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## Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

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Published online: 24 Jun 2011.

To cite this article: Oliver-D. Finch (2005) The parasitoid complex and parasitoid-induced mortality of spiders (Araneae) in a Central European woodland, *Journal of Natural History*, 39:25, 2339-2354, DOI: [10.1080/00222930502005720](https://doi.org/10.1080/00222930502005720)

To link to this article: <http://dx.doi.org/10.1080/00222930502005720>

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# The parasitoid complex and parasitoid-induced mortality of spiders (Araneae) in a Central European woodland

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(Accepted 10 January 2005)

## Abstract

The parasitoid complex of spiders was studied in three different sites of a forest and, for comparison, in open habitats in north-western Lower Saxony (Germany). Qualitative data and, for four spider species, detailed quantitative rearing data were obtained. At least 25 parasitoids of spiders were recorded (23 species of Hymenoptera and two species of Diptera). External parasitoids of spiders were rare in the woodlands; only up to 1% of the spiders collected by hand searching and sweep netting had ectoparasitoids. During the investigation 23 parasitoid species were reared from spider egg masses, 10 of them occurring in woodlands. Two species were secondary parasitoids. Several parasitoid–host relationships were recorded for the first time. Egg masses of *Floronia bucculenta* were parasitized up to 5% by two species of the genus *Gelis*. Up to 10% of the egg masses of *Linyphia hortensis* were parasitized by *Aclastus* species. Egg masses of the spider genus *Ero* were parasitized by three species, causing an overall mortality of 40%. For egg masses of *Agroeca* spp. parasitization at some locations was up to 60%. An overview of the Central European parasitoid complex of spiders is provided.

**Keywords:** *Arachnophagy, community ecology, parasitic Hymenoptera, parasitoid web*

## Introduction

The quantitative influence of natural enemies on spider populations is of special interest, as they play an important role in the mortality of spiders, and thus may be a relevant factor controlling population size (Wise 1993). Beside the fact that spiders themselves are probably their most important predators (Foelix 1992), a large number of other taxa acting as natural enemies of spiders has been recorded (e.g. Bristowe 1941; Rollard 1984, 1987; Fitton et al. 1987, 1988). Already Bristowe (1941) remarked that hymenopterous parasitoids might be the most important ones among these enemies.

Although we find several records of spider parasitoids in Central Europe, many taken from the literature are highly dubious for a variety of reasons (Shaw 1994). Several of the parasitoid genera involved, including the species of the commonly reared genus *Gelis*

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Published 29 June 2005.

ISSN 0022-2933 print/ISSN 1464-5262 online © 2005 Taylor & Francis Group Ltd  
DOI: 10.1080/00222930500101720

(Ichneumonidae: Phygadeuontini), remain flawed not only with nomenclatural incongruencies, but also with inadequate species separation (Schwarz 1998).

Consequently, the aims of this study were:

- to produce reliable host–parasitoid relationships for spiders in a Central European woodland and to investigate the diversity (species richness) of the parasitoid complex;
- to provide quantitative data on the impact of parasitoids on the mortality of spiders (parasitoid community function); and
- to get further insights into the life-history of these antagonists of spiders.

Such data are important for the construction of metapopulation models of single animal species (Topping 1997; Hanski 1999) and for the modelling of parasitoid webs as subsets of natural food webs in community ecology (Memmott and Godfray 1994; Polis and Winemiller 1996). Furthermore, these data could help in developing urgently needed strategies for the conservation of parasitic Hymenoptera (Shaw and Hochberg 2001).

## Material and methods

### *Study sites*

Spiders and their egg sacs were collected in woodlands in the vicinity of Oldenburg, Lower Saxony, Germany (Figure 1) between 1996 and 1998. Investigations were carried out mainly in the “Wildenloh”, a partially ancient woodland located 7 km west of the city of Oldenburg. Included were a 170-year-old beech stand growing on sand and boulder clay,

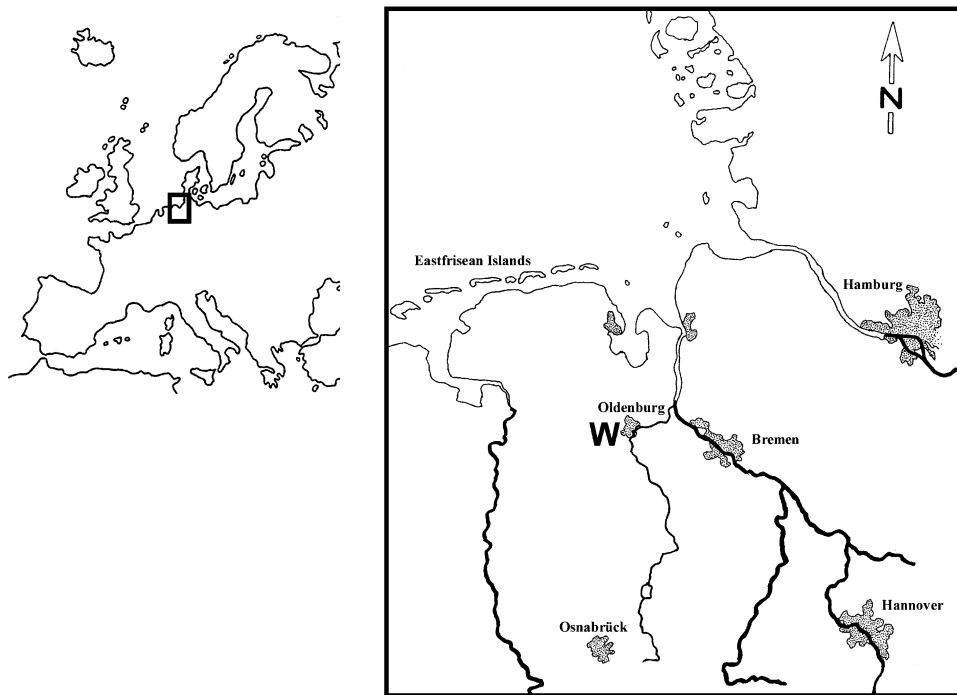


Figure 1. Map of the Oldenburg area. W indicates the main investigation site, the woodland “Wildenloh”, 7 km to the west of Oldenburg.

representing an ancient part of the Wildenloh, as well as 110-year-old pine (*Pinus sylvestris*) and 55-year-old spruce (*Picea* spp.) forests growing on peat (further details in Finch 2005). In order to get an overview of the regional species pool of spider egg sac parasitoids, further specimens were collected predominantly in abandoned grasslands of the same general region.

#### *Studied species, collecting and rearing methods*

Spider parasitoids have been defined as arthropods that do not move the host after the adult females have located it, their larvae feeding only on a single individual of the host species (Godfray 1994; O'Neill 2000). Thus the external parasitoids of immature or mature spiders are "true" parasitoids. Furthermore, following Godfray (1994), parasitoids which oviposit into cocooned spider egg masses are defined as "egg predators" if they attack more than one egg (i.e. more than one host) within the egg masses. In contrast to his definition, in agreement with other authors (Schwarz 1998; Shaw 1998), in this paper I prefer to name these insects also "parasitoids", as their larvae do not feed on several egg sacs during their development, and show no substantial behavioural differences to "true parasitoids" in all other aspects.

Due to the considerable differences regarding the requirements for their study, internal parasitoids of spiders (e.g. Diptera: Orthorrhapha: Acroceridae) were not considered in the framework of this investigation.

All species of the *Polysphincta* genus-complex (Hymenoptera: Ichneumonidae: Pimplinae: Ephialtini; see Gauld et al. 2002 for a recent phylogenetic analysis of this suprageneric group) develop externally on spiders. Their larvae live solitarily on immature or, only occasionally, on adult spiders. As koinobiont parasitoids they allow their hosts to continue growing during the development of the larvae (Nielsen 1923, 1928, 1935, 1937; Shaw 1998; Finch 2001). In order to collect larvae of this suprageneric group, spiders were sampled using intensive sweep-net catches at approximately fortnightly intervals between April and October. Individuals with ectoparasitic larvae were selected in the field and were kept alive and individually in the laboratory. Before the spider was killed by the parasitic larva it was fed with short-winged *Drosophila melanogaster* (Diptera) and *Entomobyra purpurascens* (Collembola). Pupated parasitoids were kept in the same container until the imago emerged.

The genus *Zaglyptus* shows remarkable particularities in feeding behaviour. Within a silken nest of an egg sac-guarding spider female, their larvae are able to develop on both the spider's eggs and the female (see Nielsen 1923, 1935 and Shaw 1998 for further details). As Clubionidae are known hosts of *Zaglyptus*, their nests were also sampled in the field.

Solitary or gregarious larvae of several taxa of Ichneumonidae and a few Diptera feed on successive eggs in the egg sacs of spiders. After finishing feeding, the idiobiont larvae pupate in the egg sac and in due course the imagines emerge. Spider egg sacs were searched for and collected manually in the field. If present, female spiders guarding their egg sac were collected as well, in order to determine the spider species. Spider egg sacs were kept singly in petri dishes under laboratory conditions at 19–25°C until parasitoids and/or spiderlings emerged. This way parasitoids could be linked accurately to the cocoon from which they came and further information (e.g. sexual composition of the brood) could be obtained. Overwintering was carried out in climate chambers at 5°/0°C. Juvenile spiders emerging from parasitized cocoons or from similar cocoons found in the same microhabitat and obviously made by conspecific spiders, were reared to the adult stage, when necessary for determining the host. In some cases, however, host egg sacs could not be determined.

Four spider species were investigated in detail: *Agroeca* spp. (Liocranidae; almost certainly all *A. brunnea* (Blackwall)), *Ero* spp. (Mimetidae; almost certainly all *E. furcata* (Villers)), *Floronina bucculenta* (Clerck), and *Linyphia hortensis* Sundevall (both Linyphiidae). All four species are widely distributed throughout Central Europe and occur in a wide range of habitats, including woodlands of different types (Hänggi et al. 1995). The egg sacs of *Agroeca* species are conspicuous, and in spring they can be found more often during field samplings than the spider itself. The egg cocoon has been described as looking like an inverted wineglass, before being finally completely camouflaged with soil particles by the female spider. Egg sacs of *Ero* spp. have a highly distinctive appearance and are identifiable to genus level without any difficulty. They have a 1–3 cm long, thin stalk and are pear-shaped, with a diameter of 3–5 mm. The white egg sacs of *F. bucculenta* are fusiform, 1.5–2 cm long and up to 0.5 cm high; in the literature they have repeatedly been ascribed to *Linyphia triangularis* (Clerck) (Linyphiidae), as noted by Schaefer (1976a). In the case of *L. hortensis* the “petri dish method” described by van Baarlen et al. (1994) was additionally used for the assessment of parasitization of egg sacs in the field. With a continuous food supply females of *L. hortensis* produced several (up to three) egg masses. These were left out in the beech stand for 7 days, giving parasitoids a chance to parasitize them. For this spider species egg numbers were calculated from the first of these cocoons to be laid, because in the field eggs were often lost while scraping the cocoons from the bark.

The degree of parasitization was calculated for each species using all available data from the whole investigation period. These are minimum values, because after collection egg masses could no longer be parasitized, as would have been the case in the field.

Nomenclature of parasitoids follows Fitton et al. (1988), Gauld et al. (2002), Sawoniewicz (1980), Schmitz (1943), and Schwarz and Shaw (1998, 1999, 2000), that of spiders is in conformity with Platnick (1998).

## Results

### *Ectoparasitoids of mobile spiders*

In the woodlands investigated, mobile spiders were parasitized only at a very low level. Less than 1% of the sampled individuals were parasitized by two species of parasitic wasps.

*Acrodactyla degener* (Haliday) (Ichneumonidae: Ephialtini) was recorded in the beech stand and the pine forest. In the pine forest an additional parasitoid, *Zatypota percontatoria* (Müller) (Ichneumonidae: Ephialtini), occurred. The larvae of *A. degener* were collected during spring (April, May); that of *Z. percontatoria* were found during summer (June, August). In the laboratory they killed their host and pupated within a maximum of 7 days. Not later than 17 days after collecting the larvae, the imagines emerged. Because spider individuals were immature, host species could not be definitely determined to family level for *Z. percontatoria*. *A. degener* attacked sheet web spiders (Linyphiidae) almost exclusively, and in at least one case *Neriene clathrata* (Sundevall) was the host species.

### *Parasitoids of spider egg masses*

From the spider egg masses that were sampled in the field, in 4112 cases spiders and/or parasitoids were reared successfully in the laboratory. At least 23 species (670 individuals) of parasitoids and at least 24 spider taxa were involved (Table I).

Table I. Parasitoid–host associations in spider egg masses, recorded in woodland habitats and in open habitats in north-western Germany between 1996 and 1998.

	Hymenoptera – Ichneumonidae										Diptera	Total																	
	<i>Aclastus cf. gracilis</i>	<i>Aclastus cf. micator</i>	<i>Aclastus micator</i> <sup>c</sup>	<i>Aclastus solutus</i>	<i>Aclastus</i> spp.	<i>Bathytrix formosa</i> <sup>g</sup>	<i>Bathytrix thomsoni</i>	<i>Gelis agilis</i> <sup>b</sup>	<i>Gelis bicolor</i> <sup>b,e</sup>	<i>Gelis discodens</i> <sup>b,e</sup>	<i>Gelis fasciinctus</i> <sup>b</sup>		<i>Gelis melanocephalus</i> <sup>b,e</sup>	<i>Gelis micrurus</i> <sup>b,e</sup>	<i>Gelis rufogaster</i> <sup>b,e</sup>	<i>Gelis viduus</i> <sup>b,e</sup>	<i>Hemiteles marcesca</i> <sup>c</sup>	<i>Hirryta sordida</i> <sup>a</sup>	<i>Idoliswa a. analis</i> <sup>h</sup>	<i>Polyaulon paradoxus</i> <sup>c</sup>	<i>Thaumatogelis audax</i> <sup>c,d</sup>	<i>Tromatobia ovirova</i> <sup>f</sup>	<i>Trychosia legator</i> <sup>a</sup>	<i>Trychosia cf. legator</i>	<i>Trychosia tristator</i> <sup>a</sup>	<i>Zaglyptus varipes</i> <sup>i</sup>	<i>Sarcophaga sexpunctata</i>	<i>Megeselia major</i>	
Araneae indet.	2	2	7	1	1		1*						3	8				1			1						1	28	
Araneae, cf. <i>Pachygnatha</i> spp.							1*		8		5																		14
Araneae, cf. <i>Xysticus</i> spp.																						4		2					6
Mimetidae <i>Ero cf. furcata</i>							1*	2					91		12														106
Linyphiidae Linyphiidae indet.													1																1
Linyphiidae, cf. <i>Tapinopa longidens</i>														1															1
<i>Floronia bucculenta</i>								3						15															18
<i>Labulla thoracica</i>														1															1
<i>Linyphia hortensis</i>			11		1																								12
<i>Macrargus rufus</i>														5															5
<i>Nerieni clathrata</i>		1			1																								2
<i>Nerieni peltata</i>		2			2																								6
<i>Tapinopa longidens</i>														1															1
Tetragnathidae <i>Pachygnatha</i> cf. <i>clercki</i>									13		79																		92
<i>Pachygnatha clercki</i>							2*		50		18																		70
<i>Pachygnatha listeri</i>											7																		7
<i>Tetragnatha</i> spp.								10																					10

Table 1. Continued.

	Hymenoptera – Ichneumonidae																				Diptera		Total					
	Aclastus cf. gracilis	Aclastus cf. micator <sup>c</sup>	Aclastus solutus	Aclastus spp.	Bathythrix formosa <sup>g</sup>	Bathythrix thomsoni	Gelis agilis <sup>b</sup>	Gelis bicolor <sup>b,e</sup>	Gelis discedens <sup>b,e</sup>	Gelis fasciinctus <sup>b</sup>	Gelis melanocephalus <sup>b,e</sup>	Gelis micrurus <sup>b,e</sup>	Gelis rufogaster <sup>b,e</sup>	Gelis viduus <sup>b,e</sup>	Hemiteles maricisca <sup>c</sup>	Hidryta sordida <sup>a</sup>	Idolispina a. analis <sup>h</sup>	Polyaulon paradoxus <sup>c</sup>	Thaumatogelis audax <sup>c,d</sup>	Tromatobia ovivora <sup>f</sup>	Trychosis legator <sup>a</sup>	Trychosis cf. legator		Trychosis tristator <sup>a</sup>	Zaglyptus varipes <sup>i</sup>	Megeselia major	Sarcophaga sexpunctata	
Araneidae																												
<i>Araneus</i> spp.																					2							
<i>Araneus</i> cf. <i>quadratus</i>																				4								
<i>Larinioides cornutus</i>										24																3	27	
Lycosidae																												
<i>Pardosa agrestis</i>												10															10	
<i>Pardosa amentata</i>												2					5										7	
<i>Pardosa palustris</i>																	1										1	
<i>Pardosa prativaga</i>																	2										2	
<i>Pardosa pullata</i>																1											1	
<i>Trochosa</i> spp.																											3	
<i>Trochosa terricola</i>																											3	
Pisauridae																												
<i>Pisaura mirabilis</i>																								88			88	
Liocranidae																												
<i>Agroeca</i> spp.					4					12	85			1					22								124	
Clubionidae																												
<i>Clubiona reclusa</i>																									2		2	
Philodromidae																												
<i>Tibellus</i> spp.																											1	
<i>Tibellus oblongus</i>																											1	
Thomisidae																												
<i>Xysticus cristatus</i>																							2	1			3	
<i>Xysticus ulmi</i>																							7	4			11	
Total	2	5	18	1	5	4	1	4	5	81	12	218	12	116	13	12	9	6	1	22	6	14	1	96	2	3	1	670

The quantity of reared parasitoids is given. Additionally, host records mentioned in the following recent literature are framed with a dashed line (one source) or with a solid line (two sources): <sup>a</sup>Schwarz and Shaw (1998); <sup>b</sup>Schwarz and Shaw (1999); <sup>c</sup>Schwarz and Shaw (2000); <sup>d</sup>Schwarz (1998); <sup>e</sup>Schwarz (2002); <sup>f</sup>Oehlke and Sacher (1991); <sup>g</sup>Horstmann (1998); <sup>h</sup>Schwarz (1988); <sup>i</sup>Fitton et al. (1987). \*Secondary parasitoid, though unknown ichneumonid sp.



Two of the parasitic wasps are known as hyperparasitoids, which attack a primary parasitoid: *Gelis agilis* (Fabricius) and *Bathythrix thomsoni* (Kerrich) (Ichneumonidae: Phygadeuontini). They should be accounted as secondary parasitoids (pseudohyperparasitoids) in the parasitoid complex of the hosts: *Pachygnatha clercki* Sundevall (for *G. agilis*) and *Ero* cf. *furcata* (for *B. thomsoni*).

In samples that were taken for comparative purposes from outside of the investigated woodlands, several parasitoid–host records were made solely for spider species typical of open habitats.

Egg masses of *Pachygnatha* spp. (Tetragnathidae) are available in the field between the end of April and the end of July. In an abandoned grassland, in May 1997, 122 egg sacs were collected and reared in the laboratory; 35 (28.7%) of them were parasitized. *Gelis discedens* (Foerster) and *G. melanocephalus* (Schrank) were gregarious parasitoids in these egg masses. From another abandoned grassland, 103 *Pachygnatha* spp. egg masses collected in spring 1997 and 1998 presented a degree of parasitization of 20.4% caused by the same two species. At this location *G. discedens* also attacked egg sacs of *Tetragnatha* spp. (Tetragnathidae) with an unknown intensity (two out of 25 egg sacs were parasitized).

From egg masses of Araneidae both Hymenoptera and Diptera were reared. *Tromatobia ovivora* (Boheman) (Ichneumonidae: Ephialtini), a well-known gregarious parasitoid of *Araneus* spp. and *Araneus* cf. *quadratus* (Clerck) cocoons, was recorded. Egg sacs of *Larinioides cornutus* (Clerck) were parasitized by the fly *Sarcophaga sexpunctata* (Fabricius) (Diptera: Brachychera: Calypttratae: Sarcophagidae). Both species hibernate within the spider egg sac.

Parasitoids attacking egg cocoons of Lycosidae, a spider family showing intensive brood care, seem to be restricted to this family. From egg cocoons of *Pardosa agrestis* (Westring) and *P. amentata* (Clerck), collected sparingly at river margin sites of the river Weser, the gregarious parasitoid *Gelis micrurus* (Foerster) was reared. In another 100 cocoons of lycosids from an abandoned grassland *G. micrurus* could not be found, but *Hidryta sordida* (Tschek) (Ichneumonidae: Mesostenini) occurred as a solitary parasitoid in the egg cocoons of the lycosids *Pardosa amentata*, *P. palustris* (L.), *P. prativaga* (L. Koch), and *P. pullata* (Clerck). They were collected in June and September and their cocoons were overwintered in the laboratory. Imagines emerged in the year after egg sac collection. A third species parasitizing cocoons of lycosids, *Idiolispa analis* (Gravenhorst) (Ichneumonidae: Mesostenini), was reared from *Trochosa terricola* Thorell egg sacs coming from the river margin sites. This was a further solitary parasitoid that infected its host species at an unknown level.

In the case of *Clubiona reclusa* O. P.-Cambridge (Clubionidae) *Zaglyptus varipes* (Gravenhorst) (Ichneumonidae: Ephialtini) was found in a single brood of two males collected in grassland.

Altogether 44 egg cocoons of Thomisidae from abandoned grassland were reared. *Trychosis tristator* (Tschek) and *T. legator* (Thunberg) (Ichneumonidae: Mesostenini) both attack the egg sacs of both *Xysticus cristatus* Clerck and *X. ulmi* (Hahn) as solitary parasitoids. *Tibellus oblongus* (Walckenaer) (Philodromidae) is also attacked by *T. tristator*. The adult parasitoids emerged in the year of egg sac collection or, alternatively, they hibernated suggesting that both species are partly bivoltine. *T. tristator* was also reared from *Pisaura mirabilis* (Clerck) (Pisauridae) egg cocoons (see below).

With the exception of *T. tristator* parasitizing *P. mirabilis* sacs, none of the parasitoid–host relationships found from spider egg masses in open habitats could be recorded in the investigated woodlands.

The main emphasis of this study was the investigation of spider parasitoids in a Central European woodland.

Here, at least 10 parasitoid species of spider egg masses were recorded for 10 host species.

Whereas data for *Agroeca* spp. (mainly *A. brunnea*), *Ero* spp. (mainly *E. furcata*), *Floronia bucculenta*, and *Linyphia hortensis* are extensive and will be presented separately below, the following records could not be analysed quantitatively, due to small sample sizes.

In the beech stand *Gelis rufogaster* Thunberg parasitizes egg masses of linyphiids: apart from unidentified cocoons of this spider family, recorded hosts of this solitary parasitoid are *Labulla thoracica* (Wider) and *Tapinopa longidens* (Wider). In addition, *G. rufogaster* was reared from two cocoons of *Neriere peltata* (Wider) (Linyphiidae) which had been exposed in the beech stand using the petri dish method. An undetermined species of the genus *Aclastus* also attacks cocoons of *Neriere* spp. *Gelis viduus* (Foerster) was reared from egg sacs of *Macrargus rufus* (Wider) (Linyphiidae). Furthermore, *Aclastus micator* (Gravenhorst), *Polyaulon paradoxus* (Zetterstedt) (both Ichneumonidae: Phygadeuontini), and the phorid fly *Megeselia major* (Wood) (Diptera: Phoridae) were reared from undetermined spider egg masses collected in the beech stand.

In the sparse pine forest the egg masses of *Pachygnatha listeri* (Sundevall) (Tetragnathidae) are a food resource of *Gelis melanocephalus*. *Aclastus* cf. *gracilis* (Thomson) (only tentatively identified) was reared from an unidentified spider egg sac from the same area. *Trychosia tristator* attacks the egg cocoons of *Pisaura mirabilis*, a spider species that cares intensively for its brood. In abandoned grasslands of areas surrounding the forest, the spider and the parasitoid were both much more abundant. There, parasitization rates of *P. mirabilis* cocoons were sometimes up to 70% (for more details see Finch 2001).

#### Egg masses of *Ero* cf. *furcata*

Quantitative collections of egg sacs of this spider genus were conducted in the spruce forest and in the pine forest (Table II). In the former, sweep netting led to the recording of

Table II. Results of the investigation of egg masses of *Ero* cf. *furcata*.

	Type of forest stand	
	Spruce	Pine
Unparasitized egg masses	129	40
Mean number of eggs $\pm$ SD*	6.61 $\pm$ 1.61	5.92 $\pm$ 1.59
Parasitized egg masses	88	24
Degree of parasitism (ns)	40.6%	37.5%
Percentage of eggs consumed	>99%	100%
Parasitoid species		
<i>Gelis bicolor</i>	-/1	-
<i>Gelis rufogaster</i>	50/19	13/8
<i>Hemiteles maricesca</i>	5/7	-
<i>Bathythrix thomsoni</i> <sup>a</sup>	1/-	-
Indet. (unemerged)	5	-

The mean numbers of eggs and emerged spiderlings per egg mass were assessed from 128 and 36 unparasitized egg masses in spruce and pine forests, respectively. For emerged parasitoids the numbers of males/females are given.

<sup>a</sup>Secondary parasitoid.

\*Significant difference between spruce and pine stand ( $P < 0.05$ ); ns, not significant.

specimens of *E. furcata* and *E. tuberculata* (De Geer), in the pine stand only *E. furcata* was recorded. All egg sacs almost certainly belong to *E. furcata*, because that of *E. tuberculata* are more elongated and the spider itself was very rare.

Egg sacs were collected in early spring (March to May) or, with a lower frequency, in autumn (October, November). Adults of *E. furcata* were sampled in late summer and autumn (August to November) and in spring (May). Females that had been kept in captivity for a few days after collection produced egg sacs in September/October and in April. This suggests that in the field egg sacs are produced in spring as well as in autumn. However, young spiderlings emerged only in spring.

Each egg sac contains an average of six to seven eggs, with a minimum of four and a maximum of 11. Difference in egg number is significant between sites (*U* test,  $Z = -2.033$ ,  $P = 0.042$ ). Less than 4% of the eggs failed to develop (the causes for this are unknown), so that on average six spiderlings emerged from unparasitized sacs. Three primary parasitoids were reared: *Gelis bicolor* (Villers), *G. rufogaster*, and *Hemitheles maricesca* Schwarz and Shaw (Ichneumonidae: Phygadeuontini). A single specimen of *Bathythrix thomsoni* was reared as a secondary parasitoid, it was not clear, though, which species of primary parasitoid had been attacked. All parasitoids were solitary. *H. maricesca* was recorded during this investigation only in egg masses of *Ero* spp. Only in *G. rufogaster* sex composition differs significantly from equal distribution, with more males than females emerging (spruce forest: 72% males,  $\chi^2 = 13.93$ ,  $P < 0.001$ ; pine forest: 62% males, not significant). The degree of parasitism of *Ero* cf. *furcata* egg sacs was high: up to 40% were parasitized in the two forest stands (difference between the two stands: not significant). *G. rufogaster* achieved 32% parasitization, *H. maricesca* 4.3%, *G. bicolor* 0.4%, and unemerged or hyperparasitized parasitoids 3.3%. Each parasitoid larva usually consumes the whole egg complement in the cocoon, so that the overall mortality of *Ero* spp. caused by its parasitoids was around 40% (all of the parasitized egg sacs were unsuccessful).

### Egg masses of *Floronia bucculenta*

The egg sacs of *F. bucculenta* were collected in the spruce and the pine forest during March and April of all three investigation years (Table III). Many of them were found on leaves of

Table III. Results of the investigation of egg masses of *Floronia bucculenta*.

	Type of forest stand	
	Spruce	Pine
Unparasitized egg masses	372	427
Mean number of eggs $\pm$ SD***	17.79 $\pm$ 8.61	22.52 $\pm$ 9.15
Parasitized egg masses	16	3
Degree of parasitism**	4.15%	0.7%
Percentage of eggs consumed	>95%	100%
Parasitoid species		
<i>Gelis rufogaster</i>	3/12	–
<i>Gelis bicolor</i>	–	–/3
Indet. (unemerged)	1	–

The mean numbers of eggs and emerged spiderlings per egg mass were assessed from 107 and 120 unparasitized egg masses in spruce and pine forests, respectively. For emerged parasitoids the numbers of males/females are given.

\*\* , \*\*\*Significant difference between spruce and pine stand (\*\* $P < 0.01$ , \*\*\* $P < 0.001$ ).

*Molinia caerulea* and *Vaccinium* spp. Density was roughly estimated to reach 10 egg sacs per m<sup>2</sup>. In the field, females of *F. bucculenta* start oviposition at the beginning of September. Adult individuals were also collected by sweep net sampling in late summer and autumn (August to October). Hibernation of this univoltine spider takes place in the egg stage.

The mean egg number differs significantly between the two forests and is, respectively, 18 and 23 eggs per sac (*U* test,  $Z = -4.052$ ,  $P < 0.001$ ). Between 8% and 14% of these eggs did not develop, so that on average 16–19 spiderlings emerged per sac.

*Gelis bicolor* and *G. rufogaster* were the only parasitoids found in the egg sacs of *F. bucculenta*. Both were solitary. Contrary to the results from egg masses of *Ero* cf. *furcata*, significantly more females than males of *G. rufogaster* emerged (80% females,  $\chi^2 = 5.4$ ,  $P = 0.02$ ). In comparison with other spider species, the degree of parasitization of *F. bucculenta* was low: in the spruce forest it was below 5% and in the pine forest parasitization affected even less than 1% of the egg masses ( $\chi^2 = 10.552$ ,  $P < 0.01$ ).

### Egg masses of *Linyphia hortensis*

The elliptical egg cocoons of *L. hortensis* could be sampled during June in the beech stand from trunks of oak and beech trees. They were only partially hidden in the crevices of the bark. They contained on average 35 eggs (range: 27–50 eggs), from which around 15% failed to develop so that a mean number of 30 spiderlings emerged per cocoon (Table IV).

Only *Aclastus* species were recorded as parasitoids in the egg masses of *L. hortensis*. One specimen could not be identified to species level, the others were *A. micator*. Five cocoons produced broods of two individuals each, the remaining showed only a single parasitoid each. All parasitoids emerged in the laboratory within 2 weeks after collection of egg sacs.

The degree of parasitism of egg masses collected in the field amounted to about 10%. Egg masses exposed in the field with the petri dish method were parasitized with half of this intensity (4.4%), but differences were not significant ( $\chi^2 = 2.373$ ,  $P = 0.123$ ). On average about 40% of the eggs in the parasitized cocoons were left unconsumed (60% mortality).

Table IV. Results of the investigation of egg masses of *Linyphia hortensis*.

	Beech stand	
	Collected <sup>a</sup>	Petri dish <sup>b</sup>
Unparasitized egg masses	66	152
Mean number of eggs $\pm$ SD	nc	35.47 $\pm$ 5.76
Parasitized egg masses	7	7
Degree of parasitism (ns)	9.59%	4.4%
Percentage of eggs consumed	nc	59.83%
Parasitoid species		
<i>Aclastus micator</i>	3/2	4/2
<i>Aclastus</i> sp.	1/–	–
Indet. (unemerged)	5	3

The mean numbers of eggs and emerged spiderlings per egg mass were assessed from 15 unparasitized egg masses. For emerged parasitoids the numbers of males/females are given.

<sup>a</sup>Autochthon material from the beech stand; <sup>b</sup>egg masses exposed in the beech stand using the petri dish method. nc, not counted; ns, not significant.

*Egg masses of Agroeca spp.*

Egg cocoons (mostly believed to be of *A. brunnea*) were sampled during spring (April to June) at four different locations: in the beech stand, the spruce forest, and two edges of forests in the surroundings of Oldenburg. Sacs contained 39–44 eggs on average, with a minimum of 13 and a maximum of 57 (Table V). Differences in egg numbers were significant between the beech stand and forest edge II ( $U$  test,  $Z=-2.332$ ,  $P=0.02$ ) and between the two forest edges ( $Z=-2.309$ ,  $P=0.019$ ). On average 39 spiderlings emerged from each egg sac.

With the exception of *Gelis melanocephalus*, the parasitic wasps in the egg sacs of *Agroeca* spp. showed narrow host ranges: *Bathythrix formosa* Desvignes, *Gelis fasciitinctus* (Dalla Torre), and *Thaumatogelis audax* (Olivier) (all Ichneumonidae: Phygadeuontini) were only found in the egg masses of these spiders. These three parasitoid species were solitary. *G. melanocephalus* produced gregarious broods of  $6.5 \pm 2.5$  individuals. In two cases multi-parasitism was observed, i.e. single individuals of different parasitoid species emerged from the same egg sac (*G. melanocephalus* and *T. audax*). *T. audax* and *G. melanocephalus* were the most frequent species in the cocoons of *Agroeca* species. Sex ratio was not significantly different from equal except in the case of *G. fasciitinctus* (forest edge I:  $\chi^2=4.5$ ,  $P<0.03$ ), with more females than males. *B. formosa* was hibernated in the laboratory in the spider egg masses. The imagines of *G. melanocephalus* and *T. audax* emerged a few weeks after collection of the egg sacs in spring. *G. fasciitinctus* seems to be plurivoltine: nine out of 12 individuals emerged within 3 weeks of collection, and the remaining overwintered.

In the interior of the investigated woodlands egg sacs could be found only very sparsely and no parasitoids were recorded. In contrast to that, the level of parasitization on the forest edges, where the egg masses were more abundant, was quite high (up to 66%), with differences between the two edges being not significant ( $\chi^2=2.948$ ,  $P=0.086$ ). A high proportion of the spiders' brood is consumed in parasitized sacs; larvae left (mean  $\pm$  SD): none (*B. formosa*),  $0.3 \pm 1.2$  eggs (*G. fasciitinctus*),  $1.1 \pm 2.5$  eggs (*G. melanocephalus*), or even  $10.5 \pm 7.9$  eggs (*T. audax*) in the spiders' cocoons.

Table V. Results of the investigation of egg masses of *Agroeca* spp.

	Location			
	Beech	Spruce	Forest edge I	Forest edge II
Unparasitized egg masses	20	18	7	47
Mean number of eggs $\pm$ SD	$38.88 \pm 8.81$	nc	$37.29 \pm 6.37$	$43.59 \pm 7.90$
Parasitized egg masses	0	0	15	43
Degree of parasitism	0%	0%	66.18%	47.78%
Percentage of eggs consumed	–	–	>93%	>92%
Parasitoid species				
<i>Bathythrix formosa</i>	–	–	–	3/1
<i>Gelis fasciitinctus</i>	–	–	1/7	2/2
<i>Gelis melanocephalus</i>	–	–	1/3	37/44
<i>Thaumatogelis audax</i>	–	–	3/3	8/8
Indet. (unemerged)	–	–	0	7

The mean numbers of eggs and emerged spiderlings per egg mass were assessed from 17 (beech stand), seven (forest edge I) and 34 (forest edge II) unparasitized egg masses. For emerged parasitoids the numbers of males/females are given.  
nc, not counted.

**Discussion and conclusions**

In this study, rearing records for a broad spectrum of spider parasitoids are given. For both reared species of external spider parasitoids the host associations are relatively clear: *Acrodactyla degener* is a widespread parasitoid of linyphiids (in the present case, of *Neriene clathrata*) whereas published data for *Zatypota percontatoria* indicate that this species is restricted to certain *Theridion* species (Theridiidae) (Shaw 1994, 1998).

Apart from confirming existing biological knowledge about interactions between spiders and their egg sac parasitoids, this study gives us a new, detailed insight into hitherto unknown host–parasitoid relationships (Table I). For instance, for *Idiolispa analis* the author knows of no reliable host records in the published literature. Additionally, host species lists of *Gelis discedens*, *G. melanocephalus*, *G. rufogaster*, and *Trychosis tristator* were appreciably extended. It was furthermore possible to clarify the life cycle of the parasitoid *Aclastus micator*. This species was reared from *Drapetisca socialis* (Sundevall) by Schaefer (1976b; det Horstmann) and, during this study, from the egg sacs of *Linyphia hortensis*. Hence, its life cycle should be as follows: after developing in *L. hortensis* egg sacs during spring and early summer *A. micator* passes through a short diapause during summer and develops and overwinters in *D. socialis* cocoons. In addition, a contribution to parasitoid taxonomy was made during this study, as males of *Hemiteles maricesca* were unknown before they and their females were reared from cocoons of *Ero* spp. (Schwarz and Shaw 2000; Finch 2002).

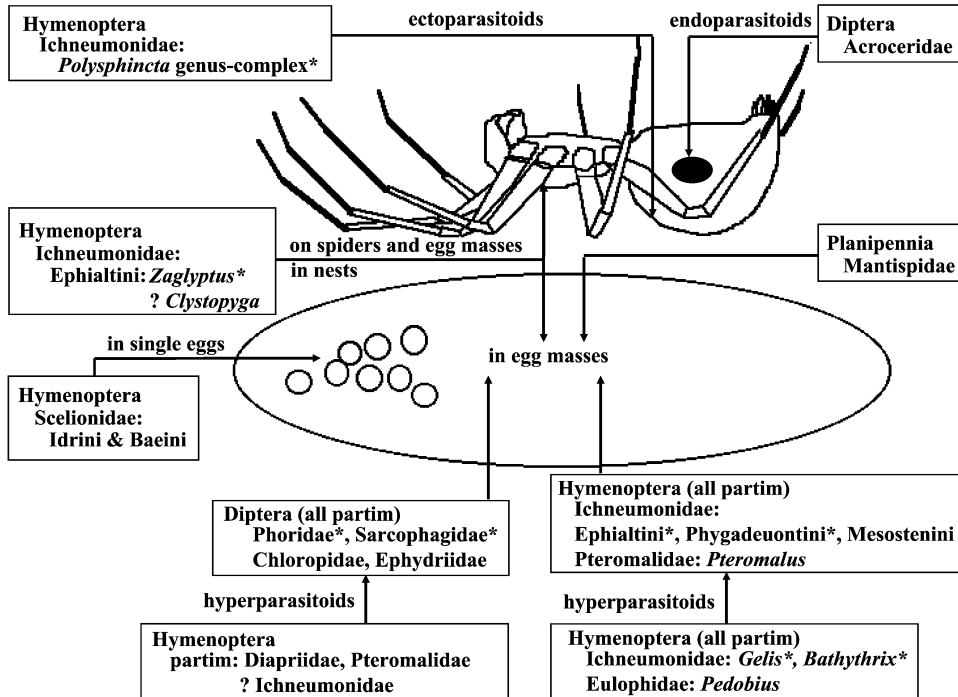


Figure 2. Qualitative parasitoid web of spiders in the Central European region. Compiled mainly from Fitton et al. (1987) and from further literature mentioned in this paper and in Finch (2001). \*Parasitoid taxa recorded during this study. ? not well-known relationship.

Figure 2 was compiled from the results presented here as well as from literature cited in this paper and in Finch (2001). It summarizes the known host–parasitoid relationships of spiders in Central Europe in the form of a qualitative parasitoid web.

On the other hand, consulting the relevant literature reveals that several families of insects well known as spider parasitoids were not recorded in the present study. Thus, the following parasitoids are missing from this study: orthorrhaphan Acroceridae (Schlinger 1987) and further cyclorrhaphan Diptera (e.g. Cyclorrhapha: Acalyptratae: Chloropidae; see Irwin 1979), Mantispidae (Neuroptera; see Wachmann and Saure 1997), Pteromalidae (Hymenoptera: Chalcidoidea) and Scelionidae (Hymenoptera: Proctotrupoidea; see Fitton et al. 1987). The Scelionidae are exceptional, for they are true parasitoids in spider eggs: each larva develops by feeding only in one egg (Austin 1984). A few species of the genera *Idris* and *Baeus* occur in Europe and are expected to be widely distributed (Fitton et al. 1987). In the present study species of the genus *Idris* were possibly not recorded since their host group (Lycosidae; see Huggert 1979) was not well represented in the material. *Baeus* species were found to parasitize Dysderidae, Agelenidae and Theridiidae (Fitton et al. 1987), as well as Linyphiidae (van Wingerden 1973; van Baarlen et al. 1994). Therefore, their absence in the material remains unexplained. The other mentioned unrecorded taxa are generally rarely observed, thus their absence in the studied material is not very surprising.

For all highly specialized Hymenoptera reported here as parasitoids of spiders, there are no reliable records from hosts other than spiders (Fitton et al. 1987; Schwarz and Shaw 1998, 1999, 2000). Especially the species with narrow host ranges, for example most parasitoids of *Argoeca* spp. egg masses, seem to be highly adapted to the life cycle and egg sacs of their hosts. In a hypothetical evolutionary process spiders should reduce the parasitoid-load of their egg masses by constructing species-specific egg cocoons; meanwhile, the species of parasitoids are acting as a selective agent and specialize on a certain form of cocoon. Here (diffusive) coevolution of parasitoids and their hosts seems to be apparent (Austin 1985; Hieber 1992).

Quantitative studies concerning parasitism of spider egg masses in Central European woodlands have rarely been published (e.g. Edgar 1971). Parasitism on various spider species has been investigated quantitatively only in a few other habitats (Kessler and Fokkinga 1973; van Wingerden 1973; Rollard 1990). Studies on the parasitism of linyphiid spiders are scarce even from arable land (van Baarlen et al. 1994; Dinter 1996). For example, Dinter (1996) noticed highest parasitization rates of *Erigone* spp. (Linyphiidae) egg sacs in winter wheat during July (up to 5.7%). In the study by van Baarlen et al. (1994) egg sacs of *Erigone* were attacked by two species of parasitoids with a mean parasitization value of 17.1%. Highest values (28.6%) were observed during July. Van Wingerden (1973) found in Dutch coastal habitats—also during July—approximately 50% of the eggs of *Erigone arctica* White to be consumed by two parasitoid species (*Aclastus minutus*, *Gelis pumilus* (Foerster)). Furthermore, in contrast to Dinter (1996), in van Wingerden's investigation the percentage of egg sac parasitism increased during the vegetation period. Rollard (1990) recorded the level of infestation by hymenopterous parasitoids for seven spider species in heathlands in northern France. Two of these spider species were also investigated in the present study. In the heathlands 35.2% of *Argoeca brunnea* egg sacs were parasitized, ranging from 30.0 to 44.1% in different years (Rollard 1990). This is fairly well in agreement with the values presented here from woodland edges for the same genus of spiders. Additionally, Rollard (1990) observed a considerably lower level of infestation of *Ero* spp. egg sacs (26.7%) than the one observed in the present study (approximately 40%). Summarizing these quantitative aspects of spider egg mass parasitization it becomes

obvious that, despite methodological variations (e.g. Dinter 1996), the degree of parasitism varies not only between spider species but also strongly spatially and temporally.

In studies on population dynamics of spiders and in (metapopulation) models based on these studies, the mortality of eggs and spiderlings has to be considered, since especially the mortality of eggs is expected to be most important for a spider's life cycle (Topping 1997). According to Topping (1997), fungi, parasitoids, and various predators (e.g. birds) are responsible for egg mortality. In this study mortality of spider eggs solely induced by parasitoids was up to 40% or even 60% for some spider species. Although the temporal variability in parasitism rates was not investigated here, overall a high proportion of spider mortality induced by parasitoids seems to be present at most locations. But such generalizing averages could be deceptive, due to the demonstrated spatially and temporally species-dependent variability in the parasitization rates.

From an ecological point of view we have to admit that until today we only have a few hints indicating that parasitoids can exert top-down control on spider populations (Wise 1993). On the other hand, for example, Schaefer (1978) found the number of available sites for web placement to be the ultimate factor in regulation of population densities of *F. bucculenta*. But there may be no general truth in this, leaving it at present unclear as to what extent, in general, the availability of sites for web placement, the food supply or other density-dependent factors may outweigh the importance of parasitoids.

### Acknowledgements

Thanks to M. Schwarz (Linz, Austria; species of the genera *Bathythrix*, *Gelis*, *Hemitheles*, *Hidryta*, *Idiolispa*, *Thaumtogelis*, and *Trychosis*), K. Horstmann (Würzburg, Germany; species of the genera *Aclastus*, *Acrodactyla*, *Tromatobia*, *Polyaulon*, and *Zatyota*), S. Prescher (Braunschweig, Germany; genus *Megeselia*), and T. Pape (Stockholm, Sweden; genus *Sarcophaga*) for their help in the determination of the parasitoids. With M. Schwarz, P. van Baarlen (Wageningen, The Netherlands), and M.R. Shaw (Edinburgh, UK) I had fruitful discussions about parasitoid biology. Special thanks to R. Biedermann (Oldenburg, Germany), N.D. Springate (London, UK) and again to M.R. Shaw who kindly improved earlier versions of this manuscript. T. Holle (Oldenburg, Germany) collected the spider egg sacs at the river margin sites of the river Weser.

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