

FUNCTIONAL WEBS BUILT BY ADULT MALE BOWL AND DOILY SPIDERS

It is generally accepted in the arachnological literature that adult female web-building spiders build species-typical webs while adult males do no web-building other than that required for courtship and sperm induction (e.g. Savory 1928, Opell 1982), though there is at least one published report that adult male uloborid spiders sometimes construct webs (Eberhard 1977). Immature bowl and doily spiders (*Frontinella pyramitela*, Linyphiidae) of both sexes as well as adult females have long been known to build relatively complex sheet webs consisting of a bowl-shaped horizontal sheet, an underlying flat sheet (the doily), and a barrier meshwork of silk that is above the bowl and doily.

We observed web-building by adult males while we were investigating the behavioral effects of the chemical constituents of webs built by *F. pyramitela* (Suter and Hirscheimer in press). In the course of those studies, we collected spiders of all ages and both sexes from webs in Poughkeepsie and Millbrook, New York, during May and June 1984. In the laboratory, the spiders were placed on glass or wooden hexapods in 3.8 l plastic jars where each could build a web (for details of techniques, see Suter 1985). Usually within a day or two after a spider built a web, the spider was removed from the web and placed on a new hexapod, and the web was stored for subsequent testing. All spiders were maintained in the laboratory on a diet of fruit flies (*Drosophila melanogaster*).

We recorded the data of construction of all webs and the molt dates of every individual spider. These data allowed us to determine the last day on which male

spiders definitely could build webs. It did not enable us to determine what the first day was on which they could not build webs. These two measures might well have been different, since a spider may not have built a web on a given day though he still had the capability to do so. Our method of measurement, the last day on which males definitely could build webs, is actually the more conservative of the two, and indeed male spiders may have had the ability to build webs on several subsequent days.

Of the six immature males that reached maturity in the laboratory, two never built species-typical webs as adults. Instead they built rudimentary platforms that consisted of a diffuse and very small (1-3 cm diameter) horizontal sheet supported by a few strands of silk below. These structures resembled crude versions of the normal "doily." Each of the remaining four adult males built a fully functional and structurally complete species-typical web soon after the final molt. One male, brought into the laboratory as an adult, also built functional and species-typical webs. The last day on which we could ascertain that adult males built species-typical webs ranged from 2 to 7 days after the final molt (Table 1). The last web built by each male tended to be truncated (i.e. the bowl was relatively flat and the vertical dimension of the entire web was reduced relative to the heights of webs constructed by adult females and juveniles), but still had an identifiable "bowl" and "doily." These webs were as functional as those of other sex and age classes in that prey items could still be captured on them.

Because adult males of this species emerge in the spring at the same time as females (Suter 1985), adult males are not dependent upon their own web-building abilities to capture food. During most of their active adult lives, males make use of females' webs for predation. This is rare among spiders because in most species the males take no food during adulthood (Bristowe 1985). Male bowl and doily spiders feed frequently while cohabiting on females' webs and capture about 37% of the prey that hit the web despite competitive activities of the females (Suter 1985). Of what benefit then, might it be to adult males to expend energy and nutrients in building webs when they could expend the same resources in search of females?

When a male comes upon a female's web that already has a resident male on it, the two males engage in an agonistic interaction which the larger (heavier) male wins most of the time (Austad 1983, Suter and Keiley 1984). And when a male comes upon a female's web with no resident male on it, the male's size will likewise determine the outcome of contests with subsequent intruder males. Thus male size is probably closely tied to male reproductive success and it will be advantageous to adult males to be as large as possible when leaving their own

Table 1.—Construction of functional webs by adult male spiders.

Spider	Date of final molt	Adult age (days) when last web was built
1	5/26	7
2	5/28	3
3	5/30	6
4	5/31	2
5	*	>5

*Captured as an adult on 5/14.

webs. Because the mass of a spider, one measure of size, is directly related to the amount of food that it consumes, a male may benefit by trying to capture as many prey as he can for as long as he can, before setting off to find females.

According to Austad (1982), first male sperm priority is operative in bowl and doily spiders; that is, the first male to inseminate a given female will fertilize about 90% of her eggs. Finding virgin females, then, is crucial to the reproductive success of a male, and any delay in beginning the search reduces the probability that the male will find a virgin female.

Thus males have to weigh the benefits of capturing more prey against the costs of delaying their search for unmated females. The optimum behavior for a male depends upon at least three variables: nutritional status, season, and size. The spider's nutritional status determines what his energy reserves are and therefore how long he can spend searching for females before starving. The time of year is an important variable because the intensity of intermale competition varies with male and virgin female densities which vary seasonally (Suter 1985). And size is important because it is the primary determinant of male success in intermale agonistic interactions. [Size can be measured both as lengths of body parts and as mass. The latter is a good predictor of the outcome of intermale interactions in bowl and doily spiders (Suter and Keiley 1984)].

Therefore, if a male were small at maturity, early encounters with females might prove futile because of competition with other males, and the addition of mass would be advantageous. In contrast, if the male were large, additional mass might be far less advantageous than early encounters with females. This putative relationship between mass at maturity and cessation of male web-building is easily tested. We plan to test the relationship during the 1985 season.

We thank William Eberhard and Steven Austad for their helpful reviews of this manuscript.

LITERATURE CITED

- Austad, S. N. 1982. First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). *Evolution*, 36:777-785.
- Austad, S. N. 1983. A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Anim. Behav.*, 31:59-73.
- Bristowe, W. S. 1958. *The World of Spiders*. Collins, London.
- Eberhard, W. G. 1977. The webs of newly emerged *Uloborus diversus* and of a male *Uloborus* sp. (Araneae, Uloboridae). *J. Arachnol.*, 4:201-206.
- Opell, B. 1982. Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae, Uloboridae). *J. Arachnol.*, 10:185-191.
- Savory, T. H. 1928. *The Biology of Spiders*. The MacMillan Company, New York.
- Suter, R. B. 1985. Intersexual competition for food in the bowl and doily spider, *Frontinella pyramitela* (Araneae, Linyphiidae). *J. Arachnol.*, 13:61-70.
- Suter, R. B. and A. J. Hirscheimer. In press. Multiple web-borne pheromones in a spider, *Frontinella pyramitela* (Araneae, Linyphiidae). *Anim. Behav.*
- Suter, R. B. and M. Keiley 1984. Agonistic interactions between male *Frontinella pyramitela* (Araneae, Linyphiidae). *Behav. Ecol. Sociobiol.*, 15:1-7.

Andrea J. Hirscheimer and Robert B. Suter, Biology Department, Vassar College, Poughkeepsie, NY 12601.