

SHORT COMMUNICATION

Araneus expletus (Araneae, Araneidae): another stabilimentum that does not function to attract prey

William G. Eberhard: Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica. E-mail: william.eberhard@gmail.com

Abstract. Juvenile *Araneus expletus* often place a visually conspicuous, disc-like white silk stabilimentum on one side of the retreat where the spider rests during the day away from its orb. Placement of the stabilimentum at this site rules out a prey attraction function and argues instead that it may function to defend the spider from visually orienting enemies.

Keywords: Orb weaver, orb web, silk, defense, camouflage

The function of the visually conspicuous white silk “decorations” or “stabilimenta” that many orb weavers add to their webs has a long history of controversy (summary, Herberstein et al. 2000). Silk stabilimenta are described by Herberstein et al. (2000) as “conspicuous silk designs on the surface of the web” (p.650). They have various forms, including straight and curved lines, tufts, and more or less circular, flat discs of white silk (Herberstein et al. 2000). All known discs and most other silk stabilimenta are placed at or near the hub of the orb where the spider rests during the day. Disc stabilimenta occur in the webs of the araneids *Argiope argentata* (Fabricius 1775) (Nentwig & Heimer 1987) and *Allo cyclosa bifurca* (McCook 1887) (Eberhard 2003), and the uloborid genera *Philoponella*, *Uloborus*, and *Zosis* (Lubin 1986).

Herberstein et al. (2000) concluded that silk stabilimenta evolved convergently at least nine times among orb weaving spiders. They argued that the prey attraction (“foraging”) hypothesis for the function of stabilimenta “has received most supporting evidence.” They noted that the independent derivations of stabilimenta may imply different functions, although this is surely not a logical necessity (Eberhard 2003). Blackledge & Wenzel (2001) argued, in contrast, that silk stabilimenta may function in roles similar to retreats in reducing predation pressure. Subsequent reports have added two additional apparently independent origins, in the genera *Molinaranea* (Levi 2001) and *Metepeira* (Piel 2001). This note presents still another apparent convergence, in *Araneus expletus* (O. Pickard-Cambridge 1889). The stabilimenta of this species are especially interesting because the site where they are placed in the spider’s web rules out the prey attraction hypothesis.

The sites in the web where the spider rests during the day and where the stabilimentum is placed can have important implications for the possible functions of stabilimenta. One general pattern in the distribution of stabilimenta among orb weavers is that among the many species of orb weavers in which the spider rests during the day at the edge of the web rather than the hub, not a single species builds a stabilimentum (Eberhard 2003). This pattern argues against a prey attraction function, because if the function of stabilimenta is to attract prey to the web, there is no obvious reason why stabilimenta should be lacking in these webs. If anything, these spiders would seem to have more rather than less need to attract prey to the web, because their attacks are necessarily slower; they must first move from the retreat to the hub before going to the prey. This association between resting away from the hub and lack of stabilimenta is, on the other hand, easily explained by the camouflage hypothesis.

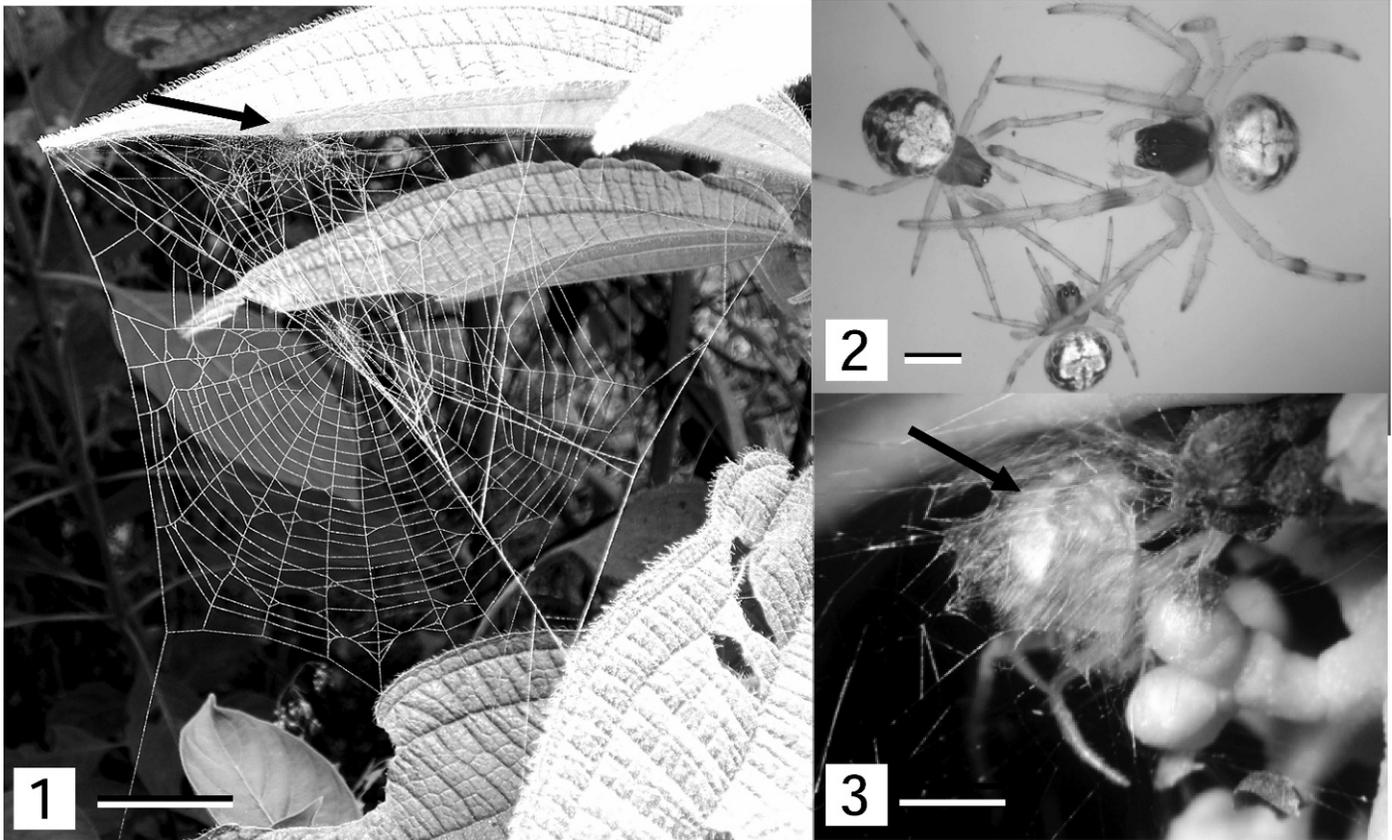
This note shows that juveniles of *A. expletus* constitute the first exception to this pattern: these spiders build disc stabilimenta, despite

the fact that they consistently rest off of the web in a retreat during the day. This exception supports the camouflage argument, however, because these spiders place their stabilimenta on the walls of their retreats, rather than on their orbs.

Araneus expletus is an orb-weaving spider that ranges from Mexico to Panama in second growth at intermediate elevations (Levi 1991). Previous observations (W. Eberhard, unpublished) indicate that in the Valle Central of Costa Rica *A. expletus* is relatively common and apparently univoltine, with young instars appearing early in the wet season (late April or early May); mature females are present late in the wet season and early in the dry season (Dec–March). Spiders of all ages build orb webs with a silk retreat in a small tangle of lines away from the orb (Fig. 1); the retreat is connected to the hub with a signal line that the spider holds with one leg. The spider rests in the retreat during the day, and rushes to the hub along the signal line to attack prey entangled in the orb. Adults and older juveniles often fold or roll green leaves to form a more or less conical retreat, while younger juveniles generally fold leaves only partially or not at all. The lines in the orbs of adults are distinctly yellow in color, and are faintly yellow in those of young juveniles. The silk in the dense walls of the retreats of older juveniles and adults is white. The orb is rebuilt in the early morning more or less daily, and is apparently used mostly during the day. Only one of 30 young juveniles checked between 8–10 PM had an apparently newly built orb; the others had removed the orb, and there were only a few radial lines in the area where the orb had been. The eggs are not laid in the retreat, and egg sacs have not been found.

Young juvenile spiders (estimated to be second and third instars) were observed near San Antonio de Escazú, San José Province, Costa Rica (elev. 1320–1400 m; ~10°20'N, 84°15'W) during the second half of May 2007. They were identified as *A. expletus* on the basis of color patterns (a distinctive central white patch and lateral brown on the anterior dorsum of the abdomen) (Fig. 2), their relative abundance, their size and the season when they were encountered, the early second growth habitat in which they occurred, the green leaves and stems to which their webs and retreats were attached (only one of 53 had a retreat in a curled dry leaf), and their web design (a more or less vertical orb with a hub that lacked a central hole and a retreat away from the orb) (Fig. 1). More than 20 years’ field experience at this site leaves little doubt about this species identification. Voucher specimens have been deposited in the Museo de Zoología of the Universidad de Costa Rica.

Of 53 young juveniles (maximum width cephalothorax ranged from 0.80 to 1.38 mm), 51% had a patch of bright white silk on the wall of the retreat; in no case was there any white patch on the orb itself (all spiders were checked in the morning, and had orbs). These patches fit



Figures 1–3.—Orb weaver *Araneus expletus* and its web: 1. Orb and retreat of a juvenile *A. expletus*; the arrow indicates the spider, which was resting on the underside of a leaf near its lateral edge. A disk stabilimentum was on the near wall of the retreat (the retreat is nearer to the viewer than the orb). Scale line = 3 cm. 2. Juvenile *A. expletus* illustrating their color patterns. Scale line = 1 mm. 3. Spider's abdomen (arrow) is obscured by stabilimentum, while its legs, which extend beyond the stabilimentum, are easily visible through the wall of the retreat. Scale line = 1 mm.

the definitions of silk stabilimenta of other orb weavers (Herberstein et al. 2000; Blackledge & Wenzel 2001) in being visually conspicuous white objects composed of a dense mat of many fine white silk lines that were apparently added to another structure (the retreat wall) (Figs. 3, 6–8). The retreat wall was thimble-shaped or conical, and some were formed when the spider pulled the edges of a leaf partly together with silk lines (Figs. 4, 6). When the leaf was not bent (as in Figs. 1, 5), the retreat consisted of an approximately conical wall of non-sticky lines, in some cases with recognizably radial and spiral orientations that resembled the hub of an orb (Fig. 5). The stabilimentum lines ran in many directions, were attached to the retreat lines (Figs. 7, 8), rather than to the leaf (Fig. 4), and occurred on retreats in which the leaf was not curled, so they did not have the mechanical function of applying tension to the leaf edges. The stabilimentum lines were whiter than the lines in the wall of the retreat, and their density was great enough to largely obscure the outline of the spider from view when it was in the retreat (Figs. 6–8). In contrast, even relatively thick retreat walls of the lines that were used to curl the leaf were relatively transparent, and left the spider more visible (compare Figs. 3, 4 and 6).

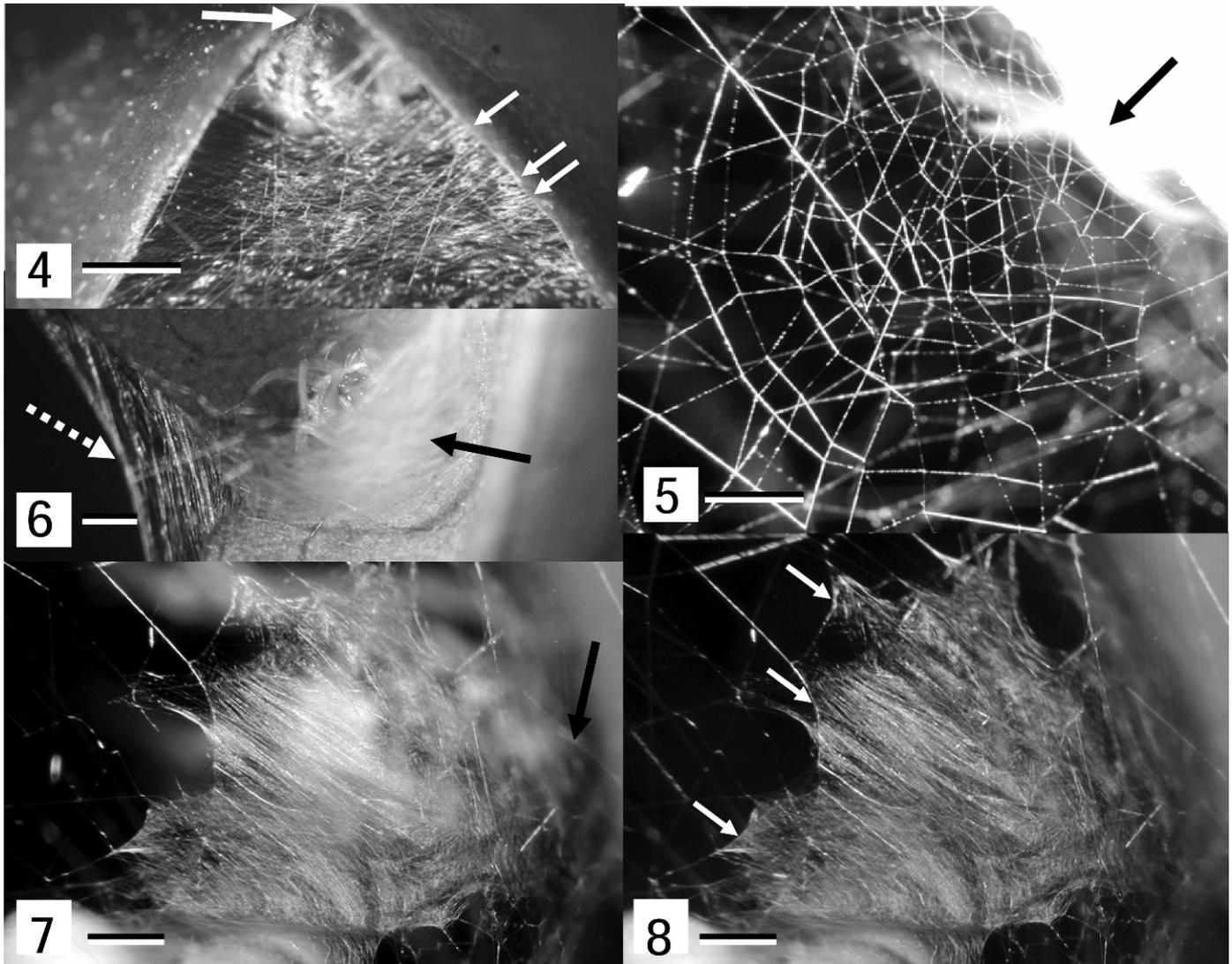
Retreats of young juveniles were found under the leaves of at least six families of plants, and the leaf was at least partly folded by the spider in 88.7% of the retreats. Of the 27 stabilimenta, 48.2% were on the wall of lines that folded the leaf, 40.7% were on the retreat wall opposite the lines that folded the leaf (Fig. 6), and 11.1% were on the wall of a retreat under an unfolded leaf (Figs. 1, 7, 8).

The fact that the silk stabilimenta of *A. expletus* juveniles are placed on their retreats demonstrates that these stabilimenta do not function

to attract prey, because the structure that captures prey is the orb, not the retreat, and the retreat was always sited away from the orb (Fig. 1). The possibility that the stabilimentum functions to camouflage or hide the spider as it rests in its retreat from visually orienting enemies is supported by the placement of the stabilimentum near the spider's resting place in the innermost portion of the retreat and on retreat walls that were relatively exposed (Figs. 1, 6–8), and by the effectiveness with which the stabilimenta obscured the outlines of the spiders (Figs. 6–8). One cannot rule out, however, the possibility that stabilimenta in this species function as physical barriers to protect the spider from predators or parasites.

These arguments are of course based on correlations rather than experiments. Data from experimental manipulations, however, do not necessarily provide more reliable information. In fact, for hypotheses such as camouflage and prey attraction, that necessarily involve so many different possible predators, parasites, and prey in a variety of habitats, experiments that achieve appropriate balances in quantifying different effects, and whose interpretations are not open to other criticisms (Eberhard 1990; Herberstein et al. 2000; Craig et al. 2001) are very difficult if not impossible to design (Eberhard 2003). On the other hand, some correlations (e.g., stabilimenta on webs or parts of webs that do not function to capture prey) can provide powerful reasons to reject particular hypotheses.

For those of us who are counting, this makes four different spider genera with independently derived silk stabilimenta in which the prey attraction hypothesis is strongly contradicted: *Philoponella* (Eberhard 2006); *Gasteracantha* (Jaffé et al. 2006; Eberhard 2006); *Alloctylosa* (Eberhard 2003); and now *A. expletus*.



Figures 4–8.—Orb weaver *Araneus expletus* and its web: 4. The thick wall of lines that folded a leaf into a cone and that lacks a stabilimentum does not obscure the abdomen of the spider resting inside (large arrow). In places where the lighting and focus on the lines are favorable, it can be seen that the numerous fine lines were all attached to the edges of the leaf (small arrows). Scale line = 1 mm. 5. Lateral wall of a retreat without a stabilimentum in which the leaf was only slightly folded, illustrating a hub-like pattern of lines; arrow indicates the spider (out of focus) in the retreat. Scale line = 0.5 mm. 6. A spider that faces outward from a folded leaf retreat is partially obscured by the retreat wall (black arrow) that has a stabilimentum (out of focus). The strong lines that bent the leaf into a cone (dotted white arrow) are on the opposite side of the retreat. Scale line = 1 mm. 7. Inner end of a retreat that is largely covered with a stabilimentum; the spider, resting in the retreat facing away from the camera, is largely obscured (black arrow indicates posterior tip of the spider's abdomen) (contrast with the relatively transparent retreat wall that lacks a stabilimentum in Fig. 4, and the wall beyond the stabilimentum in Fig. 3). 8. The same retreat as in Fig. 6 but without the spider. The similarity with Fig. 6 illustrates how well the stabilimentum hid the spider in Fig. 6. The fine white lines of the stabilimentum are attached to the tangle of lines that form the retreat wall (small white arrows). Scale lines in 6 and 7 = 0.5 mm.

ACKNOWLEDGMENTS

I thank Jonathan Coddington and Gail Stratton for useful comments on the manuscript, and the Smithsonian Tropical Research Institute and the Universidad de Costa Rica for financial support.

LITERATURE CITED

- Blackledge, T.A. & J.W. Wenzel. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasps. *Behaviour* 138:155–171.
- Craig, C.L., S.G. Wolf, J.L.D. Davis, M.E. Hauber & J.L. Maas. 2001. Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. *Evolution* 55:986–993.
- Eberhard, W.G. 2003. Substitution of silk stabilimenta for egg sacs by *Alloctyclosa bifurca* (Araneae: Araneidae) suggests that silk stabilimenta function as camouflage devices. *Behaviour* 140:847–868.
- Eberhard, W.G. 2006. Stabilimentum of *Philoponella vicina* (Araneae: Uloboridae) and *Gasteracantha cancriformis* (Araneae: Araneidae): evidence against a prey attractant function. *Biotropica* 39:216–220.
- Eberhard, W.G. 1990. Function and phylogeny of spider webs. *Annual Review of Ecology and Systematics* 21:341–372.
- Herberstein, M., C.L. Craig, J.A. Coddington & M.A. Elgar. 2000. The functional significance of silk decorations of orb-web spiders:

- a critical review of the empirical evidence. *Biological Reviews* 75:649–669.
- Jaffé, R., W. Eberhard, C. De Angelo, D. Eusse, A. Gutierrez, S. Quijas, A. Rodríguez & M. Rodríguez. 2006. Caution, webs in the way! Possible functions of stabilimenta in *Gasteracantha cancriformis* (Araneae: Araneidae). *Journal of Arachnology* 34: 448–455.
- Levi, H.W. 1991. The neotropical and Mexican species of the orb-weaver genera *Araneus*, *Dubiepeira*, and *Aculepeira* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 152:167–315.
- Levi, H.W. 2001. The orbweavers of the genera *Molinaranea* and *Nicoepeira*, a new species of *Parawixia*, and comments on orb weavers of temperate South America (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 155:445–475.
- Lubin, Y.D. 1986. Web building and prey capture in the Uloboridae. Pp. 132–171. *In Spiders: Webs, Behavior, and Evolution.* (W.A. Shear, ed.). Stanford University Press, Stanford California.
- Nentwig, W. & Heimer, S. 1987. Ecological aspects of spider webs. Pp. 211–225. *In Ecophysiology of Spiders.* (W. Nentwig, ed.). Springer Verlag, Berlin.
- Piel, W.H. 2001. The systematics of neotropical orb-weaving spiders in the genus *Metepeira* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 157:1–92.

Manuscript received 31 May 2007, revised 7 January 2008.