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Bull. Br. arachnol. Soc. (1997) **10** (9), 333–336

Web-site selection in *Drapetisca socialis* (Araneae: Linyphiidae)

Karin Schütt

Zoologisches Institut,
Universität Kiel,
Olshausenstr. 40,
D-24098 Kiel,
Germany*

Summary

The spatial pattern of web distribution in *Drapetisca socialis* on the lower part of tree trunks was investigated in a beech wood. The spider prefers regions of trunks covered with a thick layer of epiphytic algae, a finding confirmed in a laboratory choice experiment. Prey availability is assumed to be higher at these places. The results indicate that *D. socialis* uses the algal cover as a proximate cue for distinguishing prey-rich from prey-poor sites and is thus able to assess the site quality of a patch in advance, instead of sampling different habitats with the associated risk of wasting time, material and energy. The web abundance in relation to height on tree trunks is presumably caused by prey density and interspecific competition. The preferred southern exposure is assumed to be related to thermoregulation. *D. socialis* also strongly prefers places under large protuberances on the otherwise smooth surface of beech trunks, behaviour that is interpreted as providing protection against water or visibility.

Introduction

The foraging success of predators is closely linked with patch choice and thus predators should search for patches that possess high prey availability and that permit the efficient perception and capture of prey (Riechert & Gillespie, 1986). Several recent studies have shown that the rate of food acquisition directly affects survival, growth rate, size at sexual maturity and reproductive success, all of which have a strong impact on fitness (Morse, 1981; Vollrath, 1987; Orians, 1991). Therefore, natural selection is expected to have favoured those responses to cues concerning habitat quality. Relatively sedentary animals or species defending a fixed territory should spend more effort in searching for

suitable patches and settle at sites affording a high concentration of food (Riechert & Gillespie, 1986).

Sit-and-wait predators are relatively sedentary, ambush mobile prey and leave patches infrequently. Mobile predators actively search their environment for prey and often move between foraging sites. These two foraging modes occupy the endpoints of a continuum (Janetos, 1982).

Spiders that build relatively permanent webs are clear examples of sit-and-wait predators. How does such a spider locate web sites affording good conditions and how does it judge the quality of patches? Different families of web-building spiders use various habitat selection strategies (Riechert & Gillespie, 1986). Some species build “trial webs” in several patches and thus estimate the availability of prey. Other spider species are known to be associated with vegetation of a particular structure.

To be able to distinguish whether patch choice is influenced directly by prey density or by various parameters of the environment, we must determine the extent of association with proximate features of the environment in laboratory choice experiments, because proximate and ultimate factors both create a similar pattern in the field. In addition, other goals and constraints, such as a suitable microclimate, structures for web support, predation risk and competition are involved and influence the spatial pattern.

The linyphiid spider *Drapetisca socialis* (Sundevall) occurs throughout the Palaearctic and is an obligatory tree trunk dweller. It attaches a specialised web vertically to the surface of trees, especially beeches, a tree type where no other spider is as frequent as *D. socialis*. The web consists of a small sheet and surrounding signal threads that inform the spider about passing arthropods (Schütt, 1995). The spider maintains the same web for an extended period but can be driven away by conspecifics. Thus, *D. socialis* is a true sit-and-wait forager living in an approximately two-dimensional system.

In this study, I have examined the spatial and temporal pattern of web distribution in *D. socialis* on tree trunks and the cues associated with patch choice decision. I have also investigated the mechanism of the

*Present address: Museum für Naturkunde, Humboldt Universität Berlin, Invalidenstr. 43, 10115 Berlin, Germany.

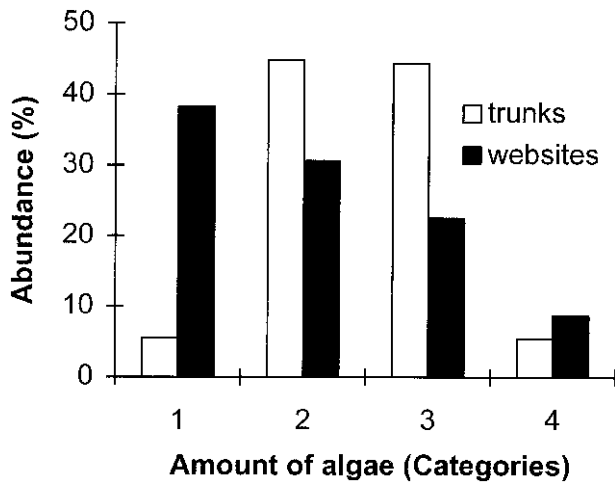


Fig. 1: Distribution of 173 webs of *D. socialis* as related to four categories of algal layer and, for comparison, the distribution of algae on beeches. Lower trunk region (up to 2 m). Categories: (1) closed cover of algae, (2) considerable amount of algae, (3) thin cover of algae, and (4) devoid of algae.

selection process using a laboratory experiment based on insights gained from field studies.

Study site and methods

Field study

Field studies and collection of specimens were performed in the Projensdorfer Gehölz, a forest near Kiel, northern Germany. The forest consists predominantly of beech standards (*Fagus sylvatica* L.) and has been coppiced with elder understorey (*Sambucus nigra* L.). The study was carried out from May to November 1993 but the web survey was restricted to June, July and August. Observations were made during daylight only on beech trunks and no higher up the trunk than 2 m above ground level.

Every *D. socialis* sitting in a web was noted and the sites were assigned to one of 16 sectors based on compass bearings and one of four classes of different thickness of algal layer assessed by eye. The heights were measured and the presence of protrusions larger than 1 cm above the web was noted. For comparison, the density of epiphytic algae on 12 m² surface of beech trunks was recorded by evaluating 19,200 squares each with a size of 6.25 cm² on eight beeches at all heights and at four main directions (north, east, west and south). The number of protrusions in the area below 2 m was counted on 12 trees.

Laboratory study

The preference for substrate with algae was tested in a choice experiment in the laboratory. Single specimens of *D. socialis* were placed in small glass boxes in which two pieces of bark of approximately the same size were fixed on one side. One piece of bark carried a cover of pleurococoid algae, the other had none. Seven of these boxes were employed and, for every single test, a new adult or subadult spider was taken. The experiments were terminated when the spider had built a web on one of the two available pieces of bark. The webs were in any case removed with a paint-brush before the next experiment started.

Results

The density of algae in regions where *Drapetisca socialis* chose web sites differed significantly from the distribution of algae over the whole trunk area, such that *D. socialis* used sites with a closed algal cover more often than expected (Fig. 1) (Kolomogorov-Smirnov Test: $D=0.32$, $n=173$, $p<0.001$).

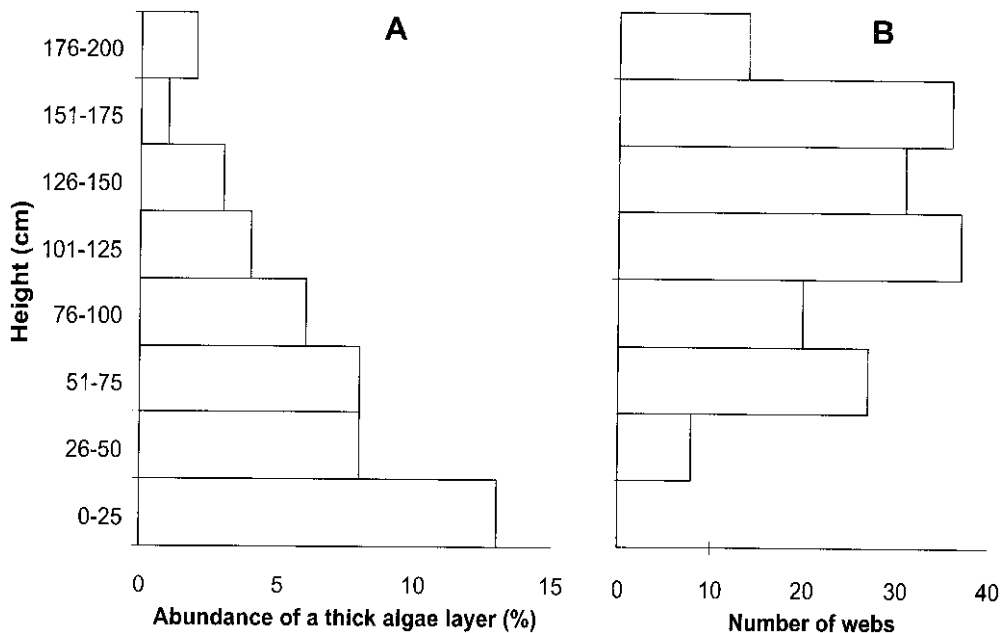


Fig. 2: **A** Abundance of a closed algal cover (Category 1 in Fig. 1) at different heights; **B** Number of webs of *D. socialis* at different heights above ground level up to 2 m.

In the choice experiment, *D. socialis* built 78 webs on the bark with algae but only 24 on bark without algae, thus the preference of *D. socialis* for the substratum with algae was highly significant ($\chi^2=28.6$, $df=1$, $p<0.001$). This supports the results of the field investigation.

Approximately seven large protrusions were found on average per tree. These protuberances were induced by fungi and are unique prominent structures on the otherwise smooth bark of the beeches. Only about 0.2% of the total area of the bark is occupied by these protuberances. Of 173 webs, 83 (48%) were found under these rare structures, indicating that *D. socialis* favours places under protuberances. The first two instars, which were not included in this sample, were found exclusively here.

The distribution of webs at different heights up to 2 m (Fig. 2B) exhibited significant selectivity ($\chi^2=58.9$, $df=7$, $p<0.001$). Approximately 7/8 of all webs were recorded between 0.50 and 1.75 m, thus in 5/8 of the total area. The lowest 25 cm were totally avoided. The pattern of web abundance was not correlated with the amount of epiphytic algae at different heights (Fig. 2A).

The spiders were mostly oriented on the south and south-east sides of trunks (Fig. 3). This bias of orientation was significantly different from random (Rayleigh Test: $n=173$, mean vector= 165° , $p<0.001$). The epiphytic plant cover was most pronounced on the west side of trunks.

Discussion

Linyphiid spiders are examples of predators that spend most of their time at a fixed place and that use their costly sheet-web for extended periods (Leclerc & Blandin, 1990). One can therefore assume that a previous patch choice decision, i.e. the active search for a suitable web site before settling, has resulted in a higher foraging success. Araneid spiders construct a new web daily, which needs less investment in time and material, and they are known to respond to changes in prey density more rapidly than linyphiids (Rypstra, 1985). Thus araneids can use their orb-webs to measure site quality and can change sites if they are not profitable. *Drapetisca socialis* is a linyphiid spider with an extremely reduced web. What strategy is used by this species to maximise prey intake?

The prey of *D. socialis* consists mainly of arthropods that graze the layer of pleurococcid algae. The most abundant are springtails (mostly the sminthurid *Allacma fusca*) and Psocoptera (Schütt, 1995). The algal layer forms an irregular spatial pattern on tree trunks and thus the prey are found in irregular clumps. The web of the ambush predator *Drapetisca* has a small extent of about 6 cm. Therefore, specimens that build their web on green parts of the tree can be expected to have a great advantage in foraging success.

Field investigations and laboratory experiments both show a highly significant positive correlation for *D. socialis* between web abundance and the amount of pleurococcid algae on the bark. There are theoretically two possible explanations of these observations: either the spider has previously often measured prey avail-

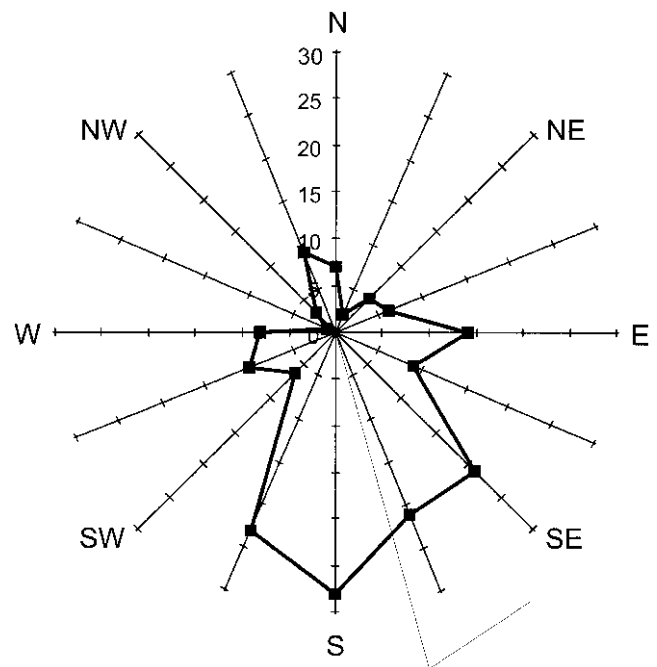


Fig. 3: Distribution of webs of *D. socialis* in the lower trunk region (up to 2 m) in relation to the points of the compass. Mean vector and 95% confidence intervals are given.

ability at different places and compared the profitability of these sites or it settles a priori at good sites by using algal cover as a proximate cue for prospectively high prey density. Before courtship, the site tenacity of *D. socialis* is relatively high, i.e. they leave their webs rarely (pers. obs.). This, together with the observation that, as early as June, the spiders sit in areas that provide a rich supply of prey, is a strong indication for the hypothesis that site quality is judged before settling.

In contrast to other linyphiids, *D. socialis* has a lower investment in her small web and catches relatively large prey infrequently (Schütt, 1995). Hence this spider, which only lives a few months, cannot afford to settle without careful consideration.

Riechert (1985) has observed, in the field, that *Agelenopsis*, an agelenid spider that builds a large and relatively permanent sheet-web, apparently chooses profitable sites before settling, by using proximate cues. *Argiope*, which however expends little time and material on its orb-web, is also able to assess site quality before settlement (Enders, 1975). Thus, trial and error is a waste of time and energy if useful cues are present to allow site quality to be estimated in advance. This is important irrespective of different foraging ecology.

Another point to be taken into account is the risk of predation during travel between web sites. A spider's web acts not only as a trap, but also as an early warning device against other predators. *D. socialis* is perfectly camouflaged on bark as long as the spider sits motionless but, by moving, they lose protection both from the web and from any camouflage.

What is the advantage of sites under protuberances? The protrusions of bark, where all specimens of the first two instars and about half of the older spiders were found, are not necessary for web support. This singular prominent structure of beech bark might provide

protection against rivulets of water running down the tree trunks during heavy rain, when all the spiders are out as usual. Another possibility is that sitting under a protrusion prevents the spider being easily visible from below, against the bright sky. The observation that the younger and smaller spiders more often use these structures is an indication for the first hypothesis.

D. socialis mainly uses the lowest tree trunk region (Braun, 1992) and rarely occurs in canopies (Hesse, 1940). As shown in this investigation, however, the increase downwards is not continuous, because an optimum height at approximately 1 m is prominent in the results. Psocoptera are in most cases obligatory tree trunk dwellers, in contrast to springtails, which live in the litter layer and which use trunks only optionally. If the trunk is wet, they spread upwards and graze on the epiphytic algae but hardly ever reach higher regions (Bauer, 1979). Thus, springtails, which are an important prey group, are more frequent at the lower trunk level and therefore the lower tree trunk provides more food for *D. socialis*.

The lowest 25 cm are totally avoided, although we could expect the highest prey density to occur in this part. Possible deterrent factors include predators and competitors that spread upwards from the ground. The trunk area is used optionally by numerous representatives of other strata. For example, in spiders, the border between field- and trunk-layer is not distinct (Łuczak, 1966).

The observation that more webs are found on the south side of trees can be explained by climatic conditions; this field study was carried out in a dense, shaded wood and not on isolated trees, where other authors have described *D. socialis* as preferring the northern or north-west aspect (Gurr, 1967; Wunderlich, 1982). Compass orientation is used by other spiders in thermoregulation (Lahoz-Beltra & Ortega, 1989).

Neither the distribution at different heights nor the orientation to cardinal points are correlated with the pattern of algal cover on trunks. The spatial pattern of algal cover on trunks is very patchy, thus a place with a

thick layer can even be found on the preferred south side and higher up the trunk.

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