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Drapetisca socialis (Araneae: Linyphiidae): Web reduction – ethological and morphological adaptations

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Abstract. The linyphiid spider *Drapetisca socialis* (Sundevall, 1832) attaches a specialized web vertically to tree trunks: A small sheet is surrounded by signal threads that inform the spider about passing arthropods. Field observations of prey composition revealed the importance of Collembola, especially Sminthuridae, as prey items. As can be seen from video recordings, *D. socialis* catches prey by a special technique, which is also employed outside the web. The spider moves carefully over its victim, which is grasped from above by means of modified chelicerae and pedipalps. They carry a setal trap, that is unique among linyphiid spiders (in spiders in general?). The tarsi of *Drapetisca* legs do not have adhesive hairs, thus not being specially adapted to seize prey. The development of triads (the spigots involved in the production of gluey capture threads) was examined in six linyphiid spiders: In three of them, including *D. socialis*, the triads are reduced to some extent, which leads to the conclusion that gluey capture threads do not play an important role in the capture of prey in Linyphiidae.

INTRODUCTION

The web of money spiders (Linyphiidae) consists of a horizontal, often vaulted and unevenly meshed sheet. An extended tangle of stopping-threads is elevated above it. The spider hangs horizontally, ventral side up, underneath the sheet which is held taut by scaffolding-threads (Hopfmann, 1935). When a flying insect hits the stopping-threads it either falls directly on to the sheet or is shaken down by the spider. Woven-in gluey capture threads hold the victim until the spider can take hold of it through the sheet from underneath (Wiehle, 1949).

This space web has been reduced many times within the Linyphiidae. Among the ground-dwelling members of this family, many species build a two-dimensional web, consisting of the sheet only. In some of these species the sheet is woven very tightly, and possibly is not used to catch prey, but rather to regulate microclimate (Heimer & Nentwig, 1982; Toft, 1980). Millidge (1988) considers reduced webs to be derived.

Until 130 years after its description it was believed that *Drapetisca socialis* (Sundevall, 1832) was one of the few Linyphiidae which had no web at all. "*Drapetisca* spinnt kein Netz, sondern jagt nach Art der Wolfspinnen an Baumstämmen" (Gerhardt & Kästner, 1938: 608; Wiehle, 1956). Kullmann (1961) was the first to describe the web of this species, which is considerably reduced in size and situated on vertical surfaces of tree trunks.

The number of obligatory tree trunk dwellers is low in comparison with soil or tree top inhabiting fauna (Funke, 1979). Only 15 species of Central European spiders are exclusive inhabitants of tree bark (Wunderlich, 1982). The trunk area, however, is used optionally by numerous representatives of other strata. Most of the obligatory inhabitants of tree trunks occur on trees with a richly structured bark. *Drapetisca socialis* is the only spider which permanently populates the smooth trunks of beech trees in high abundance, but it also lives on other types of trees (Funke, 1979; Nicolai, 1985). Funke (1973) describes *D. socialis* as one of the most significant hunting arthropods in the beech forest of Solling.

Although the web of this spider has been described, its exact structure and function has not been explained. Furthermore, the question is still open as to how the spider compensates for the small size of the web.

This paper examines the ethological and morphological adaptations of *Drapetisca socialis* to its particular habitat. *Linyphia triangularis*, a ubiquitous money spider, which builds an extensive space web, was used as a comparison. The spinnerets of the latter species in relation to their functions in web-building are well known (Peters & Kovoor, 1991). Beyond that, however, spinnerets in Linyphiidae are virtually unknown. In order to assess possible peculiarities, these structures were examined in other members of the family.

STUDY AREA, MATERIAL AND METHODS

Site of field studies and collection of specimens was the "Projensdorfer Gehölz", a beech forest near Kiel, Northern Germany.

In the laboratory, *D. socialis* built webs on vertically mounted surfaces, made of black cardboard or glass (assembled from several microscope slides). Webs on cardboard were made visible by exposing them to ammonium chloride vapour (Kullmann, 1961); those on glass surfaces were examined using a stereoscopic microscope and a compound microscope.

Field observations of prey capture were made several times between May and November 1993 in daylight. Prey composition of *D. socialis* was studied by removing freshly caught prey items from the chelicerae. Identification and measurement were carried out in the laboratory. Catching of *Drosophila* flies by *Drapetisca* was filmed in the laboratory using video equipment, that took single pictures at a rate of 24 frames per second.

Morphology of spinnerets, tarsi, female pedipalps and chelicerae of *D. socialis* and *L. triangularis* were examined by light microscopy (stereoscopic and compound) as well as SEM. Likewise the spinnerets of other four species of Linyphiidae (*Linyphia hortensis*, *Neriene peltata*, *Neriene emphana* and *Helophora insignis*) were investigated. Spinnerets of *D. socialis* were examined in both sexes and all stages, of *L. triangularis* in adult and young females and of the other species in adult females only. Before examination the spinnerets were spread out by carefully squeezing the abdomen. Carnoy solution (60% ethanol, 30% chloroform, 10% acetic acid) was used for dissection and hardening, xylol for drying. The preparations were sputtered with gold resp. gold palladium.

RESULTS

Web construction behaviour

The web of *Drapetisca socialis* is difficult to see on the tree trunk as the threads are extremely fine and lie very close to the surface of the trunk. The spiders sit in their webs facing head down. They prefer places below areas of raised bark; the first two instars are found exclusively there.

The spider sits on a small, irregularly woven sheet measuring 5 cm^2 which hardly exceeds the spread of the spider's legs. Several long threads directed to the side and diagonally upward originate from the sheet, the web thus assuming a U- or V-shape (Fig. 1). Each of these threads consists of a bundle of fibres, only a few of which are taut, while most of them run in loose loops. There are many fixation points (Fig. 1, above),

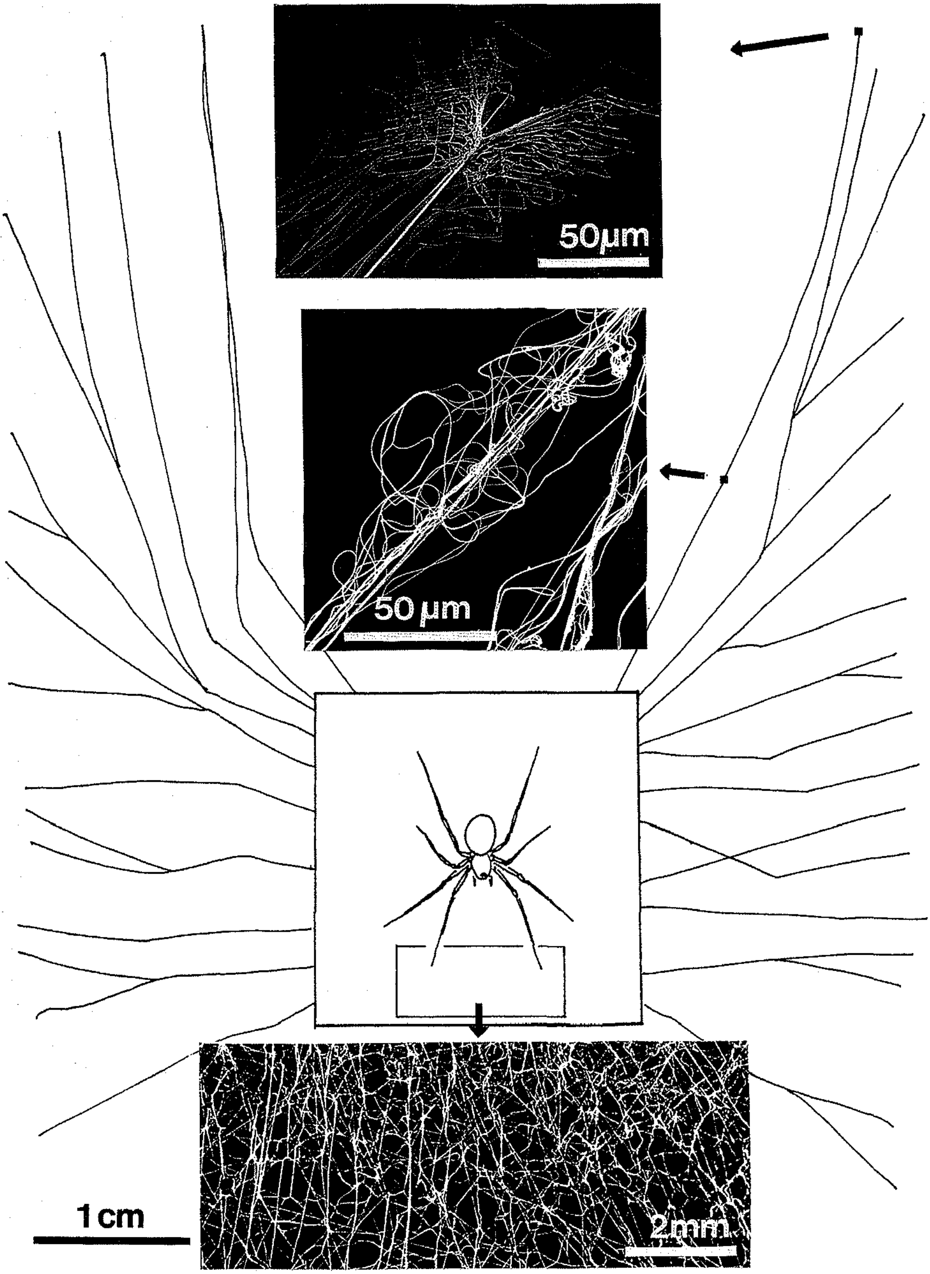

Fig. 1. Diagram of a web of *Drapetisca socialis* built on the surface of a tree trunk. Square area indicates approximate size and location of sheet and position of spider in web. Photographic sections show details of the following structures (starting from below): dense irregular mesh of sheet, taut signal threads with loose stopping threads, fixation point.

TABLE 1. Prey composition of *Drapetisca socialis*.

Systematic groups:	Number	Σ
Arachnida		
Araneae	1	6
Linyphiidae	4	
Anyphaenidae	1	
Acari		1
Oribatei: Damaeidae	1	
Insecta		
Collembola		12
Sminthuridae	9	
Isotomidae	2	
Entomobryidae	1	
Psocoptera	7	12
Lachesillidae	1	
Peripsocidae	4	
Heteroptera	3	4
Aradidae	1	
Homoptera		8
Cicadina	2	
Jassidae	2	
Aphidina		
Aphididae	1	
Phylloxeridae	1	
Pemphigidae	1	
Drepanosiphidae	1	
Coleoptera		1
Staphylinidae	1	
Hymenoptera		1
Proctotrupoidea: Platygasteridae	1	
Diptera		5
Culicidae	2	
Cecidomyiidae	1	
Psychodidae	2	

particularly in the peripheral area. Maximum length of threads is 10 cm. Gluey capture threads have not been observed.

Drapetisca may build a web at any time during the day as soon as it has found the appropriate base. The web is completed within 2–4 minutes; however, during the following days and weeks it is extended so that it becomes much denser, but keeps its form. Alien webs are accepted both in the laboratory as well as in the field. Sometimes other *Drapetisca* are driven away from their webs. Web recycling never occurs.

Prey catching behaviour

Prey composition is presented in Table 1. Most common were springtails (especially Sminthuridae) and Psocoptera, further important prey groups were leaf-hoppers and aphids, mosquitoes and the family Linyphiidae among the spiders.

The length of adult *D. socialis* is approx. 4 mm. On average the prey was about half as large as *Drapetisca*, however, a few specimens reached twice the size of the predator.

When prey approaches and touches the threads fanning out from the web, the spider leaves its waiting position and runs after the prey. Thereby the spider takes a short cut, that considers the direction of movement of the prospective victim. Adult spiders are able to follow prey for a distance of up to 30 cm beyond the area of the web.

If the chase is successful, the spider returns to its waiting position with its prey, always carrying it in the chelicerae. The victim is not wrapped in silk but consumed immediately. The digestion of large prey can take up to two hours, during which time the prey item is chewed until it is unrecognizable. During this time further potential victims passing the web are not attacked.

This behaviour can be observed at all ages and in both sexes, including adult males. Approx. 2/3 of the observed attempts (n = 20) at catching prey were unsuccessful.

Figs 2a and b show two video recordings of attacks on *Drosophila*, one of which was successful (a). It becomes apparent in both cases that the threads slow down the fly, but do not catch it. The spider turns towards it only a few seconds after it has touched the web for

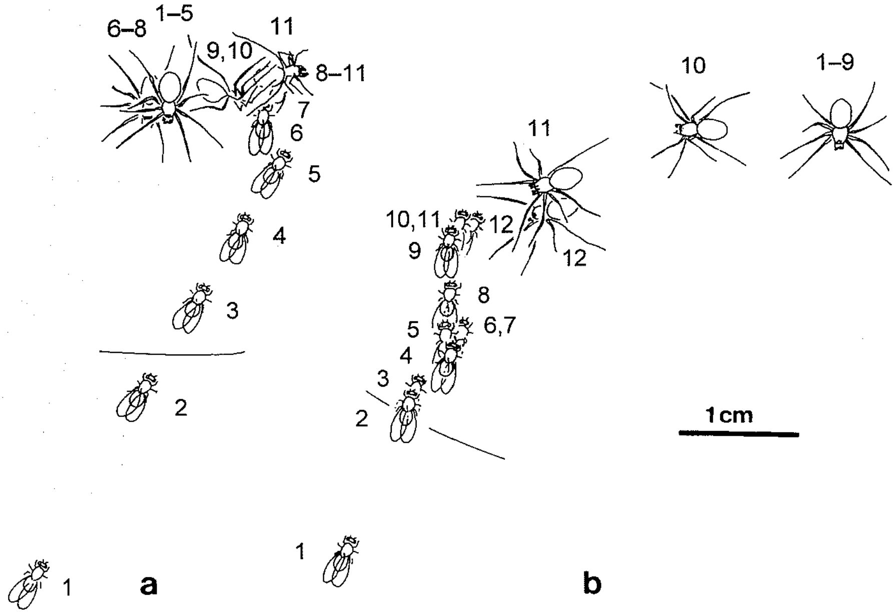

Fig. 2. Two analyses of video recordings of the behaviour concerning the catching of prey by *Drapetisca* females. The numbers correspond to the time in seconds; the line shows the boundary of the web. Only example a. was successful.

the first time and attacks in a jerky manner.

Video analysis has shown that *D. socialis* first runs over the flies on stilted legs and then catches them by a quick lowering of its body.

If the spider is separated from its web, a fly passing by does not cause any reaction; in this case a fly is attacked only if it walks directly into the spider. If such an attack is not successful the fly will be followed by the spider.

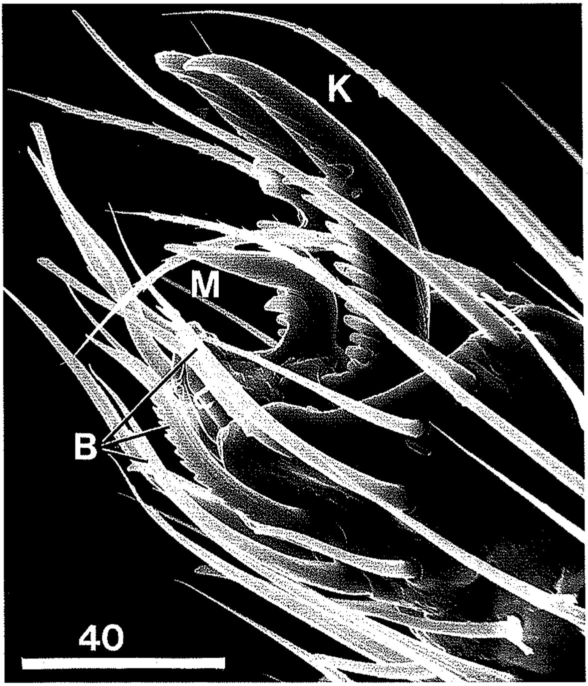

Fig. 3. The tip of a tarsus of *D. socialis*. B – serrated bristles; M – median claw; K – lateral claws. SEM, scale in μm.

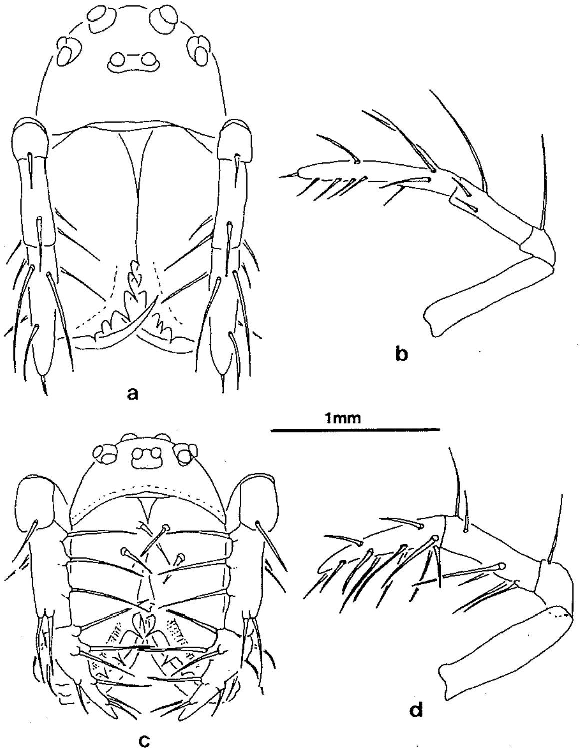

Fig. 4. Prosoma of adult females in frontal view (a, c) and right pedipalp in prolateral view (b, d). a, b – *Linyphia triangularis*; c, d – *Drapetisca socialis*.

Morphology of tarsi, pedipalps and chelicerae

Tarsi of *D. socialis* (Fig. 3) have a smaller median claw between two large claws, a feature typical for web-building spiders. The tarsi do not show any scopulae, which are present in most groups of hunting spiders.

Drapetisca has strong pedipalps terminating in cone-shaped tarsi (Fig. 4d). The pedipalps are armed with conspicuous strong setae, directed inwards and crossing each other medially (Fig. 4c). The setae are surrounded by high U-shaped sockets at their bases (Fig. 5). In *Drapetisca* the openings of the sockets are directed in such a way that they prevent the setae being bent outwards (away from chelicerae). Compared with *Drapetisca*, pedipalps of *L. triangularis* are slim, with setae not strongly developed and not crossing each

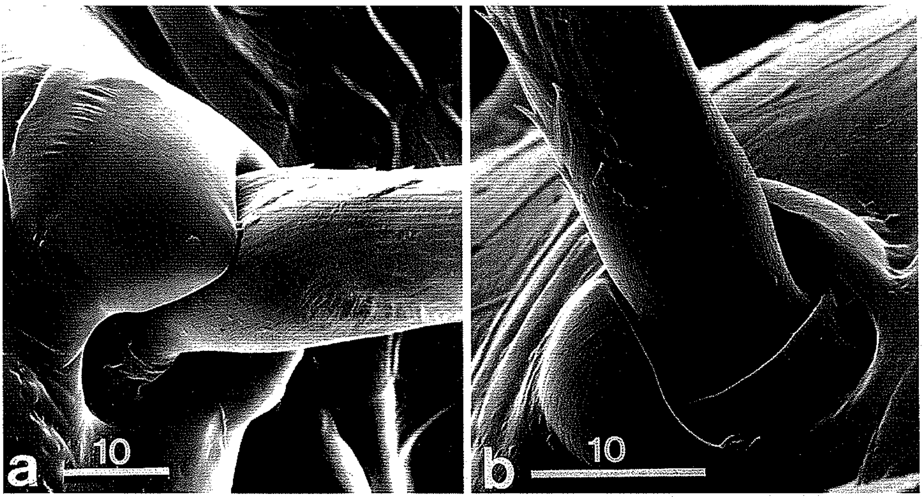

Fig. 5. Bases of two setae located on different areas of the pedipalp of *Drapetisca socialis*. a – tarsus, median; b – patella, dorsal. SEM, scales in µm.

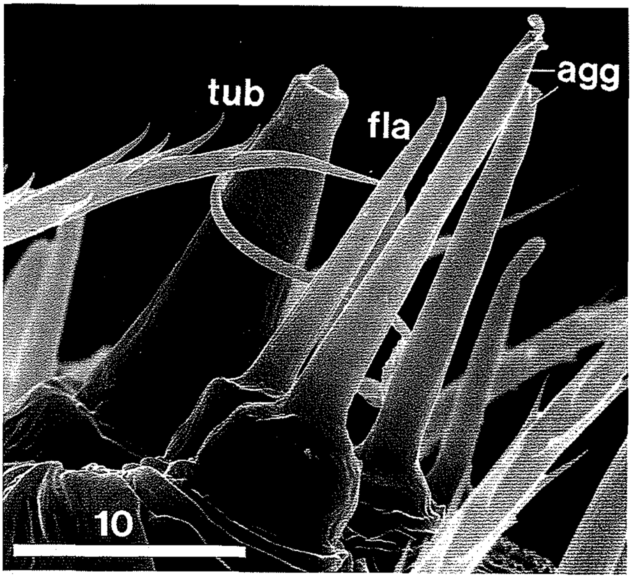

Fig. 6. Posterior spinneret of *Neriene emphana*, adult female. The abbreviations signify the spigots of the following glands: tub – Gl. tubuliformes, fla – Gl. flagelliformes and agg – Gl. aggregatae (the triad is a combination of two aggregate glands and one flagelliform gland). SEM, scales in μm.

other (Figs 4a,b). In *Linyphia* setae and sockets are smaller than in *Drapetisca*, with the sockets' openings directed distally.

Each of the large basal segments of the chelicerae of *D. socialis* also bears two strong setae surrounded by sockets (Fig. 4c). No such setae are found on the chelicerae of *L. triangularis*, but only a few thin hairs.

Morphology of spinnerets

The spinnerets of six species of Linyphiidae were examined. Among others, differences in the triads were noticed; a triad (term introduced by Kovoor & Lopez, 1982) is a combination of two spigots of aggregate glands and one spigot of a flagelliform gland located on the posterior spinnerets (Fig. 6). The spigot of the flagelliform gland is present in all species examined. The triads are completely developed in three species (Fig. 7), but in two species – namely *Drapetisca socialis* and *Neriene peltata* (Wider, 1834) – only the spigot of the flagelliform gland is present. In some specimens of *Linyphia hortensis* Sundevall, 1829 one of the spigots of the aggregate glands may still exist. The degree of reduction can thus be variable within one species. In many cases of reduction of the aggregate glands the slim spigot of the flagelliform gland is surrounded by one or two bumps and/or pores. Appearance of triads can be different on both sides of the same specimen.

In the ontogeny of the spinning apparatus of *D. socialis* the spigot which belongs to the flagelliform gland can be seen from the first instar. It is retained in the female but degenerates in the male after the last moult. Spigots of aggregate glands are absent in all postembryonic stages of *Drapetisca*.

DISCUSSION

Web reduction is common in the phylogeny of spiders. Whole families have become secondary free hunters, for example the wolf spiders and jumping spiders, among which only the first instars of some species may build a web (Eberhard, 1985). There is a tendency among the Linyphiidae, particularly among the smaller members of the family, to reduce the tangle of threads above and below the sheet, and to stretch this small sheet web over holes in the ground (Kaston, 1964). In some dwarf spiders the web has lost its

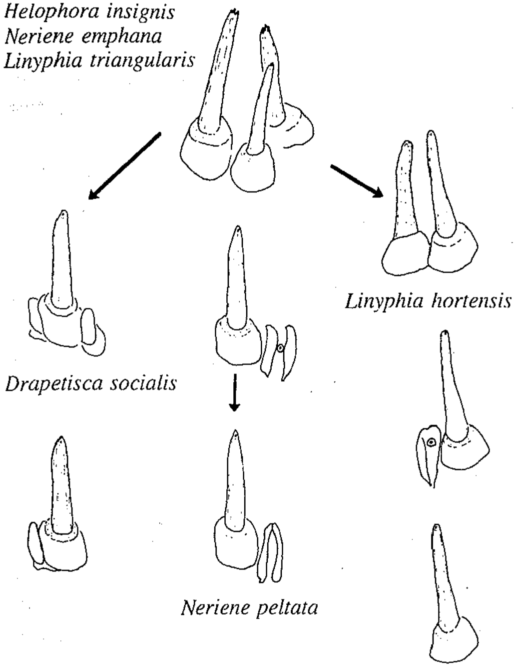

Fig. 7. Diagram of triad reductions in Linyphiidae. Upper drawing shows the original triad morphology in Linyphiidae (present in *Helophora insignis*, *Neriene emphana* and *Linyphia triangularis*). Drawings below show as examples of reduction: *Drapetisca socialis* (left), *Neriene peltata* (middle) and *Linyphia hortensis* (right).

function of catching prey and acts only as a protection or to preserve a suitable microclimate (Nentwig & Heimer, 1983). Thus, in the case of *Tapinopa*, Toft (1980) showed that its exceptionally dense sheet web holds moisture. Heydemann (1961) reported on reduced webs and secondary hunting spiders among Linyphiidae which live on flooded foreshores. Only in the case of those few dwarf spiders living in ant nests is it assumed that there is no web at all (Bristowe, 1958).

The much smaller web of *Drapetisca socialis* shows a peculiarity when compared with other reduced webs; in *Drapetisca* the function of catching prey has been retained, but the web has lost its protective function. The typical sheet web of the Linyphiidae serves not only to catch insects. The spiders hanging underneath the sheets are also protected from enemies, especially birds. In contrast *Drapetisca* is perfectly camouflaged on bark.

Theoretically there are two possibilities to compensate for a smaller web: the animal has found a way of actively luring prey, or it has chosen a place with abundant prey (e.g. the area of the tree trunk).

Most spiders have a device which can hold their prey for a short period only and which informs the predator by means of web vibration of the location of its victim. The prey must be caught and overcome quickly, before it can get away.

The few threads in the *Drapetisca* web which are tightly stretched from the centre to the upper and side edges are used to transmit vibratory stimuli caused by prey passing by. The numerous loose threads slow down the victim and sometimes hold it for a while.

There are no drops of glue in the web of *Drapetisca socialis*; in the case of *Linyphia triangularis* there are many small drops of glue. When compared with the method of catching used by orb weavers (Araneidae) these do not play an important role in Linyphiidae (Wiehle, 1949; Peters & Kovoor, 1991). This is probably also the reason why the spigots of aggregate glands, which supply the glue for capture threads, have often been reduced within the Linyphiidae. As compared with orb weavers these spigots are generally not as well developed.

With the exception of a few specialists, almost all spiders are polyphagous (Foelix, 1992). The composition of prey is mainly dependent on the habitat with its potential prey, and less on the type of web (Nentwig, 1987; Wise & Barata, 1983). Linyphiid food is correspondingly diverse, depending on which stratum it occupies. Especially for the many dwarf spiders living in the litter layer the huge number of springtails is of great importance (Bristowe, 1941).

D. socialis has on its menu obligatory tree trunk dwellers such as Psocoptera, but also animals which use tree trunks only optionally, either as a feeding place, as in the case of springtails which climb up the trunk when it is damp (Bauer, 1979), or as a resting place, as in the case of mosquitoes. Others use the trunk as a "climbing pole" when changing from one stratum to another, as in the case of Homoptera (Funke, 1979).

A remarkable feature of the composition of *Drapetisca*'s prey is that it consists of large (up to double the size of the predator), strong or fast-moving animals. Spiders which hunt without a web only rarely catch prey larger than 150% of their own size. Exceptions are the crab and jumping spiders (Nentwig, 1987).

As compared with other family members which have a space web, the hunting manner of *D. socialis* is strongly modified. Although the sheet web and its extending threads are still used as an alarm and locating system, the prey can also be overcome outside the web. This spider has developed a special catching technique: it runs over the prey and grabs it from above with the pedipalps and chelicerae.

In comparison, the typical families of hunting spiders such as Pisauridae and Lycosidae grab their prey with their front legs, and the tarsi are only placed lightly on the prey to pull it towards the chelicerae. Adhesion is ensured by the tarsal scopulae (Rovner, 1978, 1980; Melchers, 1967). These are thick bundles of hairs found at the tip of and underneath the tarsi, sometimes also on the metatarsi. They are not found on any web spiders, including *D. socialis*, whose tarsi are in no way different from those of any other web building spiders. It is noteworthy that *Drapetisca* shares two behavioural pecularities with the non web building spiders despite the morphological difference named above: *D. socialis* is able to overcome prey without a web and to walk on smooth vertical surfaces.

In adaptation to the highly developed escape mechanism of the springtails, which make up a large part of their prey, *Drapetisca socialis* has a specialised catching apparatus consisting of very strong setae on the two distalmost segments of the pedipalps as well as on the basal segment of the chelicerae. The possible movements of these setae are restricted by their sockets, thus forming a trap.

Drapetisca socialis runs on stilted legs above its prey so as not to touch it too soon and drops its body in a lightning movement at the moment of catching its prey. Thereby the setal trap prevents the prey from escaping forwards and presses it against the chelicerae. It is important that the prey is held securely at the first moment of contact, especially with regard to the Collembola, which react extremely quickly.

Carabid beetles, which have specialized in hunting hemiedaphic Collembola, show similar adaptations to some extent. *Loricera pilicornis* uses extended setae on its antennae and on the underside of its head to encircle springtails (Hintzpeter & Bauer, 1986). Certain species of the genus *Leistus* have circularly placed setae on the ventral side of the head (Bauer, 1985). The traps as a whole may have distinctive characteristics, but the details show a remarkable convergence of the structures. As in *Drapetisca socialis*, the setae of the carabids are surrounded by a cuticular collar, the opening of which points towards the inside of the trap.

Thus *Drapetisca* is a free hunter with the legs of a typical web spider (no scopulate hairs present). It uses its long legs to make a surprise attack from above and catches its prey with a specially developed setal trap.

REFERENCES

BAUER T. 1979: Die Feuchtigkeit als steuernder Faktor für das Kletterverhalten von Collembolen. *Pedobiologia* **19**: 165–175.

BAUER T. 1985: Beetles which use setal trap to hunt springtails: The hunting strategy and apparatus of Leistus (Coleoptera, Carabidae). *Pedobiologia* **28**: 275–287.

BRISTOWE W.S. 1941: *The Comity of Spiders*. Ray Soc., London, 560 pp.

BRISTOWE W.S. 1958: *The World of Spiders*. Collins, London, 304 pp.

EBERHARD W.G. 1985: The "sawtoothed" orb web of Eustala sp. (Araneae, Araneidae) with a discussion of ontogenetic changes in spiders' web-building behavior. *Psyche* **92**: 105–117.

FOELIX R.F. 1992: *Biologie der Spinnen 2. Aufl.* Thieme Verlag, Stuttgart, New York, 331 pp.

FUNKE W. 1973: Rolle der Tiere im Wald-Ökosystem des Solling. In Ellenberg H: *Ökosystemforschung*. Springer, Berlin, Heidelberg, pp. 143–174.

FUNKE W. 1979: Wälder, Objekte der Ökosystemforschung: Die Stammregion – Lebensraum und Durchgangszone der Arthropoden. *Jber. Naturwiss. Ver. Wuppertal* **32**: 45–50.

GERHARDT U. & KÄSTNER A. 1938: Araneae. In Kükenthal W. (ed.): *Handbuch der Zoologie Bd. 3.2.1.1.* T. Krumbach de Gruyter, Berlin, p. 608.

HEIMER S. & NENTWIG W. 1982: Thoughts on the phylogeny of the Araneoidea Latreille, 1806 (Arachnida, Araneae). *Z. Zool. Syst. Evolutionsforsch.* **20**: 284–295.

HEYDEMANN B. 1961: Untersuchungen über die Aktivitäts- und Besiedlungsdichte bei epigäischen Spinnen. *Verh. Dtsch. Zool. Ges.* **20**: 538–556.

HINTZPETER U. & BAUER T. 1986: The antennal setal trap of the Ground beetle Loricera pilicornis: a specialization for feeding on Collembola. *J. Zool. (London)* **208**: 615–630.

HOPFMANN S. 1935: Bau und Leistung des Spinnapparates einiger Netzspinnen. *Z. Naturwiss. (Jena)* **70**: 65–111.

KASTON B.J. 1964: The evolution of spider webs. *Am. Zool.* **4**: 191–207.

KOVOOR J. & LOPEZ A. 1982: Anatomie et histologie des glandes séricigènes des Cyrtophora (Araneae, Araneidae): affinités et correlations avec la structure et la composition de la toile. *Rev. Arachnol.* **4**: 1–21.

KULLMANN E. 1961: Über das bisher unbekannte Netz und das Werbeverhalten von Drapetisca socialis (Sundevall) (Araneae, Linyphiidae). *Decheniana* **114**: 99–104.

MELCHERS M. 1967: Der Beutefang von Cupiennius salei (Keyserling) (Ctenidae). *Z. Morph. Ökol. Tiere.* **53**: 321–346.

MILLIDGE A. 1988: The relatives of the Linyphiidae: phylogenetic problems at the family level (Araneae). *Bull. Br. Arachnol. Soc.* **7**(9): 253–268.

NENTWIG W. 1987: The prey of spiders. In Nentwig W. (ed.): *Ecophysiology of Spiders*. Springer, Berlin, Heidelberg, pp. 249–263.

NENTWIG W. & HEIMER S. 1983: Orb webs and single line webs: an economic consequence of space web reduction in spiders. *Z. Zool. Syst. Evolutionsforsch.* **21**: 26–37.

NICOLAI V. 1985: *Die ökologische Bedeutung verschiedener Rindentypen bei Bäumen.* Diss. Univ. Marburg, 198 pp.

PETERS H.M. & KOVOOR J. 1991: The silk-producing system of Linyphia triangularis (Araneae, Linyphiidae) and some comparisons with Araneidae-Structure, histochemistry and function. *Zoomorphology* **111**: 1–17.

ROVNER J.S. 1978: Adhesive hairs in spiders: behavioral functions and hydraulically mediated movement. *Symp. Zool. Soc. Lond.* **42**: 99–107.

Rovner J.S. 1980: Morphological and ethological adaptions for prey capture in wolf spiders (Araneae, Lycosidae). *J. Arachnol.* **8**: 201–220.

Toft S. 1980: Humidity retaining function of the catching web of Tapinopa longidens (Wider) (Araneae: Linyphiidae). *Entomol. Medd.* **48**: 5–7.

Wiehle H. 1949: *Vom Fanggewebe Einheimischer Spinnen 12.* Neue Brehm-Bücherei. Akademische Verlagsgesellschaft Geest & Portig, Leipzig.

Wiehle H. 1956: Spinnentiere oder Arachnoidea (Araneae). 28. Familie Linyphiidae – Baldachinspinnen. In Dahl M. & Bischoff H. (eds): *Die Tierwelt Deutschlands 44.* Gustav Fischer, Jena, 337 pp.

Wise D.H. & Barata J.L. 1983: Prey of two syntopic spiders with different web structures. *J. Arachnol.* **11**: 271–282.

Wunderlich J. 1982: Mitteleuropäische Spinnen (Araneae) der Baumrinde. *Z. Angew. Entomol.* **94**: 9–21.

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