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OVIPOSITION SITE SELECTION BY *FRONTINELLA PYRAMITELA* (ARANEAE, LINYPHIIDAE)

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ABSTRACT

In the field, the bowl and doily spider, *Frontinella pyramitela* (Araneae, Linyphiidae), deposits its eggs in a loosely-woven silk cocoon on or close to the soil. Experimental laboratory studies indicate that gravid females select that type of oviposition site in response to gravitation, soil moisture or atmospheric humidity, and the gross structure of the microhabitat. Under experimental conditions, rates of water loss from *F. pyramitela* egg cocoons are approximately double the rates from cocoons constructed by three species (*Achaearanea tepidariorum*, *Argyrodes trigonum*, and *Uloborus glomosus*) that oviposit in aerial webs well above the ground. We conclude that desiccation of developing eggs has been an important natural selective force shaping the selection of oviposition sites by bowl and doily spiders.

INTRODUCTION

Habitat selection usually refers to the suite of choices made by an organism that results in its occupation of a particular habitat (Partridge 1978). Often it is useful to partition the choices into functionally specific subsets, to refer, for example, to foraging patch selection, display arena selection, and oviposition site selection. In this more specific context it is possible to discover experimentally the stimuli to which the organism responds as it makes each choice.

Morse (1985) has correctly asserted that the selection of an oviposition site is "one of the most important decisions made by animals that deposit eggs," and that this is particularly so if most of the organism's eggs are deposited at one or only a few sites. Because most spider species do not move their eggs once they are deposited (Comstock 1948; Foelix 1982; but note the egg cocoon-transporting behaviors of the Lycosidae and Pisauridae) and usually distribute their eggs among one or a few clutches (Comstock 1948), their decisions leading to oviposition site selection are certainly crucial. And the importance of the selection process is increased by the fact that hatchlings may remain in the cocoon for long periods (Foelix 1982).

For many web-building spiders (e.g., *Cyclosa*, *Achaearanea*, *Uloborus*), the selection of oviposition site is identical to the selection of foraging site, because the egg cocoon is incorporated into the prey-capture web at the time of oviposition. For others, though, the processes of oviposition and web site selection are separate and the selected sites are qualitatively very different. We report here on the oviposition sites chosen in the field by the bowl and doily spider, *Frontinella pyramitela* (Linyphiidae), and on the environmental cues that the spider responds to during the process of selection.

MATERIALS AND METHODS

Field study.—We removed 17 gravid female *F. pyramitela* from their webs in an old field in LaGrange, NY, during July, 1985, and placed them inside a 1 m^3 cube-shaped enclosure which was located in an old field. The enclosure was screened on four sides and on the top but was open on the bottom. The wooden bottom edges of this enclosure rested on a smoothed soil bed which surrounded a one meter square of pasture vegetation (grasses and a mixture of forbes and dried stems of forbes) which had been clipped at the top and sides to fit within the enclosure. The outside of the bottom edge of the enclosure was sealed with fine sand to prevent the escape of the spiders. This entire assembly was surrounded by pasture vegetation similar to what was inside the enclosure.

Eight days after spiders were released into the enclosure, we performed a top-down search of its contents in an attempt to recover as many *F. pyramitela* egg cocoons as possible. As each cocoon was found, we recorded both its location and a description of its microhabitat. We also counted all *F. pyramitela* that we found, and noted their condition.

Laboratory studies.—Gravid female bowl and doily spiders, either mated in captivity or freshly removed from their webs in the field, were placed in 10.2 cm (diameter) by 15.3 cm plastic cylinders which gave the spiders sufficient volume both to construct prey-capture webs and to deposit eggs. In tests of the importance of gravity as a stimulus in oviposition site selection, the ends of each cylinder were covered by polyethylene plastic wrap (e.g., Saran Wrap®) and the chamber was stored horizontally in a larger container in which the atmosphere was saturated with water. Because of overhead lighting, the brightest areas of these cylinders during the day were located on the bottom near either end. In tests of the importance of substrate moisture as a stimulus, one end of each (vertical) cylinder was covered with cheesecloth and the other end rested on a divided bed of white sand, half of which was dry and half of which was moist (darker than the dry sand but with no liquid water visible). Again because of overhead lighting during the day, the sand floors of these containers were uniformly illuminated. Each morning, we recorded the locations of the egg cocoons constructed during the previous night.

Overhead fluorescent bulbs provided light during the day and no light was visible to the spiders during the night. Relative humidity in the laboratory varied between 45% and 60%.

We measured rates of water loss from 16 newly constructed egg cocoons of *F. pyramitela* by individually weighing them before and during seven days of desiccation over a 50% H_2SO_4 bath (33% RH). For contrast, we subjected 48 egg cocoons of *Argyrodes trigonum* (Theridiidae), *Achaearanea tepidariorum* (Theridiidae), and *Uloborus glomosus* (Uloboridae) to the same desiccation regime. After desiccation, the cocoons were dried to constant weight in a low-temperature oven to establish (by subtraction) the total water initially present in each cocoon. They were also opened to determine which cocoons contained only eggs (no spiderlings or parasitoids). Nineteen of the theridiid and uloborid cocoons contained only eggs, and data from only these were used in later comparisons.

RESULTS

Field study.—During the search of the field enclosure, we found eight egg cocoons belonging to *F. pyramitela*, and two dead and four live *F. pyramitela*. Of the latter, all were still gravid. None of the cocoons was found further than 2 cm from the soil: six were directly on the soil, one was 1 cm and another was 2 cm from the soil surface. All of the cocoons that were in contact with the soil had been constructed in small hollows or between the underside of the wooden frame of the enclosure and the soil (connected to both). The two cocoons found above the soil had been constructed within clumps of dead grass leaves.

Laboratory studies.—Figure 1 shows the locations of 24 egg cocoons relative to the direction of gravity. The distribution of locations is significantly different from random and the mean direction is downward (357° ± 31°; Rayleigh test, z = 17.6, $P < 0.01$). Figure 1 also indicates that > 91% of the cocoons in the gravitation experiment were constructed in contact with the polyethylene ends of the cylinders (binomial test, $P < 0.001$), and this was the case despite the inability of the silk to adhere to that plastic (Suter et al. in press).

Figure 2 shows the locations of cocoons constructed in vertical cylinders in which the bottoms were divided into moist and dry sections. The 12 spiders unanimously selected the moist side (binomial test, $P < 0.001$) and showed no obvious preference for locations far from the dry sand substrate. As in Fig. 1, Fig. 2 shows evidence that the selection of oviposition site is influenced by the gross structure of the available environment: 92% of the spiders built their cocoons in contact with both the sand and the wall of the cylinder (binomial test, P = 0.003).

Desiccation of the 16 egg cocoons of *F. pyramitela* resulted in water loss at a rate nearly twice that of the 19 cocoons of the theridiids and the uloborids (among which there were no statistical differences in rates of water loss). Egg cocoons of *F. pyramitela* lost water at a rate of 0.42% ± 0.1% per hour (70.6% in 7 days) while egg cocoons of the other taxa lost at a rate of 0.27% ± 0.2% per hour (45.4% in 7 days) (T = 3.48, $P < 0.001$).

DISCUSSION

Kaston, in his 1948 work on the spiders of Connecticut, stated that he had never seen the egg sacs of bowl and doily spiders (p. 121). His observation is not surprising given the selection of oviposition sites reported above. The placement of egg cocoons under natural conditions indicates that this aerial web-building spider uses wholly different sets of criteria in selecting sites for prey-capture webs and oviposition. The sites selected for oviposition contained high relative humidity, low light, and were near or on the ground, and all but two were partially enclosed in soil depressions or in small gaps between soil and wood.

Data from the laboratory indicate that gravity, moisture content of the air or substrate, and physical structure of the microhabitat are important variables in oviposition site selection by *F. pyramitela*.

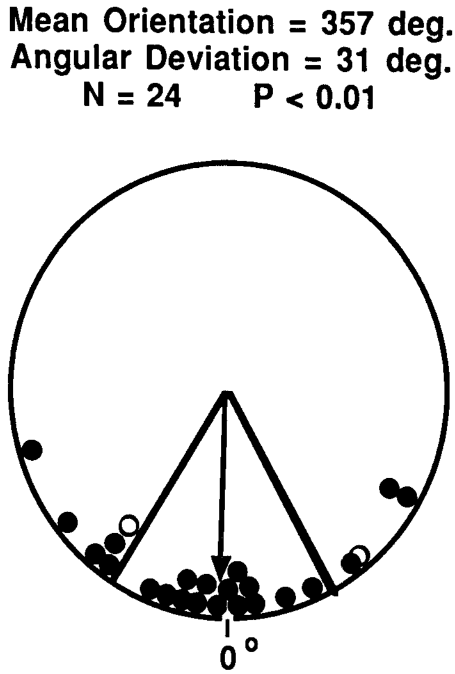

Fig. 1.—Oviposition sites chosen by 24 gravid spiders in horizontal, cylindrical chambers. In reference to the direction of gravity (0°), the mean orientation of the sites was strongly and significantly downward (357° ± 31°; Rayleigh test, $P < 0.01$). Only two of the spiders constructed egg cocoons away from the intersection of a cylinder and its plastic end (open circles; binomial test, $P < 0.001$).

In a horizontal cylindrical environment in which the RH was invariate at 100%, the spiders showed a strong preference for locations that were down (in the direction of gravity) and that had two distinct sides; they nearly always constructed their egg cocoons low against the ends of the cylinders (Fig. 1). The same location is also the brightest location in an experimental cylinder during daylight hours. We discount the importance of light as a cue, however, because nearly all egg cocoons were begun during the night and because the cocoons found in the field were in locations which had very low or negligible light levels.

In a vertical cylindrical environment open to low-RH air at the top and with a choice of moist or dry sand at the bottom, the spiders showed an unequivocal preference for the more moist of the two microhabitats; all egg cocoons were constructed in contact with the moist sand. (Note that no distinction can be made here between the moisture of the sand and the RH of the immediately surrounding air. The spiders may be capable of measuring either or both). In this experiment, too, the spiders displayed a significant tendency to oviposit where the cylinder and one of its ends joined (Fig. 2).

Thus the data from laboratory experiments coincide well with what was found in the field—in selecting a site for oviposition, a female *F. pyramitela* is positively gravitactic and, in that context, chooses a moist site that also is partially enclosed.

The choice of an off-web oviposition site places the gravid female at a risk not shared by spiders that remain on the web while laying eggs. When *F. pyramitela* leaves its web to search for an oviposition site, it leaves its primary source of information and must travel where its detection of predators is greatly hampered. Moreover, the enclosed oviposition sites chosen by *F. pyramitela*, though probably safe from visually-hunting predators, are likely to expose the cocoons to predation by rodents and ants (Hieber 1984). Thus the risk of the search for an

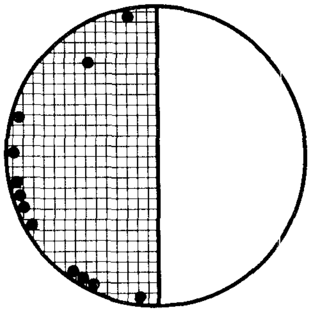

Fig. 2.—Oviposition sites chosen by 12 gravid spiders in vertical, cylindrical chambers resting on sand. All of the spiders constructed their cocoons on moist sand (cross-hatched) in preference to dry sand (binomial test, $P < 0.001$). Eleven of the spiders constructed cocoons in contact with both the sand and the vertical side of the cylinder (binomial test, $P = 0.003$).

oviposition site and the predator pressure on eggs deposited there must be outweighed by the benefits of discovery of a site that is suitable in other ways.

The presence of still, moist air, may be the most important attribute of these oviposition sites. Several authors have postulated that a primary function of egg cocoons in spiders is to retard water loss and the resulting detrimental effects of desiccation on development (Bristowe 1941; Foelix 1982; Opell 1984; Hieber in press). Our investigations of the rates of water loss from egg cocoons of *F. pyramitela* show that, in 33% RH air, about 70% of the water may be lost in seven days, a time that is about half the development time required by the species (median = 15.5 days at 22°C; Suter unpubl. data). That rate of water loss is nearly double the rate from cocoons of two species of spiders that construct their cocoons in open air. One of these, *Argyrodes trigonum*, provides a particularly apt comparison because it often suspends its egg cocoon in the web of *F. pyramitela*. Thus the cocoons of *A. trigonum* are subjected to a relatively dry microclimate (usually > 30 cm above the ground), the one where *F. pyramitela* spends most of its life, and it is not surprising that the eggs of the former become desiccated more slowly under test conditions.

The egg cocoon of *F. pyramitela* is composed of two very loosely-woven layers of silk surrounding the eggs. This covering is open enough to allow the orange color of the eggs to be seen from the outside. In contrast, the egg cocoons of *A. trigonum* and *A. tepidariorum* have as their outer coverings a densely woven and paper-like layer of tanned silk. Opell (1984) and Hieber (in press) have shown that this sort of covering retards water loss from cocoons of some spiders. The absence of such a covering on cocoons of *F. pyramitela* and their high rate of water loss suggests that this spider has evolved orientation behaviors rather than silk spinning behaviors in answer to selective pressures resulting from egg desiccation.

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