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The Ecology of the Web of *Uloborus diversus* (Araneae: Uloboridae)*

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Summary. The distribution of *Uloborus diversus* webs around pack rat nests on the desert near Cave Creek, Arizona, differences between webs there and in nearby residential Phoenix, and differences between the webs of large and small individuals indicate that these spiders select web sites and designs to minimize web damage by wind. The frequency of web construction decreased when spiders in captivity were exposed to wind or to relatively bright (5 Lamberts) nights. Observations of web sites on the desert revealed high rates of web-turnover and substantial frequencies of movements of spiders from one site to another. Much lower rates of web-turnover and spider movement occurred in less windy situations in the laboratory, and in suburban Phoenix. Partial web replacement and the extension of web construction over two nights are apparently methods used to improve catching ability of sheltered (longer lived) webs by extending their surface and/or tightening their mesh.

A spider’s web is an easily observable and measurable sum of its predatory behavior. As such it offers a rare opportunity for quantitative studies of predatory strategies under natural conditions. Several basic questions about the ecology of the orb web of *Uloborus diversus* are investigated in this paper: how the spider decides where to hunt; how long a given web stays intact; and how often a spider changes hunting sites.

The one detailed study of web ecology is that of Turnbull (1964) on the cob-web spider *Achaearanea tepidariorum* (Theridiidae). It indicates that, at least indoors, the spider conducts a systematic search for prey, changing web sites until it builds in one where it catches more than a certain minimum of prey. The literature on orb webs, whose highly organized, planar form lends itself to precise measurements, is sparse and consists mainly of passing observations with little supporting data.

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Various factors have been proposed as being important in site selection: the size of open space must be at least that of the web in *Cyrtophora citricola* (Kullmann, 1958) and *Araneus diadematus* (Szlep, 1958); *Argiope bruennichi* prefers more rigid attachment sites for bridge threads (Tilquin, 1942); *Cyclosa conica* (Marples and Marples, 1937) and *Uloborus glomosus* (=*americus*, McCook, 1889) select dead rather than living attachment sites. Many orb weavers, including *Cyclosa* (McCook, 1889), *Araneus* (Peters, 1953; Breed *et al.*, 1964), *Zilla* (Mayer, 1952), and *Eucta* (Crome, 1954) usually replace their webs daily. Except for anecdotal notes of individual spiders remaining at the same site for days or weeks, movements between web sites are largely unstudied. Poetzsch (1966) found that movements rates changed seasonally in *Meta menardi* living in cellars; Marson (1947) indicates (without giving data) that *Cyclosa insulana* will move away if its web is “seriously” damaged.

**Methods**

Field observations were made on and around the more or less conical nests of pack rats (*Neotoma lepida*) (Fig. 1) in high Sonoran desert (elevation 1000 m) about 1 km W of Wildcat Hill (NE of Cave Creek), Arizona. Additional observations were made about 60 km away in residential Phoenix, Arizona (elevation 365 m). The physical characteristics of these areas differed in several respects: Phoenix had higher (3–6° C) temperatures, higher humidity, and more thick vegetation; the wind on the desert was usually steady around 4–8 kmph from the S and SW, while the wind in Phoenix was usually weaker and more erratic in direction.

I made a survey of 438 webs, each at a different site, on the desert, and of 59 webs, also at different sites, in Phoenix between 10 July and 23 August, 1966. About 110 desert sites were observed daily (in the late afternoon) between 25 August and 2 September, 1967, with individual sites being observed for from 2 to 8 days. I attempted to record all the webs on each pack rat nest investigated during the survey in 1966, but only followed easily accessible sites in 1967. Sites were marked with paint spots on prominent supports, and webs were marked with small patches of dry powdered paint applied with the powder-covered point of a pair of forceps. The area of each web was approximated by the area of a rectangle whose dimensions were the length and width of the web viewed looking directly toward the pack rat nest. Although a web was often not perfectly planar, usually a large fraction of its area was at least very nearly planar; the largest angle this plane made with horizontal was measured with a level mounted on a protractor. The straight edge of the protractor was held parallel to the plane of the web, the level moved until it was horizontal, and the angle between the two read from the scale on the protractor.

The spiders were grouped into four size classes: 1, probably corresponding to first and second instar spiders; 4, probably corresponding to penultimate and mature females; and 2 and 3, intermediate instars. The size of a spider was estimated visually, and there were thus no rigid boundaries between the size classes. The first legs of sample spiders placed in the four classes were 1.8, 2.5, 3.1, and 4.8 mm long.

Experiments on the effect of wind on the frequency of web construction were performed indoors in residential Phoenix between 24 August and 6 September, 1967. The wind was produced by a blower which pulled air from outdoors into the room
and blew it approximately horizontally past spiders caged in $18 \times 18 \times 8.5$ cm screen-sided cages with saranwrap tops and bottoms. Experiments on the effect of night light intensity were performed from 15 October to 6 November, 1968 in Cambridge, Massachusetts with 14 hours of light and 8 hours of darkness each day. All tests of significance are two-tailed Chi-squared tests (Spiegel, 1961).

Selection of Web Site and Design

A. Effects of Wind

*Uloborus diversus* webs on the desert were most common among the debris of well-sheltered pack rat nests (under the thick, hanging branches of a paloverde, *Cercidium* sp., for example), and absent from unsheltered nests. The number of webs of post-first instar spiders per nest ranged up to about 30. The webs were not distributed in equal numbers on all
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Before storms (296 cases) \( p < 0.01 \)

After storms (142 cases) \( p = 0.7 \)

Fig. 2. Distribution of webs around pack rat nests on the desert before and after storms

sides of the nests, but were found more often \( p < 0.01 \) on the sides least exposed to the prevailing S and SW winds (Fig. 2, "before storms"). There are several possible reasons for selecting sites sheltered from the wind: prey may be more abundant there; dessication may be reduced below a tolerance level; or web damage may be minimized. There are several indications from web designs that avoidance of web damage may be an important factor.

As shown by Fig. 3, the webs of smaller individuals, which spin thinner threads and whose webs are thus more fragile, tended to be closer to the ground \( p < 0.01 \) for size class 1 vs. size class 4) where the wind was probably weaker. Smaller spiders also spun more nearly horizontal webs (Fig. 4, \( p < 0.02 \) for size classes 1 and 2 vs. 3 and 4). In addition, webs of spiders of a single size on windward sides of nests also tended \( p < 0.1 \) to be more nearly horizontal than those on lee sides (Fig. 5). As argued elsewhere (Eberhard in prep.), more nearly vertical webs may be better traps for flying insects and may be favored when wind damage is not frequent, but more nearly horizontal webs would probably be stressed less by wind which is probably more or less horizontal (see "web longevity" below). Webs in Phoenix (low wind levels) were larger \( p < 0.02 \) than those of the same sized spiders on the
Larger webs built by the same sized spiders would also probably be better traps but would have greater air resistance and thus be more susceptible to wind damage.

Results of experiments in which spiders kept in screen cages were exposed to different durations of wind showed a correlation between the amount of air movement and the frequency of web construction. The spiders, which built their webs one or two hours before dawn, were exposed on alternate days to no wind, wind (about 11 kmph) during only the day before web construction, and wind (about 11 kmph) the day and night before and during actual web construction. Fourteen newly captured spiders of size classes 2–4 were used, and each spider was fed one fruit fly (*Drosophila melanogaster*) the day each web was built, and the web was then destroyed. Webs were constructed in 49% of 53 cases with no wind, 32% of 38 cases with wind during the preceding...
day only, and 22% of 41 cases with wind the preceding day and night (wind day and night differs from no wind, $p < 0.01$). Thus the frequency of web construction was lowered by windy conditions during the time of construction, and slightly (but not significantly) by wind during the preceding day.

B. Effects of Light

Laboratory experiments also demonstrated that the intensity of ambient light during the night affected the design of webs and the frequency of their construction. About 25 spiders (size classes 3 and 4) were exposed to night light intensities of 4.5 Lamberts and <1 Lambert on alternating nights. Each day the webs spun that morning were measured, the spiders which built them were each fed one fruit fly, and all webs were destroyed. Web building frequency was 77% ($N = 152$) following <1 Lambert nights, and 43% ($N = 139$) after 4.5 Lamberts nights ($p < 0.01$). Web sizes were also correlated with night light intensity.
Webs after < 1 L. nights averaged 124 cm² ($N = 69$), while those after 4.5 L. nights averaged 83 cm² ($N = 25$). Since the intensity of moonlight on clear nights is often above 25 L., the change in web building frequency may indicate that $U. diversus$ avoids building webs at sites most exposed to the night sky. Smaller webs at brighter sites might also be better able to survive more the rigorous conditions likely to prevail at these sites. These data are fragmentary however, and more work will be needed before their significance can be established.

**Web Longevity**

The length of time a given web remained intact was measured on the desert by marking webs and observing them daily. The study period
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(25 August to 1 September, 1967) was stormless (one short, gentle rain fell the morning of 30 August), but followed rain storms on 22 and 24 August. I assumed that only one spider occupied a given site as long as the spider there was in the same size class as the original occupant. Since no obvious usurpations were observed (sites were never occupied by different sized spiders on successive days), this is probably a reasonable assumption. Each day the spiders either spun new orbs, repaired or left the old ones unaltered, or deserted them (Table 1). Deserted webs usually became seriously damaged much more quickly than occupied webs, apparently because the maintenance activities of the spiders (removing all heavy

<table>
<thead>
<tr>
<th>Size class of spider</th>
<th>New web (%)</th>
<th>Same web (%)</th>
<th>Partial replacement of web (%)</th>
<th>Desertion of web (%)</th>
<th>Total observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>46 (25)</td>
<td>15 (25)</td>
<td>20 (13)</td>
<td>18 (37)</td>
<td>99 (8)</td>
</tr>
<tr>
<td>2 and 3</td>
<td>34 (100)</td>
<td>34 (0)</td>
<td>9 (0)</td>
<td>23 (0)</td>
<td>50 (1)</td>
</tr>
<tr>
<td>4</td>
<td>37 (19)</td>
<td>25 (34)</td>
<td>23 (22)</td>
<td>15 (25)</td>
<td>176 (32)</td>
</tr>
<tr>
<td>Total</td>
<td>39 (20)</td>
<td>23 (32)</td>
<td>20 (20)</td>
<td>17 (27)</td>
<td>325 (41)</td>
</tr>
</tbody>
</table>

(*) = spider was observed feeding in late afternoon of previous day.
objects from the web, tightening broken threads near holes in the web) prevented the wind from ripping small holes into larger ones. Spiders which deserted their webs usually either built another web at the same site within two days, or apparently abandoned the site (Table 2).

A. Correlation with Spider Size

Small (size class 1) spiders had spun new webs in 46% of the observations \((N = 99)\), slightly more often \((p < 0.1)\) than large (size class 4) spiders \((37\%, N = 176)\). This trend supports the idea that since webs of smaller spiders are more fragile they need replacement more often. However smaller spider's webs did not have large holes \((\geq 1/10\) of web destroyed) more often than large spiders' webs (see below), and the more frequent replacement may be due to the thinner threads of the smaller spiders fatiguing more quickly, losing their elasticity or strength from over-extension or drying out (R. M. Langer, pers. comm.).

B. Correlation with Prey Capture

Identification of feeding spiders was easy, as \(U. \diversus\) always feeds with legs I spread to form a distinctive “V” with the food mass at the mouth at the point of the “V”. Feeding time, which lasts up to two hours or more, correlates at least roughly with the relative sizes of the spider and the prey (unpublished observations). The frequency of observations of feeding spiders is thus at least a very rough approximation of the spiders’ food intake.

Spiders in size class 4 were observed feeding most often \((21\%, N = 149)\), size class 1 less often \((10\%, N = 81)\), and intermediates least often \((3\%, N = 39)\). Prey capture apparently lowered the frequency of web construction the following day. Individuals with food (in the late afternoon) built new webs the next day slightly less frequently \((p = 0.1)\) than others of the same size (Table 1). The difference in frequencies may

Table 2. Lengths of "inactive" periods following desertion of web

<table>
<thead>
<tr>
<th>Size class of spider</th>
<th>New web within 2 days</th>
<th>New web within 3/5 days</th>
<th>No new web within 5 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>2 and 3</td>
<td>3</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
<td>2</td>
<td>19</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>2</td>
<td>41</td>
</tr>
</tbody>
</table>
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indicate that food eaten late in the day inhibits new web construction. When spiders had their webs destroyed daily in the laboratory however, feeding did not have this effect. Eight mature female spiders whose webs were all destroyed the day of construction were fed one fruit fly per web on alternate days. The frequency of web construction was, if anything, higher rather than lower on days following feeding 

Smaller spiders which had eaten the previous day built new webs more frequently and left old webs intact less frequently than older spiders which had eaten the previous day 

C. Correlation with Web Damage

Almost all webs observed on the desert were at least slightly damaged (had broken threads). About 29% of the webs spun on a given morning had at least an estimated 1/10 of their surface missing by late that afternoon. Neither frequency nor amount of web damage was correlated with spider size. The sample was not large enough to test whether more nearly horizontal webs sustained less wind damage. Damage of 1/10 or more may be correlated with decreased web life, as damaged webs were left up unaltered slightly less often than usual and deserted slightly more often (p < 0.1) (Compare Tables 1 and 3).

<table>
<thead>
<tr>
<th>Size class of spider</th>
<th>New web</th>
<th>Same web</th>
<th>Partial replacement</th>
<th>Desertion of web</th>
<th>Total observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>58</td>
<td>0</td>
<td>19</td>
<td>23</td>
<td>26</td>
</tr>
<tr>
<td>2 and 3</td>
<td>31</td>
<td>15</td>
<td>15</td>
<td>38</td>
<td>13</td>
</tr>
<tr>
<td>4</td>
<td>35</td>
<td>19</td>
<td>14</td>
<td>32</td>
<td>37</td>
</tr>
<tr>
<td>Total</td>
<td>42</td>
<td>12</td>
<td>16</td>
<td>30</td>
<td>76</td>
</tr>
</tbody>
</table>

D. Differences between the Study Areas

Some of the older sectors of Phoenix webs were much dustier than any webs found on the desert, and having seen how quickly dust accumulated on new webs in both areas, I judged that many of the webs (or at least sectors of them) in Phoenix were much older then those on the desert.

Spiders in the laboratory made webs similar to those found in Phoenix. They almost never completely replaced webs; old webs were always
patchworks of several partial replacements, and since the oldest part of a web was not always the part replaced, some sections of these webs were much older than others. One web of a mature female free in the laboratory had sectors more than a month old. The stimuli which release partial replacement thus do not appear to originate in the accumulation of dust on the spiral threads (and the resulting reduction of their stickiness).

Some araneids replace their orb webs regularly once every one or two days in the laboratory (Mayer, 1952; Breed et al., 1964). This difference may stem from the fact that uloborid sticky silk is not wet and probably does not lose its stickiness as rapidly as does that of the araneids.

E. Changes in Design

Although some individuals apparently occupied given sites for several days, the designs of successive webs at a given site often changed substantially. The average difference between the largest and smallest webs spun by (apparently) a single individual at a given site was 75 cm², or an average range equal to 56% of the mean web size for that individual (N of webs = 158). Changes of similar magnitude in web area were observed in successive webs of individuals in the laboratory. Web slants also changed, with the average range just under 13°. The relative variation in both web size and slant in the field was about the same for large and small spiders.

The amount of wind during the day may have affected the slants of small spiders’ webs but not those of large spiders built the next night. The distribution of slants following moderately windy days preceding the storms in 1966 (see below) was the same (p > 0.9) as that following nearly windless days just after the storms for size class 4 spiders, but was somewhat different (p < 0.1) for size class 1 spiders. No such changes were observed in the webs of spiders subjected to varying wind regimes in the laboratory however. Other, as yet undetermined factors are probably involved in the marked day to day changes in web design.

The large variation in design implies that even though webs in the field were largely intact at the end of the day, spiders often did not use the same frame threads for successive webs. Uloborus diversus thus differs from Araneus diadematus and other araneids which apparently use the same frame threads for many successive webs (McCook, 1889; Wiehle, 1927; Peters, 1932; Mayer, 1952). The reason for the frequent change of frame threads is not clear, as damaged frame threads were only rarely observed in occupied webs. Perhaps the threads fatigue in some way (above). Tests have not been performed on the susceptibility of spider
threads to fatigue, but Pointing (1965) had the impression that newly
spun webs of the linyphiid Frontinella communis were less susceptible
to damage than older webs.

F. Web Repair and Extension

Healthy spiders always eventually replaced parts of their webs in
the laboratory. Although these replacements were identical to a common
type of repair of damaged webs (Eberhard, in prep.), they were made
even when there was no damage to the web. The new section was usually
larger and more tightly meshed than the one it replaced, and it thus
appears that partial web replacement not only functions to replace
damaged parts of webs but also to increase the size and effectiveness
of the web beyond that which the spider produces in a single day. Many
webs in Phoenix and in the laboratory contained several partial replace-
ments, and these replacements may be at least partially responsible for
the larger size of Phoenix webs (Fig. 6). Multiple repairs of a single web
are apparently common in Nephila (Wiehle, 1931, p. 370), but rare in
Araneus diadematus (Peters, 1932) and probably many other orb weavers.

Uloborus diversus sometimes only partially filled particularly large
webs with sticky spiral the night they were built in the laboratory, and
finished filling them the night. This behavior (seen rarely in the field)
may also serve to increase the area of a sheltered web (one with a presum-
ably long life expectancy) beyond that which can be made with a single
day's supply of silk. Many spiders which do not spin orb webs also
continue to add to their webs over an extended period of time; this has
been noted in Linyphia (Linyphiidae–Wiehle, 1929), Latrodectus (Theridi-
idae–Szlep, 1965), Cytophora citricola (Araneidae–Wiehle, 1929; Kull-
mann, 1958), Pholcus sp. (Pholcidae–Duncan, 1949), and Duguetia
canities (Duguetidae) and Dictyna sp. (Dictynidae) (unpublished data),
and probably occurs in many others. Extended construction of orb webs
however appears to be rare and perhaps hitherto unknown.

Movements between Web Sites

The periods of "inactivity" following web desertion (Tables 1 and 2)
may have resulted from movements to new web sites, or pauses in web
construction, perhaps due to egg laying or moulting. Egg sacs were
placed deep in the pack rat nest debris where I could not see them during
the survey, but I did find newly cast skins at two sites. It seems likely
however that most of the observations of desertions, especially those
which lasted more than two days, were the result of movements to new
sites (Table 2). Thus the daily rate of movement to new web sites during
the study period in 1967 can probably be taken to be a large fraction but not all of the frequency of observed web desertions (17% in Table 1).

The results of a cosmic experiment on the desert in 1966 demonstrated that spiders may sometimes shift sites in even larger numbers. After several weeks of moderate S and SW winds during the day and little wind at night, there were violent evening thunderstorms with strong winds (est. 45–80 kmph) from the N and E and heavy rains on the evenings of 17, 18, and 20 August. There was little or no wind on August 21st and 22nd, then a steady SSW wind on the 23rd. One hundred and forty two webs at as many sites were observed on 21–23 August. Their distribution around pack rat nests was different from that of webs observed earlier; webs were equally common on all sides of the nests (Fig. 2). The storms, which almost certainly destroyed all webs, apparently caused many spiders to move to new web sites.

Spiders in the laboratory did not change web sites often. Several individuals free in the room did two or three fruit flies per week and stayed at their web sites for periods of weeks and months. The spiders even tended to build their webs near the site where they were introduced into 20 × 20 × 5 cm wooden cages; mature females (N = 15) introduced into one corner of a previously unoccupied frame built more webs in that corner than in the opposite corner (57% vs. 16%, N = 352, p < 0.01).

Discussion

Although several of the lines of evidence above indicate that certain web sites and designs are favored to avoid possible wind damage, other factors not considered in this study are also undoubtedly important. In particular, it is possible that at least some types of insects are concentrated behind the windbreaks formed by pack rat nests (Lewis, 1969), and that the uneven distribution of webs around the nests was partly due to uneven distribution of prey.

It is not clear whether the distributions of web sites, slants, and sizes presented above resulted from orientation and construction behavior by the spiders which positioned webs with appropriate slants and sizes at appropriate sites, or whether the webs observed were the survivors of a continuing selective process in which "inappropriate" webs were destroyed and the spiders responded by either changing web site or design. Probably both phenomena occur in nature. Certainly in some circumstances (following storms for example) large numbers of spiders of all sizes change web sites after web destruction. It also seems likely that spiders actively seek out sites best suited for their webs. Even after storms, most webs were found at relatively sheltered sites. Lower frequencies of web construction and smaller webs after bright nights,
and fewer webs after exposure to wind at web construction time in the laboratory all imply that spiders may use both light and air movement in such a search. Uloborids apparently discard the silk of old webs rather than ingesting it as araneids do before they spin new webs (unpublished data), so not only time and energy, but also protein is wasted by spiders which build inappropriate webs at inappropriate sites, and the construction of such webs is almost certainly selected against.

Bibliography


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