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Structure and function of the web of *Bathyphantes simillimus* (Araneae: Linyphiidae) in an isolated population in the Stołowe Mountains, SW Poland

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Summary

Bathyphantes simillimus inhabits deep sandstone rock crevices. Field and laboratory observations of juveniles and adults showed four web structures and two related, completely different, prey capture strategies. The original function of the web occurs only in the young. Communal webs are reported for the first time in a linyphiid. The disparity of web structures and prey capture strategies proves behavioural flexibility in *B. simillimus*; additionally it shows that this species is able to adjust to the type of dwelling site, as well as to the type and number of prey. Data on the prey spectrum, abundance both of *B. simillimus* and its prey, and a comparison of the population densities of *B. simillimus* and another linyphiid species are also presented.

Introduction

According to Bristowe (1958), Ford (1977), Roberts (1993), Schütt (1995) and Foelix (1996) the Linyphiidae are distinguished biologically from other families by a characteristic web structure. In most cases, the webs of Linyphiinae consist of a three-dimensional sheet with an irregular mesh and crossed threads (barrier threads or knock-down structure) stretched above them, the purpose of which is to stop the prey (Wiehle, 1949). Two-dimensional linyphiid webs have been found in ground-inhabiting members of the Erigoninae living in the moss and lichen layer (Kaston, 1964; Schütt, 1995; Alderweireldt, 1994) and in one representative of the Linyphiinae, *Drapestica socialis* (Sundevall) (Schütt, 1995).

The genus *Bathyphantes* includes 35 Palaearctic species (Platnick, 2005). Woźny & Czajka (1985) described *B. simillimus* as a synonym of *Bathyphantes eumenis* (L. Koch, 1879), and the latter name still occurs in Polish literature. Initially, this name was also used by Růžička (1988). Eskov (1988), however, recommended using the name *B. simillimus* (L. Koch, 1879) for Central European populations, and Růžička (1992, 1994) applied the name *B. simillimus* to his findings from the Czech Republic. Eskov and Růžička's view is not widely accepted. Blick (1991) and Blick & Molenda (1997) followed the name proposed by Woźny & Czajka (1985). As the taxonomic status of this species is still ambiguous I decided to use the name proposed by Eskov and Růžička. Voucher specimens have been deposited in the Zoological Institute, University of Wrocław.

The only species of this genus whose web structure and function has already been described is *Bathyphantes gracilis* (Blackwall). Its web is similar to those typical of other linypiids, e.g. *Linyphia triangularis* (Clerck), but its central part is much denser (Alderweireldt, 1994). The web of *B. simillimus* could be expected to have a similar structure. Until now the structure of the web, the prey spectrum and the prey catching technique of the species have not been studied. *Bathyphantes simillimus* is distributed in northern Eurasia and America, between 40 and 70°N (Marusik *et al.*, 1993). In Central Europe it is restricted to a few regions with low temperatures throughout the year. It has been found among stony debris and rocks in the Czech Republic, Slovakia, Germany, France and Belgium (Růžička, 1988; Blick, 1991; Blick & Molenda, 1997). In northern areas the species has been found in stone belts and on cliffs (Koponen, 1977). In Central Europe *B. simillimus* is believed to be a relict of periglacial or early postglacial times (Woźny & Czajka, 1985; Růžička, 1988; Blick & Molenda, 1997). In Poland, it is known only from the Stołowe Mountains, where it inhabits the central parts of the sandstone boulder area (the "Stone Town"). At these localities there are rock fissures, which are usually tens of metres deep and only tens of centimetres wide. The species is abundant in dark, moist and cold crevices.

In this paper the structure and function of the web of *B. simillimus*, as well as some other biological aspects (the prey spectrum and certain aspects of the life cycle and ethological adaptations to its habitat), are presented.

Material and methods

The site of field studies and collection of specimens was the Błędne Skały (850 m a.s.l., 50°29′N, 16°17′E), part of the Stołowe Mountains National Park in the central part of the Sudety Mountains.

The spider population was observed under natural conditions for at least 24 h per week from March–November 2000. Simultaneously, spiders were randomly caught and taken to the laboratory, where observations were continued at different times of day and night throughout the year. In the laboratory, 37 adult individuals (19 females and 18 males) were kept in jars (various sizes), while juveniles (56 specimens) were maintained in Petri dishes (5 cm diameter) singly, in twos, or in groups (from 4 up to 10). Photoperiod was 16L:8D, humidity varied from 90–100% (cotton wool soaked with water) and temperature was maintained at 5–10°C. Prey, 30 springtails per week, given all at once (Isotomidae, Hypogastruridae, Onychiuridae and Entomobryidae) were collected with an aspirator in a nearby park.

The life cycle of *B. simillimus* in the field spans three years. Young individuals hatch between April and July and become adults after their first winter. The adults reproduce from April to July in the second year of their lives. They die during the spring and summer after their second winter (Rybak, pers. obs.).

The examined specimens, both females and males, belonged to three age groups: first year juveniles (before overwintering), second year individuals (after the first overwintering, juveniles and adults) and third year adults (after the second overwintering).

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The field and laboratory investigations also included estimating the area of four types of webs, the prey spectrum and the hunting strategies of *B. simillimus.* The web structure was observed in the laboratory with a Citoval 2 stereoscopic microscope. Webs were sprayed with paint (a car varnish) to better reveal their structure. The web area was estimated by measuring two dimensions (length and width). From ten to twenty webs (made by different individuals) were measured in the laboratory and in nature for each of three categories: juvenile webs and two types of adult webs. The webs were measured three times (on the same occasion) to an accuracy of from 0.1 cm^2 to 1 cm^2. Three-dimensional webs of single adult individuals (retreat web), for the sake of simplicity, were measured in two dimensions for comparison with the other types of webs; the volume of these webs was significantly larger than the other webs owing to their irregular structure. Differences in web sizes between sexes were estimated in nature and in the laboratory. The areas of twenty webs were measured three times on the same occasion (10 for each sex) to an accuracy of 0.25 cm^2.

The prey composition of *B. simillimus* was determined by removing newly caught prey and preserving them in 70% ethanol. Identification of individuals was carried out in the laboratory. Prey capture frequency (per month) depending on the type of web structure was estimated by isolating in captivity 12 individuals (8 adults, 4 first year juveniles), and supplying 30 springtails per week, only prey consumed by the spiders being counted. To estimate the effectiveness of the group web (communal web), four individuals were kept together until they had woven a web, then three of them were moved to another jar, and one was left to catch prey; only prey which had been fed on was counted.

Results

Different types of webs

Four types of web structures were found:

Retreat — typical for single adult individuals: The preferred locations for this kind of web are shallow fissures in the rock surface ($n=30$). It usually consists of several irregularly crossed threads (Figs. 1a, 2a). Sometimes, the structure contains quite large empty spaces interspersed with densely woven areas and areas with various grades of density. Prey capture activities were never observed there ($n=45$). A comparison of the mean web sizes for single individuals in nature and in laboratory conditions is shown in Fig. 3. The web sizes under favourable laboratory conditions were considerably larger than those observed in nature (Mann–Whitney U-test; $p=0.0008$) (where they were probably limited by the size of the crevice). As shown in Fig. 6, no significant differences were found between the sexes in the sizes of their retreats (Mann–Whitney U-test, $p=0.47$).

Communal web — typical for some adult individuals and juveniles before their last moult: Periodically, up to a few dozen individuals gather in deeper and wider crevices (fissures of this type are rather rare). They construct a communal two-dimensional, uniform, compact web as shown in Figs. 1a and 2b. The web size and density depends on the number of its inhabitants (Mann–Whitney U-test; $p=0.00037$). These webs are significantly larger than the webs constructed by single individuals (communal webs approximately 15 times larger; Mann–Whitney U-test $p=0.000157$), as shown in Fig. 4. The last moults of juveniles were also found in these webs. Individuals placed together in one jar in the laboratory built a communal web too. The spiders (females and males) do not show antagonistic interactions. When they met and touched, they jumped aside and made way for each other. They do not cooperate in the prey-catching process and do not engage in joint feeding on one prey ($n=37$). During the reproduction period, females and males stay near the cocoons, but they do not guard them. They do not react to the removal or destruction of the cocoons ($n=19$). The sizes of communal webs in nature and under laboratory conditions are compared in Fig. 5. Unlike the sizes of individual spiders' webs, the web sizes for groups and pairs in laboratory conditions were not found to be larger than those observed in nature (Mann–Whitney U-test, $p=0.1987$).

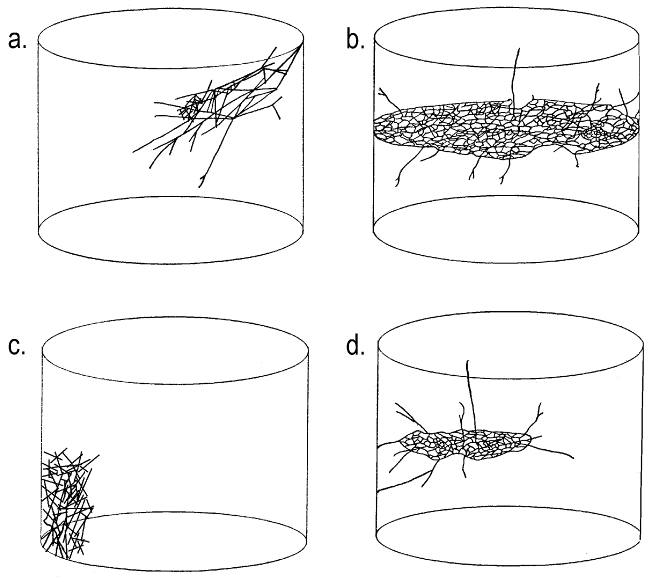

Fig. 1: Schematic drawings of web types of *B. simillimus*. **a** Retreat; **b** Communal web; **c** Warp; **d** Juvenile web.

Warp — typical for some adult individuals: A smooth rock face (excluding crevices) is covered with very thin threads, forming an irregular structure with wide meshes (Figs. 1c, 2c). Most of the threads in this structure are short and fixed to the rock surface. This type of web covers the rock just above its surface.

Juvenile web — characteristic for young individuals: The structure of these two-dimensional webs is regular and they have an even density (Figs. 1d, 2d). Their size is very small, proportional to the spider's size ($n=32$). A comparison of the sizes of webs woven by juveniles (first free instar) under natural and laboratory conditions is shown in Fig. 7. Under laboratory conditions juveniles weave webs of similar sizes to those observed in nature (t-test, $p=0.282$).It was observed that young individuals

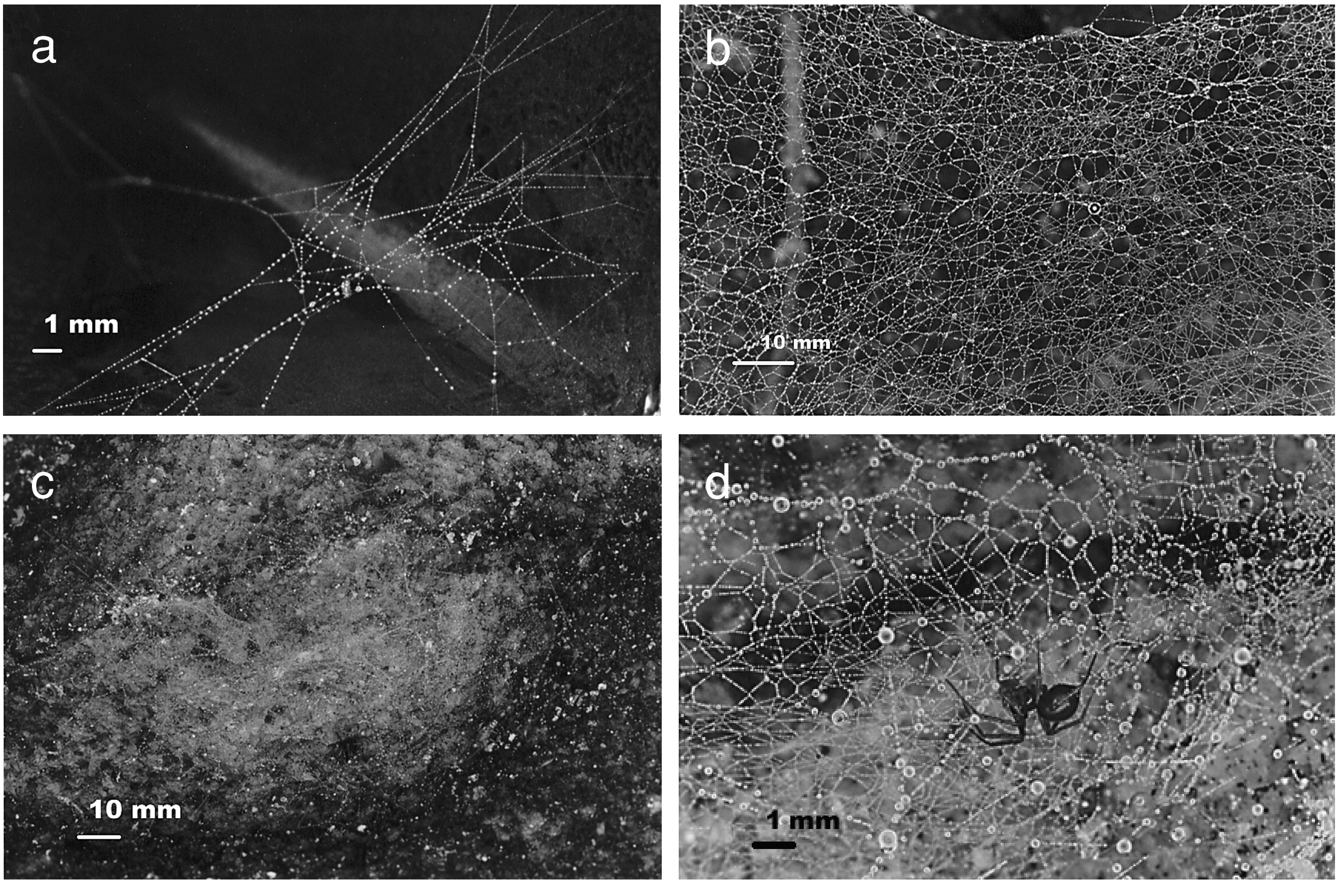

Fig. 2: Web types of *B. simillimus*. **a** Retreat; **b** Communal web; **c** Warp; **d** Juvenile web.

move to webs left by other individuals. Young spiders may change webs several times. A substantial number of moults were found there; thus shedding takes place on the web. Juveniles occurred in communal webs in nature only in the last instar before maturity.

Prey composition

Prey composition is presented in Table 1. *Orchesella alticola* (Uzel, 1890) was the main prey. The concentration of *O. alticola* on the rock surface was relatively high. Occasionally, other representatives of the Collembola (mainly from the families Isotomidae, Hypogastruridae and Entomobryidae), Diptera (small) and Aphididae were also caught. Table 1 shows that springtails made up 86.7% of the total prey caught by *B. simillimus*, with Diptera and Homoptera accounting for 8.5% and 4.8%, respectively.

Prey catching strategies

According to the type of web structure, two different prey catching strategies were identified:

Strategy 1 — "web capture": characteristic for spiders inhabiting structural webs (retreat, juvenile and communal web). The hairs and bristles covering the body of the prey (springtails) get so entangled that the insect is detained in the web. To free itself, the springtail makes a series of rapid movements, alerting the spider. After noticing the vibrations emitted by a struggling prey, *B. simillimus* makes a few precise movements towards the prey, followed by biting.

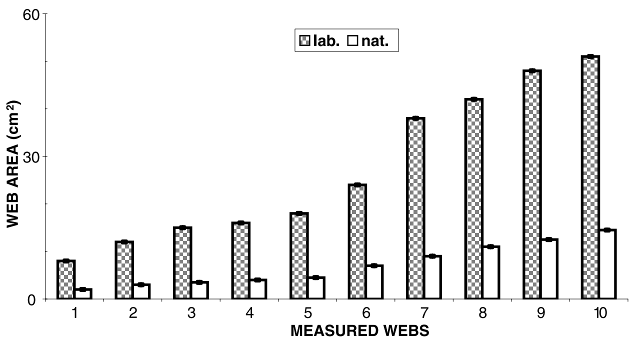

Fig. 3: Web areas of single individuals of *B. simillimus* in nature and under laboratory conditions (± 0.25 cm^2; $n=20$, i.e. 10 webs in each category, each measured 3 times).

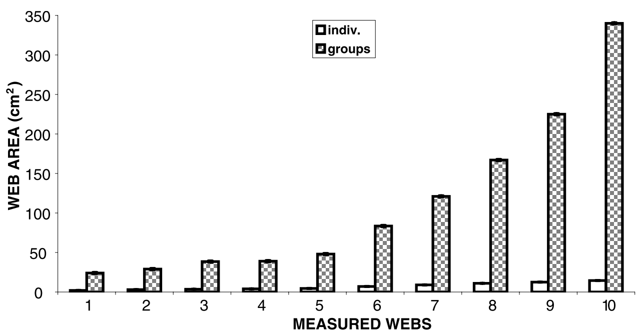

Fig. 4: Web areas of single individuals and groups of *B. simillimus* in nature (± 1 cm^2; $n=20$, i.e. 10 webs in each category, each measured 3 times).

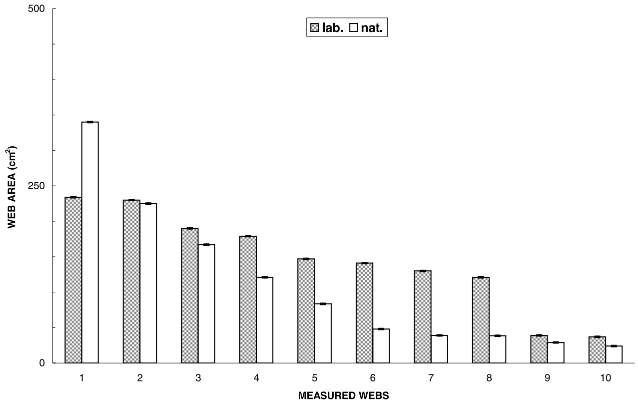

Fig. 5: Web areas of groups of *B. simillimus* in nature and under laboratory conditions (± 1 cm^2; n=20, i.e. 10 webs in each catetory, each measured 3 times).

Adult individuals do not attack another prey while feeding. However, in the case of juveniles positive reactions to web vibration were noticed even during feeding. In laboratory observations it was found that young spiders bothered by web vibrations either leave the previously caught prey in the web or attack the new victim whilst holding in the chelicerae the one caught earlier. The mean ($\pm$ SE) time for an adult individual before grasping struggling prey was 219.9 ± 59.3 s (n=10). In contrast, juveniles responded to web vibrations more rapidly (7.7 ± 1.2 s, n=28).

Prey capture frequency depending on the type of web is summarised in Table 2. When unlimited food was available (in the laboratory), juveniles caught up to 77 prey items per month. However, in the same conditions adult individuals using a communal web or retreat caught only up to 4 prey items per month! Thus the catching efficiency observed for both adult single individuals and groups is low and similar (two-way ANOVA; p=0.775) in comparison with the inhabitants of the juvenile webs. The latter are approximately 30 times more efficient at prey capture (Wilcoxon signed–ranks test; p=0.0022). Moreover, as shown in Table 2, no difference was found in feeding frequency related to the spider's sex (Mann–Whitney U-test, p=0.566). Both adult males and adult females feed rarely.

Strategy 2 — "direct contact capture": Characteristic for adult residents of warp webs. Because of its structure (wide meshes and short threads fixed to the rock surface), the rock-covering warp of *B. simillimus* enables springtails to move freely under the warp without touching the stretched threads. After dusk adult individuals leave their retreat and move into the warp to wait for accidental, direct contact with the prey. A springtail must touch the spider's leg to initiate attack; a potential victim passing at a distance of more than 1 cm does not elicit any reaction from the predator. The efficiency of this strategy is fairly high; out of the sample of 110 hunting attempts, 32 were successful.

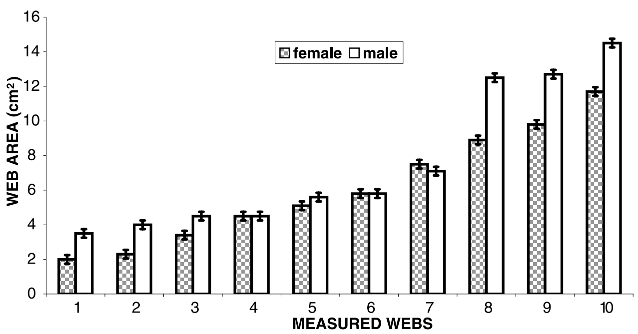

Fig. 6: Comparison of web areas of adult females and males of *B. simillimus* in nature (± 0.25 cm^2; n=20, 10 webs of each sex, each measured 3 times.

Taxonomic group/species	Number of specimens	Total (%)
Collembola		143 (86.7%)
Entomobryidae:		102 (61.7%)
Orchesella alticola (Uzel, 1890)	89	
Entomobrya nivalis (Linnaeus, 1758)	6	
Willowsia buski (Lubbock, 1870)	7	
Hypogastruridae:		17 (10.3%)
Ceratophysella denticulata (Bagnal, 1941)	16	
Willemia anophthalma (Borner, 1901)	1	
Isotomidae:		23 (13.9%)
Pseudisotoma sensibilis (Tullberg, 1876)	11	
Isotomiella minor (Schaffer, 1896)	12	
Onychiuridae:		1 (0.6%)
Mesaphorura tenuisensillata (Rusek, 1974)	1	
Diptera:		14 (8.5%)
Cecidomyiidae		8
Mycetophilidae		4
Fungivoridae		2
Homoptera:		8 (4.8%)
Aphididae		8
Total		165

Table 1: Prey composition of *B. simillimus*. All specimens were collected in one season (from April to November 2000).

Conclusion

Bathyphantes simillimus constructs four different types of webs and uses two different prey capture strategies. So far no other related species has been found to exhibit as many structural and functional web modifications as *B. simillimus*.

Earlier studies (Chant, 1956; Bristowe, 1958; Wheeler, 1973; Ford, 1977; Toft, 1980; Heimer & Nentwig, 1982; Jocqué, 1984; Thornhill, 1983; Alderweireldt, 1994; Schütt, 1995) have shown the existence of various modifications with regard to the web structure and function among different species of Linyphiidae. However, species closely related to *B. simillimus* (*B. gracilis*, *Lepthyphantes tenuis* (Blackwall), *Linyphia clathrata* (Sundevall)) have a web structure resembling that of

Web type		Prey capture frequency (per month)												
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Retreat	♀	0	0	1	1	2	2	1	2	1	2	0	0	12
	♀	0	0	0	2	2	1	2	1	0	0	0	0	8
	♂	0	1	1	1	3	4	1	2	0	1	1	0	15
	♂	0	0	1	1	1	3	1	0	1	1	0	0	9
Comm. web	♀	0	1	0	1	1	2	0	0	1	1	0	0	7
	♀	0	0	1	0	2	1	2	1	1	1	1	2	12
	♂	0	0	0	2	1	3	3	2	2	0	0	1	14
	♂	1	0	0	1	1	2	1	0	1	1	1	0	9
Juvenile web	j	7	9	4	8	4	61	71	54	57	45	12	7	339
	j	4	8	5	8	56	50	34	42	22	21	14	12	276
	j	5	4	2	6	11	77	65	60	66	38	21	17	372
	j	7	4	4	5	5	9	11	75	63	65	34	10	292

Table 2: Prey capture frequency. Number of prey caught by *B. simillimus* individuals per month in each web type under laboratory conditions (humidity 100%, temperature 10–12 °C, 16L:8D), only prey consumed were counted. Twelve individuals were used: second year adult females and males and juveniles. Prey provided: 30 springtails per week to each spider.

Linyphia triangularis. They are completely dependent on their web for capturing prey (Peters & Kovoor, 1991; Alderweireldt, 1994).

The function of the web of *B. simillimus* changes as the spider gets older: juveniles are the main feeding stage of this species. The observations clearly demonstrated that young individuals are more active than adults and feed more often (faster average response to web vibration, positive reactions to web vibrations during feeding, higher hunting efficiency). Similar observations have been made for *Oedothorax* (Alderweireldt, 1994). The young of *Oedothorax* weave small regular webs, while adult individuals make no webs at all. These ontogenetic changes in webs follow the pattern described in many other spider families (Eberhard, 1990).

Communal web construction is unusual among linyphiids and requires further study. Spiders inhabiting the web do not show any aggressive behaviour to each other, but neither do they cooperate. Such behaviour is called semisocial (Shear, 1970) or parasocial (Foelix, 1996). In the literature there are many examples of species that are normally solitary but which may form groups (Witt & Rovner, 1982); like *B. simillimus*, they use a communal web. So far such a phenomenon has never been observed in other linyphiid species.

Prey capture in the retreat is not very efficient but possible (Fig. 2a, Table 2). The threads in some areas of that structure or over its whole surface are so loose that

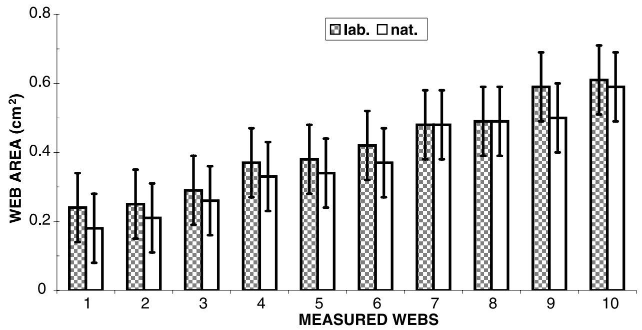

Fig. 7: Web areas of juvenile *B. simillimus* in nature and under laboratory conditions (± 0.1 cm^2; $n=20$, i.e. 10 webs in each category, each measured 3 times).

stopping the prey is impossible. Probably the basic function of this structure is to create a kind of retreat for the spider.

The warp structure may also be communal. This type of web forms a permanent retreat for *B. simillimus*. Spiders can exhibit courtship behaviour and mate there. This structure also aids hunting. The method of catching prey without using web vibrations (strategy 2) involves a technique similar to the "sit and wait" strategy. *Bathyphantes simillimus* does not have to weave large dense webs, as the probability of incidental contact with springtails is high. The efficiency of this strategy is fairly high (out of 110 attempts, 32 successful), good enough considering the low nutritional demands of adult individuals and the abundance of prey (see Table 2). Collembola are the most abundant group inhabiting the sandstone rocks with their low temperatures throughout the year. Other Linyphiidae catch Aphididae, Diptera, Acari and Homoptera more often than Collembola (Turnbull, 1960; Nentwig, 1980, 1982). In low temperatures springtails exhibit their normal activity, while individuals of the other groups often move slowly and may rarely occur in such an environment. This affects the prey spectrum of *B. simillimus*. Aggregation because of increased prey density is well known among spiders (Witt & Rovner, 1982), but it has not been found among the Linyphiidae. Living in a mass may also simplify the task of finding mates.

Bathyphantes simillimus has developed two hunting strategies related to four web types. Adult individuals use both strategies, of which "direct contact capture" is dominant. The second strategy ("web capture") is used only occasionally. All web types can be regarded as retreats. Hence, the most likely conclusion is that adult spiders have adapted their hunting behaviour to the dwelling site requirements, which consequently led to minimisation of the web area. The small size and low density of the web is compensated for by the high concentration of potential victims on the rock surface (Schütt, 1995). Most probably small web sizes amongst species of the subfamily Erigoninae are related to their nutritional preferences. It is well known that spiders of this group feed mostly on springtails (Bristowe, 1941). Moreover, substantial reduction in the web (warp structure) may represent an intermediate stage in the transition to the lack of webs observed in some other linyphiids.

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