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Cues guiding placement of the first loop of the sticky spiral in orbs of *Micrathena duodecimspinosa* (Araneidae) and *Leucauge mariana* (Tetragnathidae)

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Summary

Several of the cues generally used by orb-weaving spiders to guide sticky spiral placement are missing when the spider lays the first loop of sticky spiral in an orb. This study combines behavioural observations and web measurements to suggest that two species of spiders use the distance between the outer loop of temporary spiral and the frame line to guide placement of the first loop. The correlation between these two variables occurred, however, only in a context in which spiders contacted the frame—when the outer loop of temporary spiral was near the frame. The correlation was absent when the temporary spiral–frame distance was large, and spiders generally failed to contact the frame line. The cue used to produce the correlation is thus probably sensed when the spider contacts the frame line while laying the first loop.

Introduction

Orb construction behaviour has been studied for more than 100 years (see reviews and summaries in McCook 1889; Hingston 1920; Peters 1939; Witt *et al*. 1968; Eberhard 1972, 1982; Vollrath 1992; Zschokke 1996; Kuntner *et al*. 2008; Blackledge *et al*. 2009). The cues that guide some of the aspects of orb construction, such as sticky spiral placement, are better understood in some respects than those that guide many other invertebrate behaviour patterns. Every time an orb-weaving spider encounters a radius while laying sticky spiral, she attaches the sticky line to the radius, and then moves on to the next radius. At least six different cues have been shown by experiments and direct observations to influence a spider's decision regarding where on the radius to attach the sticky spiral line. These cues include: the amount of silk in the spider's glands, the lengths of the spider's legs, her position in the web (near or far from the hub, above or below the hub), and two cues from sticky lines already present in the web that are sensed anew on each radius—the site where the preceding loop of sticky line was attached to the radius, and the distance from the outer loop of temporary spiral to this inner loop of sticky spiral (Hingston 1920; Peters 1939; LeGuelte 1966; Witt *et al*. 1968; Eberhard 1972, 1988a; Vollrath 1987; Eberhard & Hesselberg in press). In at least one species the time of day may also influence sticky spiral spacing (Sandoval 1994), and evidence from correlations suggests additional possible cues (Herberstein & Tso 2011). This seems an unusually large array of stimuli to affect a single decision by an invertebrate, but perhaps it is not atypical, and due only to the relative ease of studying behavioural decisions during sticky spiral construction (Eberhard 1969; Zschokke & Vollrath 1995a).

Decisions that determine the placement of the first, outermost loop of sticky spiral differ from those concerning all subsequent loops, because neither of the two cues from previous sticky lines is available to the spider. These decisions are especially important in determining how well the orb functions, because they determine the size of the area where prey can be trapped, and the area which the spider must subsequently cover with her limited supply of sticky silk (Eberhard 1988a).

Several previous studies have indicated that the placement of the first loop of sticky spiral is guided instead by the outer loop of temporary spiral, which the spider is thought to use like a handrail (Zschokke 1993). Direct behavioural observations show that, throughout Araneidae, the spider maintains contact with the temporary spiral during the entire time she lays the first loop of sticky spiral (Eberhard 1982). In addition, experimental modifications of the site of the outer loop of temporary spiral in the araneid *Araneus diadematus* and the uloborid *Uloborus diversus* produced corresponding displacements of the first sticky spiral loop (Peters 1970; Eberhard 1972; Zschokke 1993).

While this handrail function seems well established in at least some orbweavers, closer examination shows that the situation is more complicated. In the first place, there are several families of orbweavers in which the spider does not maintain contact with the temporary spiral while laying the first sticky loop. In Tetragnathidae and Theridiosomatidae, the spider consistently moves farther outward along many radii, beyond where she can maintain contact with the outer temporary spiral loop when she attaches the first sticky spiral loop (Eberhard 1982). In other orbweaver families, including Anapidae, Symphytognathidae, and Mysmenidae, the spider does not even build a temporary spiral. She returns to the hub after each sticky spiral attachment, then moves out the next radius to make the next attachment.

In addition, even in araneids in which the spider maintains contact with the temporary spiral, the distance between the outer loop of temporary spiral and the first loop of sticky spiral varies substantially (see Fig. 1), rather than being constant, as implied by the handrail analogy. Thus, in none of these groups does placement of the first spiral loop involve simply maintaining a constant distance from the outer temporary spiral loop by holding onto it.

Nor do frame lines appear to consistently guide placement of the first loop. On at least some radii, spiders in all of these families stop short of the frame line (deduced from direct observations, and web photos: Platnick & Shadab 1979; Platnick & Forster 1989; Coddington 1986a,b; Eberhard 1987, 1988a, 2007; Lopardo *et al*. 2011). In *U. diversus* and *U. walckenaerius*, in contrast, the first loop of sticky spiral is laid on top of the frame line in some parts of the orb (Eberhard 1972, Zschokke & Vollrath 1995b).

In summary, there are still questions concerning the cues that guide placement of the first loop of sticky spiral in orb webs. This paper combines descriptions of details of sticky spiral construction behaviour and correlations in the intact webs to suggest cues that guide placement of the first loop in an araneid and a tetragnathid spider in placing the first loop.

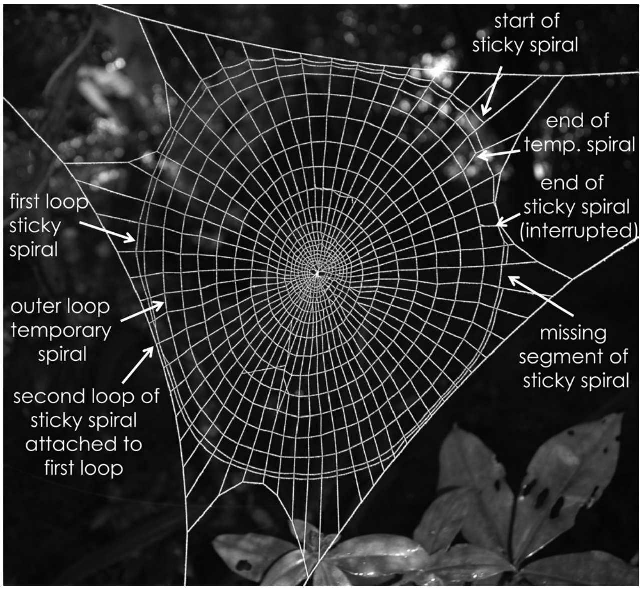

Fig. 1: *M. duodecimspinosa* web in which construction was interrupted when two loops of sticky spiral had been completed, before any temporary spiral lines had been broken. The distance of the outer (first) loop of sticky spiral from the last (outer) loop of temporary spiral varies substantially. The spider built the sticky spiral in a counterclockwise direction (after laying a clockwise temporary spiral).

Methods

The behaviour of adult female spiders was observed and video-taped, and their webs were coated with white powder and photographed near San Antonio de Escazu, San José Province, Costa Rica (1325 m a.s.l.). Webs of *Micrathena duodecimspinosa* (Araneidae) were photographed in the field (angles with horizontal varied between 60° and 85°). Those of *Leucauge mariana* (Tetragnathidae) were built in horizontal, approximately 50 cm diameter wire hoops hung in an outdoor screen cage. Only a single web was photographed for each spider.

Web construction was interrupted after the first few loops of sticky spiral had been laid, before any segments of temporary spiral had been broken. It was thus possible to measure in the photographs the distance along each radius between the outer loop of the temporary spiral and the frame line (TS-F distance in Fig. 2) that the spider encountered while laying the first loop of sticky spiral. In addition, her decision regarding how far beyond the outer loop of temporary spiral to attach the first loop of sticky spiral (TS-L1 distance in Fig. 2) could be measured. To compare the webs of different spiders, both TS-F and TS-L1 distances in each web were standardized by dividing them by the median TS-F and TS-L1 distances for that web.

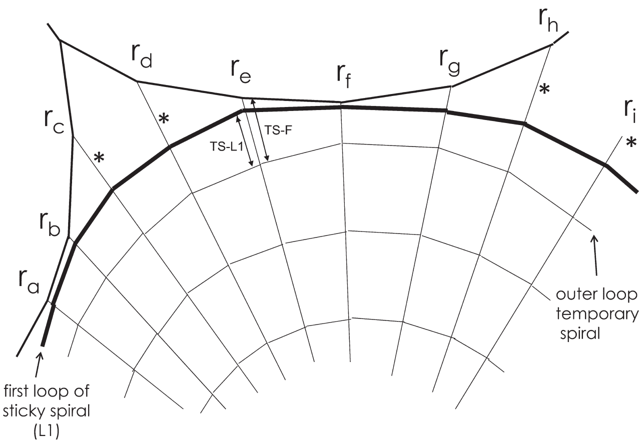

Fig. 2: Schematic drawing of a partially finished orb (sticky line is thicker). On longer radii (*), the TS-F distance was larger, and the spider did not contact the frame line during construction of the first loop of sticky spiral. On shorter radii, the TS-F distance was smaller, and the spider contacted the frame while laying the first sticky spiral loop.

Voucher specimens of these species have been placed in the Museum of Comparative Zoology in Cambridge, MA and the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica in Ciudad Universitaria, Costa Rica.

Results

The construction behaviour of the two species resembled that of other confamilial species. As in other araneids, *M. duodecimspinosa* remained in contact with the outer loop of temporary spiral during construction of the entire first loop of sticky spiral. The spider was never out of contact with the temporary spiral while she built the outermost sticky spiral loop, and she used the outer loop of the temporary spiral as a bridge as she moved from one radius to the next. When the radius was relatively short and the TS-F distance was short (ra, rb, re, rf and rg in Fig. 2), she also contacted the frame line while holding the temporary spiral. She did not contact the frame, however, when the TS-F distance was more than approximately the maximum distance between loops of temporary spiral (radii with * in Fig. 2). Similarly, *L. mariana* behaved as a typical tetragnathid, and did not always maintain contact with the temporary spiral. On many radii, the spider moved out of contact with the temporary spiral when she attached the first loop of sticky line. On shorter radii, she contacted the frame line, while on longer radii she attached the sticky spiral without having touched the frame.

In summary, behavioural observations showed that in both species the site of the frame line was only available as a cue through direct contact during construction of the first loop of sticky spiral when the spider was on shorter radii, where the TS-F distance was relatively low. Information regarding the site of the outer loop of temporary spiral may have been available in all cases, either through direct contact or path integration involving the distance moved away from the temporary spiral along the radius.

Measurements of photographs of webs of both *M. duodecimspinosa* and *L. mariana* showed that, under some conditions but not others, the TS-F distance correlated with the placement of the first loop (the TS-L1 distance in Fig. 2). There was a positive correlation between the TS-F distance and the TS-L1 loop distance on radii in which the TS-F distance was relatively small (Fig. 3). However, when the TS-F distance was relatively large, there was no relation between the TS-F distance and the site where the first loop of sticky spiral was attached (Fig. 3).

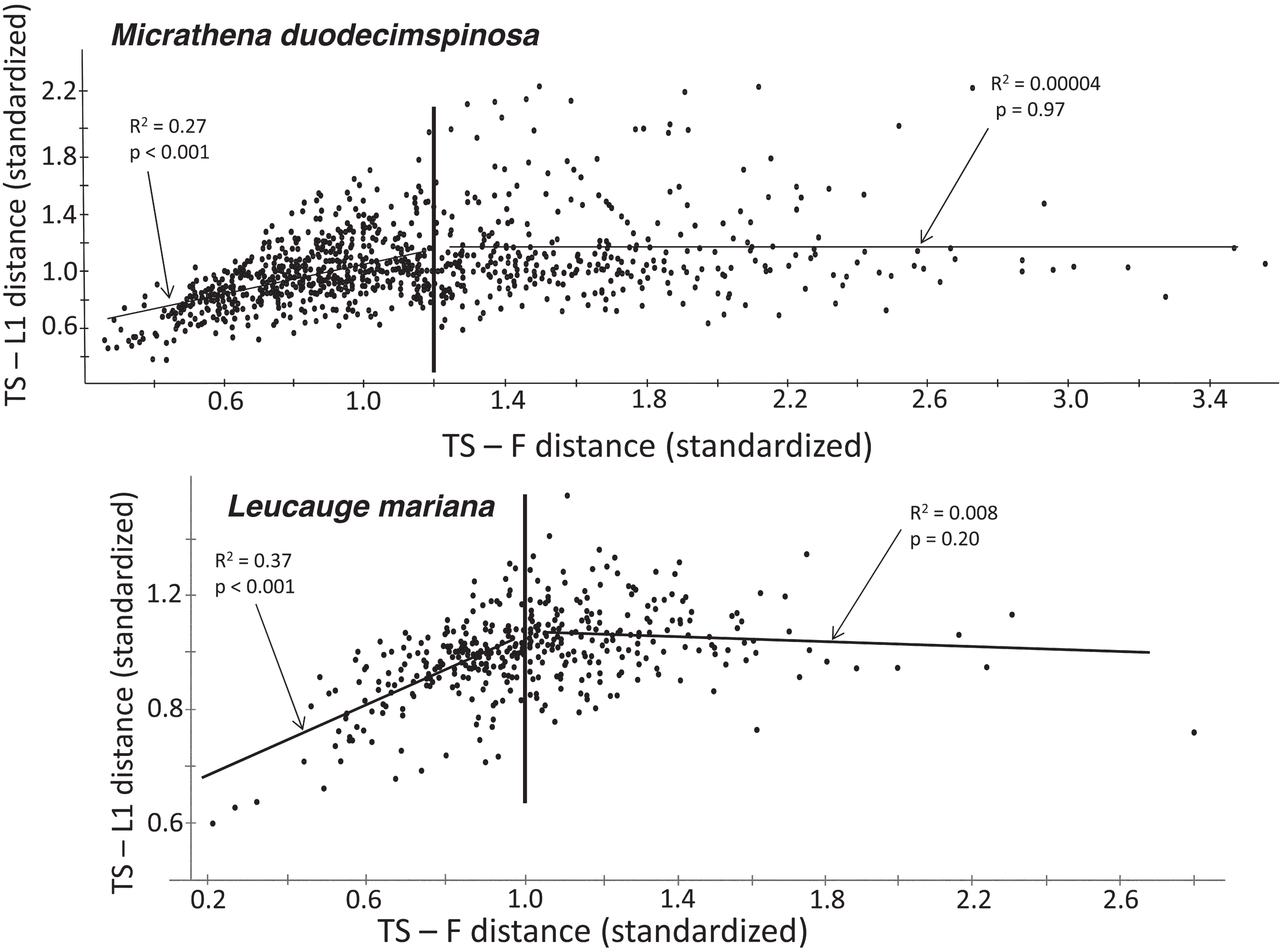

Fig. 3: The relations between the distance between the TS-F distance and the distance from the outer loop of temporary spiral at which the first loop of sticky spiral was attached (TS-L1 distance) in 19 webs of *M. duodecimspinosa* and 18 webs of *L. mariana*. When the data were split according to the relative TS-F distance, there was a significant positive relationship in each species with smaller TS-F values (lines on left) but no significant relationship with larger TS-F values (lines on right).

Discussion

The trends in the placement of the first loop of sticky spiral (Fig. 3) are probably associated with behavioural details during its construction. Presumably, when the spider could sense the position of the frame by touching it (when the TS-F distance was small), she used information on the TS-F distance to produce the correlation between the TS-L1 distance and the TS-F distance (Fig. 3). On the other hand, when the spider did not contact the frame (when the TS-F distance was large), the attachment of the first loop of sticky spiral tended to be independent of the TS-F distance (Fig. 3). Careful web measurements were not performed on the same webs where behavioural observations were made, however, so the association between the behavioural detail and the placement of the first loop of sticky spiral is only speculative for intermediate values of TS-F. It is certain to have occurred, however, at the two ends of the distribution of TS-F: at low TS-F values, spiders consistently contacted the frame, and at high TS-F values they consistently did not contact the frame.

By reducing the TS-L1 distance when the TS-F distance was smaller, the spider may benefit from keeping the sticky line separate from the frame line and thus preserve its high extensibility, which makes it a more effective trap (Witt *et al*. 1968). Also, combined with subsequent positive correlations between the sticky spiral spacing and the distance between the temporary spiral and the inner loop of sticky spiral (Eberhard & Hesselberg in press), she provides a smoother inner profile of the sticky spiral as it is built, and avoids the more irregular spacing that results from turnbacks (Eberhard 1969).

Presumably, when the spider did not contact the frame, she instead used the site of the outer loop of TS as a reference point (as in the handrail analogy. The large amount of scatter in this context (Fig 3c,f) suggests, however, that other factors had important effects. Some L1-F values in orbs built by *L. mariana* and the related *L. argyra* in very confined spaces even become negative, with the outer loop placed beyond the frame lines in some portions of the orb (Barrantes & Eberhard in press).

The mechanism by which spiders measured TS-L1 distances may have differed in the two species. In *M. duodecimspinosa* the distance was presumably measured using the spider's own body and legs (e.g. the degree to which the legs holding the outer loop of temporary spiral were extended). In *L. mariana*, the measurements made when the spider moved beyond the temporary spiral and lost contact with it were probably made instead by ideothetic sensing of the distance the spider had moved along the radius.

Presumably, the spiders in the other orb-weaving families in which contact with the outer loop of temporary spiral is routinely lost, or which do not build temporary spirals, also use ideothetic cues to lay the first loop of sticky spiral. This proposed use of distance measurements is in accord with demonstrations that distance measurements are used to guide orb construction in other contexts, including temporary spiral spacing in *L. mariana* (Eberhard 1988b), and sticky spiral spacing in *L. mariana* and *M. duodecimspinosa* (Eberhard & Hesselberg in press); the TS-L1 distance also provided useful cues to obtain spider-like web designs in simulations of temporary spiral and sticky spiral construction by the araneid *Araneus diadematus* (Gotts & Vollrath 1991; Krink & Vollrath 1999).

The temporary spiral probably has three different functions in the species of this study: as a bridge used by the spider to move between radii; as a support that ties the radii together so that their positions relative to each other are not too severely distorted by the spider's weight during construction (perhaps especially important in more nearly vertical orbs); and as a guide for placement of both the first and subsequent loops of sticky lines in a regular array that takes advantage of the space outlined by the frame lines of the orb.

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