

# Patch size, fine-scale co-occurrence and competition in forest litter linyphiids

Jacques Leclerc<sup>1</sup> & Patrick Blandin<sup>2</sup>

<sup>1</sup>Station Biologique de Foljuif, Ecole Normale Supérieure, Rue du Château, F-77140 Saint-Pierre-les-Nemours, France

<sup>2</sup>Laboratoire d'Ecologie Générale, Muséum National d'Histoire Naturelle, 4 Ave. du Petit Château, F-91800 Brunoy, France

The fine-scale repartition and co-occurrence of the different species of sheet-web spiders found in a deciduous forest litter is estimated by means of transect sampling at two fixed stations and three periods of the year (spring, mid-summer and fall). A variance to mean ratio test was applied on blocked data to find the scale of aggregation which is a function of the microhabitat patch size. Probability of co-occurrence between species was calculated at each block size. One of the predictions is that similar species should co-occur at the patch size scale but should replace one another at a finer scale if interference competition is effective.

## 1. Introduction

Sheet-web spiders are examples of predators which spend most of their time at a fixed place, namely the web (Vollrath 1987), so one can assume that web positions are important attributes both in foraging ecology (Caraco & Gillespie 1986) and in community organization (Spiller 1984, Toft 1987). In this paper, we look for web position patterns in a guild of sheet-web spiders which occupy a deciduous forest litter. The first pattern sought for is the type of spatial dispersion (aggregation, randomness or overdispersion) of each species while the second is the type of between-species co-occurrence (negative, random or positive association). Block-size analysis (Greig-Smith 1979) is used to determine the spatial scale of

these patterns. Our null hypothesis is that there is no such pattern in the observed guild of sheet-web spiders. Results are compared with predictions of competition theory.

## 2. Methods

The study was undertaken at the Station Biologique de Foljuif, 80 km south of Paris, France, in a 4 ha mixed forest plot. Dominant species are oak (*Quercus sessiflora*), hornbeam (*Carpinus betulus*) and pine (*Pinus sylvestris*). Details on climate, vegetation structure and litter can be found in Blandin et al. (1980).

Our goal was to obtain the best estimates of web position at a reasonable cost. Mapping tech-

niques provide the most precise point estimates (Diggle 1983) but are too time-expensive for sheet-webs. On the other hand, quadrat sampling does not seem appropriate because the area commonly sampled (1/16 m<sup>2</sup>) is possibly one or two orders of magnitude greater than most sheet-webs in the study area (unpubl. data). The chosen compromise was to pick up litter by hand and to enclose it very rapidly in a bag with its spider contents. Two sampling sites were selected in seemingly uniform areas without undergrowth to facilitate the picking. One of the sites was nearly horizontal (site H) while a small slope characterized the second (site S). A 256-handful transect was sampled at each site in fall (October 14 and 21, 1987), spring (April 20 and 27, 1988) and summer (July 6 and 8, 1988). The same day and the following day, spiders were manually extracted from the numbered bags. They were still alive and could be easily detected; furthermore, a handful of litter is sufficiently small to find most if not all of the spiders. All adult spiders were identified at the species level; immature *Lepthyphantes* were pooled; other immature linyphiids were put in a single group with the exception of immature *Macrargus rufus* which can be safely recognized (Christophe 1974). As an abundant species in the samples, the non-linyphiid *Hahnia helveola* was included in the analysis.

Handfuls were blocked by 1,2,4,...,64 and an index of dispersion (variance to mean ratio) was

calculated at each block size for total spider counts and for each species count. Formal significance tests for departure from randomness are not available (Diggle 1983) so we have used a Monte Carlo procedure to simulate complete spatial randomness at all scales. This was done by reshuffling the transect positions (1...256) in a pseudotransect and then calculating the dispersion index of the pseudotransect. This procedure was repeated 100 times: at each block size, the dispersion index was significant if it was greater than 95% (aggregation) or lower than 5% (overdispersion) of the corresponding pseudoindeces. The block size with that significant dispersion index indicated patch size. Species co-occurrences were analysed with the same approach, replacing the dispersion index by the probability of co-occurrence calculated by the method of Mac Nally & Doolan (1986). The probability of detecting deviation from randomness becomes independent of sampling size at about 15 (*t*-test between no patch and patch cases;  $P=0.09$ ). Thus, both indices were calculated only when 15 or more spiders of each species were caught in a transect.

### 3. Results

Transect lengths divided by 256 gave a handful length of 10 to 15 cm. In our analysis we used the handful length of 12.5 cm; therefore, the succes-

Table 1. Catch of the main species of spiders in hand transects at two selected sites (S = slope; H = horizontal) and three dates (fall, spring and summer). a = adult; i = immature.

	Fall		Spring		Summer	
	S	H	S	H	S	H
<i>Hahnia helveola</i> (a)	51	25	13	3	2	5
<i>H. helveola</i> (i)	21	8	34	13	30	25
<i>Microneta viaria</i> (a)	37	36	16	9	5	19
<i>Centromerus serratus</i> (a)	4	38	1	7	0	7
<i>C. aequalis</i> (a)	3	22	0	9	0	6
<i>C. dilutus</i> (a)	0	16	0	0	0	0
<i>Macrargus rufus</i> (a)	28	16	1	4	0	1
<i>M. rufus</i> (i)	11	1	0	0	72	124
<i>Lepthyphantes flavipes</i> (a)	11	7	6	7	5	11
<i>Lepthyphantes sp</i> (i)	18	12	23	15	15	37
Other Linyphiidae (i)	40	46	58	69	15	74
Total	224	227	152	136	144	309

sive scales were 0.125, 0.25, 0.5, 1, 2, 4 and 8 meters. Handful transect catches are reported in Table 1. Differences between sites and between dates are apparent (no statistical tests made). We did not find any case of overdispersion. Random and aggregated cases with their patch sizes are shown in Table 2: it appears that patchiness is minimal in spring and becomes larger in summer or fall. Predominant scales are 0.5–4 m which are found more frequently than small scales (<0.5 m) or large scales (>4 m). There also exist multispecies patches in summer and fall (Table 2, all species).

Species association is scale-dependent (Fig. 1). Associations (positive and negative) are more frequent at the smallest scale (0.125 m) and then at the 1–2 m scale. Positive associations are more frequent than negative associations at all scales. Table 3 shows that associations at different scales are probably not independent ( $P=0.06$ ) mainly because small scale positive associations are associated with larger scale positive associations (Table 3, last line).

#### 4. Discussion

As terrestrial predators, sheet-web spiders that are found in deciduous forest litter should be affected by interspecific competition (Hairston et al. 1960).

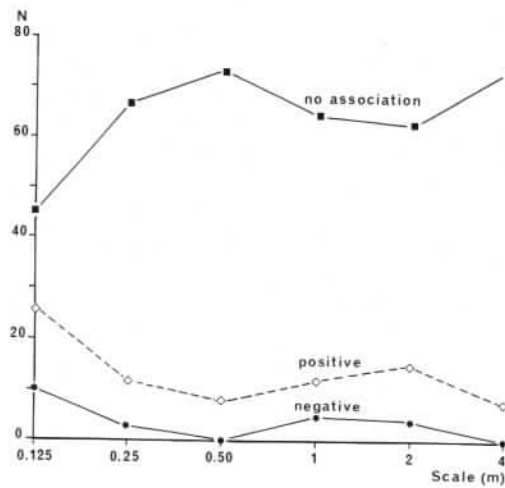


Fig. 1. Number (N) of cases of positive, negative or no association between pairs of species as a function of scale.

As “sit and wait” predators (Vollrath 1987) linked to specific web sites possibly in short supply, this competition should be a competition for space (Yodzis 1986). Resource competition is unlikely if one assumes that there is a high variability in prey capture both in time and space (Caraco &

Table 2. Patch sizes (m) of the main species of spiders. Size is expressed either as a single number or as a range (where necessary). R = no patch found; – = insufficient sampling (catch < 15).

	Fall		Spring		Summer	
	S	H	S	H	S	H
<i>Hahnna helveola</i> (a)	R	0.5	–	–	–	–
<i>H. helveola</i> (i)	R	–	R	–	0.25–2	4
<i>Microneta viaria</i> (a)	8	0.5–2	R	–	–	2–8
<i>Centromerus serratus</i> (a)	–	0.5–1	–	–	–	–
<i>C. aequalis</i> (a)	–	0.25	–	–	–	–
<i>C. dilutus</i> (a)	–	R	–	–	–	–
<i>Macrargus rufus</i> (a)	R	R	–	–	–	–
<i>M. rufus</i> (i)	–	–	–	–	R	4
<i>Lepthyphantes</i> sp (i)	R	–	0.25	R	R	R
Other Linyphiidae (i)	2–4	R	2	R	R	2–4
All species	1–8	0.5–4	R	R	1–2	1–8

Table 3. Cross-tabulation of small scale (0.125 m) association with large-scale (2–4 m) association for species pairs with more than 15 individuals for each species. Numbers in parentheses are expected under independence. – = negative association; 0 = no association found; + = positive association.  $\chi^2 = 8.6$ ;  $P = 0.06$ .

		Large		Total	
		–	0	+	
Small	–	2 (0.6)	6 (7.0)	2 (2.4)	10
	0	2 (2.8)	36 (31.7)	7 (10.5)	45
	+	1 (1.6)	15 (18.3)	10 (6.1)	26
Total		5	57	19	81

Gillespie 1986) with several prey species, mainly in diptera and collembola (personal field observations, Moulder & Reichle 1972, Aitchison 1984).

Species co-occurrences (Fig. 1) in relation with patch sizes (Table 2) do not support the hypothesis of competition as a major force in the guild organization. Competition for web sites predicts that co-occurrence at a larger scale (shared microhabitat) should be coupled with species replacement at the shortest scale (web size scale) because the dominant species push the subordinate out of the rare web sites (variance deficit at short scale of Wilson et al. 1987). This is not what is found in most of the cases (Table 3). Positive associations are more common at all scales, which can be explained by a microhabitat selection process based on litter depth and complexity (Bultman & Uetz 1982) with web sites in excess.

Although our results do not disprove the importance of interference competition in forest litter linyphiids, they point out that hypothetical competition processes must be looked for at scales smaller than 0.125 meter. At those scales, vertical distribution probably becomes an important variable, though no differences were observed between *Centromerus* sp. Territoriality overdispersion (Riechert 1978), if present, would also be found only at those scales.

*Acknowledgements.* J. Leclerc thanks Fonds pour la formation de chercheurs et l'aide à la recherche, Gouvernement du Québec, for a scholarship supporting this study.

## References

- Aitchison, C. W. 1984: Low temperature feeding by winter-active spiders. — *J. Arachnol.* 12:297–305.
- Blandin, P., Abbadie, L., Courault, S., Garay, I. & Geoffroy, J. J. 1980: Etude d'un écosystème forestier mixte I. Climat, structure de la végétation et retombées de litière. — *Rev. Ecol. Biol. Sol* 17:181–198.
- Bultman, T. L. & Uetz, G. W. 1982: Abundance and community structure of forest floor spiders following litter manipulation. — *Oecologia* 55:34–41.
- Caraco, T. & Gillespie, R. G. 1986: Risk-sensitivity: foraging mode in an ambush predator. — *Ecology* 67:1180–1185.
- Christophe, T. 1974: Etude écologique du peuplement d'araignées d'une litière de Châtaigneraie (Forêt de Montmorency, Val d'Oise). — Thèse 3è Cycle Biol. Anim. (Entomol.), Orsay. Publ. Lab. Zool. ENS 3:1–144.
- Diggle, P. J. 1983: Statistical analysis of spatial point patterns. — Academic Press, London. 148 pp.
- Greig-Smith, P. 1979: Pattern in vegetation. — *J. Ecol.* 67:755–779.
- Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960: Community structure, population control and competition. — *Amer. Nat.* 94:421–425.
- Mac Nally, R. C. & Doolan, J. M. 1986: An empirical approach to guild structure: habitat relationships in nine species of eastern-Australian cicadas. — *Oikos* 47:33–46.
- Moulder, B. C. & Reichle, D. E. 1972: Significance of spider predation in the energy dynamics of forest-floor arthropod communities. — *Ecol. Monogr.* 42:236–243.
- Riechert, S. E. 1978: Energy-based territoriality in populations of the desert spider *Agelenopsis aperta* (Gertsch). — *J. Anim. Ecol.* 46:729–749.
- Spiller, D. A. 1984: Competition between two spider species: experimental field study. — *Ecology* 65:909–919.
- Toft, S. 1987: Microhabitat identity of two species of sheet-web spiders: field experimental demonstration. — *Oecologia* 72:216–220.
- Vollrath, F. 1987: Growth, foraging and reproductive success. — In: Nentwig, W. (ed.), *Ecophysiology of spiders*: 357–370. Springer Verlag, Berlin Heidelberg.
- Wilson, J. B., Gitay, H. & Agnew, A. D. Q. 1987: Does niche limitation exist? — *Functional Ecol.* 1:391–397.
- Yodzis, P. 1986: Competition, mortality and community structure. — In: Diamond, J. & Case, T. J. (eds.), *Community ecology*: 480–491. Harper & Row, New York.