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Web density is related to prey abundance in cellar spiders, *Pholcus phalangioides* (Fuesslin) (Araneae: Pholcidae)

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Summary

Spider predatory success is known to depend on web-site selection and on an appropriate "decision" of when to leave an established site. However, there are few data on another potentially effective strategy — investing more in webs at productive sites. The hypothesis that long-bodied cellar spiders (*Pholcus phalangioides* (Fuesslin)) will build larger and/or denser webs on prey-abundant sites was tested. In the laboratory, fed spiders added significantly more strands to their webs than did unfed spiders.

Introduction

Spiders can increase their chances of survival and reproduction by responding to prey abundance (Morse, 1988). In web-building spiders, the best-studied expressions of this resource sensitivity are site selection and site persistence. Some spiders may be able to sense prey directly (Riechert & Gillespie, 1986); in other species, prey capture rate probably affects how long a spider remains at a site rather than where it chooses to build. It appears that many web-builders construct a "test trap" with little or no direct information about prey abundance; they spin in any site furnished with an interacting collection of suitable physical attributes such as adequate web supports, preferred temperature and humidity, etc. (Turnbull, 1964, 1973; Riechert & Tracy, 1975; Enders, 1977; Janetos, 1986). The spiders then assess the quality of the site based on the web's yield. Finally, productivity of the site, and negative factors, such as competition, web destruction, predation, and parasitoid presence influence whether the spider stays or leaves (Janetos, 1982, 1986; Riechert & Gillespie, 1986).

In addition to site choice and site persistence, there is a third, but largely unstudied, factor that might improve a spider's efficiency: adapting web structure. Spiders at good sites might further enhance their chances of prey capture by enlarging or altering the structure of their webs. We here report an example of web enhancement at good sites by the long-bodied cellar spider, *Pholcus phalangioides*.

Methods

Pholcus phalangioides is a cosmopolitan species most often found associated with human habitations. Its feeding biology has been outlined by Jackson & Brassington (1987) and Kirchner (1990), and a detailed description of its tangled space web is provided by Kirchner (1986).

Twenty specimens collected from a population established in Ohio Wesleyan University's greenhouse were fed to satiation with fruit flies, then sealed individually into 21 × 26 × 36 cm terraria. Each terrarium contained an open dish of water to maintain high humidity, and six vertical wooden dowels (Fig. 1). The dowels provided attachment sites for web strands, and they also "partitioned" the terrarium into four subsections, an aid in counting the strands (see below).

The spiders were randomly assigned to one of two groups. Ten of the spiders were not fed for the duration of the study. The other ten were provided with an excess of fruit flies, ad lib. Temperatures ranged between 20–22°C, and the animals were exposed to a normal day/night photoperiod.

We estimated web density in all terraria at weekly intervals over a six-week period. We counted the number of web strands that crossed established "transect" lines in all three dimensions of each terrarium's four subsections. Only threads within 45° of a right angle with the transect lines were counted. Illuminating the webs from one side and sighting along a straight-edge made the otherwise faint threads visible. A "total web density" estimate for each terrarium was obtained by summing counts for all three dimensions in all four subsections. Figures for each spider's weekly additions were obtained simply by subtracting the previous week's totals. Examination of subsection subtotals allowed us to look for differences in dispersion of threads within each terrarium.

One spider in the unfed group produced an egg sac during the study and was eliminated from the analysis.

Results

Webs of fed spiders did not contain more strands at the end of week 1; means were 69.1 for unfed subjects vs. 52.6 for fed spiders ($t = 1.58$, $p = 0.93$). By the end of the study however, webs of fed spiders had significantly higher densities than those of unfed spiders (means of 274.8 vs. 191.4, $t = 2.97$, $p = 0.0045$). Total web density increased linearly with time in both fed and unfed groups (Fig. 2). Correlation coefficients of individuals' web densities vs.

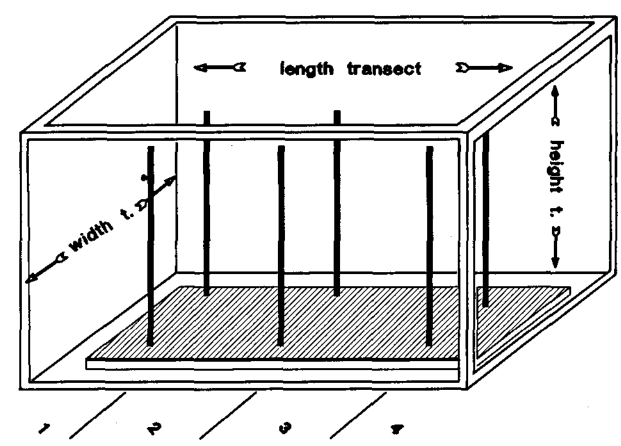

Fig. 1: Experimental chamber. Vertical wooden dowels separating the terraria into four sub-sections provided web attachment sites and facilitated thread counts. Estimates of thread densities were obtained by sighting along pre-determined "transect lines" in each of three dimensions.

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week number were highly significant ($n=60$, $r=0.891$, $p<0.001$ for fed spiders; $n=54$, $r=0.707$, $p<0.001$ for unfed). Mean web densities plotted against week number (Fig. 3) yielded extremely high correlation coefficients (0.995 and 0.998 for fed and unfed groups respectively, $n=6$, both groups).

The slope of the increase in web density over time was significantly steeper for fed than for unfed spiders ($t=189.3$ with 110 d.f., $p<0.001$, small sample t-test for parallelism, Kleinbaum & Kupper, 1978).

Fed spiders not only added web strands at higher rates, but they also produced webs whose spatial patterns of strands differed from those of unfed spiders (Table 1). At the end of the first week, all spiders had produced more threads in one sub-section (called the "core") than in any of the other three (called "peripheral") sub-sections. By the study's end, core densities of fed vs. unfed spiders were about the same ($t=1.24$, $p=0.12$, one-tailed test). However, fed spiders finished with significantly more threads in peripheral sections ($t=2.87$, $p=0.0056$). The core sections for most (7 of 9) unfed spiders remained the area of highest thread density. Most (7 of 10) fed spiders expanded their webs so extensively that at least one of the three peripheral sections attained a higher density than the core, though mean peripheral densities remained lower.

Discussion

Fed spiders added to web density at higher rates than unfed spiders, as predicted. Proximate factors that contribute to the differences may include relatively simple cell-nutrition mechanisms (secrete silk if "adequate" protein and calories exist), to more complex neural mechanisms involving sensory feedback and integration (expand web if prey are abundant). Our data cannot distinguish between possibilities, but either way the spider should benefit.

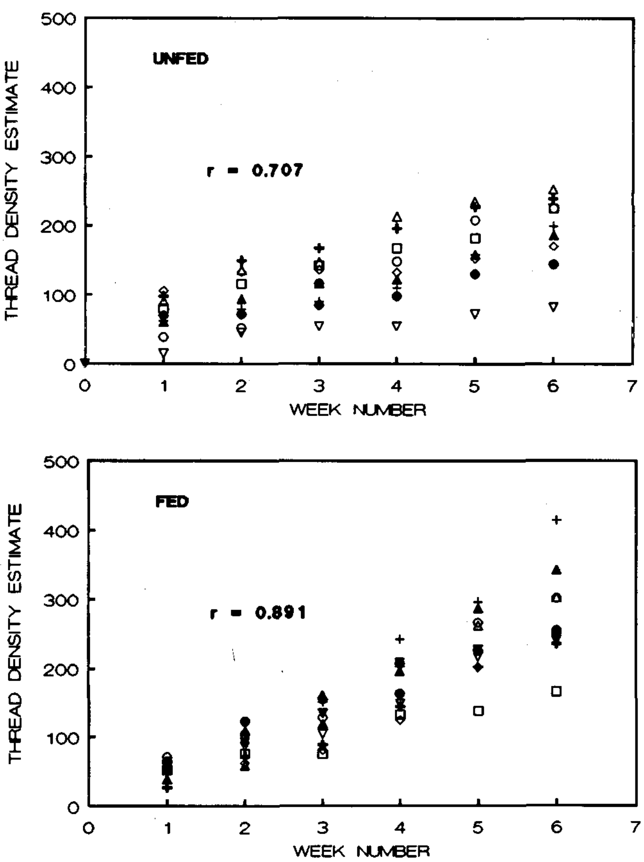

Fig. 2: Increase in total thread density over time in individual unfed (top) and fed spiders; $n=9$ for unfed group, and 10 for fed group. Points for each individual are indicated by different symbols.

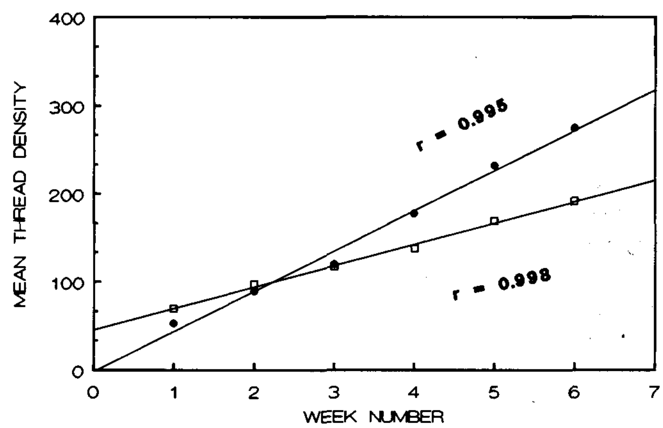

Fig. 3: Changes in mean thread density over time in fed ● vs. unfed □ spiders. Increases were strongly linear in both groups; the slope of the line representing fed spiders is significantly steeper ($p<0.001$) than that representing unfed spiders.

An underlying assumption is that higher web density will increase capture rates. Rypstra's (1982) data support that assumption for tangle webs up to a density of 900 thread/cc; she argued that increasing web density beyond that point may become disadvantageous because webs become more visible, hence avoidable, to flying *Drosophila*. In our study, the web densities fell well below 900 threads/cc. In any case, *Pholcus* may not be limited by the above-mentioned point of diminishing returns, for it preys on many non-flying species (Nentwig, 1983), and has more than one set of predatory tactics (Jackson & Brassington, 1987), and often builds in relatively dark habitats.

Other authors have noted that spiders may continue to add silk to established webs (Turnbull, 1964; Jackson, 1986; Kirchner, 1986). However, no previous studies appear to have elaborated on the connection between prey abundance and web density. One possible reason for this curious lack of published data is that most detailed analyses of web structure concern orb webs,

	Core density		Mean peripheral density	
	Unfed	Fed	Unfed	Fed
Week 1	35.2 (±4.82)	26.3 (±2.22)	11.4 (±1.97)	8.8 (±1.2)
Week 6	72.1 (±5.5)	85.8 (±9.57)	39.6 (±5.44)	63.0 (±6.09)

Table 1: Thread densities and dispersions in webs of fed vs. unfed spiders at beginning and end of the study. Numbers are means (with SE in parentheses). At the study's end, peripheral densities of fed spiders' webs were significantly higher than those of unfed subjects, but core densities of fed vs. unfed spiders were not significantly different (see text for definitions of "core" and "peripheral").

whose forms are highly stereotyped. Indeed, orb construction is often used as an illustration of behavioural rigidity (Turnbull, 1973; Shear, 1986). Witt's (1963) study provides an exception; low feeding levels result in webs with smaller diameters. Otherwise however, the structural variation reported in orbs has been related to factors other than food abundance (summarised by Eberhard, 1990).

Non-orb webs then, may be better candidates for seeking a prey abundance–web density relationship, but they present difficulties of their own. Because their residents continue to add silk, estimation of web densities becomes an intimidating task. Nevertheless, Rypstra (1982) has shown that such measurements can be taken in the field, and our study should be repeated with this, or another appropriate species, under natural conditions.

That unfed spiders continued to add to the web throughout six weeks is intriguing, for silk is metabolically expensive, particularly for *P. phalangioides* and other spiders that do not re-ingest and rebuild their webs (Enders, 1975). Perhaps the methodical addition of silk serves to repair the average minor damage done daily to webs in natural settings, and/or to increase the chances of prey capture in the future. Since no environmental damage occurred in our sheltered terraria, a "web-repair programme" would result in the observed steady, slow increase in thread density. We re-emphasise however, that field observations on unconfined spiders are needed to corroborate our results; individuals at unproductive sites may simply abandon and move, rather than stay and add silk.

The observed increase in peripheral density of fed spiders' webs may have been an artefact of confinement. We suspect that fed spiders would have extended the boundaries of their webs, but were blocked by terrarium walls. The result was a deposition of additional web strands in the only available space, which led to a relatively uniform thread dispersion. If this is true, then web size, rather than, or in addition to, web density, may be an important variable to study in the field. Webs in the field differ in size, but do not have uniform web densities throughout (personal observation).

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