

Long-term fluctuations of the spider populations (Araneida) in a northern German woodland¹

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Summary

During a seven year period, from 1989 to 1995, spider populations were investigated by hand sorting and Macfadyen extraction from 0.1 m² of litter in three woods situated along a cross section from an alder wood at Lake Belau to a beech wood on a hilltop. In total, 68 adult spider species were recorded with average yearly densities ranging between 17 ind./m² in the alder wood and 37 ind./m² in the beech wood. Average yearly densities of juvenile spiders ranged between 43 ind./m² in the alder wood and 127 ind./m² in the beech wood. Most of both juvenile spiders and adult species showed a distinct seasonality with maximum densities of juvenile spiders in summer and of adult species in late autumn or winter. Intervals between maximum of juvenile spiders and six analysed species ranged between three and six months, which were also significant in long-term analyses. Effects of rainfall, temperature, litter fall, collembolan density, and groundwater level fluctuations on spider populations were analysed by time series statistics. Rainfall was the most frequently effective climatic parameter and was negatively correlated with the densities of each spider species investigated. Litter fall and collembolan densities were commonly found to have a positive influence on the spider populations. It is supposed that adult spider populations are regulated by litter fall via collembolan density and juvenile spider abundance in the beech wood, while groundwater fluctuations effects juvenile spider abundance via collembolan density in the alder wood.

Introduction

According to the predicted global change of climate, increasing rainfalls and temperatures are expected that will also influence the communities of northern German ecosystems. The spatial reduction of the salt marsh communities have been derived from the changing dynamics of low and high tides (NEUHAUS et al. 1998, IRMLER et al. 2002). Geographical displacements of species, a changing species composition and activity, as well as dependent ecological processes, e.g. litter breakdown or energy

¹ Professor Dr. Berndt Heydemann to his 75th anniversary

turnover in the food web, will occur in mainland ecosystems (BOCK et al. 1995). Concerning birds, for example, migration behaviour and breeding success will change (BAIRLEIN & WINKEL 1998, MOSS 1998). In phytophagous insects, e.g. leaf hoppers (Auchenorrhyncha) and butterflies (Lepidoptera), an earlier seasonal occurrence has been presumed by long-term investigations, which will amount to 11.6 days within 20 years for butterflies (SPARKS & CARY 1995) and will result in an increase of the yearly number of generations of leaf hoppers (HANSSEN & IRMLER 1995, MASTERS et al. 1998).

At present, long-term investigations regarding climate-based fluctuations of soil faunal populations are rare and hardly allow general conclusions on the reaction of the fauna. BERG et al. (1998) assumed that climate changes will have an effect on functional groups of the soil fauna, but that differentiation of microhabitats or decomposition of the organic substances will be of greater importance. Similar results were published for the nematod fauna based on displacement experiments in the Nordic tundra (SOHLENIUS & BOSTROM 1999). Concerning climate-related fluctuations of the predatory soil fauna, e.g. spiders, no investigations are available.

The present study, which is based on a 7-year investigation of three wood types in Schleswig-Holstein, mainly focuses on the relations between the density fluctuations in the spider fauna and climate factors, litter fall, and density of their collembolan prey. Thus, probable predator-prey relations will also be analysed. The following questions should be answered:

- 1) Which environmental parameters influence the fluctuations in the spider populations?
- 2) How long is the reaction time to impact parameters?

Sites and methods

The investigations were performed in a woodland at Lake Belau about 30 km south of Kiel (northern Germany) between 1989 and 1995. The woodland was divided into three areas. A beech forest with acidic Dystric Cambisol soils (pH 3.5) was situated on the hilltop, an afforested, young coniferous forest, also containing hazel and oak, followed at the hillside and an alder forest, which had a characteristic spatial pattern of soil moisture due to a central depression of the floor, was at the lake margin. Further characterisations of the three woodland areas, the vegetation and other groups of the soil fauna are described by IRMLER (1995). The soils were characterised in detail by SCHLEUSS (1992).

Spiders were sampled from litter at a 0.1 m² frame. In the laboratory, the spiders were collected from the litter by hand-sorting, subsequently followed by heat extraction in a Macfadyen apparatus for 10 days (MACFADYEN 1962). Sampling was performed monthly in 1989 and 1990, and every two months between 1991 and 1995, with exception of 1992, where, again, a monthly sampling was executed in the alder wood. The number of replicate samples were 4 in the beech and alder wood, and 2 in the mixed forest at the hillside. Within the alder wood each of the 4 sampling sites was situated along a cross section in different distances to groundwater level (Fig. 1).

Climate data were obtained using the data from the climate station at Wankendorf, a village in 2.5 km distance from the investigated woodland. Litter was sampled by 1 m² funnel collectors directly adjacent to the spider sample area and analysed in detail (SPRANGER 1992). Only the data on leaf litter and total litter have been used for further investigation in this study. Additionally, groundwater level was determined monthly

at each site in the alder wood using 50 cm long groundwater pipes with openings at intervals of 5 cm.

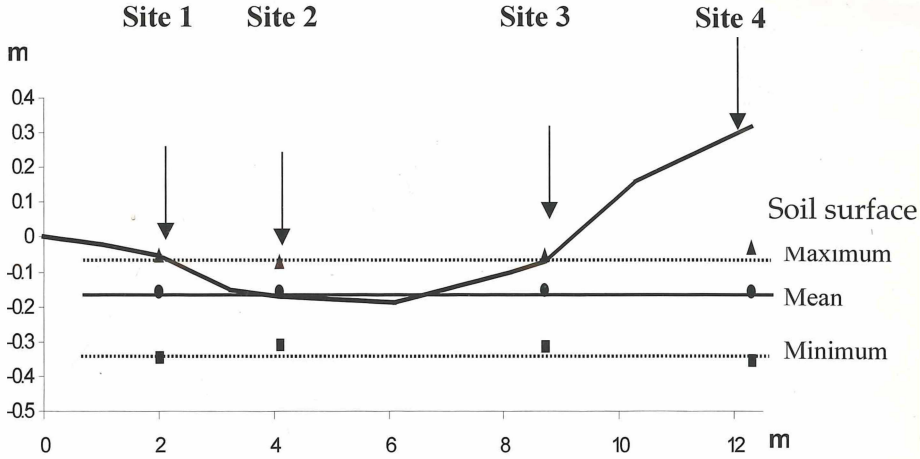


Fig. 1: Situation of sampling sites in the alder wood along a cross section with distance to the lake margin. The data on maximum, mean and minimum refer to the average groundwater level during the seven year study period.

The program Statistica was used for the statistical analyses (STATSOFT 1996). A time series analysis was performed to determine long-term trends in order to calculate seasonally adjusted curves and to correlate climatic changes with the fluctuating abundance of the spider species. The seasonally adjusted curves were chosen to focus on long-term trends and to avoid the correlation between the endogenous seasonality of species with the seasonality of climate factors. The additive model was selected to produce the seasonally adjusted trend curve. Cross correlation was performed to calculate the lag time. In cross correlation, the environmental parameters analysed are successively correlated at monthly intervals with the abundance of the species. The shortest significant ($p < 0.05$) period between the environmental parameters and the abundance of the species was taken as lag time, which can be regarded as the reaction time between the abundance of the spider species and the respective environmental factor. Lag time reflects the time between the occurrence of a triggering environmental situation, e.g. rainfall, and the reaction of the species, which is expressed in changes in abundance. The reaction time may be influenced either by different developmental times, or by migration and the population dynamics affected by the ecological conditions. Lag times longer than 12 months were omitted. Counter plots of abundance were achieved by using distance weighted smoothing of smallest quadrates.

Results

Changes of the environmental parameters during the investigated time period

The investigated years (from 1989 to 1995) provided different climatic situations (Fig. 2). The year 1990 was relatively warm, which had to do with the very warm winter (mean January temperature: 3.7 °C), whereas the summer was relatively cool. The year 1994 was also warm as a result of the warm summer. Both years were characterised by extremely strong rainfall. The years 1991 and 1994 represented the coldest winter periods, while 1994 and 1995 reached high summer temperatures. The driest year of the studied period was 1993.

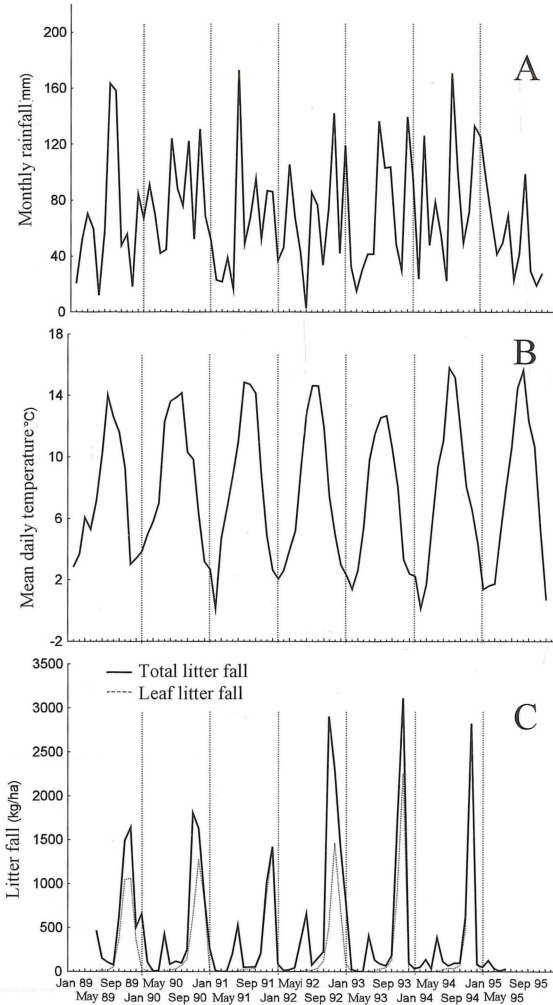


Fig. 2: Fluctuation of the rainfall (A), the temperature (B), and total litter fall and leaf litter fall (C) in the beech wood during the 7 years studied.

Litter fall showed high fluctuations between the years as well. In 1992, litter fall was

nearly twice as high as in the preceding year, 1991. The year 1993 was also characterised by very high litter fall. The yearly litter input into the beech wood, the mixed wood at the hillside and the alder wood amounted to averagely 5500 kg/ha, 4500 kg/ha, and 6500 kg/ha, respectively.

The groundwater level fluctuated according to the seasons, with high levels in the early spring and low levels in autumn (Fig. 3). In 1994 and 1995, groundwater levels were above average, causing the stations 2 and 1 in the alder wood to be waterlogged for a long time period. In contrast, the years 1991 and 1992 were relatively dry and the groundwater level was below soil surface throughout the entire year.

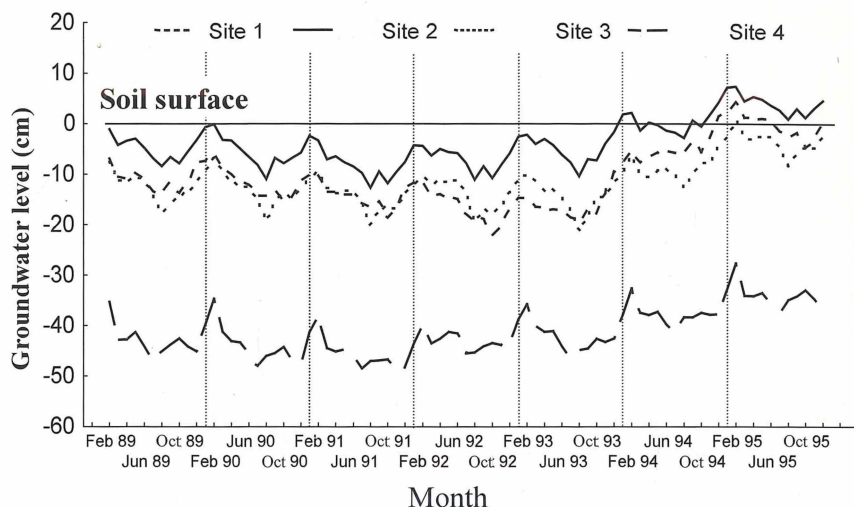


Fig. 3: Fluctuation of the groundwater level at the 4 stations along the cross section in the alder wood.

The composition of the spider fauna

Overall, the average yearly densities of adult spiders decreased continuously from the beech wood to the alder wood, with 37 ind./m² at the beech wood, 30 ind./m² at the mixed wood at the hillside, and 11 ind./m² at the alder wood (Table 1). Juvenile spiders showed a corresponding reduction from 127 ind./m² in the beech wood, to 72 ind./m² in the mixed wood at the hillside, and then 43 ind./m² in the alder wood. The spiders in the woodland that occurred most frequently were *Robertus lividus*, *Microneta viaria*, *Saloca diceros*, and *Macrargus rufus*, with an average between 8 and 15 ind./m². Typical species of the beech wood were *Macrargus rufus* and *Coelotes terrestris*, whereas *Saloca diceros* and *Gongylidium rufipes* dominated in the alder wood. *Microneta viaria* occurred in relatively high densities throughout the complete woodland area. The mixed wood at the hillside can be regarded as a transitional area between the beech wood on the hilltop and the alder wood at the lake margin, because *Gongylidium rufipes*, frequently found in the alder wood, and *Robertus lividus*, commonly found in the beech wood, were also represented by high densities in this area. According to their high densities, *Micrargus herbigradus* can be considered as the typical spider species of the mixed wood at the hillside.

Table 1: Mean densities (ind. m⁻²) of spider species in the investigated woodland.

Species	Beech wood		Hillside wood		Alder wood	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
<i>Macrargus rufus</i>	7.0	1.8	0.4	0.0	0.1	0.2
<i>Microneta viaria</i>	6.1	0.7	4.2	0.8	1.4	1.0
<i>Robertus lividus</i>	6.1	0.5	3.6	3.7	0.6	0.4
<i>Centromerus dilutus</i>	4.1	1.4	1.5	1.0	.	.
<i>Coelotes terrestris</i>	3.4	0.8
<i>Saloca diceros</i>	1.4	1.5	0.5	0.1	3.5	3.1
<i>Bathypantes parvulus</i>	1.1	0.6	2.8	0.6	0.2	0.4
<i>Tapinocyba insecta</i>	1.1	0.8	2.6	0.3	.	.
<i>Walckenaeria cucullata</i>	0.9	0.2	0.1	0.1	.	.
<i>Walckenaeria dysderoides</i>	0.8	0.6	0.9	0.1	.	.
<i>Centromerus sylvaticus</i>	0.8	0.4	0.8	0.6	0.2	0.2
<i>Walckenaeria antica</i>	0.7	0.4	0.1	0.1	.	.
<i>Lepthyphantes tenebricola</i>	0.6	0.4	0.1	0.1	0.1	0.2
<i>Clubiona terrestris</i>	0.4	0.3	0.3	0.1	0.3	0.3
<i>Porrhomma pygmaeum</i>	0.4	0.2	0.1	0.1	.	.
<i>Diplocephalus picinus</i>	0.3	0.2	0.2	.	0.4	0.2
<i>Helophora insignis</i>	0.3	0.3	.	.	0.2	0.3
<i>Porrhomma pallidum</i>	0.2	0.2	0.4	0.3	0.1	0.1
<i>Erigone atra</i>	0.2	0.2	0.2	0.0	.	.
<i>Bathypantes nigrinus</i>	0.2	0.2	.	.	0.2	0.3
<i>Erigonea hiemalis</i>	0.2	0.2	.	.	0.1	0.1
<i>Walckenaeria obtusa</i>	0.2	0.2
<i>Micrargus herbigradus</i>	0.1	0.1	2.5	0.4	0.1	0.1
<i>Meta segmentata</i>	0.1	0.1	0.6	0.3	0.1	0.1
<i>Maso sundevalli</i>	0.1	0.1	0.5	0.4	0.4	0.2
<i>Lepthyphantes pallidus</i>	0.1	0.1	0.4	0.3	0.3	0.2
<i>Gonatium rubellum</i>	0.1	0.1	0.4	0.0	.	.
<i>Walckenaeria acuminata</i>	0.1	0.1	0.2	0.3	0.1	0.1
<i>Lepthyphantes zimmermanni</i>	0.1	0.1	0.1	0.1	.	.
<i>Porrhomma microphthalmum</i>	0.1	0.1	0.1	0.1	.	.
<i>Lepthyphantes alacris</i>	0.1	0.2	0.1	0.1	.	.
<i>Centromerus pabulator</i>	0.1	0.1
<i>Anyphaena accentuata</i>	0.1	0.1
<i>Lepthyphantes cristatus</i>	0.1	0.1	0.1	0.1	0.1	0.2
<i>Linyphia hortensis</i>	0.1	0.1	0.1	0.1	.	.
<i>Xysticus ulmi</i>	0.1	0.1	.	.	0.1	0.3
<i>Walckenaeria corniculans</i>	0.1	0.1
<i>Lepthyphantes flavipes</i>	0.1	0.1
<i>Asthenargus paganus</i>	0.1	0.1
<i>Zora spinimana</i>	0.1	0.1
<i>Linyphia triangularis</i>	0.1	0.1
<i>Erigone dentipalpis</i>	0.1	0.1
<i>Gongylidium rufipes</i>	.	.	2.3	0.4	3.9	1.1

Species	Beech wood		Hillside wood		Alder wood	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
<i>Clubiona comta</i>	.	.	0.8	0.0	.	.
<i>Agyneta subtilis</i>	.	.	0.6	0.8	.	.
<i>Tapinocyba bispissa</i>	.	.	0.5	0.7	.	.
<i>Diplostyla concolor</i>	.	.	0.3	0.1	0.7	0.6
<i>Ceratinella brevis</i>	.	.	0.2	0.0	0.5	0.3
<i>Clubiona lutescens</i>	.	.	0.2	0.3	0.2	0.4
<i>Clubiona stagnatilis</i>	.	.	0.2	0.0	0.2	0.2
<i>Lepthyphantes angulipalpis</i>	.	.	0.2	0.3	.	.
<i>Agyneta decora</i>	.	.	0.2	0.0	.	.
<i>Pachygnatha clercki</i>	.	.	0.1	0.1	0.6	0.7
<i>Trochosa terricola</i>	.	.	0.1	0.1	0.4	0.6
<i>Zygiella atrica</i>	.	.	0.1	0.1	.	.
<i>Porrhomma convexum</i>	.	.	0.1	0.1	.	.
<i>Pelecopsis parallela</i>	.	.	0.1	0.1	.	.
<i>Lethyphantes angulatus</i>	.	.	0.1	0.1	.	.
<i>Hilaira pervicax</i>	.	.	0.1	0.1	.	.
<i>Agyneta conigera</i>	.	.	0.1	0.1	.	.
<i>Tetragnatha montana</i>	0.3	0.2
<i>Pirata piraticus</i>	0.2	0.2
<i>Dicymbium tibiale</i>	0.1	0.1
<i>Pachygnatha degeeri</i>	0.1	0.1
<i>Meioneta saxatilis</i>	0.1	0.2
<i>Diplocephalus latifrons</i>	0.1	0.2
<i>Clubiona subtilis</i>	0.1	0.2
<i>Clubiona phragmitis</i>	0.1	0.1
Sum	37.0	14.3	30.2	14.4	16.9	14.2

The long-term fluctuations of the spider species

All spider species investigated showed seasonal dynamics, which were expressed differently in the single species (Fig. 4 and 5). The maximum of juvenile spiders was in summer at all three parts of the wood, while the maximum of adult spiders was in autumn or winter. Within the beech and alder wood, juvenile spiders reached their maximum in June or July; in the hillside wood they reached their maximum in August - distinctly later. Compared to juvenile spiders, the peaks of the most frequently found adult spiders in the beech wood occurred much later: 4 months later for *Macrargus rufus* and *Robertus lividus* (October), 5 months later for *Microneta viaria* (November), or even 6 months later for the distinctly larger species *Coelotes terrestris* (December). A longer developmental period by *Microneta viaria* in comparison to the similarly large *Macrargus rufus* and *Robertus lividus* can be concluded from this longer interval, which was also recognizable in the long-term trend. The time lag by adult species on the long-term density changes in juvenile spiders amounted to 6 months ($r = 0.72$) in *Microneta viaria*, and 3 months ($r = 0.60$) in *Macrargus rufus* and *Robertus lividus* ($r = 0.66$).

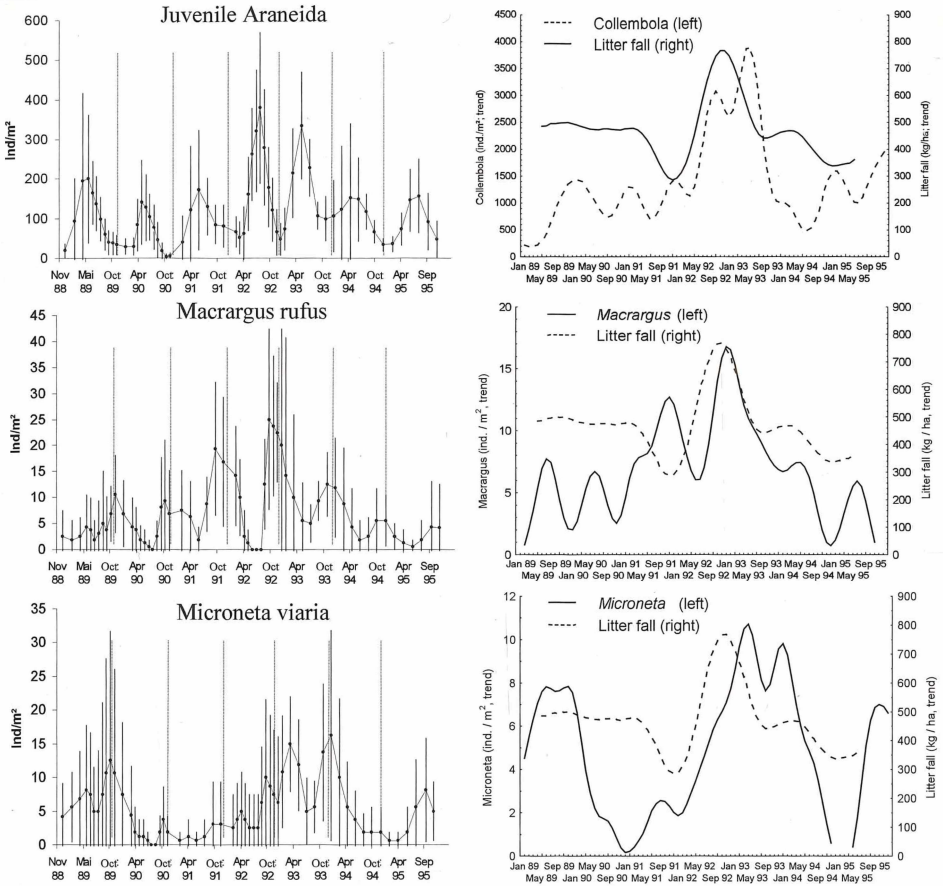


Fig. 4: Density fluctuations of juvenile spiders and the spider species *Macrargus rufus* und *Microneta viaria* (left side), as well as trend results between the two spider species and Collembola as prey organisms and litter in the beech wood (right side).

The seasonal maximum of adult *Microneta viaria* on the hillside and in the beech wood was in November, while maximum of juvenile spiders was in August on the hillside wood and in June in the beech wood. Thus, on average, reproduction seems to be later on the hillside than in the beech wood, but can be compensated by a faster development in the summer. Concerning the long-term trend at the hillside wood, the abundance of adult *Microneta viaria* correlated with that of juvenile spiders with a lag time of 12 months ($r = 0,37$), which is much longer than in the beech wood. For *Robertus lividus*, no significant correlation at the hillside wood was calculated due to the low abundance.

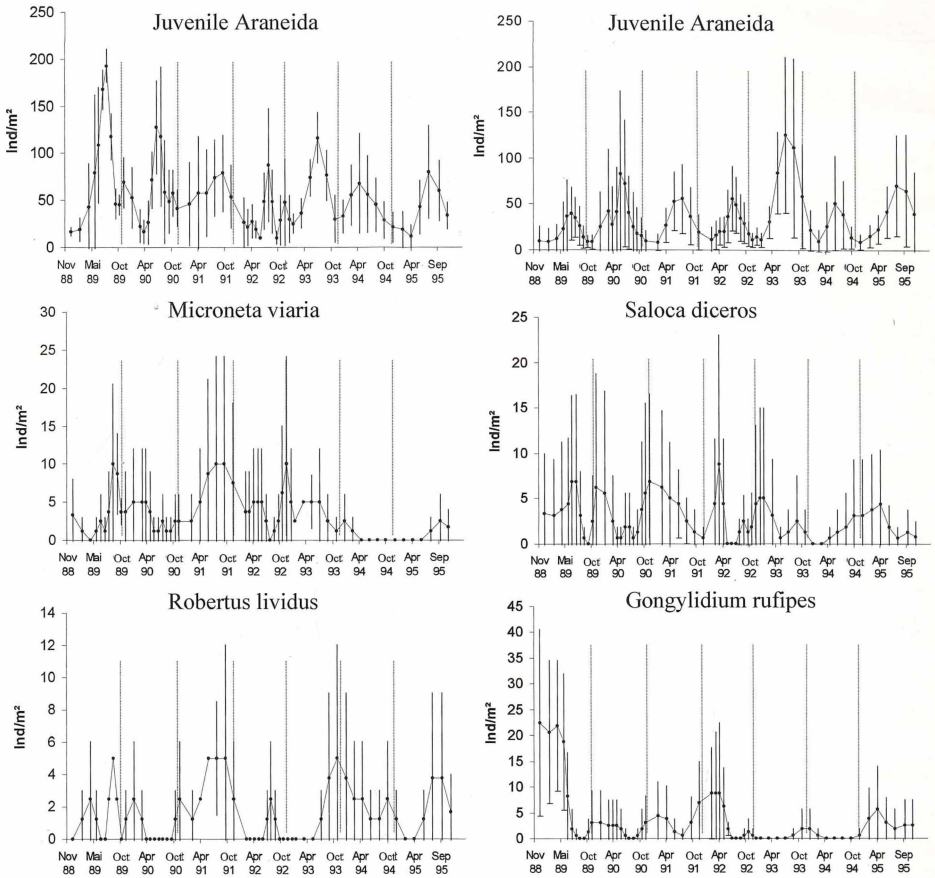


Fig. 5: Abundance fluctuations of juvenile spiders and of 4 adult spider species in the hillside wood (left) and the alder wood (right).

A different seasonality in the spider fauna was observed in the alder wood. The very small species *Saloca diceros* passed two seasonal peaks: the first in June at the maximum of juvenile spiders, and the second in December/January. There was no relation recorded between the juvenile spiders and the adult *Saloca diceros* seasonality. In contrast, adult *Gongylidium rufipes* passed an obvious abundance depression during the maximum of juvenile spiders in June/July, subsequently followed by a density increase after November and reached its maximum abundance in the wintertime between February and April. Thus, the maximum abundance was nearly 5 months later than the juvenile spider maximum. A similar time lag of 4 months was determined between juvenile spiders and adult *Gongylidium rufipes* for the 7 investigated years by using cross correlation ($r = 0.27$).

Table 2: Results of cross correlations between the abundance of juvenile spiders or several spider species and environmental parameters. The lag data lists the retarded reaction of spiders in months (R = correlation coefficient; only significant results with $p < 0.05$ are listed).

Species	Site	Rainfall		Temperature		Litter fall		Collembola		Groundwater level	
		Lag	r	Lag	r	Lag	r	Lag	r	Lag	r
Araneida juvenile	Beech	3	-0.27			0	0.53	0	0.71		
Araneida juvenile	Mixed	2	-0.35					0	0.30		
Araneida juvenile	Alder	4	-0.26					1	0.85	2	-0.39
<i>Macrargus rufus</i>	Beech	6	-0.32	12	0.37	3	0.51	3	0.51		
<i>Microneta viaria</i>	Beech	3	-0.29	3	-0.64	3	0.63	7	0.61		
<i>Microneta viaria</i>	Mixed	3	-0.56					1	0.51		
<i>Robertus lividus</i>	Beech	3	-0.25	3	-0.57	12	0.29	2	0.44		
<i>Robertus lividus</i>	Mixed	2	-0.26	4	-0.49						
<i>Coelotes terrestris</i>	Beech	6	-0.43								
<i>Saloca diceros</i>	Alder			6	0.56						
Species richness	Beech	6	-0.27								
Species richness	Mixed	2	-0.33	12	0.70						
Species richness	Alder	1	-0.48	12	0.29					12	-0.31

Relations between spider populations and environmental parameters

Significant results in the trend correlation of the time series analyses were frequently revealed (Table 2). Abundance trends were negatively correlated with rainfall in all cases, implying that high rainfall caused low spider abundance (Fig. 6). Concerning rainfall, time lags of juvenile spiders were between 2 and 4 months, whereas time lags of adult spider species ranged between 3 and 6 months. The relations between temperature and spider abundance were less uniform. Neither negative nor positive relations were found. In the beech and in the hillside wood, high temperatures seemed to impact *Robertus lividus* negatively. Thus, warm years resulted in a decrease of the abundance of this species.

Uniformly positive relations also occurred between spider abundance and litter fall or collembolan density in all three wood areas (Fig. 4 and 6). In particular, close relations with short time lags between 0 and 3 months existed between spider abundance and collembolan density (Table 2). Time lag of *Microneta viaria* in the beech wood was comparably long - 7 months. The absence of a significant relation between adult spider abundance and groundwater level in the alder wood was astonishing. A weakly significant correlation with a time lag of 2 months was only found for juvenile spiders (Fig. 6). A still closer correlation was determined between abundance fluctuation of Collembola and the juvenile spiders. The time lag between these two soilfaunal groups was 1 month.

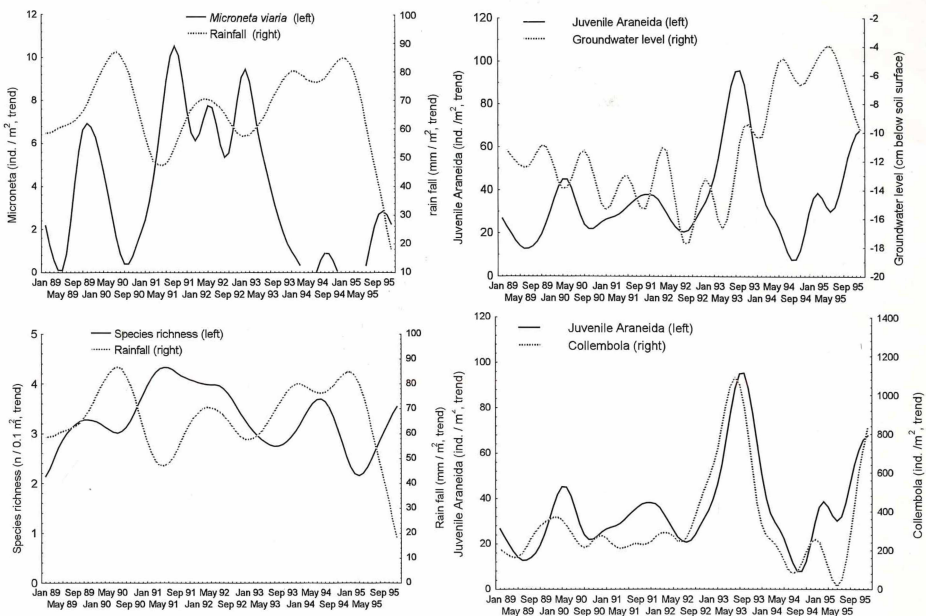


Fig. 6: Trend-curves for rainfall, abundance of *Microneta viaria* and species richness in the hillside wood (left), and those for juvenile spiders, groundwater level and collembolan density in the alder wood (right).

The contour plots of *Saloca diceros* and *Gongylidium rufipes* suggested high temporal and spatial dynamics of spiders in the alder wood (Fig. 7). During the investigated period, *Saloca diceros* reached highest densities in the upper part of the alder wood and seemed to migrate downwards in periods of low groundwater level, such as in 1991 and 1992. At the beginning of the investigation, *Gongylidium rufipes* inhabited the entire alder wood area, but subsequently retreated during the following period.

Fluctuations of species richness were also related to the climate parameters (Table 2). Rainfall had a negative effect and temperature had a positive effect in all three parts of the wood, with exception of the beech wood. In the alder wood, a negative effect of the groundwater level was observed.

Discussion

The global climate change has already resulted in a considerable shift in the spider fauna of Schleswig-Holstein. The web spider *Argiope bruennichi*, for example, has expanded into northern parts of Schleswig-Holstein during the past 10 years (WINKLER 1998). Spiders are dependent upon climate conditions in many different ways. Particularly linyphiid spiders are quite dependent upon weather conditions due to their dispersion by ballooning. THOMAS et al. (2003) found interdependencies between behaviour and weather. According to their investigations, spiders cover distances of up to 30 km when the weather conditions are suitable. In particular, rough temperature declines seem to impact the ballooning (BISHOP 1990). Therefore, spiders have adapted well in order to disperse fast, implying that a relatively rapid immigration of new species can occur. This behaviour was mainly observed in species of the open landscape, but BISHOP (1990) noticed very high densities in levels of 33 m and 44 m above the canopy of forests during spring time, which led to the assumption that the fauna of woods can be affected by this behaviour as well.

Within the two areas nearest to the lake, fluctuation of species richness was both positively and negatively related to temperature and rainfall, respectively. As ballooning is mainly initiated by dry and windy weather conditions, a negative relation to the rainfall was expected. The close, positive correlation of species richness to the temperature at the hillside wood can be explained by the invasions of spiders across the lake due to the wind-exposed situation of the site. Spiders with ballooning behaviour may pass the lake by the wind impinging on the hillside. This also explains the lacking correlation between the species richness and the temperature in the beech wood, which is less affected by the dispersion due to its more sheltered situation on the hilltop. The alder wood seems to profit from the high dispersion potential by being openly exposed to the lake, too. Most spider species prefer warm and dry sites, which explains the negative relation of species abundance to the groundwater level in the alder wood. Particularly long, waterlogged situations result in a decrease of spiders such as in the year 1994.

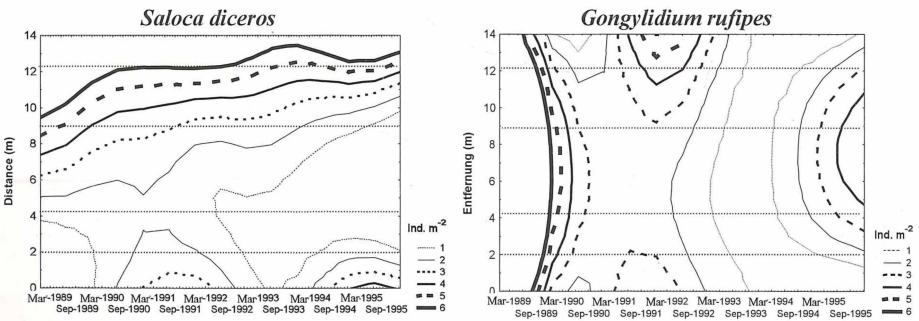


Fig. 7: Contour plots (ind./m²) of *Saloca diceros* and *Gongylidium rufipes* in the alder wood. Distance data refers to the distance from the lake margin. The dotted horizontal lines indicate the 4 investigated sites.

Furthermore, spider populations are indirectly affected by the climate-based fluctuations of their prey organisms or their predators, because of their involvement in the food web. One such indirect relation was found by SPILLER & SCHOENER (1995),

who observed climate-based population fluctuations of lizards feeding on spiders. In their investigations, rainfall on islands with lizards had a smaller impact on the spider populations than rainfall on islands without lizards, which shows that biotic relations influence the abiotic effects. The lag time by the rainfall amounted to 6 months in their study.

The influence of predator populations on spiders was not investigated in the present study, but the prey population of spiders, which is mainly Collembola for the small litter-dwelling species, obviously effected the spider density. In particular, juvenile spiders reacted to the fluctuation of the collembolan density with an extremely short delay of one month. Retardation of adult spiders was distinctly longer, ranging between 1 and 7 months, and can be referred to the development of juvenile spiders. As in the beech wood, a relation was found between collembolan density and litter fall; it can be assumed that the amount of litter fall influences the energy flow in the food web. It seems that the litter fall regulates the density of Collembola, the main prey organisms, and controls the density of juvenile spiders and, therewith, the density of adult species.

A direct influence of Collembola on adult spiders in *Microneta viaria* may exist at the hillside wood. There they responded to the collembolan density with a lag time of one month. This time lag is considerably shorter than the development period derived from the lag time between the maximum of juvenile spiders and the peak of adult *Microneta*.

In the alder wood, very complex relations seem to exist between the long-term fluctuations of Collembola, rainfall, temperature, and the groundwater level, which cause spatially and temporally oppositional patterns (IRMLER 2004). These complex relations may be the reason that collembolan density in the alder wood only correlated with juvenile spiders. This correlation showed a closer relationship than the correlation with the climate parameters and leads to the assumption that the groundwater level regulates the collembolan density, which subsequently controls the adult spider density via juvenile spiders in a more spatially and temporally diverse pattern than in the beech forest.

Short-term relations between the spider fauna and climate factors have been detected in Finland (NIEMELÄ et al. 1994), where similar results as in the presented study were found. In the Finnish investigations, spider activities showed a negative correlation with rainfall and were not related to temperature. *Macragus rufus* that was also most frequently found in the Finnish forests exhibited a positive relation to the temperature in the investigated beech forest of northern Germany. The influence of temperature has developed differently in several spider families. BAYRAM & LUFF (1993) found relatively high sensibilities to super-cooling in Lycosidae. Linyphiid spiders tolerate distinctly lower temperatures than lycosid spiders do. BLISS (1988) also stressed that lycosid spiders prefer higher temperatures. He investigated *Pardosa lugubris* living at open wood or wood margins in Schleswig-Holstein (REINKE & IRMLER 1994). No differences were detected between males and females or between adult and juvenile spiders in either investigation. The species *Gongylidium rufipes*, which occurs frequently in the alder wood, was investigated in detail by BAERT (1980, 1981). He found that the species exhibited seasonal vertical migrations between soil surface and the canopy of shrubs. Inhabitation of the soil layer occurred by juvenile spiders during leaf fall. According to his investigations, the optimal temperature for species' development was 22.5 °C. However, during the investigated period no relation was determined for the temperature fluctuations in the alder wood. Also, no other environ-

mental factor investigated provided an explanation for the density fluctuation of the species.

When referring to the potential changes of the climate, the following effects can be derived for the spider fauna of forests in Schleswig-Holstein. On the one hand, species seem to exist that exhibit positive and negative reactions on temperature fluctuations. On the other hand, it seems unlikely that small changes of temperature will cause an extinction of species. In particular, fluctuations of the prey organisms in the beech and in the alder wood seem to be responsible for the fluctuations of spider densities. In this respect, both litter fall and groundwater level in the beech and the alder wood, respectively, may be the triggering parameters. Moreover, the dispersion potentials of the species can change and cause a development of species-rich communities at wind-exposed sites, although this may be more unstable. The potentially higher rainfall and the climate warming seem to be more important, particularly in the summer months. All investigated spider species exhibited negative effects with an increase in rainfall. As the dispersion by ballooning is also negatively influenced by the increase in rainfall, the overall consequences for the spider fauna of forests, derived from the climate changes, will be most likely negative.

Zusammenfassung

Langfristige Schwankungen der Spinnen Populationen (Araneida) in einem Waldgebiet Norddeutschlands

Während eines Zeitraums von sieben Jahren von 1989 bis 1995 wurde in drei Waldbereichen, die auf einem Transekt von einem Erlenwald am Ufer des Belauer Sees bis zu einem Buchenwald auf der Hochfläche reichen, die Spinnenpopulation durch Handsortierung mit anschließender Trockenextraktion nach Macfadyen aus einem 0,1 m² großen Quadrat erfaßt. Insgesamt wurden 68 Spinnenarten mit Dichten zwischen 17 Ind./m² in dem Erlenwald bis zu 37 Ind./m² in dem Buchenwald nachgewiesen. Die Dichte der juvenilen Spinnen lag zwischen 43 Ind./m² im Erlenwald und 127 Ind./m² im Buchenwald. Sowohl juvenile als auch die adulten Spinnen zeigten ausgeprägte saisonale Abundanzschwankungen mit Maxima im Sommer bei den juvenilen Spinnen und im späten Herbst oder Winter bei den adulten Spinnen. Der Zeitraum zwischen dem Maximum der juvenilen Spinnen und dem von sechs adulten Spinnenarten reichte von drei bis sechs Monaten und war auch im langjährigen Verlauf signifikant. Die Wirkung von Niederschlag, Temperatur, Streufall, Dichte der Collembolen und Grundwasserschwankungen auf die Spinnenpopulation wurde mit Hilfe der Zeitreihen Statistik analysiert. Der Niederschlag war der am häufigsten signifikante Klimafaktor. Er war immer negativ mit der Spinnenabundanz korreliert. Der Streufall und die Collembolendichte hatte häufig einen positiven Einfluß auf die Spinnendichte. Im Erlenwald wurde die Spinnendichte von der Collembolendichte und den Grundwasserschwankungen bestimmt. Für den Buchenwald läßt sich folgendes Beziehungsgefüge vermuten. Der Streufall reguliert die Collembolendichte, die wiederum über die Dichte juveniler Spinnen die Abundanz der adulten Arten beeinflusst. Im Erlenwald wird die Abundanz juveniler Spinnen über die Collembolendichte reguliert, die von den Grundwasserstandsschwankungen bestimmt wird.

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