Microhabitat identity of two species of sheet-web spiders: field experimental demonstration

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Summary. Descriptive studies reveal that web-site characteristics of two sympatric species of sheet-web spiders, Linyphia triangularis and L. tenuipalpis are similar, even though their body sizes and web sizes are significantly different. The hypothesis of identical web-sites were tested by a species exchange experiment in the field. Here the residence times of adult females of each species released in webs of the other species were compared to the residence times of other females released in own species' webs. As there was no differences between the species-exchange series and the control series, the experimental results supported the conclusions of the descriptive studies. The utility of testing habitat parameter differences experimentally, and the significance of the results to the ecology of the species, in particular to their interspecific interactions, are discussed.

Key words: Linyphia – Niche-separation – Spiders

One of the dogmas of community ecology is that no two species have exactly identical ecologies. Therefore, if we measure a sufficient number of niche or habitat parameters, we will always find one difference or another. A question then arises, however: Is the particular difference that we have found of real importance in the ecology of the two species?

In the standard procedures of comparative ecology, for example in the computation of overlap indices based on information about habitat and resource utilizations, all information is valued equally (cf. Pianka 1981). This is so because experimental information usually is not available to evaluate the relevance of the selected parameters. Clearly, food partitioning is more important among food-limited species, and microhabitat partitioning has particular significance among mutually aggressive species. Likewise, some microhabitat differences may be more important than others, though this is hard to evaluate as in most cases they are known only as statistical realities. Analytically, we may pose the question in the following way: Will we interfere significantly more with the population dynamics of the species if we experimentally eliminate one rather than another ecological difference between them?

Some web spiders offer a unique opportunity to answer such a question, because to some extent they are willing to accept the web of other individuals, in some cases even of other, though not very different, species. It is thus possible to release individual spiders in webs showing other web-site characteristics than those of their own web, and see how they behave under these new conditions.

In this paper, I report on a series of experiments in which individuals of one species have been released in webs of another species, i.e. their microhabitats have been exchanged. The experiments were designed to test the hypothesis that the web-site requirements of the two sympatric species are identical, as descriptive information (also given here) and other observations suggest. The experiments relies on the assumption that the time the spiders stay in a web reflects the acceptability of the web-site chosen by another individual.

Spiders and study area

Linyphia triangularis Clerck is a ubiquitous and extremely abundant spider in all of Northern Europe, frequenting nearly all kinds of habitats offering sufficient support for its space web. It is an annual spider, being adult in August to October and overwintering in the egg-sac (Toft 1978). As an adult it is 6–10 mm in total length. This is slightly larger than Linyphia tenuipalpis Simon (4.5–8 mm) which is also much more restricted in macrohabitat occupation. In Denmark this species occurs only on Calluna heaths (Toft 1980b), nearly always mixed with L. triangularis. Apart from their only statistical size difference (Toft 1980a), they are very similar in general appearance, though usually recognizable on the colour pattern on the dorsal side of the abdomen. In areas with mixed populations their webs seem identical in general shape and with no immediate differences as to how they are placed in the vegetation.

The life-cycle of L. tenuipalpis is similar to that of L. triangularis (Toft, unpublished work). In all phenophases, instars, moults, mating, and egg-laying, L. tenuipalpis is slightly earlier than L. triangularis, but the difference is only one or two weeks.

The webs are typical sheet-webs consisting of a rather densely woven horizontal sheet while vertical or oblique threads form a barrier web above. The spider is moving about upside-down on the underside of the sheet. The web is attached to surrounding vegetation at all possible supports along the circumference of the sheet as well as by the barrier threads above, and by some scattered attachment threads below the sheet. In the adult stage only females build webs, and all results given in this paper refer to adult females.

The studies to be reported here were performed in the heaths belonging to the Mols Laboratory in Eastern Jut-
land, Denmark. In this area, L. ten is particularly abundant in the heather on warm south-facing slopes; here it may be the dominant species particularly in small patches of Calluna isolated by bare areas grown with tufts of Corynephorus concolor. However, which species dominates may change within few meters.

Methods

Web and web-site characteristics

In the month of September, i.e. in the adult period of both species, measurements of webs and web site characteristics were made. These included:

1. length (l) and width (w) of web sheet; from this sheet-area is computed (l·w),
2. height of barrier web (hb); web volume is then computed as \( h_b \cdot l \cdot w \),
3. height of sheet (h) above the ground,
4. height of vegetation (hv) at the place of the web; relative web height is then given as \( h/h_v > 100 \),
5. vegetational coverage, i.e. the percentage of the sheet-area that is covered by overhanging vegetation. This measure intends to indicate the degree to which the web is hidden within the Calluna bushes, and
6. percentage importance of different plant species as web support; here I distinguished only heather (Calluna), grass, and “other plants”.

I took measurements of webs in two Calluna habitats, viz. in an area of continuous heather, and in isolated patches of Calluna, separated by area of bare ground with Corynephorus.

Spider exchange experiment

The area selected for experiments were mainly a border line between continuous and patchy Calluna, in which the two species were mixed and represented in about equal numbers. Several adult females of each species were collect-

ed in the field and in the laboratory marked on the belly with a small dot of enamel paint, after anaestesizing with carbon dioxide. For the experiments these marked spiders were then released in a new web, from which the owner had just been removed without damaging the web.

I started three series of these experiments on different dates between August 26 and September 3, 1984. The first and third I call the species-exchange series, while the second forms a control series. In the species-exchange experiments the marked L. triangularis were released in webs from which L. ten was removed, and marked L. ten were released in webs from which L. triangularis were removed. In control experiments every L. triangularis were released in a web from which an L. triangularis were removed, but not in its own web, and L. ten were released in webs formerly held by other L. ten.

After releasing the spiders, webs were visited daily and the presence or absence of the marked spider was noted. In this way I obtained the residence time of the marked spiders in their new webs. The spiders were not individually marked, but as they were released with distances of several webs, the chances of movements between experimental webs were small.

Results

Table 1 compares data on the relevant web and web site parameters for each habitat. As statistical test for differences between the two species I have used the Mann-Whitney U-test. It is seen that sheet area and web volume show highly significant differences, with L. triangularis having the larger webs. This finding is not surprising in view of the fact that this species is also the larger of the two.

As regards characteristics associated with web-sites only one comparison shows significance, viz. vegetation height in the Calluna-patch habitat, all others being far from significance. The difference found is probably not a reliable one, however. As my procedure was to take measurements from all webs present in a (then necessarily) small number

| Table 1. Data on web size and web site characteristics for Linyphia triangularis (L. tri) and and Linyphia ten (L. ten) in two Calluna habitats, continuous and patchy heather |
|---------------------------------|---------------------|---------------------|
|                                 | Continuous Calluna  | Calluna patch       |
| Sheet area (cm²)                | \( x \pm SD \)       | \( x \pm SD \)       |
| L. tri                          | 420.1 ± 124.3        | 380.6 ± 147.3        |
| L. ten                          | 269.3 ± 159.9        | 267.9 ± 138.6        |
| Web volume (cm³)                |                     |                     |
| L. tri                          | 4115.5 ± 2319.1      | 3136.8 ± 2026.6      |
| L. ten                          | 2353.0 ± 1739.1      | 2020.4 ± 1566.4      |
| Sheet height (cm)               |                     |                     |
| L. tri                          | 25.4 ± 5.3           | 28.5 ± 8.9           |
| L. ten                          | 23.9 ± 4.2           | 26.5 ± 6.5           |
| Veg. height (cm)                |                     |                     |
| L. tri                          | 40.9 ± 9.6           | 42.5 ± 11.1          |
| L. ten                          | 37.8 ± 6.9           | 37.8 ± 8.5           |
| Web rel. height (%)             |                     |                     |
| L. tri                          | 64.3 ± 10.8          | 67.6 ± 13.9          |
| L. ten                          | 64.3 ± 11.3          | 70.7 ± 12.0          |
| Veg. coverage (%)               |                     |                     |
| L. tri                          | 10.8 ± 14.2          | 22.7 ± 29.0          |
| L. ten                          | 13.3 ± 12.2          | 16.3 ± 20.9          |
| Web support, heather (%)        |                     |                     |
| L. tri                          | 97.6 ± 4.7           | 92.5 ± 15.7          |
| L. ten                          | 94.5 ± 14.7          | 90.8 ± 14.8          |
| Web support, grass (%)          |                     |                     |
| L. tri                          | 2.4 ± 4.7            | 6.0 ± 14.4           |
| L. ten                          | 5.5 ± 14.7           | 8.0 ± 12.8           |
| Web support, other plants (%)   |                     |                     |
| L. tri                          | 0 ± 0                | 1.5 ± 6.4            |
| L. ten                          | 0.1 ± 0.7            | 1.2 ± 8.7            |

Each parameter has been tested for species difference by means of the Mann-Whitney U-test, significance level given by P. Sample sizes all through the table are: Continuous Calluna, L. tri n = 55; L. ten n = 50; Calluna patch; L. tri n = 50, L. ten n = 65