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## Niche partitioning in three sympatric web-building spiders (Araneae: Linyphiidae)

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### Summary

Three sympatric species of linyphiid spiders, *Frontinellina frutetorum*, *Neriene radiata* and *Linyphia triangularis* were observed in eastern Austria. Their phenology, web height, prey capture and web structure were measured and compared. The adults of *F. frutetorum* and *N. radiata* were active in early summer, while adults of *L. triangularis* were seasonally isolated, being active in autumn. The spiders were also observed to utilise different web heights and to capture different types of prey. In contrast, aspects of web size, prey size and prey capture rates were similar. It is postulated that differences in the spiders' spatial and temporal distribution resulted in further prey capture differences.

### Introduction

The utilisation of distinct niches in terms of temporal segregation, web structure, web placement and prey capture has been reported for many different web-building spiders (Brown, 1981; Enders, 1974; Herberstein & Elgar, 1994; Malt *et al.*, 1990; Olive, 1980; Pasquet, 1984; Uetz *et al.*, 1978; Ward & Lubin, 1992; Wise & Barata, 1983). The suggested mechanism responsible for the observed patterns is the competitive exclusion principle, stating that no two species can occupy the same niche as a result of competition, leading to some form of displacement (Begon *et al.*, 1990).

Niche theory has, however, recently come under attack. Studies have found extensive prey and niche overlap (Kajak, 1965; Nyffeler & Benz, 1979, 1989), providing strong arguments against competition theory and questioning the importance of niche partitioning (Wise, 1993).

Investigating niche parameters brings with it some practical difficulties, as the niche occupied by any organism has an infinite number of dimensions which cannot be completely assessed (Krebs, 1970). Measuring a vast

array of niche parameters for the purpose of comparing two or more organisms will, however, probably find a number of differences, though some of these may not be of great importance to the ecology of the animals studied (Toft, 1987).

Nevertheless, while these arguments may deter further investigations into niche partitioning, a careful selection of niche parameters can provide important and conclusive results, which in turn are a necessary basis for the design of further studies into the forces driving the observed patterns.

Herein, I report on a number of niche parameters, such as prey capture, web structure, web placement and seasonality, utilised by three linyphiid spiders, *Frontinellina frutetorum* (C. L. Koch), *Neriene radiata* (Walckenaer) and *Linyphia triangularis* (Clerck). The spiders construct typical linyphiid webs with a centrally located sheet beneath which the spider hangs. Entangling threads are spun above the sheet to intercept prey which tumbles down on to the sheet, where it is attacked by the spider.

### Material and methods

The spiders were studied from March to October (1993 and 1994) in a mixed deciduous forest in eastern Austria near the town of Hartberg (Herberstein, 1995). The study site consisted of an area of forest regrowth planted with fir trees (mostly Douglas fir, *Pseudotsuga menziesii*). The trees were surrounded by a dense understorey, composed of grasses, ferns, raspberry and blackberry bushes.

### Phenology

The species-specific phenologies were estimated using density measures (individuals per square metre). Ten transects (10 × 1 m) were randomly chosen each month and the number of spiders found along the transects counted. The average monthly densities sampled from March to October 1994 were plotted to show the emergence and disappearance of the spiders. A more precise measure of the phenologies of the spiders could have been achieved by regular samples of their size. However, this would have been a very disruptive method, causing the destruction of webs and probably an exodus of spiders and was therefore not used.

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### Web height

The utilisation of space on fir trees was investigated by describing web height — the distance from the ground to the sheet of the web. From March to October 1993, ten transects (10 × 1 m) were randomly chosen each month and the height of each inhabited web found along the transects was recorded. The median monthly web heights were compared using Mann–Whitney *U*-tests.

### Prey spectra

The prey captured was sampled from the end of May to the beginning of July 1993 for *F. frutetorum* and *N. radiata* and from August to September 1993 for *L. triangularis*. The sampled spiders were mostly adult but also included some subadults. Webs were surveyed at 1- to 2-hour intervals throughout the observation periods, which ranged from 4 to 12 hours, covering the spiders' entire foraging period. At least 10 individuals of each species were surveyed on more than 20 days. As old carcasses are often left hanging in the webs, only those prey items on which the spiders had been feeding were carefully removed from the webs and later identified. The body length of each prey item was also measured.

The species-specific prey spectra were compared using hierarchical log linear tests. The analyses only considered prey types sampled at frequencies greater than 5%. The test also calculated *z*-values with 95% confidence intervals at  $\pm 1.96$  to reveal which of the individual insect groups showed differences in frequency. The median prey size, pooling all items collected, was compared using Kruskal–Wallis tests.

### Prey capture rates

Prey capture rates were obtained by counting the number of prey subdued per hour. Prey items were not removed from the web, in order to maintain natural prey capture conditions. At least five randomly chosen adult individuals of each species were observed for a 2-hour period and checked at 30-minute intervals. Capture rates were measured at the following times: 0700–0900, 0900–1100, 1400–1600, 1600–1800 on at least 10 separate days. Only prey items on which spiders were feeding were considered captured. The median prey capture rates were analysed with Kruskal–Wallis tests.

### Web size and spider size

The species-specific web structure of randomly selected adult female spiders was investigated in the field by measuring sheet length, sheet breadth and the height of the entangling threads above the sheet. The size of the spiders inhabiting these webs was also sampled by measuring the length of leg I (right side), carapace length and total body length under a dissecting microscope. Differences in web and spider size were analysed using an Analysis of Variance, and individual

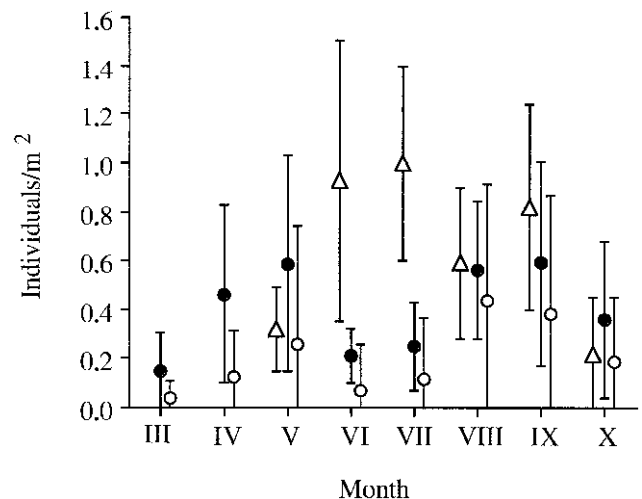


Fig. 1: Average ( $\pm$  SD) densities (individuals per  $m^2$ ) per month for juvenile and adult *F. frutetorum* (○), *N. radiata* (●) and *L. triangularis* (△).

Scheffe *F*-tests to indicate which species contributed significantly to overall differences.

## Results

### Phenology

Juveniles of *F. frutetorum* and *N. radiata* first appeared in March (Fig. 1). After a growth period of 2 to 3 months, the spiders reached the adult stage in May, when the males started to cohabit in the webs of the females. From June to July the densities of *F. frutetorum* and *N. radiata* decreased as females laid eggs and died. In contrast, juveniles of *L. triangularis* emerged in May (Fig. 1), when they coexisted with the adults of *F. frutetorum* and *N. radiata* for a short period. After a four-month growth period, *L. triangularis* reached the adult stage in August/September and males were frequently found in the webs of the females, where copulation occurred. By October the spiders laid their eggs, which overwintered, while the adults died. The new generation of juvenile *F. frutetorum* and *N. radiata* emerged in July/August (Fig. 1), coexisting with subadult or adult *L. triangularis* until October when spiders ceased activity until the following spring.

### Web height

95% of the webs of *F. frutetorum* and *L. triangularis* were constructed on fir trees, whereas *N. radiata* placed only 47% of its webs on fir trees, the rest being found in the shrub vegetation. For comparative reasons, however, only webs constructed on fir trees were considered in the following analyses.

Comparing the median web heights revealed some significant differences (Fig. 2, Table 1). *F. frutetorum* placed its webs significantly higher than *N. radiata* throughout the entire season except for the June sample, a period when their densities declined (see Fig. 1). In July, not enough webs were available to conduct a meaningful comparison.

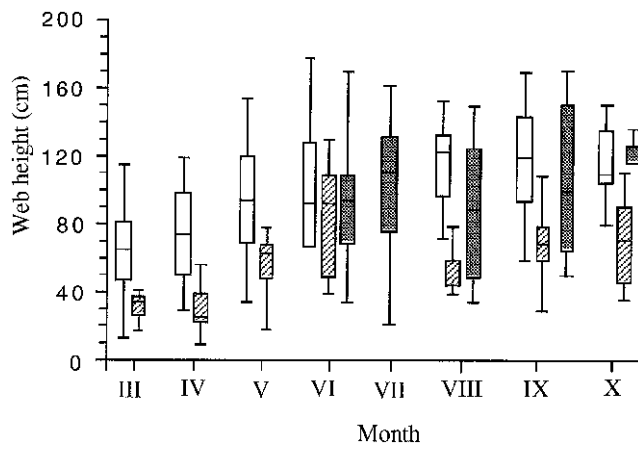


Fig. 2: Box plots describing the first quartile, the median (second quartile), the third quartile and the range of web height above ground level for juvenile and adult *F. frutetorum* (□), *N. radiata* (▨) and *L. triangularis* (▩).

In contrast to *F. frutetorum* and *N. radiata*, web placement by *L. triangularis* was more variable. In early summer (June–August), *L. triangularis* constructed its webs more or less between those of *F. frutetorum* and *N. radiata*, and no significant difference in web height was observed (Table 1). In late summer (September–October) the web height of *L. triangularis* was still not different from that of *F. frutetorum* but significantly higher than the web height of *N. radiata* (Table 1).

*Prey spectra*

A total of 151 prey items were collected from the webs of *F. frutetorum*, 82 items from the webs of *N. radiata* and 138 prey items from the webs of *L. triangularis*. The major (>5% of the total) prey types captured were Aphidina, Cicadellidae, Myrmicinae and Sciaridae, along with other taxa of minor frequencies (Table 2).

Comparison of prey spectra revealed significant differences ( $\chi^2=54.5$ ,  $df=6$ ,  $p<0.01$ ). The individual  $z$ -values indicated that *N. radiata* captured significantly more Sciaridae than expected, while *L. triangularis*

Prey type	<i>F. frutetorum</i>	<i>N. radiata</i>	<i>L. triangularis</i>
Aphidina	39 (1.32)	35.4 (-1.27)	35 (-0.24)
Cicadellidae	6 (-0.28)	18.3 (1.5)	2.2 (-1.01)
Myrmicinae	0 (-2.7**)	0 (-2.3*)	14.5 (4.7**)
Sciaridae	10.6 (-0.27)	22 (2.86**)	9.4 (-2.18*)
Psocoptera	3.3	0	3.6
Delphacidae	3.3	1.2	2.9
Miridae	0	1.2	2.9
Cantharidae	2.6	0	1.4
Staphylinidae	0	0	4.3
Eurythomidae	1.3	4.9	1.4
Ichneumonidae	3.3	0	0
Formicinae	2	1.2	4.3
Anthomyiidae	0	3.7	1.4
Helomyzidae	4	0	0
Lauxaniidae	3.3	0	1.4
Muscidae	0	2.4	0
Others	21.3	9.7	15.3
Total number of prey items	151	82	138

Table 2: Percentages of prey types captured in the webs of *F. frutetorum*, *N. radiata* and *L. triangularis*. Individual  $z$ -values are given in parentheses (\* $p<0.05$ , \*\* $p<0.01$ ).

captured significantly more Myrmicinae than expected (Table 2). Although the spiders captured different prey types, no significant difference in the median prey size ( $H=1.11$ ,  $df=2$ ,  $p>0.05$ ) was found (Fig. 3).

*Prey capture rates*

As the species-specific prey capture rates were sampled at different times (0700–0900, 0900–1100, 1400–1600, 1600–1800), the first analysis looked for any temporal differences within each species while the second analysis looked at species-specific differences. There was no time effect on the prey capture rates for *F. frutetorum* ( $H=0.69$ ,  $df=3$ ,  $p>0.05$ ), *N. radiata* ( $H=2.65$ ,  $df=3$ ,  $p>0.05$ ) or *L. triangularis* ( $H=0.12$ ,  $df=3$ ,  $p>0.05$ ). They were therefore pooled for an interspecific comparison which showed that prey capture rates were similar for all three spider species ( $H=1.22$ ,  $df=2$ ,  $p>0.05$ ) (Fig. 4).

Month	Comparison	Significance
March	<i>F. frutetorum</i> : <i>N. radiata</i>	$U_{21,9} = 18^{**}$
April	<i>F. frutetorum</i> : <i>N. radiata</i>	$U_{19,13} = 13^{**}$
May	<i>F. frutetorum</i> : <i>N. radiata</i>	$U_{26,21} = 106^{**}$
June	<i>F. frutetorum</i> : <i>N. radiata</i>	$U_{9,8} = 18$
	<i>F. frutetorum</i> : <i>L. triangularis</i>	$U_{9,17} = 73$
	<i>L. triangularis</i> : <i>N. radiata</i>	$U_{17,8} = 57$
July	NA	
August	<i>F. frutetorum</i> : <i>N. radiata</i>	$U_{22,13} = 6^{**}$
	<i>F. frutetorum</i> : <i>L. triangularis</i>	$U_{22,27} = 172^*$
	<i>L. triangularis</i> : <i>N. radiata</i>	$U_{27,13} = 118$
September	<i>F. frutetorum</i> : <i>N. radiata</i>	$U_{29,19} = 49^{**}$
	<i>F. frutetorum</i> : <i>L. triangularis</i>	$U_{29,16} = 189$
	<i>L. triangularis</i> : <i>N. radiata</i>	$U_{16,19} = 63^{**}$
October	<i>F. frutetorum</i> : <i>N. radiata</i>	$U_{10,16} = 13^{**}$
	<i>F. frutetorum</i> : <i>L. triangularis</i>	$U_{10,7} = 30$
	<i>L. triangularis</i> : <i>N. radiata</i>	$U_{7,16} = 4^{**}$

Table 1: Summary of the web height analyses for *F. frutetorum*, *N. radiata* and *L. triangularis* (\* $p<0.05$ , \*\* $p<0.01$ ).

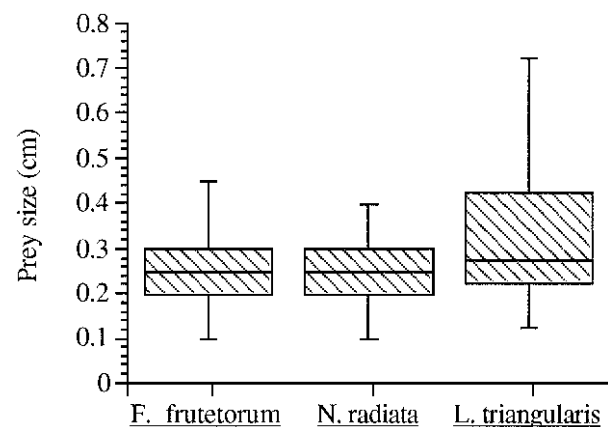


Fig. 3: Box plots describing the first quartile, the median (second quartile), the third quartile and the range of prey size (body length) for adult and subadult female *F. frutetorum*, *N. radiata* and *L. triangularis*.

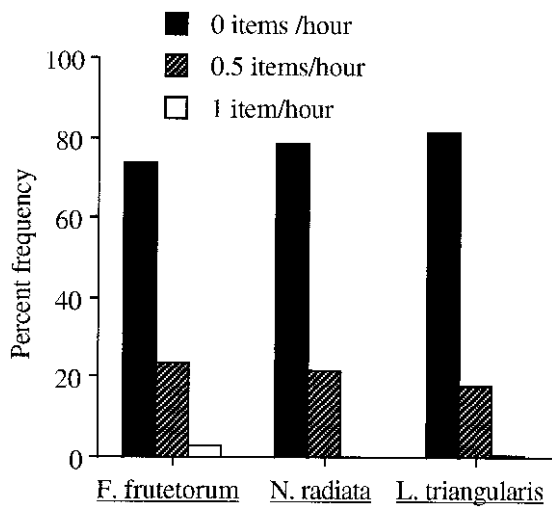


Fig. 4. Percentage frequency of the number of prey items captured per hour for adult female *F. frutetorum*, *N. radiata* and *L. triangularis*.

#### Web size and spider size

The spiders constructed species-specific webs. Most notably, viewing the web from the side, the centrally located sheet was shaped in a concave manner for *F. frutetorum*, convexly for *N. radiata* and more or less irregularly saddle-shaped for *L. triangularis*. Sheet length ( $F=23.3$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ) and sheet breadth ( $F=22.8$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ) differed significantly between the species, while the height of the entangling threads above the sheet was similar ( $F=0.68$ ,  $df=2$ ,  $57$ ,  $p>0.05$ ) (Fig. 5). *L. triangularis* constructed web sheets of greater length than *F. frutetorum* ( $F=13.7$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ) and *N. radiata* ( $F=20.6$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ) as well as greater breadth than *F. frutetorum* ( $F=16.2$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ) and *N. radiata* ( $F=17.9$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ). In contrast, sheet length and sheet breadth for *F. frutetorum* and *N. radiata* were similar ( $F=0.7$ ,  $df=2$ ,  $57$ ,  $p>0.05$ ;  $F=0.05$ ,  $df=2$ ,  $57$ ,  $p>0.05$  respectively).

The adult females of all three species showed significant differences in their leg length ( $F=53.9$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ), carapace length ( $F=11.7$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ) and total body length ( $F=6.2$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ) (Table 3).

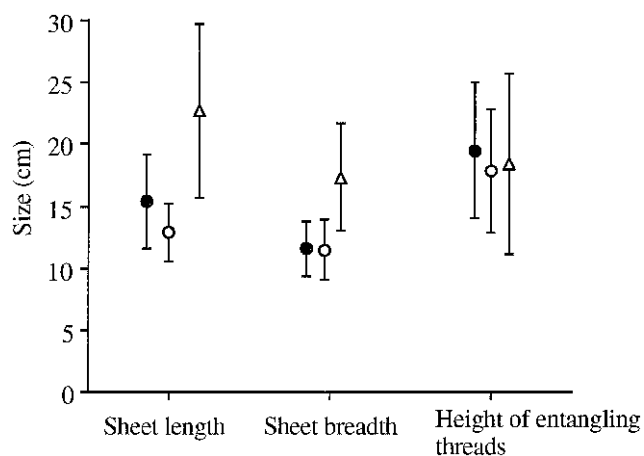


Fig. 5. Average ( $\pm$ SD) sheet length, sheet breadth and height of the entangling threads for adult female *F. frutetorum* (○), *N. radiata* (●) and *L. triangularis* (△).

Parameter (cm)	<i>F. frutetorum</i> (n=20)	<i>N. radiata</i> (n=20)	<i>L. triangularis</i> (n=20)
Leg I length	0.845 $\pm$ 0.074	1.403 $\pm$ 0.08	1.302 $\pm$ 0.294
Carapace length	0.2 $\pm$ 0	0.195 $\pm$ 0.048	0.245 $\pm$ 0.039
Total body length	0.465 $\pm$ 0.052	0.515 $\pm$ 0.056	0.532 $\pm$ 0.078

Table 3: Average ( $\pm$ SD) leg I length, carapace length and total body length for adult female *F. frutetorum*, *N. radiata* and *L. triangularis*.

The leg length of *N. radiata* and *L. triangularis* was significantly larger than that of *F. frutetorum* ( $F=47.4$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ;  $F=31.9$ ,  $df=2$ ,  $57$ ,  $p<0.01$  respectively), while no difference in leg length between *N. radiata* and *L. triangularis* was observed ( $F=1.5$ ,  $df=2$ ,  $57$ ,  $p>0.05$ ). The carapace length of *F. frutetorum* and *N. radiata* was significantly smaller than that of *L. triangularis* ( $F=7.8$ ,  $df=2$ ,  $57$ ,  $p<0.01$ ;  $F=9.6$ ,  $df=2$ ,  $57$ ,  $p<0.01$  respectively) but there was no difference in carapace length between *F. frutetorum* and *N. radiata* ( $F=0.1$ ,  $df=2$ ,  $57$ ,  $p>0.05$ ). The total body length of *N. radiata* and *L. triangularis* was significantly larger than that of *F. frutetorum* ( $F=3.1$ ,  $df=2$ ,  $57$ ,  $p<0.05$ ;  $F=5.7$ ,  $df=2$ ,  $57$ ,  $p<0.01$  respectively), while no difference in total body length between *N. radiata* and *L. triangularis* was observed ( $F=0.4$ ,  $df=2$ ,  $57$ ,  $p>0.05$ ).

#### Discussion

The niches occupied by a number of ecologically similar species living in the same habitat can be differentiated through resource partitioning, where each utilises different resources (Begon *et al.*, 1990). The three linyphiid spiders studied are considered to be closely related and were previously included within the same genus (Van Helsdingen, 1969). All three constructed typical sheet webs, suggesting a similar mode of prey capture. These aspects, as well as their high population densities within a small but well-defined area (pine plantation) make them ideal subjects for an investigation of resource partitioning.

Considering the requirements of web-building spiders, food and space can become limiting (Bradley, 1993; Miyashita, 1992; Ward & Lubin, 1992; Wise, 1975, 1979) and both are thus of particular interest when describing a species' niche. As it is virtually impossible to describe all niche parameters, this study concentrated on the use of space and on the spiders' foraging behaviour, including web architecture which can also influence prey capture (Chacón & Eberhard, 1980; Miyashita & Shinkai, 1995). Additionally, the temporal use of the habitat in terms of species-specific phenology was also investigated as some resources used may be separated in time.

The most notable differences between the three linyphiid spiders were observed in the temporal use of the habitat, web placement and type of prey captured. In contrast, the three species demonstrated similar web characteristics, size of prey and prey capture rates. Another interesting point is that half of the webs of *N. radiata* were placed in the shrub vegetation while the

other two spider species almost exclusively utilised the pine trees. This suggests that *N. radiata* does not have a strict preference for pine trees and may have moved to the shrub vegetation in order to avoid high spider densities on the pine trees.

*F. frutetorum* and *N. radiata* are seasonally isolated from *L. triangularis* to such an extent that they never co-occur as adults. Juveniles of *L. triangularis* were present with adult *F. frutetorum* and *N. radiata* (early summer). When *L. triangularis* matured (autumn) the new generation juveniles of *F. frutetorum* and *N. radiata* hatched. In favourable conditions, *N. radiata* has been found to produce two mature generations within one season (Wise, 1974), which was not apparent in the present study, possibly reflecting less favourable climatic conditions.

Tretzel (1955, quoted in Wise, 1993) argues that competition for food and space has led to spatial and temporal isolation among spiders and that the evolution of differences in the seasonal timing of reproduction permits the coexistence of species that would otherwise compete. Whether the distinct phenologies of *F. frutetorum*, *N. radiata* and *L. triangularis* evolved due to competitive pressures is, however, purely speculative.

Differences in web height were most distinct between *F. frutetorum* and *N. radiata*, which matured concurrently. In contrast, the web heights of *L. triangularis* were generally similar to those of *F. frutetorum* with little indication of space partitioning. However, it must be noted that *F. frutetorum* and *L. triangularis* never co-occurred as adults. The distinction into separate size classes and developmental stages may result in the utilisation of different resources and allow the exploitation of similar web heights.

Enders (1974) also observed differences in web height among orb-weaving spiders and suggested that vertical stratification allows competing species to coexist by exploiting different prey (see also Brown, 1981; Olive, 1980; Wise, 1993). Accordingly, the differences in web height between *F. frutetorum* and *N. radiata* and the exploitation of different prey types also suggests the possibility of species coexistence through vertical stratification. However, experimental approaches are needed in order to provide more conclusive evidence.

The types of prey captured support the description of web-building spiders as generalist predators (Kajak, 1965; Nyffeler & Benz, 1989; Robinson & Robinson, 1970; Wise & Barata, 1983) since they utilise prey from a wide range of taxa.

Although the spiders captured different prey, there was no difference in the average size of prey captured or the prey capture rates, which were low compared with those of orb-weaving spiders (Herberstein & Elgar, 1994; Kajak, 1965; Olive, 1980). Consequently, using different web heights or maturing at different seasons did not seem to offer any energetic advantage, using only prey size and prey encounter rates as indicators.

Differences in web architecture, particularly the sheet size, were not reflected in prey size or prey capture rates. The vertical spread of the web has been shown to increase prey capture success (Chacón & Eberhard,

1980; Herberstein & Elgar, 1994) in orb-weaving spiders. Therefore, the height of the entangling threads, which was similar for all three linyphiid species, may affect the spiders' foraging success more than sheet size. Unlike the symmetrical webs of orb-weavers, few studies have been devoted to web structure in linyphiid webs and those that exist do not specify which part of the web is most likely to affect prey capture (Alderweireldt, 1994; Toft, 1987). Furthermore, based on the present results, it is unclear to what extent species-specific body size affects web architecture, both of which may influence the type of prey captured.

The distinct spatial and temporal distributions of *F. frutetorum*, *N. radiata* and *L. triangularis* may be the main influence on their foraging behaviour, exposing each species to different prey resources, as the abundance and type of insect prey also varies throughout the season and across different vegetation heights (Herberstein, 1996).

The results of niche partitioning studies are frequently used as indirect evidence in support of competition theory (see Wise, 1993 for a summary). While the present results also provide evidence of resource partitioning, they cannot provide any evidence for or against competition. They are purely descriptive, but provide useful starting points for the design of appropriate manipulative experiments investigating the possible role of competition in forming community patterns such as those reported herein.

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