

## SENESCENCE OF WEB CONSTRUCTION BEHAVIOR IN MALE *FRONTINELLA PYRAMITELA* (ARANEAE, LINYPHIIDAE)

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### ABSTRACT

Female bowl and doily spiders, *Frontinella pyramitela*, build species-typical webs throughout their lives. In contrast, males of the species cease the construction of prey capture webs soon after they become adults, though they continue to be capable of producing sperm-induction webs and draglines. In this report we describe the timing of the senescence of web construction, analyze the structure and utility of the webs built by adult males, and eliminate two variables, mass at maturity and adult feeding history, as important contributors to the variability in rate of senescence.

### INTRODUCTION

The species-typical prey-capture web of the bowl and doily spider, *Frontinella pyramitela* (Walckenaer), consists of a concave upward, bowl-shaped sheet that lies between two silken meshworks. The upper of these can be vertically quite extensive and acts as a knockdown structure, while the lower of the meshworks (the doily) appears to function primarily as an anchoring structure to which the bowl is attached. Tension in threads (called "tensors") that are attached both to the bowl and to the doily cause deformation of the otherwise flat sheet and give the sheet its characteristic shape and tension profile (Suter 1984).

Until recently, it had appeared that male *F. pyramitela*, like most other male spiders (Savory 1928; Opell 1982), ceased building prey-capture webs upon molting to adulthood, and thereafter built only draglines and sperm-induction webs. But a recent report (Hirscheimer and Suter 1986) has indicated that this species is relatively unusual among the Araneae in that adult males readily build prey-capture webs under laboratory conditions. In that respect, *F. pyramitela* resembles a uloborid species (*Uloborus* sp.) in which adult males also build prey-capture webs (Eberhard 1977).

We report here the results of investigations into the characteristics of webs built by adult male bowl and doily spiders and into the timing of the cessation of prey-capture web-building by males.

### MATERIALS AND METHODS

**Animal manipulations.**—During the last half of April, 1985, 64 immature bowl and doily spiders were captured from webs in the vicinity of Vassar College,

Poughkeepsie, New York. They were reared to adulthood during the subsequent few weeks on webs of their own making and on a diet of vinegar flies (*Drosophila melanogaster*). Every morning and evening, we checked each web for the presence of a newly shed exuvium and the emerged animal, if adult, was weighed under CO<sub>2</sub> anesthesia and sexed. Adult males were immediately transferred to plastic cylinders 10.2 cm in diameter and 15.3 cm long. These enclosures were sealed on both ends with polyethylene plastic wrap held in place with elastic bands and were placed on a platform that kept their long axis in a horizontal orientation. Males so enclosed were checked every 12 h. We evicted (with a water gun) a male from its cylinder if it had built a prey-capture web since the last check or if it had been in the cylinder for more than 48 h without constructing a web. Because the spiders would not, and perhaps could not, attach silk to the plastic wrap that enclosed the cylinders, we could remove the wrap on both ends to facilitate eviction of the spiders without damaging the newly-constructed silk.

We placed each evicted male on the vacant web of an immature conspecific and there fed it one vinegar fly prior to transferring the spider to a fresh cylinder. (A subset consisting of five adult males was manipulated as described, but was not fed at all during adulthood.) Males remained in this build-evict-feed-new cylinder cycle until they failed, during 48 hours of occupancy, to construct anything more complex than draglines.

**Web manipulations and analyses.**—Webs of adult male spiders were preserved intact in the cylinders in which they had been constructed. We lightly dusted the majority of these with air-blown cornstarch, then photographed them using standardized backlighting, lens, and web-to-focal plane distance. The negatives derived from this procedure were mounted perpendicular to the beam of a helium-neon laser and the intensity of the beam, diminished in proportion to the density of the negative, was measured by a photocell and recorded by computer. The computer recorded between 300 and 1000 data points during the single vertical transection of each negative, smoothed the data by performing continuous averaging of 10-point series, and corrected for the background density of the negative. We analyzed the same negatives by direct measurement to ascertain knockdown diameters (= bowl diameters), knockdown height, and number of tensors attached to the bowl.

On the remainder of the webs, we used a hot needle to destroy the silk that connected a portion of the bowl sheet with both the knockdown meshwork and the underlying "doily". We then caught the freed section of bowl on the perimeter of a circular brass frame (diameter 1.5 cm). It adhered to the frame and could then be removed from the surrounding portions of the sheet without causing any visible distortion of the silken sheet that was attached to the frame. Each mounted bowl section was photographed under a dissecting microscope and the silk threads visible on the resulting negative were counted across two randomly chosen diameters. The two counts from a particular web section were averaged to derive a value of thread density for that bowl sheet.

## RESULTS

During this study, 30 adult male bowl and doily spiders constructed 154 webs. Figure 1 shows that all of the males constructed at least one prey-capture web

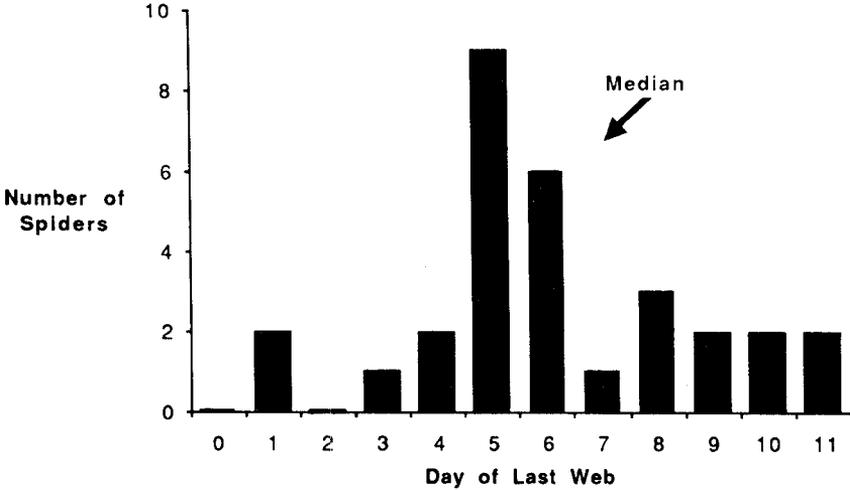


Fig. 1.—Longevity of web-construction behavior. Adult male bowl and doily spiders are capable of constructing prey-capture webs immediately after emergence as adults and under laboratory conditions may continue to build webs for up to 11 days thereafter. Most adult males cease web-construction on day 5 or day 6.

after the final molt, that no spider constructed webs after the 11th post-molt day, and that half the spiders ceased web construction at day 5 or day 6 (median = 6 days). The five spiders that had been starved during adulthood all ceased web construction between 5 and 5.5 days after the final molt (median = 5.5 days). There was no significant difference in the timing of cessation of construction between the starved and fed groups of adult males. Male mass, immediately after the final molt, was not correlated with the number of days of web construction (mean mass  $\pm$  SD =  $4.38 \pm 0.7$  mg; correlation coefficient =  $-0.006$ ,  $P > 0.05$ ).

Figure 2 shows the first (A) and last (B) webs built by a single spider after its final molt. The first of these is typical of initial prey-capture webs constructed by

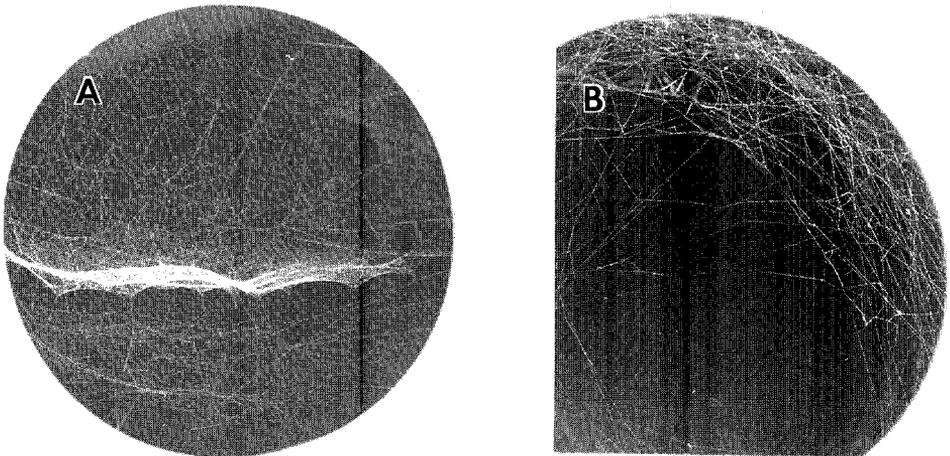


Fig. 2.—The first (A) and last (B) webs constructed by one male that ultimately built seven webs over the first 10 days of adulthood. Densitometric profiles of these and the spider's other five webs are shown in Fig. 3.

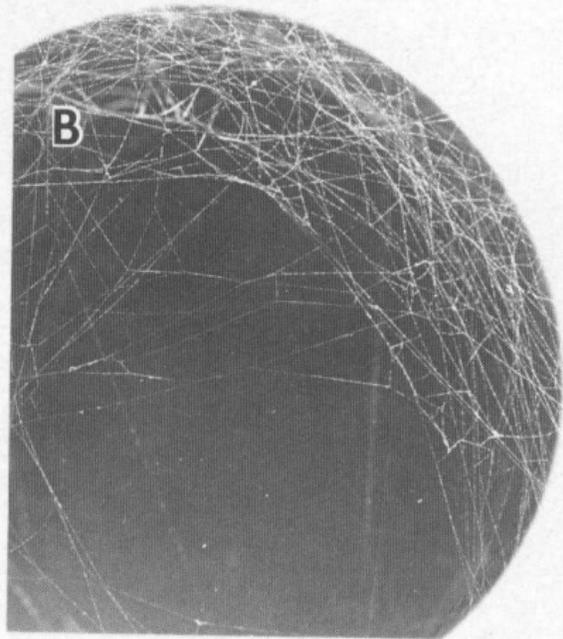
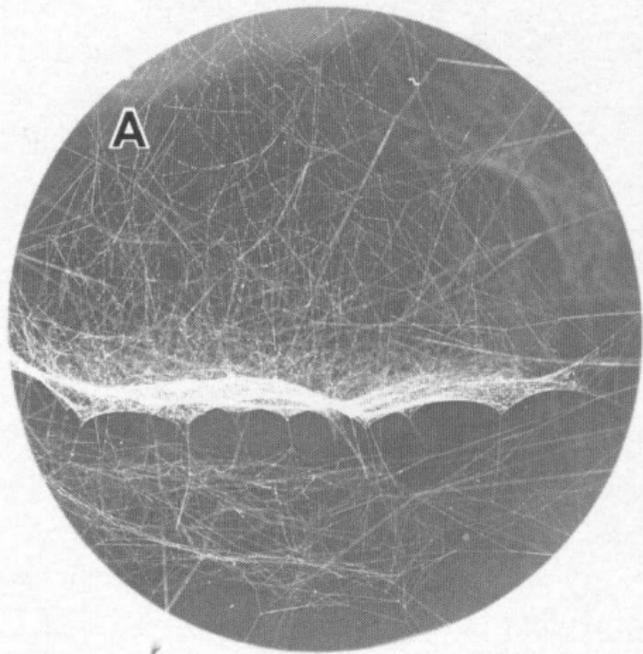
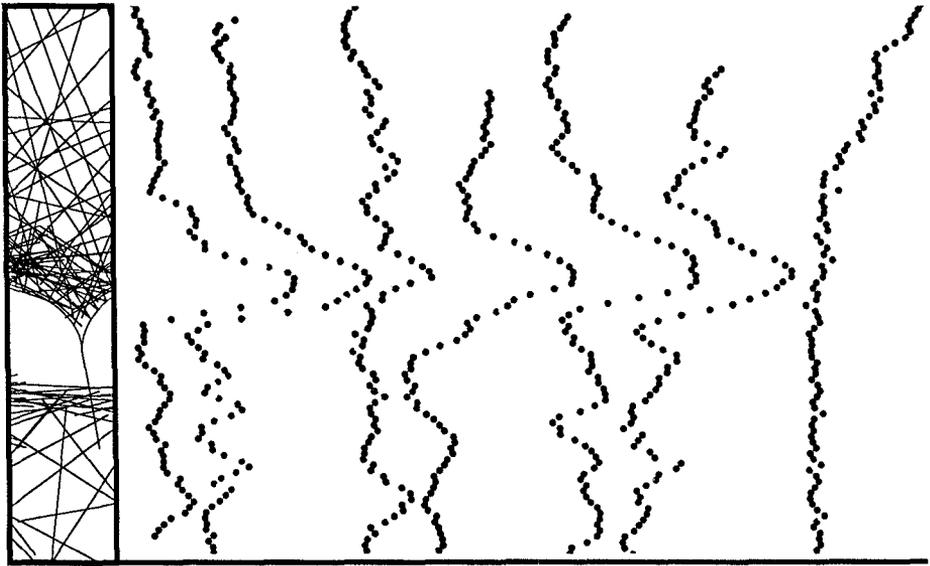


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### Relative Density

Fig. 3.—Densitometric profiles of the seven webs built by a single adult male over the first 10 days of adulthood. Each profile represents the densities measured along a vertical transect at approximately the middle of the web. For clarity of presentation, the maxima of the profiles are aligned with the maximum density of the schematic web that forms the ordinate. The first (left) and last (right) of these profiles correspond to the webs (A and B) shown in Fig. 2.

newly molted adult males. Though final webs varied more in size and structure, the web shown in Fig. 2B is not atypical. (Some final webs were little more than collections of draglines while others were more obviously prey-capture webs in that they contained a recognizable sheet). The data from densitometric analyses of all of the webs constructed by that spider are shown in Fig. 3. Densitometric profiles of 18 first webs and 21 penultimate webs are shown in Fig. 4 (penultimate rather than ultimate webs were analyzed as “late” webs because often the last web constructed was indistinguishable from a collection of draglines). The profiles represent means and standard deviations of the two sets of individual profiles which were aligned, for analysis, with respect to their maximum (highest density) values.

Of the 154 webs constructed in this study, 93 made up series that could be analyzed with respect to number of tensors, bowl diameter, etc. Using these 93 as our sample, we found that all measures, except bowl-silk density, decreased significantly as number of post-molt webs (and time) increased (Table 1).

### DISCUSSION

All adult male bowl and doily spiders appear to be capable of constructing species-typical webs immediately after emergence as adults (Fig. 1). Webs constructed early in a male's adult life are superficially indistinguishable from those built by juveniles and adult females. The penultimate webs, and usually even the last webs of adult males, persist in having a species-typical form

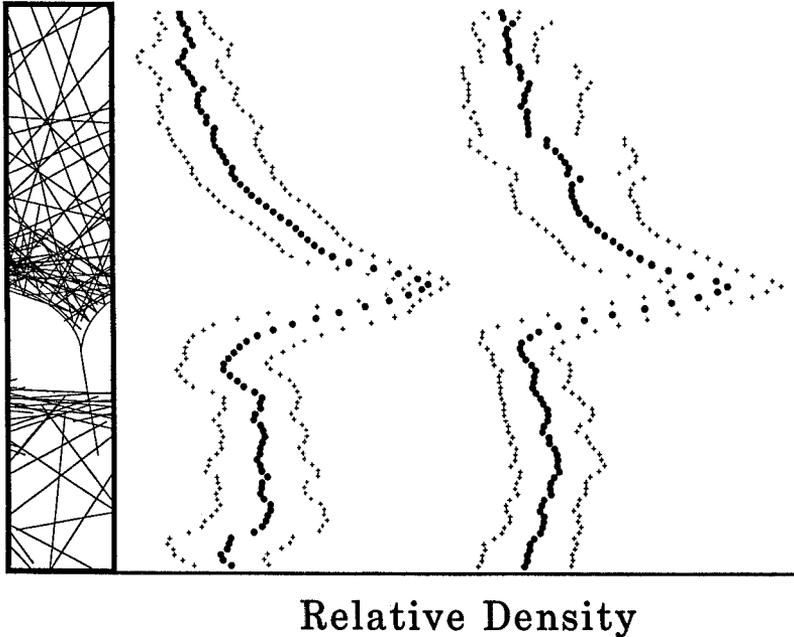


Fig. 4.—Means and standard deviations (point by point) of 18 first (left profile) and 21 penultimate (right profile) webs built by adult male bowl and doily spiders in the laboratory. The maxima of the webs were aligned prior to averaging. In both profiles, the species-typical prey-capture form is evident: an increase in density as the transect approaches the bowl from above, maximum density at the bowl, a rapid decrease in density as the transect leaves the bowl and passes through the space below the bowl where the spider normally rests, and an area of variable density occupied by the doily and its substructure.

consisting of knockdown threads, a bowl sheet, and a doily (Figs. 3 and 4). Despite this persistence of form, new construction by males changes measurably as the male builds additional webs: later webs are progressively smaller (decreased bowl diameters), flatter (fewer tensors), and can intersect the paths of fewer prey (knockdown silk less extensive) than the first web (Table 1). Because the utility of a web as a snare is limited both by its size (smaller webs intersect the paths of fewer prey) and its form (males cannot pursue prey as rapidly in a meshwork of threads as they can under the surface of a sheet), the value of web-construction to a male *F. pyramitela* must decrease as the male ages.

For the males used in this study, which became adults early in the reproductive season, differences in mass did not influence the length of time spent in the web-construction phase of their adulthood. Even with large differences in adult male mass (3.3 to 5.8 mg) we could demonstrate no correlation between mass and web-construction behavior.

Hirscheimer and Suter (1986) suggested that the time and energy spent by an adult male *F. pyramitela* in web construction would be minimized by a male that was large because its chances of discovering and productively fertilizing a female were high. The rationale behind that suggestion was that a larger male has greater nutrient and water reserves for the lengthy search that may be necessary and, if the search is successful, a greater probability of being able to displace a male already in residence (Austad 1983, Suter and Keiley 1984). A smaller male, in contrast, might benefit by increasing its mass through web-construction and

Table 1.—Correlations of web structure variables with sequence of construction. In all tests,  $N = 93$  webs.

Variable	Range	Corr. with Seq.	Probability
Knockdown Height (cm)	0 - 9.5	-0.56	< 0.001
Knockdown Diameter (cm)	0 - 8.4	-0.66	< 0.001
Capture Area ( $H \times D$ ) (cm <sup>2</sup> )	0 - 68.7	-0.54	< 0.001
Number of Tensors	0 - 15	-0.61	< 0.001
Bowl Silk Density (threads/mm)	1.3 - 5.2	-0.10	> 0.05

predation, and only then beginning the search. For all sizes of males, there would be pressure to begin the search early because previously inseminated females are reproductively less available to subsequent males - first male sperm priority characterizes the reproductive dynamics of bowl and doily spiders, and a secondary male can fertilize no more than 5-10% of the lifetime reproductive output of a female (Austad 1982).

Apparently, under laboratory conditions at least, the senescence of web-construction behavior is neither significantly hastened in larger male bowl and doily spiders nor delayed in smaller ones. Yet it is unlikely that newly molted males remain on their own webs for five or six days under natural conditions. The first adult males we have found on webs in the spring are found cohabiting with females, not alone on what could be male-constructed webs, and throughout the season adult males are rarely seen alone on webs. Thus we conclude that a) many adult males found on females' webs in the field are physiologically and behaviorally capable of constructing prey-capture webs and b) the conditions that could elicit early abandonment of webs in the field (e.g. unavailability of prey, desiccation, freedom of movement) are not present in strength in the laboratory. Supplemental feeding and misting experiments on marked males in the field may be able to elucidate the variables that stimulate early abandonment of male-constructed webs.

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