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What do orb webs catch?

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Summary

Insects were removed from the webs of the orb-weaving spiders *Araneus diadematus* Clerck and *Zygiella x-notata* (Clerck) to compare the size-distribution of the catches with the size-distribution of the insect fauna likely to be available to the webs (determined using water traps). Both species were found to be selective with respect to insect size, in that they caught a disproportionate number of small insects. *A. diadematus* was able to catch slightly larger insects than *Z. x-notata*. The two species use different web architectures, *Z. x-notata* having webs with a greater density of threads but a smaller overall area. The revelance of this for prey capture is discussed, together with the influence of physical characteristics of the potential prey.

Introduction

There have been a number of investigations into the effects of web architecture on prey size selection by spiders' webs (e.g. Kajak, 1965b; Uetz & Biere, 1980; Nentwig, 1982). Orb webs are selective in respect to insect size, in that they take prey sizes in ratios which are very different from the ratios available in their environment (Kajak, 1965a; Robinson & Robinson, 1970; Nentwig, 1985; Eberhard, 1986). The web has the effect of filtering the insects from the available insect fauna flying in the vicinity, while the spider itself selects some of the items from the web catch to eat (Nentwig, 1985).

Bristowe (1971) describes a typical orb web: a hub of densely meshed threads is surrounded by a narrow spiral, of about 6 or 7 turns, which is known as the strengthening zone. Outside of this and before the main spirals begin there is a small space called the free zone. The sticky spirals are laid across 25 to 35 radial threads connected with the hub and stretching outwards to stout threads forming the frame of the web.

Successful prey capture requires that the flight path of the prey must bring it to intercept a thread or threads and that the prey must be retained for enough time for the spider to subdue it (or for the prey to be small enough to be retained in the web without intervention from the spider). Both the radial and spiral threads of the web are involved in the interception and retention of prey and each should be considered separately. The radial threads have two functions: firstly to support the sticky spiral threads, and secondly to absorb most of the kinetic energy of the prey when it is intercepted by the web. Webs with a greater density of radial threads are better able to catch heavier and faster-moving insects because these threads can absorb an order of magnitude more energy than can the spiral threads (Craig, 1987; Eberhard, 1986).

An orb web has a far greater length of spiral thread than radial thread, and the density of the mesh of spiral thread is central in determining the size of prey intercepted and retained by the web. Chacon & Eberhard (1980) suggested that maximum prey interception occurs with the threads spaced further apart than the widest dimension of the largest prey as this increases the area "searched" by the web. It would be expected that webs with a smaller spiral thread spacing will tend to specialise on prey which is more difficult to intercept and retain, as the impact of the prey is shared by more threads and, by having a greater number of threads in contact with the struggling insect, it will make the insect's escape less likely. Increasing the thread density will also allow smaller insects to be caught (Olive, 1980).

Most predators have an optimum prey size range, and prey which are much smaller or larger than this range are either ignored or not easily captured (Murakami, 1983). The mechanical properties of a web ensure that insects which are too large to be tackled, or which might destroy the web, are not detained by the web (Denny, 1976).

Thread separation will have some effect on the lower threshold of prey size caught by the web. Having large spaces between the silk threads may increase the area "searched" by a web (Chacon & Eberhard, 1980) but it will allow some insects to fly through unimpeded. Thus the spider may lose many small potential prey, but this is of little significance, given that the larger insects that the spider is able to handle constitute by far the largest proportion of prey biomass available to the spider (Olive, 1980).

The aim of this study is to compare the prey sizes caught by two orb webs of different architecture, and to compare the catches in each with an independent assessment of the flying insects in the vicinity of the webs. The species used were *Araneus diadematus* Clerck and *Zygiella x-notata* (Clerck). *A. diadematus* builds a standard orb web with relatively wide spacing of the coils in the sticky spiral, but *Z. x-notata* builds a modified orb web with two adjacent sectors which have no spiral threads and the coils of the spiral are relatively close. The radius between these two blank sectors constitutes the signal thread and leads to the spider's retreat (Savory, 1952).

Methods

The experiment was conducted over a 39-day period from 28 August to 5 October 1989.

Because the two species were not present together in a single locality in large enough numbers, it was necessary to study them at two sites, separated by about 60 m. The flying insect populations at each site were sampled using water traps (6 in each site) so as to determine the distribution of body lengths of the insects which were potentially available for capture by the orb webs. The water traps consisted of 1–2 cm of dilute detergent solution in white plastic containers (20 × 15 cm). They were positioned at 0.5 and 1.5 m above ground for *A. diadematus* and *Z. x-notata* respectively. It was expected that the insect populations in the two sites would be very similar, given both that the surrounding vegetation was similar (a hawthorn-based hedge with 6 woody species, planted and tended bushes of redcurrant, blackcurrant and gooseberry, and large areas of grass) and that the two sites were close together. At about mid-afternoon of each day the

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contents of the six water traps at each of the two sites were emptied into a large funnel containing filter paper (one funnel for each site), so as to separate the insects from the detergent solution. The filter papers were air-dried overnight so that the next day the insects could be brushed carefully into sample bottles (one bottle for each site for each day) and preserved in 70% ethanol.

The insects caught by ten webs of each of the two species were removed daily (at about mid-afternoon) using a mounted needle, pooled separately for each species, and then preserved in 70% ethanol. Usually only webs containing 3 or more insects were used for collection, although this was not possible on some days. The webs used were at approximately the same height above ground as the water traps. Each site was divided into ten approximately equal areas and every day one suitable web was used from each of these areas. A web in the same location was not used for more than two successive days.

The body lengths of the insects collected from the water traps and webs over the 39 days of the experiment were measured under a dissecting microscope using an eyepiece graticule. The body lengths (from front of head to tip of abdomen, excluding appendages such as antennae) were measured to the nearest 0.5 mm, and a separate tally of insect body lengths was kept for the 4 sample bottles for each day of the experiment (one for each species' web

Length (mm)	Water traps	*Araneus diadematus*	*Zygiella x-notata*
0.5	344	131	168
1.0	309	124	150
1.5	282	130	171
2.0	236	136	158
2.5	233	164	126
3.0	238	155	110
3.5	232	151	102
4.0	240	128	84
4.5	201	105	67
5.0	217	74	38
5.5	212	45	26
6.0	202	38	18
6.5	224	21	7
7.0	205	8	5
7.5	202	10	2
8.0	199	12	1
8.5	212		
9.0	192		
9.5	187		
10.0	198		
10.5	178		
11.0	146		
11.5	133		
12.0	128		
12.5	126		
13.0	94		
13.5	87		
14.0	85		
14.5+	167		
Totals	5709	1432	1232

Table 1: The abundance of insects of different lengths in spiders' webs and water traps. The insects collected during the whole experiment are grouped into 0.5 mm size classes. The data for the water traps are for both sites pooled. For the two spider species, the data in the 8 mm size class include all insects over 7.75 mm.

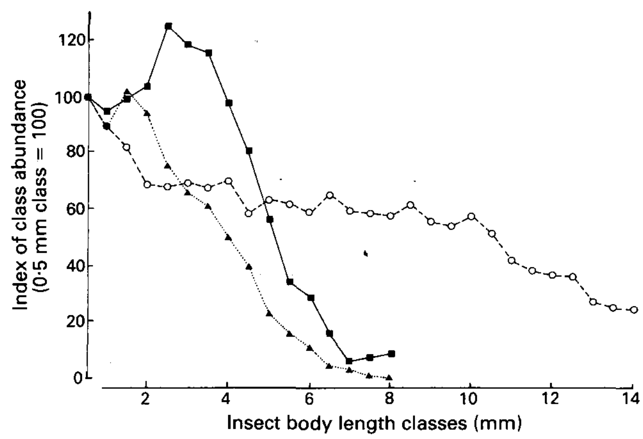

Fig. 1: The abundance of insects of different lengths in spiders' webs and water traps. The insects are grouped into 0.5 mm size classes. The abundances have been standardised so that the number in the smallest (0.5 mm) class is 100. Water trap catches are shown by a dashed line and circles; *A. diadematus* by a continuous line and squares; and *Z. x-notata* by a dotted line and triangles.

catches and the two sets of water traps). Squashed insects or insects which had incomplete bodies were ignored, as were spiders and other non-flying invertebrates caught in the water traps or webs.

To allow analysis of aspects of web architecture, four webs of each species were collected intact. This was done by first spraying the silk with black paint and then pressing a white piece of card, covered with spray glue, against the web. When the spiral threads of the web had stuck against the card the frame threads were carefully cut or broken with scissors. Various parameters of web architecture were measured: diameter of catching spiral (mean of height and width), from which spiral area was estimated, number of radii, density of spiral thread, overall thread density (calculated in both cases from the length of thread in five 2 cm square quadrats, placed on each web using random coordinates), and mean spiral spacing.

Ten spiders of each species were collected at the end of the period of the experiment and their body lengths measured from front of cephalothorax to tip of abdomen.

Results

The data for the web and water trap catches were pooled into 5 sample periods for statistical analysis, four periods of 8 days each and one of 7 days. Table 1 summarises the data, showing the total numbers of insects of each size class caught by each species and by the water traps over the period of the experiment. Insects with body lengths over 7.75 mm (for the web catches) and 14.25 mm (for the water traps) were pooled for each sample period. For the water trap catches there was no significant difference between the two sites ($\chi^2 = 180.85$, 256 d.f., $p > 0.05$; see Everitt (1977) for details about analysis of three-dimensional contingency tables). The insect fauna in the two sites can therefore be considered to be identical, and the water trap data have accordingly been pooled in Table 1. A significant difference was, however, found for the web-catches ($\chi^2 = 173.10$, 139 d.f., $p < 0.05$).

Figure 1 shows the distibution of prey sizes caught by the two spider species and by the water traps (the data have been standardised so that the smallest size class is given the value of 100 in each case). It shows two important points. First, the webs caught very few insects larger than the 7.5 mm class (0.5% of the catch), while the water traps caught many larger insects, up to the 23.5 mm class (37.3% of the catch in the 8 mm class or above). Secondly, *A. diadematus* caught more of the larger insects, over about 3 mm body length, than *Z. x-notata*. The proportion of the prey of these two species that are larger than 5 mm body length are 15% and 8% for *A. diadematus* and *Z. x-notata* respectively. However, 59% of the potential prey (insects caught by water traps) are greater than 5 mm long.

Table 2 shows the results of t-tests used to analyse aspects of the web architectures of the two species. The webs of *A. diadematus* had a significantly larger mean area than the webs of *Z. x-notata*. *A. diadematus* had webs with fewer radii than *Z. x-notata*, but the difference was not statistically significant and would not be expected, as the gaps between the radii of *A. diadematus* webs will be large at the periphery and they will not be able to support the spiral threads as effectively as the greater number of radii in the smaller web of *Z. x-notata*.

Both the length of spiral thread per unit area and the total thread (including radii) per unit area were significantly greater for *Z. x-notata*, which in both cases had about 40% more thread than *A. diadematus*. *A. diadematus* has a greater spiral spacing in its webs than does *Z. x-notata*.

The mean body lengths of the two spider species were found to be 9 mm for *A. diadematus* and 4 mm for *Z. x-notata*.

Discussion

The webs of *A. diadematus* have a higher cut-off point for prey size than those of *Z. x-notata*. Both spider species caught about the same number of prey over the period of the experiment and both had the same range of potential prey available to them. The two species appear to use quite different, though apparently effective, web design strategies to catch their prey. *A. diadematus* builds a web with a low thread density, suggesting that it will be less effective at retaining prey, but its snare is spread wide to maximise interception of prey which are of an optimal size for the spider to handle. *Z. x-notata* has a smaller web, so it will intercept fewer insects, but perhaps the greater thread density will allow it to catch more prey per unit web area. In Fig. 1, the curve for *A. diadematus* peaks at the 2.5 mm point, while *Z. x-notata* does not peak, or has a peak in the 1.5 mm class, suggesting that *Z. x-notata* catches more very small prey which are able to fly through the mesh of the web of *A. diadematus*.

	Araneus diadematus	*Zygiella x-notata*	Significance
Mean area (cm^2)	379	147	yes ($p<0.05$)
Mean number of radii	31.5	35.0	no ($p>0.05$)
Spiral length/ unit area (cm/cm^2)	2.16	3.07	yes ($p<0.001$)
Total thread/ unit area (cm/cm^2)	3.25	4.64	yes ($p<0.01$)
Spiral spacing (mm)	5.6	3.4	yes ($p<0.001$)

Table 2: Results of analysis of web architecture (t-tests).

Denny (1976) suggested that a web should be designed to catch prey up to the size of the spider and should not retain very large insects when they are intercepted by the web. The results from this experiment roughly agree with this, both species catching prey up to little more than their own size. It is possible that the size of orb-weaving spiders, or the lengths of their legs, may determine the spacing of spiral threads and therefore indirectly determine the range of prey sizes available to the spider. However, a study of spider morphology and web architecture for a number of species of different morphology (e.g. Araneidae, Tetragnathidae and Uloboridae) would be needed before any such relationship could be established.

A possible source of error in this study may arise from the fact that spiders are known to cut dangerous or distasteful prey from their webs (Turnbull, 1973). Therefore the catch of a spider's web consists of two parts: prey that are consumed and those that are refused. An underestimate of the number of large prey caught by the web could have resulted if the spiders selected larger prey caught in their webs to feed on and removed the remains from the web (Nentwig, 1985). Holes were seen in many webs during this study, but it was rarely possible to be certain whether they were made by the spider excising unwanted insects (or remains of prey) or by insects escaping from the web or breaking through threads without being detained. A spider may in fact feed preferentially on smaller individuals among the insects that become caught in the web because of the reduced handling time involved in killing and consuming them (Shelly, 1984). If this is the case then small insects may possibly be under-represented in the prey taken from the webs in this experiment.

Within each size class of potential prey, some insects are less susceptible than others to capture in a given web owing to differences in their physical characteristics. Faster and heavier insects are more likely to be able to break through a web owing to their higher kinetic energy (e.g. Craig, 1987). Insects with many projections from their bodies such as long wings, antennae, spines and legs are more likely to be captured than insects with more compact body forms (Turnbull, 1960). This seems to be supported by the small number of beetles (heavy, compact insects) found in the webs used in this study compared with the large numbers found in the water traps. For any web there is a threshold value of kinetic energy per unit length of wing-span that will allow an insect to pass through the web (Nentwig, 1982). In this study, body length is assumed to be both a function of wing span and a function of body mass, but these relationships should be established.

There are two notable groups of insects which are rarely found in spiders' webs (Eisner *et al.*, 1964; Robinson & Robinson, 1970; Chacon & Eberhard, 1980; Olive, 1980; Nentwig, 1982). These are Lepidoptera, which have scales which prevent adhesion to the web, and Tipulidae, which can escape at the expense of losing legs which become stuck to the web. The long legs of Tipulidae were often seen in the webs, and threads covered with scales were observed under the microscope in samples of web which did not contain whole Lepidoptera. Both of these groups were rarely encountered whole in webs in this study, although they were found in large numbers in the water traps (especially Tipulidae).

This study has shown that both species of spider caught a disproportionate number of small insects in comparison with the range of sizes in the available insect fauna. The two species caught about the same range of insect sizes, but *A. diadematus* was able to catch slightly larger insects than *Z. x-notata*. Even though it is less than half the length of *A. diadematus* and builds a much smaller web, *Z. x-notata* was still able to catch prey nearly as long as those caught by *A. diadematus*, and both species caught about the same total number of insects. The reason for this could be that the design of the web of *Z. x-notata* allows it to catch more prey per unit web area than *A. diadematus*.

There appear to have been no investigations into the strengths of the threads used by *Z. x-notata* or *A. diadematus*. However, there have been investigations into the relationships between web design, the mechanical properties of web silk and prey capture by other araneoids (e.g. Craig, 1987; Denny, 1976). Craig (1987) found that the energy-absorbing capability of web silk was proportional to the diameter of the silk fibres, and suggested that web silk diameter was dependent on spider size. It is possible that *A. diadematus* is able to catch larger insects than *Z. x-notata*, even though its web has a lower thread density, as a result of its greater body size: its threads may be thicker and therefore stronger.

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