

Influences of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck)

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Summary. The distribution of the spider *Zygiella x-notata* was examined using field populations of adult females occupying the outside frames of windows. The structure of the populations was aggregative, and the distribution of individuals on the window frames and the size of the webs were density dependent. Also, the sizes of the webs of neighbouring spiders on the same window alternated. This spatial organization involves interactions between neighbours. If one spider out of two is removed, and if all the webs are destroyed, remaining spiders that previously had small webs significantly increase the size of their construction. In contrast, individuals that previously had large webs do not modify the size of their construction. This shows that individuals of *Z. x-notata* respond to the presence of neighbours. The influence of intraspecific interactions in such a population is discussed.

Introduction

Animals are generally divided into solitary and social species, but there is a continuum between these two states. This is well illustrated in spiders, where it is possible to distinguish between different types of population structures, with a continuum from solitary to social species (Krafft 1979; Buskirk 1981). In solitary species, individuals disperse after a variable period in the gregarious juvenile stages. Afterwards, they seem to live independently of one another except for sexual encounters and their distribution may be random, regular or aggregative as defined by Pielou (1960).

Various studies of spider distribution have shown that spiders may be more evenly spaced than they would be according to a random distri-

bution (Burgess 1979; Burgess and Uetz 1982; Riechert et al. 1973; Pasquet 1984). This pattern can reflect territorial behavior (Davies 1978) as described for *Agelenopsis aperta* (Agelenidae) (Riechert 1981) and *Araneus marmoreus* (Araneidae) (Pasquet 1984).

Some solitary spiders of the genus *Metepeira* (Araneidae) are facultatively aggregative (Uetz et al. 1982; Schoener and Toft 1983). Their webs are characterized by a barrier-web which can be shared between several individuals and by a capture-surface which is never shared. Such aggregations are not correlated with habitat resources and could reflect a rudimentary social tendency on the part of the spiders (Schoener and Toft 1983) which assumes attraction between individuals. As each orb-weaving spider must build its own orb-web, it may be asked whether it takes into account what its conspecific neighbours do.

In the orb-weaving spider *Zygiella x-notata* (Clerck) (Araneae, Araneidae), we observed that the individuals are more clumped than predicted by a random distribution, and we tested the consequences on space occupation by each spider.

Methods

Zygiella x-notata (Clerck) is a solitary orb-weaving spider which frequently occupies areas inhabited by humans. The webs are built on a great variety of human constructions (e.g. window frames, gates, railings, gratings) or on urban vegetation (e.g. hedges, small conifers). The study populations were naturally distributed on the outside frames of trapezoidal windows ($L=2.05$ m, $l=1.24$ m, $H=2.05$ m) with aluminium frames. Two groups of five windows each, on opposite north- and south-facing concrete walls, were investigated. All these windows had the same physical structure and thus offer identical substrates for the spiders. In fact, all the webs observed were fastened to the concrete wall and the window pane. The web hub was connected by a signal thread to a retreat built in the chink (depth = 1 cm) of the window-frame junction. For each window,

the supports for webs and retreats can be considered as a linearly and continuously distributed resource which is potentially totally exploitable by the spiders.

The study was done during September and October 1982 and 1983 on the campus of the University of Nancy, France. At the end of the 1982 studies, we removed all the adults, leaving only the cocoons which were deposited in the chink.

Space occupation and distribution of individuals

The minimal space occupation for each spider is determined by both web and retreat. The position of the retreats reveals the distribution of individuals on the habitat supports. The position of the webs and some of their characteristics may indicate space utilisation. We used various parameters to characterize web structure and the locations of individuals and their webs.

We measured the height of the hub of the web and of the retreat above ground. Web structure was characterized by the lengths of the longest diameter, of the signal thread, and by counting the number of radii and of turns of the sticky spiral of the largest sector of the lower part of the web.

On the window frames, all the webs were of different sizes and small and large webs seemed to alternate. To test this observation, we compared two sets of webs, made up as follows: on each part of the window frame which supported more than three webs, we compared the first two, and assigned an even number to the largest. Webs were then numbered sequentially in a line from this even number irrespective of size. This gave two sets: one even and one odd.

The retreat of *Z. x-notata* is outside the web. Thus, it is possible to study either retreat distribution or web distribution. These were measured by recording the inter-retreat distances (DIR) and the webs inter-hub distances (DIC) between nearest neighbours.

Influence of the nearest neighbour on web size

In order to test the hypothesis that neighbours influence the size of the web built by an individual, we made simultaneous comparisons of natural populations of spiders through the following manipulations:

Set A: controls, no intervention (1982)

Set B: all the webs were destroyed without disturbing the spiders (1982: B1, 1983: B2)

Sets C+D: all the webs were destroyed and one spider out of two was removed. Set C (1982: C1, 1983: C2) corresponds to the remaining individuals in the population while set D (1982: D1, 1983: D2) includes the individuals removed.

Just before the intervention and 5 days after it we noted all the parameters previously mentioned and the removed spiders were weighed.

Data analysis

We used non-parametric tests for statistical analysis: Wilcoxon matched-pairs signed rank test and sign test for the related samples, Kruskal-Wallis one-way analysis of variance and Mann-Whitney *U*-test for the independent samples (Siegel 1956).

To determine the pattern of individual spacing, the observed distribution of nearest neighbour distances is compared with a random one of expected distances determined for a population of the same density as the natural one. We considered the individuals as linearly distributed along the window frame. A random distribution was obtained by the method explained by Crips (1979). A χ^2 goodness of fit test (Campbell and Clark 1971) was used to compare the observed distribution with the expected one.

Results

Distribution of the individuals

Webs of juvenile spiders appear on the windows from March, but during our study periods (September–October) males had disappeared and the populations of *Z. x-notata* on the windows consisted of adult females only.

Comparison of inter-retreat (DIR) and inter-hub (DIC) distances showed no significant differences; they had similar means and were significantly correlated (Table 1). This shows that webs and retreats have the same type of distribution in terms of nearest neighbour distance. Accordingly, hereafter, we use only the nearest neighbour inter-retreat distances.

If we consider the whole window frame as potential support, spider density was 0.79 and 0.76 individuals per meter for 1982 and 1983 respectively. The observed distributions of the nearest neighbour inter-retreat distances are significantly different from a random distribution at $P < 0.01$ (Table 2A). The higher than expected frequency of retreats with nearest neighbour between 0 and 22 cm indicates aggregation (χ^2 test; 1982: $P < 0.001$; 1983: $P < 0.01$). As the retreats were distributed on the upright only, (we observed a maximum of 9 individuals on an upright), we can consider these vertical structures only. Now, the densities for 1982

Table 1. Comparisons and relations between inter-retreat (DIR) and inter-hub (DIC) distances of the 1982 and 1983 populations of *Zygiella x-notata*. *n*, sample size; SD, standard deviation; *z*, value of the Mann-Whitney *U*-test for large samples; *r*, coefficient of correlation; *P*, level of significance; NS, not significant

		DIR (cm)	DIC (cm)	Comparisons DIR/DIC	Correlations DIR/DIC
1982 <i>n</i> =41	Means	32.7	32.5	<i>z</i> =0.11	<i>r</i> =0.98
	SD	20.3	18.4	NS	$P < 0.001$
1983 <i>n</i> =45	Means	52.6	51.3	<i>z</i> =0.05	<i>r</i> =0.99
	SD	33.5	30.7	NS	$P < 0.001$
Comparisons 1982/1983		<i>z</i> =2.68 $P=0.0037$	<i>z</i> =3.12 $P=0.0009$		

Table 2. Comparisons of the observed distribution of nearest neighbour distances of spider retreats with that expected for a random population of the same size and density; **A** when the whole window frame is considered as potential supports for the spiders; **B** when only the uprights are considered as potential supports for the spiders. The class intervals (22 cm and 13 cm) were chosen as suitable since they give expected frequency greater than 5 in the first classes, the smallest expected frequency acceptable for the goodness of fit test

	Class limits (cm)	1982		1983	
		Observed frequency	Expected frequency	Observed frequency	Expected frequency
A	0–22.0	15	6.5	14	6.9
	22.1–44.0	18	5.5	9	5.9
	>44.0	8	29	22	32.2
B	0–13.0	4	9.4	2	8.3
	13.1–26.0	18	7.3	12	6.8
	26.1–39.0	6	5.6	7	5.5
	>39.0	13	18.7	24	24.4

and 1983 were respectively 2.0 and 1.6 individuals per meter. The observed distributions of the inter-retreat distances were still different (1982: $P < 0.001$; 1983: $P < 0.05$) from random distributions (Table 2B). The lower than expected frequency of retreats with nearest neighbour distances between 0 and 13 cm (χ^2 test; 1982: $P < 0.05$; 1983: $P < 0.02$) and the greater than expected frequencies between 13 and 26 cm (χ^2 test; 1982: $P < 0.001$; 1983: $P < 0.05$) show that in the habitat studied, the spatial distribution of the *Z. x-notata* individuals tends towards aggregation, with a minimum distance between nearest neighbours (very few webs have threads in common).

Relations between individual distribution and web-size

The web parameters measured give the average characteristics of the webs of *Z. x-notata* (mean \pm SD): diameter 22.0 ± 5.7 cm, length of signal thread 6.7 ± 3.1 cm, number of turns of spiral 33.6 ± 9.1 , number of radii 31.9 ± 6.5 . As these parameters are all correlated at $P < 0.001$, we consider the diameter a good indicator of web structure and therefore we use it alone to characterize the webs. On the other hand, we found no significant correlation between the weight of the spiders and their web sizes (1982: $n = 29$, $r = 0.054$, NS; 1983: $n = 17$, $r = 0.176$, NS).

According to the mean densities, the upright, in 1982 and 1983, could be divided into zones of "low" density (2 or fewer individuals per meter) and of "high" density (more than 2 individuals per meter) which respectively correspond to the uprights with four or fewer spiders and to uprights with more than four spiders.

There was no important difference between the populations of the two years; the pattern of space occupation by the individuals was constant. In

fact, the nearest neighbour distances and the web diameters in the "high" density zones of 1982 were not different from those of 1983 (Table 3). On the other hand, in the "low" density zones there was no difference between the two years for the diameters of the webs, but there was a significant difference ($P < 0.006$) for the nearest neighbour distances; they were higher in 1982 than in 1983.

For both years, the nearest neighbour distances and the web diameters were significantly greater in the "low" density zones than in the "high" density zones (Table 3). Hence, the individuals' distribution on the window frames and web size are density dependent (Fig. 1). In addition, in both years the web sizes of the even and odd sets (see Methods) were significantly different (1982: even set 23.4 ± 4.6 cm, $n = 20$; odd set 17.8 ± 5.1 cm, $n = 15$; $P < 0.001$; 1983: even set 23.9 ± 5.3 cm, $n = 18$; odd set 19.7 ± 5.3 cm, $n = 17$; $P < 0.05$). That is, in the sequences of webs along the uprights there is an alternation of webs size: a given web is flanked by two larger or two smaller ones.

All these results, and particularly the relation between web size and individual spacing, allow us to conclude that the space occupation behaviour of an individual can depend on the behaviour of others nearby. This assumption is confirmed by the significant ($P < 0.01$) relation between the available free space and web size (1982: $r = 0.50$, $n = 42$; 1983: $r = 0.50$, $n = 45$; free space is defined as the distance between the hub of a spider's web and the hub of the web of its nearest neighbour, minus half the diameter of the web of this neighbour).

Influence of the neighbour on the web size

To corroborate the hypothesis that presence of a neighbour influences web size, we modified the population's structure by removing one individual out of two.

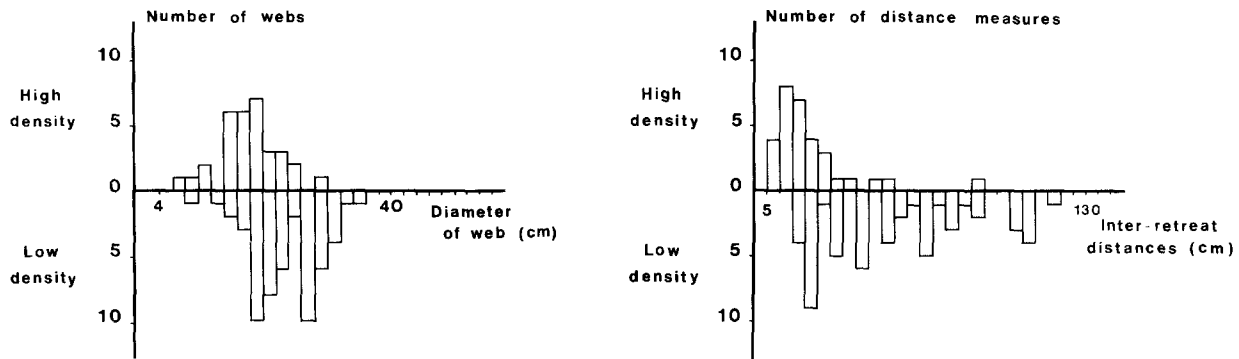


Fig. 1. Influence of the density of spiders on web size (diameter) and on nearest neighbour distances (inter-retreat distances). *High density*: window uprights with more than 2 individuals per meter. *Low density*: window uprights with 2 or fewer individuals per meter

Table 3. Comparisons between “low density” and “high density” zones concerning the diameter of the webs and the inter-retreat distances to nearest neighbours (DIR) in 1982 and 1983 populations of *Zygiella x-notata*. Abbreviations as in Table 1

	Low density zone		High density zone		Comparisons
	Means	(SD)	Means	(SD)	
1982					
<i>n</i>	22		19		
Diameter (cm)	23.9	(4.4)	18.3	(4.5)	$z = 3.22$ $P = 0.0007$
DIR (cm)	40.6	(17.9)	23.6	(19.3)	$z = 3.61$ $P = 0.0002$
1983					
<i>n</i>	33		12		
Diameter (cm)	24.0	(5.9)	18.6	(4.9)	$z = 2.94$ $P = 0.0016$
DIR (cm)	63.8	(32.1)	21.7	(8.4)	$z = 3.84$ $P = 0.00007$

Table 4. Effect of removing one spider out of two on the diameter of the web built by the remaining spiders (set C1: remaining spiders with small webs; set C2: remaining spiders with large webs). In 1982, the spiders with large webs were removed (set D1); in 1983 the spiders with small webs were removed (set D2). Set A: control; sets B1 and B2: webs destroyed without disturbing the spiders. Abbreviations as in Table 1

	<i>n</i>	Before intervention		After intervention		Comparisons
		Means	(SD)	Means	(SD)	
1982						
A	14	23.8	(3.1)	23.4	(2.0)	NS
B1	22	22.1	(5.6)	21.0	(5.9)	NS
C1	12	17.9	(4.6)	22.4	(5.3)	$P < 0.01$
D1	17	22.0	(3.7)			
1983						
B2	17	25.3	(4.3)	18.8	(4.4)	$P < 0.01$
C2	9	22.9	(5.7)	19.1	(4.5)	NS
D2	12	17.0	(5.1)			

Since there was an alternation in web size, we could remove either the spiders with a large web or the spiders with a small one.

Removing the spiders with large webs (1982). In the reference sets A (without intervention) and B1

(web destroyed), comparison of the diameters of the webs build before and after intervention shows no difference (Table 4). Thus there is no important natural variation in size after intervention (set A) and the destruction of the webs does not modify web size (set B1).

On the other hand, after removing one individual out of two, the remaining spiders (set C1) spin a web significantly larger than their previous web (Table 4). Moreover, the size of these new webs is not significantly different from the size of the webs of the removed spiders (set D1, Table 4). Thus, the individuals which previously had a small web, now build a web of similar size to the large webs of the removed spiders (set D1) and to the webs of the other sets (A, B1).

Removing the spiders with small webs (1983). For the spiders which build a large web, the removal of their nearest neighbours does not modify the size of their construction. After destruction of their web, and removing their neighbours, the size of the new webs does not differ from the size of the previous web (Table 4).

In the different experiments (1982, 1983) there was no appreciable change in the positioning of the retreat or web of the remaining spiders, and we did not find reoccupation of the sites of the removing spiders. This suggests that the previous differences of web sizes (alternation) cannot be due to the occupation of a particular site and are more likely due to constraints exerted by the nearest neighbours.

Discussion

Adult females of *Zygiella x-notata* distributed around the windows of our study area in a way more clumped than random. One possible explanation would be that spiders select particular sites to build their webs, and that the distribution of the habitat features may affect the positioning of each individual. Several studies have provided direct evidence of this. Different environmental factors have been investigated separately by various authors (for review see Burgess and Uetz 1982; Pasquet and Leborgne 1985). In some spider species, these factors (e.g. climatic conditions, abundance of potential web-attachments, richness in potential prey) can influence the living pattern – i.e. in some species individuals may be solitary or live in communal groups (Uetz et al. 1982; Smith 1983; Rypstra 1985). In contrast, Schoener and Toft (1983) suggest that *Metepeira datona* (Araneidae) aggregate independently of habitat features. As discussed below, this is probably also true of the aggregation observed in our study population of *Z. x-notata*.

It seems unlikely that there are marked differences between the right and left sides of the windows according to their orientation. Similarly, the structural features necessary for web construction are homogeneous and continuously distributed. It

is not possible to detect preferred sites along the windows, as evidenced by the fact that the clumped spiders occupy right and left sides equally. Furthermore, the spiders did not occupy the same segments of each part in 1982 and 1983, so we can exclude the existence of particular permanent microhabitats around the windows. Neither these environmental features nor available space, would limit the spiders with respect to positioning (retreat) or trap construction (web); where three or four individuals were aggregated they could have positioned themselves differently, with greater interindividual distances. The existence of a localized differential in prey availability over the window can also be discounted; using sticky traps we found no significant difference between occupied and unoccupied sites (Pasquet and Leborgne 1986).

Therefore, as environmental factors (climatic, structural and potential prey) are not sufficient to explain the distribution *Z. x-notata*, it remains to be seen whether interindividual relations could have an influence – as in some other species (Buskirk 1975a; Riechert 1978, 1979; Pasquet 1984) – because individuals within a population interact with each other as well as with environment. This can influence their positioning directly. In laboratory experiments on the effect of silk structures produced by already settled individuals on the positioning of spiders, we showed that individuals of *Z. x-notata* preferred to settle where there was conspecific silk (Leborgne and Pasquet, in press). Aggregation in *Z. x-notata* is a natural phenomenon at least in some populations. This may be attributable to interindividual attraction as Schoener and Toft (1983) suggested for *Metepeira datona*.

Several authors have given possible adaptive explanations for such aggregations in spiders, generally emphasizing the benefits; but social or colonial life can also produce disadvantages. These costs and benefits are generally investigated by comparing solitary individuals and group living as a whole. For example, Smith (1983) showed in *Philoponella oweni* (Uloboridae) that solitary and communal females did not differ in the size of the orb. On the other hand, Lahmann and Eberhard (1979) found in *Philoponella semiplumosa* that communal spiders had smaller orbs than solitary spiders. These authors did not study the effect of the aggregation on individual constructions. The question remains whether, when aggregated, all individuals build the web they “want” or if coloniality limits the activities of all or some of them.

In spiders with orb webs, and so in aggregations of *Z. x-notata*, space must be shared because each individual needs a web for prey capture. This appears to be true also for social-territorial orb-weaving spiders where individuals have a commu-

nal retreat but each defends its orb, e.g. *Metabus gravidus* (Araneidae) (Buskirk 1975b) or *Cyrtophora citricola* (Araneidae) (Rypstra 1979). In a clump of orb-weaving spiders this can lead to constraints on space occupation and web construction by individuals. The alternation of web sizes along the uprights of the windows suggests such constraints in *Z. x-notata*. There are individuals with large webs and others with small ones: this is independent of the weight of the individuals, but we can indicate that the larger are built first (paper in preparation).

Our field experiments showed that in the aggregations, some individuals of *Z. x-notata* spin smaller webs than they would do if their nearest neighbour were absent, while the spiders with the larger webs do not modify the size of their construction when their neighbours are removed. Therefore, all individuals in the aggregation are not equivalent.

As the spiders which built the small webs were able to build larger ones in the absence of their nearest neighbour, these individuals are not limited in their ability to spin larger webs. If we consider that these spiders could position themselves elsewhere along the windows, without very close neighbours, it strongly suggests that these individuals "accept" a reduction in web size in exchange for being part of a group. The variability in spacing pattern and in the size of webs inside a clump displayed by the spider *Zygiella x-notata* makes it a valuable model system to clarify the progression to spider sociality.

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