiders (Lycosidae) and the small erigonid spiders (Linyphiidae: Erigoninae) were excluded from the investigations, because they could not be registered representatively by this method.

Tab. 1. Number of study plots in different habitat types and study areas.

Habitat type	Experimental farm	Further 6 study areas
field margins	13	84 (12-17 in each area)
wood edges	2	
fallow land	5	
abandoned grassland	5	
cultivated grassland	8	

The investigations were carried out in seven agricultural landscapes situated in the same geographic region, a hilly landscape between the rivers Isar and Danube in the North of Munich (Southern Germany, see maps in: Barthel & Plachter 1996). Until 1992 one of these study areas was an experimental farm

consisting mainly of large fields up to 25 ha. At the end of 1992, field size was reduced to a maximum of 6.5 ha. In consequence, new hedges and field margins were created and the margin density increased. Furthermore, some field and grassland plots were excluded from cultivation. Therefore, the percentage of uncultivated areas increased as well. The study areas are situated at an altitude of 400 to 520 m and yearly precipitation is about 833 mm.

On the experimental farm, the study plots in various habitat types (see Tab. 1) were monitored once per month from May to September from 1993 to 1995. In the other six study areas, study plots were parts of field margins and sampled once per month from May to September in 1994 and either in 1993 or 1995, because not all of the study plots had already been fixed for investigation since May 1993. Thus, data are based on a total of 10 sampling periods per study plot comparing all study areas together, while analysis of data concerning only the experimental farm are based on 15 sampling periods.

In the study areas, the 'margin density' (m/ha) was defined as the length of all margins with at least 50 cm in width divided by the size of the study area. Four study areas have a low margin density between 90 and 160 m/ha, the margin density of the other three areas varies between 230 and 300 m/ha. At each study plot the margin width, mechanical treatments by farmers, the cover of herbs, Ellenberg's indicator values for moisture and nitrogen (Ellenberg *et al.* 1992) and the exposure of inclined margins were determined. The parameter 'mechanical treatments' includes the number of observed treatments without discriminating between different types of treatments, e.g. mowing, cutting, ploughing or trampling.

The indicator values of Ellenberg (Ellenberg *et al.* 1992) reflect the response of plant species to an environmental gradient, e.g. moisture or nitrogen. Plant species which are not indifferent to the investigated gradient got a value between 1 (very dry) and 12 (submerge) for moisture and 1 (low nitrogen amount) to 9 (high nitrogen amount) for nitrogen amount. At each study plot, the indicator values for moisture and nitrogen of all plant species were averaged and used as an indirect measured habitat parameter for moisture and nitrogen amount. Spearman rank correlation (two-tailed) and regression analysis of the statistic program WinSTAT 3.0 (Kalmia Company, USA) were used to analyse relations between *Enoplognatha* species and studied habitat characteristics and the total spider species number, respectively. Margins with an inclination of at least 10° were classified into one of eight direction classes (N, NE, E, SE, S, SW, W, NW). Correlation between the abundance of *Enoplognatha* species and the directions were calculated for each direction separately. Margins with the tested direction class got the value 1. Margins which did not have the tested exposure got the value 0. These values were correlated with the abundance of both *Enoplognatha* species at each study plot by Spearman-rank-correlation.

RESULTS

In the whole study, 1,935 *Enoplognatha* specimens were collected (Tab. 2), 54 % were adults of *Enoplognatha ovata* and 34 % belonged to *Enoplognatha latimana*. The remaining 12 % were indeterminate juveniles or adults, which escaped while catching in the field. For data analysis, the indeterminate specimens were added to either *E. ovata* or *E. latimana* according to the calculated percentage of both species at each study plot. The first part of the result analysis deals with the distribution and habitat requirements of both *Enoplognatha* species in field margins, whereas the second part focuses on distribution and abundance in different habitat types of agricultural landscapes. In the third part, data are presented that support the significance of both *Enoplognatha* species for the assessment of field margins as habitat for foliage-dwelling spiders.

Tab. 2. Number of adult and juvenile specimens of studied *Enoplognatha* species from 1993 to 1995.

		Number of specimens	%
<i>Enoplognatha ovata</i>	adults	1040	54
<i>Enoplognatha latimana</i>	adults	663	34
<i>Enoplognatha</i> sp.	adults	96	5
	juveniles	136	7
Total		1935	100

At 97 studied field margins in seven study areas, 75 species with 18,458 specimens were recorded. In Tab. 3, the 20 most frequently found species were listed according to their frequency in the 97 studied field margins. The most abundant spiders were *Theridion impressum* and *Argiope bruennichi* with 12.8 and 13.1 % of the total catch. Both spider species occurred on nearly all field margins. *E. ovata* and *E. latimana* were the 10th and 11th most frequent species with an overall abundance of 4.3 % and 3.3 %. Although both species occurred in all seven study areas (Tab. 3), they were found only on about 50 % of the study plots (Tab. 3). At 35 study plots both *Enoplognatha* species were recorded as common, although the abundance of these species differed at these syntopic occurrences. The abundance of both species varied from 0 to 58 specimens in *E. ovata* and 0 to 51 specimens per study plot (50 m², 10 sampling periods) in *E. latimana*. Focusing on a comparison of single study areas, the frequency of *E. ovata* is much more balanced: *E. ovata* occurred in 31 % to 79 % of the study plots of one area, *E. latimana* was found in one study area on all study plots and in another area only on one study plot (Fig. 1). Conclusively, both species are widespread, but seem to

have specific habitat requirements. For analysing these habitat requirements, the abundance of *E. ovata* and *E. latimana* at each study plot were correlated with habitat parameters. Both *Enoplognatha* species were significantly more abundant in areas with a high margin density and on wider margins as well as on margins with a high herbaceous cover (Tab. 4). In particular, *E. latimana* occurred more frequently in study areas with a high margin density (Fig. 1). Frequent mechanical treatments of the margins had a negative influence on the abundance of both *Enoplognatha* species. With respect to other habitat parameters both species do not react similarly. *E. latimana* was more abundant on study plots with a low average moisture, i.e. drier habitats, and a low average nitrogen amount, whereas *E. ovata* showed a significantly low negative correlation ($p < 0.05$) only with the nitrogen amount. The average moisture indicator value varied from 3.8 to 6.7, the average nitrogen indicator value from 3.6 to 7.3 at the 97 study plots.

Tab. 3. Frequency in study plots (97), presence in study areas (7) and relative abundance of the 20 most frequent foliage-dwelling spider species on field margins between 1993 and 1995. Each study plot (50 m²) was sampled 10 times. Species are listed according to decreasing frequency in the plots. Data of *Enoplognatha* species, which are the main subject of this paper, are printed in big letters.

Spider species	Frequency	Presence	Number of species	Abundance %
<i>Theridion impressum</i>	96	7	2,367	12.8
<i>Argiope bruennichi</i>	95	7	2,423	13.1
<i>Aculepeira ceropegia</i>	88	7	737	4.0
<i>Mangora acalypha</i>	88	7	555	3.0
<i>Tetragnatha pinicola</i>	79	7	520	2.8
<i>Pisaura mirabilis</i>	76	7	1,632	8.8
<i>Linyphia triangularis</i>	67	7	609	3.3
<i>Clubiona reclusa</i>	66	7	809	4.4
<i>Larinioides folium</i>	56	6	1,895	10.3
<i>Enoplognatha ovata</i>	54	7	795	4.3
<i>Enoplognatha latimana</i>	50	7	617	3.3
<i>Microlinyphia pusilla</i>	48	7	111	0.6
<i>Evarcha arcuata</i>	47	7	1,062	5.8
<i>Xysticus ulmi</i>	45	7	252	1.4
<i>Araneus quadratus</i>	41	7	1,271	6.9
<i>Metellina segmentata</i>	41	7	277	1.5
<i>Xysticus cristatus</i>	38	7	147	0.8
<i>Theridion bimaculatum</i>	35	7	56	0.3
<i>Xysticus kochi</i>	34	7	61	0.3
<i>Agelena labyrinthica</i>	30	6	686	3.7
55 further spider species			1,576	
Total sum of specimens			18,458	

E. ovata is significantly more abundant on margins with north to north-western exposures, whereas *E. latimana* occurred more frequently on margins with south to south-western exposures (Tab. 4).

On the experimental farm additional study plots in fallow land, abandoned grassland and cultivated grassland were investigated. Both species were recorded from the herbaceous layer of two investigated wood edges (Fig. 2). In abandoned grassland, only *E. ovata* was found, whereas *E. latimana* occurred more abundant in fallow land formerly used as arable land. In cultivated grassland only one specimen of *E. ovata* was recorded during the investigation period of three years between 1993 and 1995. On the fallow land plots, cultivation was stopped after the harvest in 1992. In the first years the vegetation of these fallow land plots was sparse with only a sparse moss or litter layer. In contrast, the abandoned grassland already had a thick moss and litter layer and provided well-balanced humidity conditions.

Tab. 4. Spearman rank correlations between the abundance of *Enoplognatha ovata* and *E. latimana*, respectively, and habitat parameters of 97 investigated field margins. It gives the correlation coefficient (C.C.) and the level of the significance (l.s.). Significant positive/negative correlations: +++/---: $p < 0.001$, ++/--: $p < 0.01$, +/-: $p < 0.05$.

Habitat parameters	<i>Enoplognatha ovata</i>		<i>Enoplognatha latimana</i>	
	C.C.	l.s.	C.C.	l.s.
margin density	0.32	+++	0.39	+++
margin width	0.42	+++	0.27	++
mechanical treatment	-0.46	---	-0.29	--
cover of herbs	0.36	+++	0.34	+++
humidity number			-0.31	---
nitrogen number		-	-0.36	---
exposition:				
S			0.18	+
SW			0.19	+
NW	0.32	+++		
N	0.31	+++		

On field margins, the total number of foliage-dwelling spider species ranged between 5 and 29 species per study plot (50 m² and 10 sampling periods). Thus, differences in species number exist between the field margins. For practical evaluation tasks in nature conservation it is necessary to get information on the number of spider species of single field margins with a minimized expenditure. Therefore it is of concern as to whether a few spider

species can indicate the total species number on field margins with sufficient accuracy. A correlation between the total species number and the abundance of *E. ovata* and *E. latimana* resulted in correlation coefficients (Spearman rank correlation) of 0.60 and 0.68, respectively. Similarly, the presence of one or both *Enoplognatha* species is significantly correlated to the total spider species number, too (correlation coefficient: 0.73, $p < 0.001$, Spearman rank correlation). In the next step, the connection between total number of foliage-dwelling spider species and the presence of both *Enoplognatha* species was studied by regression analysis (Fig. 3). At each study plot the total species number (range between 5 and 29 species) is known as well as the number of *Enoplognatha* species, which ranges between 0 and 2. The best suited regression (maximum r^2) between the total number of species and the number of *Enoplognatha* species is a linear regression. The response line and the equation is given in Fig. 3. The coefficient of determination r^2 has a value of 0.45. That means that 45 % of the variation in number of *Enoplognatha* species at each study plot is caused by the total number of spider species at this study plot, although causality between both parameters cannot be inferred by regression analysis. It is possible to convert the interpretation of the diagram given in Fig. 3. By the reason of linearity the coefficient of determination r^2 remains the same. If only the number of *Enoplognatha* species was recorded in the field, the range of the spider species number can be fixed at a 95 % probability level (given by the interval between the broken lines in Fig. 3), although these ranges still have a large overlap. If none of the *Enoplognatha* species was present on a field margin, a maximum of only 15 spider species were recorded there in 2 years. On the other hand, both *Enoplognatha* species found on one margin resulted in at least 13 spider species and a maximum of 29 species at this study plot. Thus, *Enoplognatha* species are suitable for the evaluation of field margins with respect to spider communities. In combination with other spider species, both *Enoplognatha* species may serve as an indicator species set for foliage-dwelling spiders in the agricultural landscape.

DISCUSSION

On field margins in Southern Bavaria, *E. latimana* is nearly as widespread as *E. ovata*. Oxford (1992) investigated ten sites in Great Britain where *E. ovata* was recorded. At six sites *E. latimana* was present as well. He concluded that *E. latimana* was fairly widely distributed in that area. This corresponds with the distribution in southern Bavaria, where each of both species was collected in about 50 % of the margins. At 36 % of all investigated field margins even both species occurred in common. Nährig (1991) collected both *Enoplognatha* species in hedges in Baden-Württemberg (southwest Germany). In this habitat type, both species were more frequent in the lower

strata (0-50 cm) than in the higher vegetation (more than 1 m above ground level). Furthermore, he found six times more *E. ovata* than *E. latimana* specimens in hedges.

Oxford (1992) describes for *E. latimana* at British sites an association with more open and drier habitats without shade to be the preferred habitat. This corresponds with the negative correlation to the average moisture indicator value and the high abundance of *E. latimana* on southward inclined margins in this study. Similarly, in the sparse vegetation of the 'new' fallow land more specimens of *E. latimana* were found. Therefore, 'open' does not only refer to the amount of shrubs and trees, but to sparser vegetation as well. In Switzerland, Maurer and Hänggi (1990) identified the herbaceous layer of open and dry sites as habitat for *E. latimana*, too. They consider *E. latimana* as mesophotophilous with respect to light and temperature and mesoxerophilous with respect to moisture, which is confirmed by the results presented in this paper. Habitat requirements of *E. ovata* bordering roads and tracks were investigated by Oxford (1993). He found a negative correlation between the abundance of *E. ovata* and the hours of bright sunshine during the summer. For Switzerland, Maurer and Hänggi (1990) consider *E. ovata* to be a mesoombrophilous species. Both statements coincide with the high abundance of this species in northward inclined margins in Southern Bavaria. With respect to moisture Maurer and Hänggi (1990) mention *E. ovata* to be a mesoxerophilous species, which cannot be confirmed by the data of this study, where *E. ovata* was abundant in some damp areas with *Juncus effusus* and *Cirsium oleraceum*. The negative impact of human disturbance by cutting and removing vegetation on population size of *E. ovata* was already mentioned by Oxford (1993). On one hand, the reason for this negative impact is the direct removal of the rolled leaves with the nursery retreats in July and August, when the females stay nearby the cocoons till the juveniles emerge. On the other hand, the mowing of the vegetation quite probably changes the micro-climate of the sites. This might have a specific influence on population size of *E. ovata*, which is associated with more shade than *E. latimana*.

A multivariate analysis (Canonical correspondence analysis) between habitat parameters and foliage-dwelling spider composition proves that margin density had the strongest influence on spider species composition (Anderlik-Wesinger *et al.* 1996). But the influence of the margin density on frequency and population size of both *Enoplognatha* species may be a side effect. In study areas with a high margin density (more than 200 m/ha), cultivation intensity is often lower and average margin width larger than in areas with a low margin density. Both species need an undisturbed zone within the margins to build up populations. If suitable conditions are given, even margins in areas with a low margin density were colonized (see study

area 'GV' in Fig. 1). Of course, the probability of extinction on a single margin is higher if it is isolated by the reason of a low connectivity of suitable habitats (Hovestadt *et al.* 1991). Similarly, Thomas *et al.* (1992) explained the distribution of occupied and vacant butterfly habitats by landscape fragmentation.

In agricultural landscapes, the influence of farming practices, either intensive or organic, and also the mowing and grazing system of grassland and land consolidation are immense. To reduce the human impact of cultivation, farmers receive governmental subsidies for special management strategies, e.g. herbicide free buffer strips in fields or a late mowing of damp meadows. Whether these measures have real positive consequences on fauna and flora is often not controlled as well as the influence of changes by land consolidation. Therefore, it is important to develop indicator species systems for monitoring habitat qualities. A survey on suitability of various taxa (family or order level) is given by Plachter (1989), but a proposal of indicator species is presented only for three habitat types not concerning the 'normal' agricultural landscape. Some detailed suggestions of indicator species for grassland management are made by Eyre *et al.* (1989) and Siepel *et al.* (1992). Both selected invertebrates, e. g. Coleoptera and Araneae, as indicator species. In habitat types covering small areas, e.g. field margins, invertebrates can also be relevant species for monitoring. If species indicate a good habitat quality of field margins, e.g. a high species diversity in the impoverished agricultural landscape, why should a farmer not be supported by subsidies, if there exist various populations of indicator species in his agricultural area? *Enoplognatha ovata* and *E. latimana* may be two species of such an indicator species set, because they occur on margins, where a lot of other spider species are present and the herbaceous cover is high. Of course, two indicator species cannot reflect a broad scale in habitat qualities, because only three degrees (neither, one or both species present) are possible. As shown in the results, the prediction of the total spider species number by the presence of only two indicator species is not very precise, it still has a wide range. Therefore, a more detailed prediction of the total species number on field margins requires a set of some more species.

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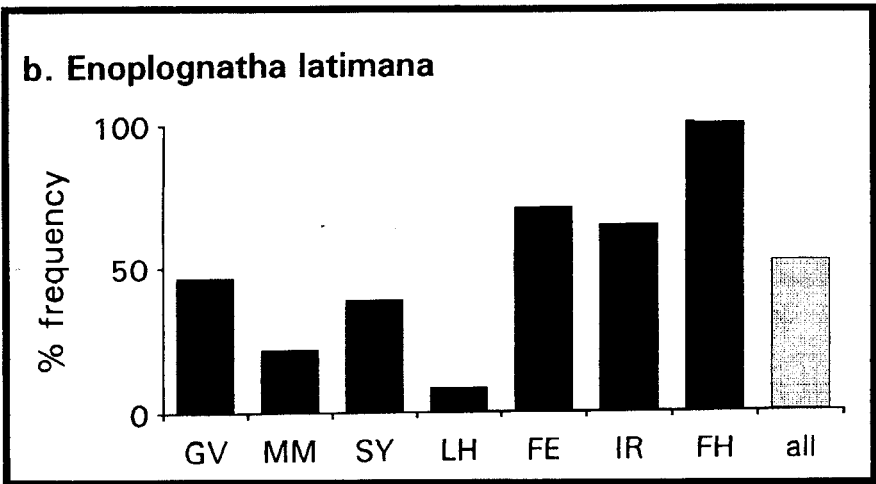
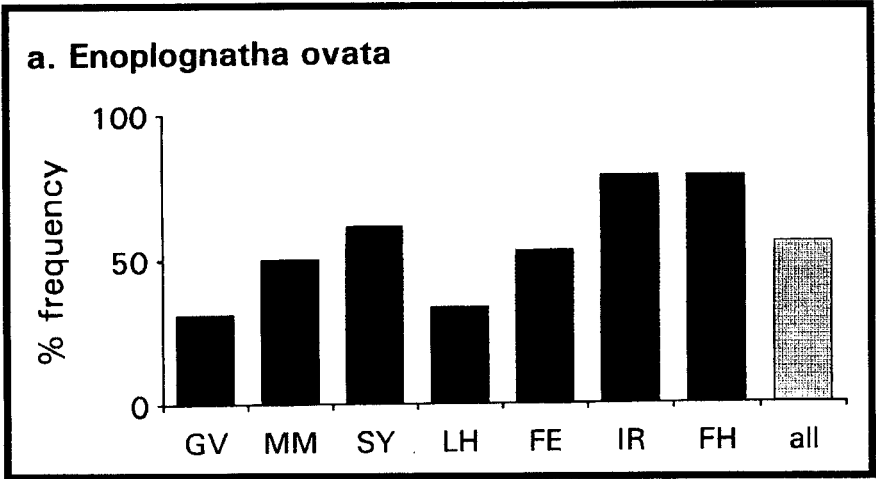


Fig. 1. Frequency of *Enoplognatha* species in the study areas. The study areas are abbreviated by two letters at the bottom. They are listed according to increasing margin density. The average frequency of each species in the whole study is given at the right side.

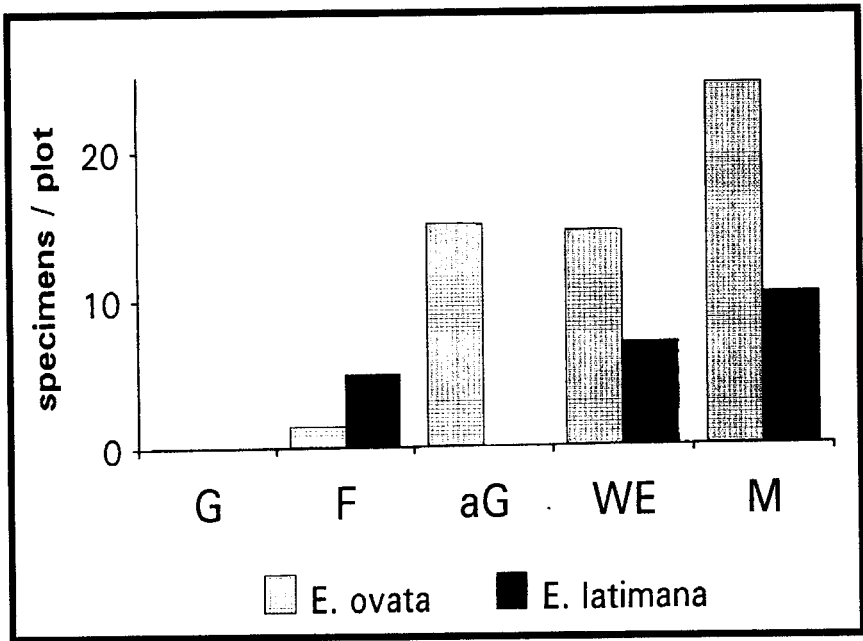


Fig. 2. Number of specimens of *Enoplognatha ovata* and *E. latimana* per study plot in different habitat types in the experimental farm between 1993 and 1995. G: grassland (number of investigated study plots N = 8), F: fallow land (used as arable land until 1992; N = 5), aG: abandoned grassland (N = 5), WE: wood edge (N = 2), M: field margin (N = 13).

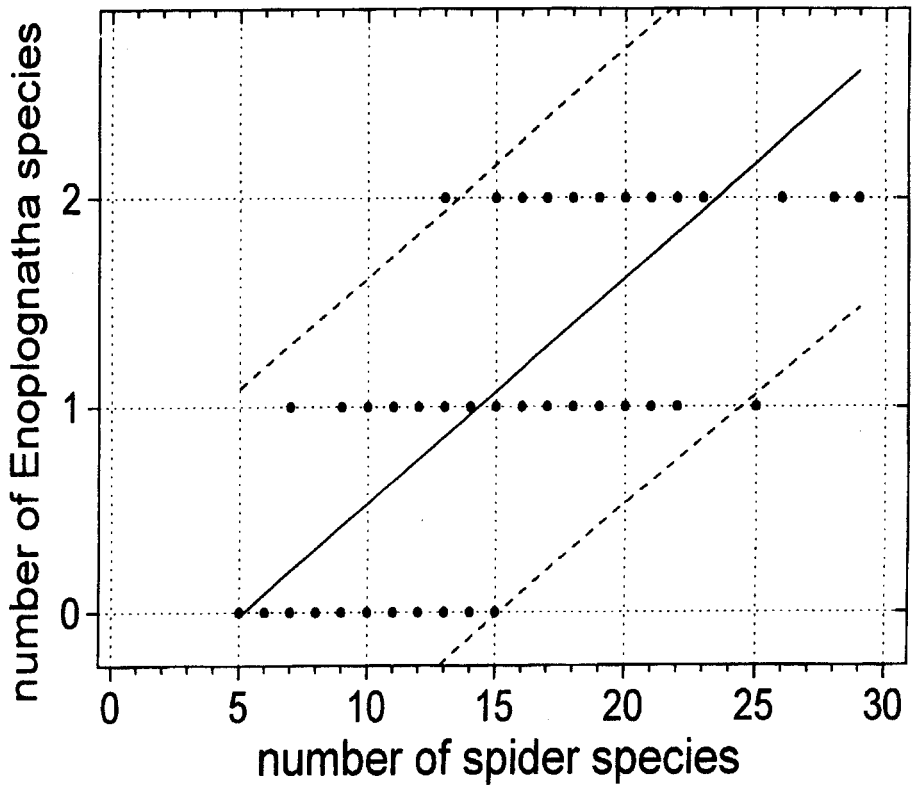


Fig. 3. Regression analysis between the total number of foliage-dwelling spider species and the presence of *Enoplognatha* species. The solid line indicates the regression line, which bases on the regression equation $Y = -0.56 + 0.10 * X$ ($r^2 = 0.45$, $p < 0.001$). The broken lines limit the 95 % range of data.

REFERENCES

- Anderlik-Wesinger G, Barthel J, Pfadenhäuer J. & Plachter H 1996. Einfluß struktureller und floristischer Ausprägung von Rainen der Agrarlandschaft auf die Spinnen (Araneae) der Krautschicht. *Verh. Ges. Ökol.*, **26**: 711-720.
- Barthel J. & Plachter H. 1995. Distribution of foliage-dwelling spiders in uncultivated areas of agricultural landscapes (Southern Bavaria, Germany) (Arachnida, Araneae). In: Růžička V. (ed.), *Proc. 15th Europ. Coll. Arachnol.* 1994, České Budějovice, pp. 11-21.
- Barthel J. & Plachter H. 1996. Significance of field margins for foliage-dwelling spiders (Arachnida, Araneae) in an agricultural landscape of Germany. *Rev. Suisse Zool.*, **vol. hors série**: 45-59.

- Ellenberg H., Weber H. E., Düll R., Wirth V., Werner W. & Paulißen D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Scr. Geobot., vol. 18, Verlag Erich Glotze KG, Göttingen, 248 pp.
- Eyre M. D., Luff M. L., Rushton S. P. & Topping C. J. 1989. Ground beetles and weevils (Carabidae and Curculionidae) as indicators of grassland management practices. J. Appl. Ent., **107**: 508-517.
- Hippa, H. & Oksala I. 1982. Definition and revision of the *Enoplognatha ovata* (Clerck) group (Araneae: Theridiidae). Ent. scand., **13**: 213-222.
- Hovestadt T., Roeser J. & Mühlenberg M. 1991. Flächenbedarf von Tierpopulationen. Ber. ökol. Forsch., 1. Forschungszentrum Jülich, 277 pp.
- Maurer R. & Hänggi A. 1990. Katalog der schweizerischen Spinnen. Schweizerischer Bund für Naturschutz, Schweizer. Zentrum für die kartographische Erfassung der Fauna (SZKF), Neuchâtel.
- Nährig D. 1991. Zur Phänologie und Ökologie der *Enoplognatha ovata* - Gruppe (Araneae: Theridiidae). Caroleina, **49**: 131-133.
- Oxford G. S. 1992. A comparison of their phenologies and genetics in the Norfolk populations. Bull. Br. arachnol. Soc., **9**: 13-18.
- Oxford G. S. 1993. Components of variation in population size in the spider *Enoplognatha ovata* (Clerck) *sensu stricto* (Araneae: Theridiidae). Bull. Br. arachnol. Soc., **9**: 193-202.
- Oxford G. S. & Reillo P. R. 1993. Trans-continental visible morph-frequency variation at homologous loci in two species of spider, *Enoplognatha ovata s. s.* & *E. latimana*. Biol. J. linn. Soc., **50**: 235-253.
- Oxford G. S. & Reillo P. R. 1994. The world distributions of species within the *Enoplognatha ovata* group (Araneae: Theridiidae): implications for their evolution and for previous research. Bull. Br. arachnol. Soc., **9**: 226-232.
- Plachter H. 1989. Zur biologischen Schnellansprache und Bewertung von Gebieten. Schr.-R. f. Landschaftspfl. u. Natursch., **29**: 107-135.
- Siepel H., van Wingerden W. K. R. E. & Maaskamp F. I. M. 1992. Grassland management evaluation with invertebrate indicator species. In: Bohác J. (ed.), Proc. VIth Int. Conf. Bioindicators Deteriorationis Regionis. Institute of Landscape Ecology, České Budějovice, pp. 243-248.
- Thomas C. D., Thomas J. A. & Warren M. S. 1992. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. Oecologia, **92**: 563-567.