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THE WEB AND BUILDING BEHAVIOR OF *SYNOTAXUS ECUADORENSIS* (ARANEAE, SYNOTAXIDAE)

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ABSTRACT. Webs and building behavior of *Synotaxus ecuadorensis* are highly ordered and complex. Their webs differ from those of other *Synotaxus* species, but there are several apparent homologies in building behavior. The overall construction sequence differs from that of many other spiders in not being organized around a central portion or retreat. Instead, lines are added to one leading edge in a crochet-like fashion. Comparison with other *Synotaxus* species suggests how building behavior is organized within the spider.

RESUMEN. La tela y el proceso de construcción de la tela de *Synotaxus ecuadorensis* son complejas y altamente organizadas. La tela de esta especie difiere de las de otras especies de *Synotaxus*, pero el comportamiento de construcción muestra varias posibles homologías. La secuencia de pasos en la construcción difiere de muchas otras arañas en no estar organizada alrededor de un punto o area central. Al contrario, la araña agrega hilos al borde de la tela, en un proceso semejante a lo de la crochet. Se sugiere, a base de una comparición entre los comportamientos de las diferentes especies de *Synotaxus*, como esta organizada el comportamiento de construcción dentro de la araña.

Synotaxus is a small neotropical genus containing five described and at least one undescribed species (H. W. Levi, pers. comm.). A recent study suggests that this genus, which has traditionally been placed in the family Theridiidae, is part of a small group of genera (nearly all from New Zealand and Australia) that is the sister group of Nesticidae plus Theridiidae (Forster et al. 1990). The webs of two species, *S. turbinatus* Simon, and *Synotaxus* sp., include highly regular arrays of approximately vertical and horizontal sticky and non-sticky lines (Eberhard 1977). Webs are built as a series of approximately rectangular modules or "unit webs". Each unit begins with a pair of more or less parallel vertical, non-sticky lines. These are then joined by a series of more or less horizontal non-sticky lines, which are laid along with one to three zig-zag, sticky vertical lines in a complex series of events (Eberhard 1977).

Both the geometric design of the web and the construction behavior of the species of this study, *Synotaxus ecuadorensis* Exline, are simpler. The construction behavior is of special interest because it illustrates an overall building tactic (and thus a possible evolutionary route) which differs from that of many (perhaps most) other spiders, including those which make orbs (e. g., Foelix 1982; Eberhard 1990), those which make sheet webs, such as the theridiids *Latrodectus* spp. (Szlep 1965; Lamoral 1968), the psechrid *Psechrus* sp. (Eberhard 1987), and the pholcid *Modisimus* sp. (Eberhard 1992; Eberhard & Briceño 1985), and those which make other centrally organized webs such as *Titanoeca albomaculata* (Szlep 1966) and *Filistata* spp. (Comstock 1948; Eberhard 1987, 1988). Instead of returning repeatedly to a central point during construction, *S. ecuadorensis* adds to its web by moving back and forth along one edge, gradually extending it in a manner analogous to crocheting.

METHODS

Observations were made between 25 June and 3 July 1992 in the Reserva Natural La Planada (elev. 1800 m), 8 km S. of Chuconés, Nariño, Colombia, in an area classified as montane wet forest in the Holdridgean system (Espinal & Montenegro 1963). Webs were in grassy second growth and early secondary forest. Twelve webs of eight different spiders (four of which were adult females) were observed. Most of the construction of two of these webs (both of adult females) was observed using the white light of a headlamp. Web initiation appeared to be inhibited by illuminating the spider, but once construction had begun the spider was apparently undisturbed by bright light. The use of bright light, plus the fact that spiders moved relatively slowly and used stereotyped movements which were frequently

repeated, made it possible to understand and record their actions in detail.

Voucher specimens of the spiders observed (numbers 3638, 3645, 3646) and mature males are deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts 02138, USA.

RESULTS

Webs were built under long (>15 cm), more or less horizontal leaves. The upper portion of the web was a tangle of non-sticky lines attached to the underside of the leaf. The lines of the mesh were more closely spaced in the area where the spider rested during the day against the underside of the leaf. The spider's pale green color and its elongate abdomen, which it laid flat against the leaf, made it extremely cryptic. Egg sacs had thin walls with projecting processes, and the sphere of pale green eggs was plainly visible inside. The sacs (up to four per female) were suspended in the mesh under the leaf.

The approximately planar prey capture web, strung vertically below the mesh, varied to some extent (Fig. 1). The lateral edges of the capture web were formed by two long, more or less vertical, non-sticky "frame" lines. The interior portions contained more or less regularly spaced lines, most of which had many short (0.2–0.5 cm) segments of adhesive on them.

Initiation of capture web construction was not observed. Judging both by the lines present in the webs when first observed, and by the order in which subsequent lines were laid, it is probable that the first lines laid were the approximately vertical frame lines. One spider with only a mesh descended twice at the end of her dragline as if to begin construction early in the evening, but failed to contact a substrate below and climbed back up without making an attachment (and later abandoned the website).

Subsequent lines were added in a highly stereotyped order (Fig. 2). The spider began by attaching a dry line at the top of the capture web, usually near one edge. She then walked downward along the innermost line already present (this was the frame line in the first descent, and a line with adhesive segments in subsequent descents), attaching the non-sticky dragline she was laying periodically to the line along which she was walking (Fig. 2A). Immediately after each of these attachments, the spider backed up a short distance along the dragline and attached her dragline to it (Fig. 2A), thus making a short, more or less horizontal line (a "rung"), and then continued her descent. In one case the spider broke and replaced the distal portion of the frame line along which she was walking as she neared the bottom of the capture web.

After making the lowermost attachment to the line along which she was descending, the spider turned and began to climb the line she had just laid. She broke this line soon after she turned, and began reeling it up, replacing it with a new "sticky" line which consisted of a non-sticky line with evenly spaced short segments of sticky material. Each sticky segment was produced as both legs IV held the dragline and appeared to pull a short length from the spinnerets; the spider took one step forward with each leg IV (thus drawing out further silk), and then laid another sticky segment. Each time she reached a rung line, the spider broke it and performed a quick series of movements which I was unable to decipher, and then continued her upward climb. Judging by the pattern of lines when she was finished (Fig. 2B), probably the spider attached her dragline to the broken end of the rung line, paid out a short length of silk, and then attached her dragline to this line. A short segment of doubled line may have thus been produced, in a manner similar to the doubled lines laid during the descent (steps 2 and 3, and 4 and 5 in Fig. 2A). Each finished rung had a single spot of white near the middle, apparently corresponding to the broken end of the line to which the spider had attached her dragline.

In one web the spider alternated descents on the right and then the left side of the web. In another web she made several descents on one side (the larger of the two) before making any on the other. In both webs later lines with sticky material were progressively less vertical, as the spider filled in the central portion of the web (Fig. 2D). The final line was made following construction of the lowermost sticky line. The spider moved more or less directly upward through the middle of the capture web to the mesh above, laying a sticky line as she went. In one web the spider clearly broke all of the lines she encountered as she climbed, reattaching each to the sticky line she was laying. A short length of silk was paid out just before each reattachment, thus lowering the tension on these lines.

DISCUSSION

Although the prey capture webs of *S. ecuadorensis* are different from those of *S. turbinatus* and *S.* sp. (compare Figs. 1 and 2 with Fig. 3),

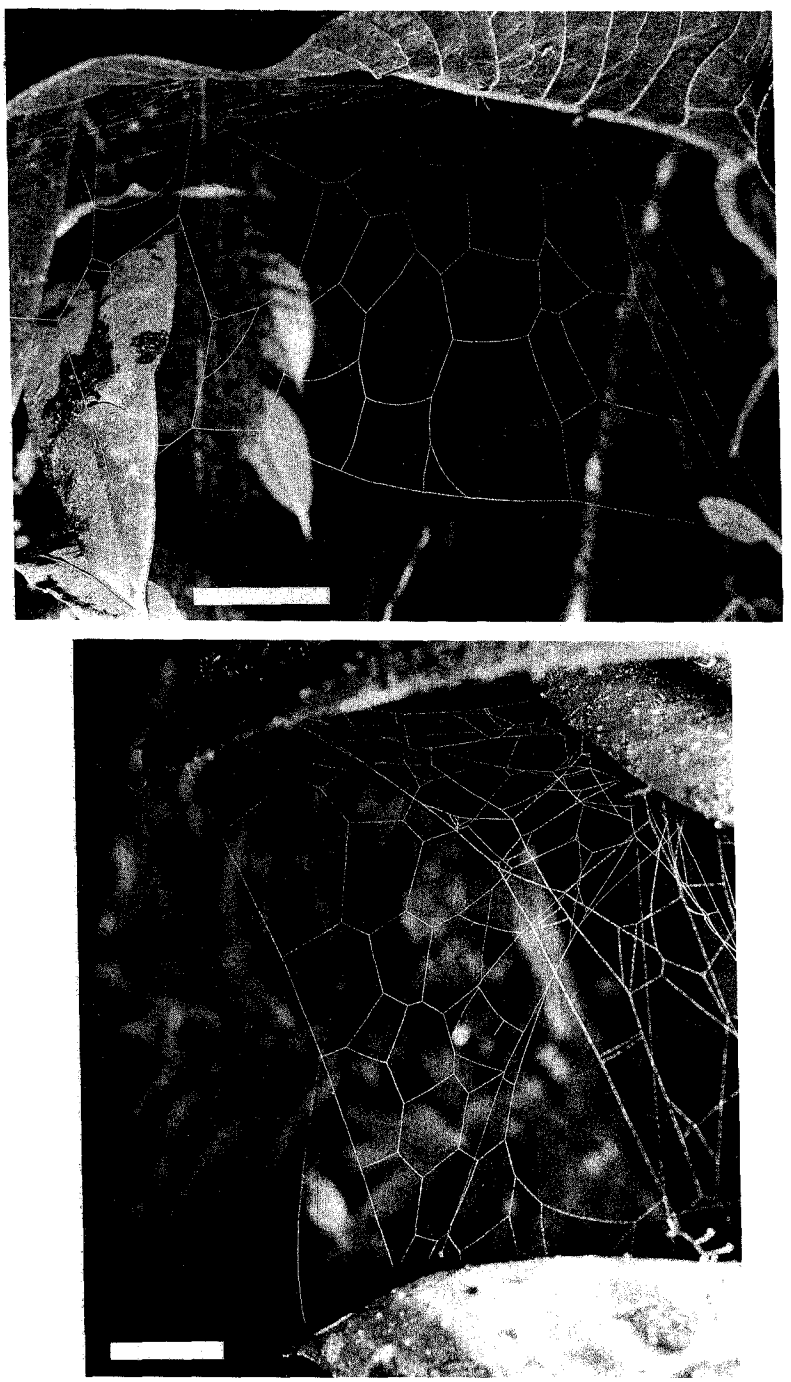

Figure 1.—Two newly-built capture webs of mature female *Synotaxus ecuadorensis* coated with cornstarch. The spider is just visible at the top of the upper web. In the lower web the lines at the right and the curved line from the tip of the leaf at the left are out of the plane of the capture web (scale lines = 5.0 and 6.0 cm for upper and lower webs).

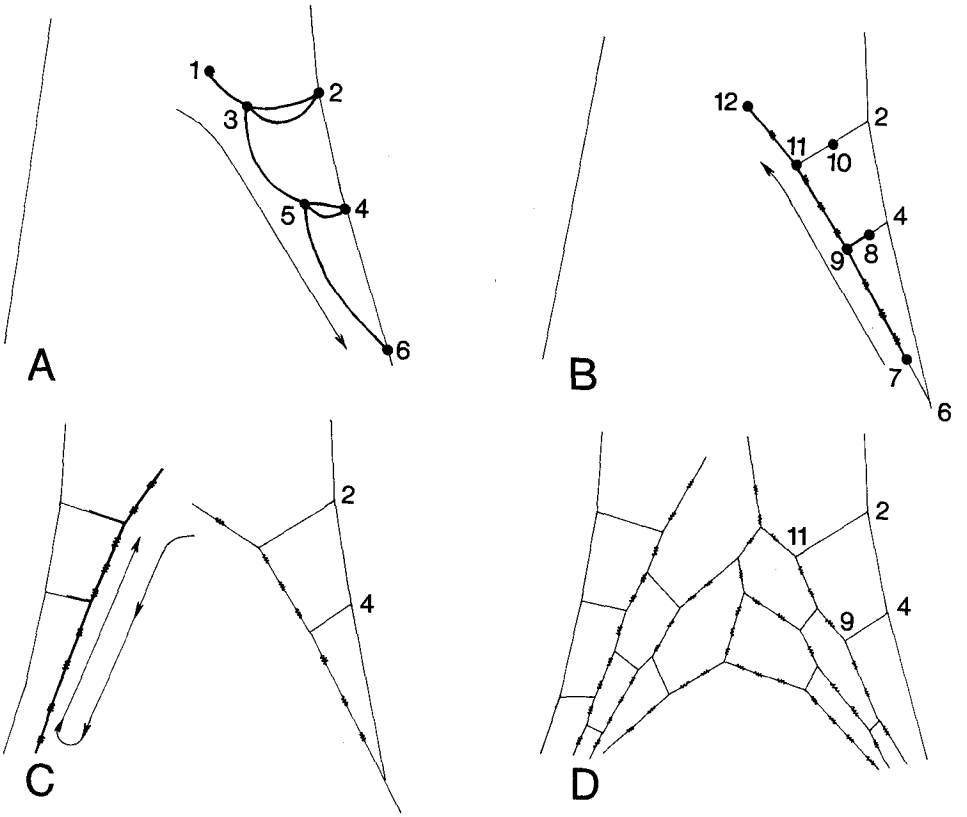

Figure 2.—Diagrammatic representation of the probable order of operations by *Synotaxus ecuadorensis* building a prey capture web. Thicker lines and large dots indicate the lines and attachments made during the period represented by each drawing; wiggly lines represent patches of adhesive; and numbers refer to the order of attachments. **A**. The spider starts from the mesh under the leaf along one of the two long non-sticky, more or less vertical lines that form the lateral borders of the web, laying a non-sticky dragline. Periodically she attaches the dragline to the frame (e. g., 2, 4), and backs up slightly and attaches to the line just laid (e. g., 3, 5) forming a "rung". She then continues downward to make a final attachment to the frame (e. g., 6). **B**. Turning back immediately, the spider breaks the line she has just laid, attaches her trail line to the broken end (7), and begins laying another line with sticky patches on it as she climbs back up along the line she just laid. She breaks each rung and attaches her dragline to the broken end (e. g., 8). Backing up slightly, she attaches to the line she just laid (e. g., 9) and continues upward, finally attaching the sticky line to the mesh near where she started (12). **C**. Subsequent lines are laid on the same or the opposite side of the web with a simIlar series of movements. **D**. Sticky lines laid later are progressively less vertical. The attachments 9 and 12 were deduced from the positions of lines in finished webs, while all others, and the breaking of lines at 7, 8 and 10 were confirmed by direct observations.

several details indicate that the prey capture web of *S. ecuadorensis* is homologous with a single "unit" of the web design of the others (Eberhard 1977) (Fig. 3). Both types of web are initiated with a pair of long, more or less vertical, straight, non-sticky lines which form their lateral margins. A complex sequence of behavior follows, in which construction of non-sticky and sticky lines alternate, with the sticky lines bearing widely spaced segments or dots of adhesive. One detail of this process in all three species is apparently unique to *Synotaxus* among all araneoid web builders studied to date: after attaching its dragline to another line, the spider backs up a short distance and makes another attachment to the line it just laid, then continues onward (e. g., Fig. 2 A, B). A further similarity is that sticky lines are laid as the spider climbs upward, each replacing a non-sticky line laid during an immediately preceding descent. Construction ends with placement of a central sticky line laid as the spider ascends. Lines already present are apparently

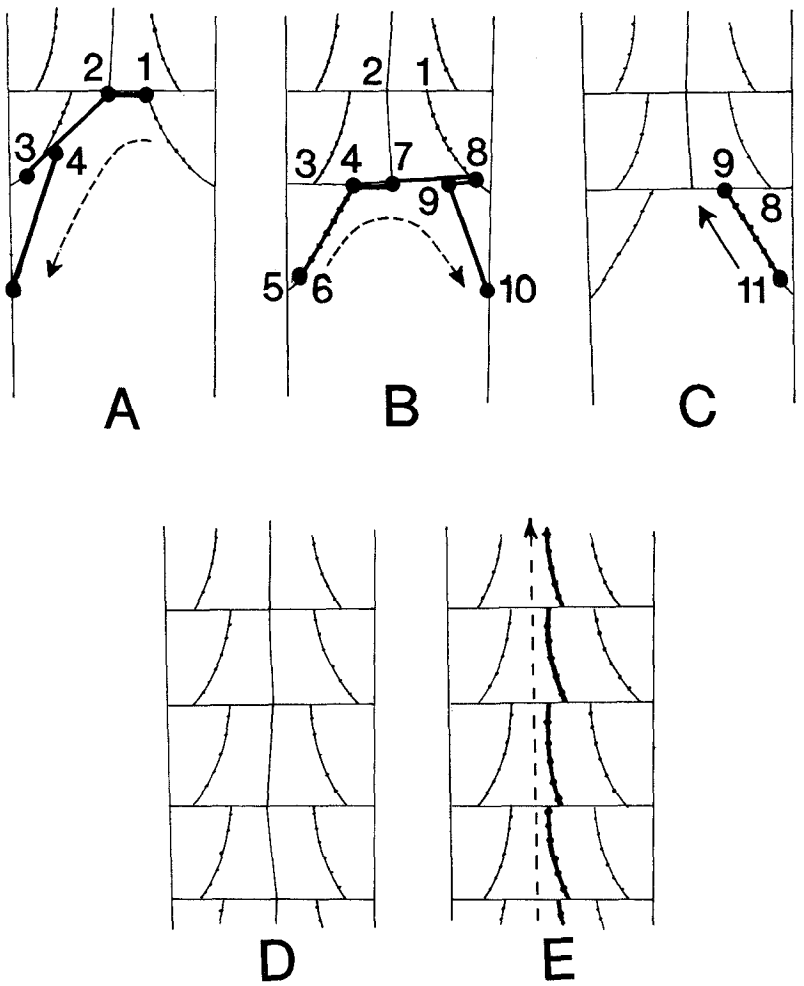

Figure 3.—Tentative order of operations in the construction of a unit web of *Synotaxus turbinatus* (after Eberhard 1977). The spider moves from side to side as she descends, laying both sticky and non-sticky lines (A, B, C). After reaching the bottom (D), she climbs up the middle of the web, replacing the non-sticky line with a sticky line (E).

broken and reattached to this central line. Both types of webs are vertical, more or less planar, and relatively fragile arrays that are rebuilt daily, and are located immediately below a more permanent mesh of non-sticky lines near the underside of a large leaf where the spider rests. These proposed homologies must remain tentative, however, until further data on *Synotaxus* and related genera become available. The apparent homology of the *S. ecuadorensis* web to a unit of the webs of other *Synotaxus* species indicates that the "units" of these species are not simply abstractions, but that web construction may be also organized in the spider's nervous system as units.

Differences between the webs and construction behavior of *S. ecuadorensis* and that of other *Synotaxus* are also substantial. They include the following: the web is constructed as a single unit, with only a single pair of vertical frame lines rather than as a series of modules; a long, uninterrupted non-sticky line is laid during each descent and is nearly completely removed during the ensuing ascent; placement of adhesive material is in short segments rather than single balls on the sticky lines; and there is no non-sticky "frame" line at the bottom of the web (also sometimes lacking in other *Synotaxus*).

The construction behavior of *S. ecuadorensis* is to my knowledge the clearest described ex-

ample in which a spider does not organize its activities around a central area. Instead, after establishing three sides of the planar web (the mesh above and the two lateral frames), the spider moves back and forth across the fourth side, gradually extending the web in a process analogous to crocheting. I have seen a similar process only one other spider (a species of the theridiid *Chrosiothes* which repairs holes in its sheet in this manner) (Eberhard, pers. obs.).

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