SUBSTITUTION OF SILK STABILIMENTA FOR EGG SACS BY ALLOCYCLOSA BIFURCA (ARANEAE: ARANEIDAE) SUGGESTS THAT SILK STABILIMENTA FUNCTION AS CAMOUFLAGE DEVICES

by

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Summary
The matching form and orientation of egg sacs and spiders, the match between egg sac color and that of the spider, ontogenetic changes in spider coloration that occur when egg sacs begin to be produced, differences in the positions of the spiders’ legs during the day and at night, and coordinated changes in spider and egg sac colors in different populations all indicated that the egg sac and detritus stabilimenta near the hub function as camouflage in Allocyclosa bifurca. Silk stabilimentum construction was induced by experimental removal of egg sac stabilimenta, and was inhibited by addition of egg sacs. This implies that silk stabilimenta also function as camouflage devices.

Introduction
The name stabilimentum long has been used, in its widest sense, to include structures of silk, egg sacs, and plant and animal detritus which are placed at or near the hubs of orb webs (Hingston, 1927; Marson, 1947). Detritus and egg sac stabilimenta are generally thought to camouflage the spider

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(e.g. Marson, 1947; Comstock, 1967; Marples, 1969; Robinson & Robinson, 1970; Rovner, 1976; Edmunds, 1986; Neet, 1990), although evidence seems to be limited to evaluations based on human vision. The function of silk stabilimenta has been more controversial. Most recent discussions have specifically excluded all forms of stabilimenta except those made of silk (e.g. Blackledge, 1998a, b; Herberstein et al., 2000; Seah & Li, 2001; Bruce et al., 2001). This was a reasonable tactic, since it is possible that the term stabilimentum is a linguistic trap, with a single name being applied to traits that have entirely different functions (Robinson & Robinson, 1970; Neet, 1990). This paper presents data, however, which indicate that in one group of orb-weavers the three different types of stabilimentum have the same function.

Despite earlier, more general discussions which included many different genera, most of the recent debate concerning the function of stabilimenta in spiders webs has focused on the genus *Argiope* (Edmunds, 1986; Craig & Bernard, 1990; Craig, 1991; Schoener & Spiller, 1992; Kerr, 1993; Tso, 1996; Blackledge, 1998a, b; Blackledge & Wenzel, 1999; Craig et al., 2001; Seah & Li, 2001; Bruce et al., 2001 — see review of Herberstein et al., 2000). Stabilimenta have apparently evolved independently in several groups of orb weavers (Herberstein et al., 2000), and are still being discovered in additional genera (e.g. *Molinaranea* — Levi, 2001; *Metepeira* — Piel, 2001), so comparative studies may help improve understanding.

In the monotypic genus *Allocyclosa* and the large, closely related genus *Cyclosa* (in which *Allocyclosa* was formerly included, Levi, 1999), detritus, egg sac, and silk stabilimenta have long been known (Wiehle, 1927, 1928, 1929; Nielsen, 1931; Marples & Marples, 1937; Marson, 1947; Kaston, 1948; Comstock, 1967; Marples, 1969; Robinson & Robinson, 1970; Rovner, 1976; Shinkai & Takaji, 1984; Neet, 1990; Tso, 1998; McClintock & Dodson, 1999). The evolutionary origin of the stabilimenta made by spiders in these two genera is apparently independent of that of stabilimenta made by other araneids (Herberstein et al., 2000). Previous descriptions of the orbs of *A. bifurca* (McCook), a species which ranges from the southern United States to Panama (Levi, 1999), have mentioned vertical strings of egg sacs and detritus, which were said to appear to camouflage the spider at the hub (Comstock, 1967; Levi, 1999). The female actively defends her egg sacs (Eberhard, in prep.).

Little has been published on the functional significance of stabilimenta in *Cyclosa* and *Allocyclosa*, other than repeated mention that egg sac and
detritus stabilimenta make the spider difficult for the human eye to see (Marson, 1947; Comstock, 1967; Marples, 1969; Robinson & Robinson, 1970; Rovner, 1976; Neet, 1990; Levi, 1999; McClintock & Dodson, 1999). Such evaluations of function are somewhat risky, however, given the differences in human vision and that of other animals such as birds, insects and salticid spiders that may prey on and parasitize these spiders. As also occurs in *Argiope* (Robinson & Robinson, 1970), the frequencies of different kinds of stabilimenta apparently differ in different populations of some species (Comstock, 1967 and Tso, 1998 on *C. conica*; Marson, 1947, Neet, 1990, and McClintock & Dodson, 1999 on *C. insulana*). Neet (1990) found that ‘circular’ silk stabilimenta in *C. insulana* (consisting of both straight lines along radii and curving lines crossing radii) were more common in windy weather than in calm weather, and argued that they serve to reinforce the web. Tso (1998) argued that silk stabilimenta in *C. conica* function to attract prey because orbs with stabilimenta captured more prey than those without. As noted by Blackledge & Wenzel (1999), however, correlations of this sort are not sufficient to demonstrate cause-effect relations. It is possible that the silk stabilimenta did not attract prey (or even repelled them), and that they occurred at web sites with more prey because spiders at such sites were better fed. Tso attempted to address this problem, but the small sample of web sites (13) and the failure to group sites with and without stabilimenta weakened this analysis.

In addition, McClintock & Dodson (1999) tested, but failed to find support for another possible function, that the predominantly vertical and horizontal detritus and egg sac stabilimenta of *C. insulana* serve to warn off large animals that might damage the orbs. They concluded that their data did not provide support for this hypothesis. Still further hypotheses that have been proposed are food storage (detritus stabilimenta) (Herberstein *et al.*, 2000), and shading the spider (Humphrey, 1992). In this article I use data from *A. bifurca* to examine all of these ideas, and argue that in this species egg sac, detritus, and silk stabilimenta all function as camouflage devices.

**Materials and methods**

Spiders were identified according to Levi (1999), and voucher specimens have been deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, MA. Web designs and spider colors were surveyed at two sites in San José Province, Costa Rica: on the sides of a house near San Antonio de Escazú (el. 1325 m) and on Agave, *Yucca*, and bromeliad plants growing in the open in San Pedro de Montes de Oca (el. 1100 m) in August — October,
Fig. 1. Schematic drawing of the abdomen of a mature female in dorsal view, showing the two pairs of antero-dorsal protuberances (arrows), and the two zones (hatched) in which color was recorded.

2001 and September, 2002, and at another site in Cartago Province, on a house near Chitaria (el. about 1000 m) in December, 2001. Unless otherwise specified, observations of webs and experiments were performed near San Antonio de Escazú, between August, 2001 and January, 2002. The webs of spiders which had not been previously manipulated were surveyed for stabilimenta on 12 Sept. \((N = 76)\) and 10 Oct. \((N = 104)\). The colors of two areas of the abdomen (Fig. 1) were noted in the field using a 10× hand magnifier. Experiments involved mature females (abdomen \(\geq 5\) mm long) and large immatures (abdomen \(\geq 3\) mm long).

Spiders were marked by placing unique combinations of dots of fast-drying paint or india ink on their abdomens. Experimental manipulation of the stabilimenta of mature females was performed by removing or adding strings of egg sacs. An egg sac stabilimentum (and any detritus that was present) was removed by grasping one end of the string with a fine forceps and carefully cutting it free with a fine scissors, taking care to damage the orb as little as possible. Webs checked for stabilimenta on both the following day and the day after (to control for possible effects of disturbance caused by removal). Then a stabilimentum was
 added to the orb by placing a string of egg sacs in the outer half of the sticky spirals to one side of the hub, and the webs on the next two days were checked. In a further control for the possible effects of damaging the web, the egg sacs were removed and then immediately returned to the webs of a different group of spiders.

Mature and penultimate female *Cyclosa monteverde* Levi were collected with their egg sac and detritus stabilimenta from *Agave* plants above San Antonio de Escazú (el. 1500 m) and induced to build orbs in captivity. They were fed the next day, and the stabilimentum was removed from the orb that evening; the web built the next night was checked for a silk stabilimentum.

**Results**

The spider rested day and night at the hub of its nearly vertical orb (Figs 2-4) as in all *Cyclosa* species observed. The spider always faced downward, and it tended to rest on the exposed side of the orb when the web was near a large object; of 31 webs of females built near and more or less parallel to walls and windows near San Antonio, the spider was on the ‘outer’ side of her web (*e.g.* the side away from the window) in all but one (97.0%). At night adults and juveniles always rested with their legs spread (Fig. 5b). During the day, the spider’s legs were usually folded tightly against its body (Figs 2b-d, 3, 4a) (85.7% of 49 mature females, 93.8% of 32 immatures with abdomens 2-4 mm long, and 90.0% 40 of immatures with abdomens \( \leq 1 \) mm long). Occasionally a mature female stretched her legs I and II anteriorly, pressing herself against an egg sac (Fig. 5a).

Stabilimenta included detritus, egg sacs, and silk (Figs 2-4). Detritus stabilimenta were generally more or less brown in color, and had two more or less distinct forms. The most frequent (Fig. 2b, c) was a vertical line of detritus, either above, below, or both above and below the hub, sometimes combined with silk stabilimenta (Fig. 2c). A less common type, apparently limited to larger spiders was a blob of detritus above, below, or at the center of the hub (Fig. 2d). Most of the identifiable objects in detritus stabilimenta were small pieces of plant (leaf and stem fragments, tiny flower parts), and spider exuvia (always smaller than the spider) (Fig. 2b). Of 16 detritus stabilimenta examined under dissecting and compound microscopes, all but one contained at least one moulted spider exuvium; the maximum was three. Recognizable prey remains were absent from most detritus stabilimenta.

Egg sac stabilimenta consisted of one or more sacs in a vertical line above, below, or both above and below the hub (Fig. 3). There was almost always an
Fig. 2.  (a) Orb web of mature female *A. bifurca* with an egg sac stabilimentum above the hub (scale = 3 cm); (b) Immature spider with a linear detritus stabilimentum above and below the hub (arrows mark molted spider cuticles); (c) Spider rests on a silk disc stabilimentum at the hub (arrow), with a linear detritus stabilimentum above, and three blobs of detritus below; (d) Spider at hub with blob of detritus at hub (scales for b-c = 0.3 cm).
Fig. 3. Egg sac stabilimentum. (a) The first egg sac in the web has a long extension above (arrow marks tuft of green silk); (b) and (c) Dorsal and lateral views of spider resting in the open space at the center of the hub with an egg sac stabilimentum above and below (arrow marks protruding tuft of green silk) (scale for all = 0.5 cm).
Fig. 4. Silk stabilimenta. (a) Spider crouches at the hub on a silk stabilimentum disc with a silk line stabilimentum above (scale = 0.3 cm); (b) Silk disc with a line stabilimentum above (scale = 0.5 cm); (c) Closeup of a disc stabilimentum; it is a mat of fine lines with multiple attachments to hub lines (scale = 0.2 cm); (d) Closeup of a silk stabilimentum line; it is a mat of fine lines attached to a radius, and that broadens to attach to lines (hub spiral, sticky spiral) that cross this radius (scale = 0.1 cm).
Fig. 5. (a) Elongate posture of a mature female with an egg sac stabilimentum; (b) Spread, non-crouching posture that all spiders adopted at night (arrow indicates silk stabilimentum disc); (c) Mature female *C. monteverde* at the hub of a web with a silk stabilimentum line spun after the spider’s egg sac stabilimentum was removed (scales in all = 0.2 cm).
open space at the center of the hub when there were egg sacs above and below (Fig. 3b, c). Each sac was lens-shaped in cross section, with its maximum diameter in the plane of the orb. Egg sacs were composed of two types of silk. The outermost layer consisted of a thin layer of dark green silk lines. On one side of the sac but not the other the green silk was piled into several protruding dark green tufts (Fig. 3a, c). Tufts on newly built sacs in webs built near the side of a house were always on the same, more exposed side (e.g. the side away from the window) on which the spider rested ($N > 50$) (the orientation of older sacs was less consistent). The other side of the sac, which slightly overlapped the sac immediately below it when there were several sacs in a string, was flat; it also had areas where green silk was more abundant, but there were no tufts.

The inner portion of the sac was composed of tightly meshed grey-white silk, and was the functional retainer of the pearly grey spherical eggs which were completely hidden from view. The inner surface of this grey-white wall had a thin fluffy layer, made of apparently the same grey-white silk. Egg sacs never had pieces of detritus on the surface, as in many species of *Cyclosa*. The first egg sac in a web usually (14 of 15 cases) had a long flat, upward-directed extension (Fig. 3a) composed of grey-white silk that was partially covered with green silk. Such extensions never occurred in subsequent sacs, each of which was usually added at the bottom end of the string of sacs above the hub. Egg sac colors did not change appreciably over the first several weeks, then very gradually acquired a dark rusty brown tinge over the next 1-3 months.

Silk stabilimenta were bright white, and formed either lines or circular discs (Fig. 4). Linear stabilimenta were nearly always directly above or below the hub. Stabilimentum lines were composed of many fine lines that were usually attached to one radius and to lines crossing that radius (Fig. 4b, d); occasionally they zig-zagged for at least part of their length between two adjacent radii. The lines to which stabilimentum silk was attached were not visibly displaced, and individual lines in both disc and line stabilimenta were often curved rather than straight when viewed under a microscope, thus indicating that they were slack. Disc stabilimenta consisted of more or less uniform mats of thin white silk lines attached at many places to the central portion of the hub (Fig. 4b, c).

Stabilimentum type and form changed as spiders grew (Fig. 6). The stabilimenta of mature females were almost exclusively egg sacs, occasionally
FACULTATIVE SILK STABILIMENTUM IN A. BIFURCA

combined with detritus or more rarely with white silk. In younger spiders most stabilimenta were composed of detritus. Silk stabilimenta were much more common both above and below the hub in the webs of immature spiders ($\chi^2 = 24.6$, df = 1, $p < 0.0001$).

The shape and color of the spider’s abdomen also changed as spiders grew (Table 1). Early instar nymphs lacked the dorso-lateral protuberances of older spiders (Fig. 1). Intermediate-sized spiders were more brown in color on both the anterior protuberances and the central dorsal region (A and B in Fig. 1), while adult females were more grey and green. Comparing intermediate-sized spiders (abdomens were 2-4 mm long) vs. mature females, intermediate-sized spiders were more likely to have brown in both areas ($\chi^2 = 27.4$ and 40.0, df = 1, $p \leq 0.001$ in both cases), and were less likely to have green in both areas ($\chi^2 = 12.6$ and 9.6, df = 1, $p < 0.001$ and $= 0.002$).

Color changes from brown to grey and green occurred during the adult stage in 55 marked adult females that were checked once a week for an av-

Fig. 6. Distribution of different types of stabilimenta in the orbs of A. bifurca spiders of different sizes. Silk stabilimenta were significantly less common in orbs of mature females than in any immature stage ($p < 0.001$ in all cases), while different sizes of immatures did not differ.
TABLE 1. Percentages of individuals of different sizes that had different colors in two areas of the abdomen (see Fig. 1).

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<thead>
<tr>
<th>Length of abdomen</th>
<th>brown</th>
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<td>green</td>
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<td>63</td>
<td>0</td>
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In two different instars (‘1 small’ and ‘1 large’) the abdomen was ≤1 mm.

verage of 7.9 weeks/spider. On comparing the same spider from one week to the next (N = 405), the color usually did not change (17% were brown at beginning and end of the week, 77% were grey or green at the start and the end of the week). Of the 24 transitions, 23 were from brown to grey or green, and 1 from green to brown (this spider then changed to grey-green the next week and remained grey and green for the 7 weeks thereafter).

The change from brown to green occurred near the beginning of egg sac production. Of the 20 individuals whose color change and oviposition history were determined (the spider was first seen on an orb lacking egg sacs or on an orb with only old and empty sacs that were probably produced by a different individual), the first appearance of a green color usually occurred either the same week as the first egg sac (7 individuals) or one week earlier than the first egg sac (10 individuals) (1 transformation occurred two weeks before the first egg sac, and 2 occurred one week after). Five individuals that were followed from their final moult took 2.8 ± 0.8 weeks to change color from brown to green, and 3.4 ± 1.5 weeks to lay their first clutch of eggs.
**Chitaria**

The colors of the spiders at Chitaria differed (Table 1). Both areas A and B of the abdomen of adult females were more often brown than in the spiders from other sites (76.2% and 81.0% of 21 spiders, compared with 13.1% and 15.8% of 38 females from other sites ($\chi^2 = 23.4$ and 24.1, both df = 1, $p < 0.001$). Immatures, in contrast, were more often white on the dorsal prominence (63.2% of 19) and grey in the posterior portion (60% of 20) than those from other sites, combining data for spiders 2-4 mm abdomen length, the corresponding percentages for 45 individuals at other sites were 8.9% and 2.3% ($\chi^2 = 29.7$ and 28.9, both df = 1, $p < 0.0001$).

Orbs of immature spiders at Chitaria were more likely to include silk stabilimenta. Of 24 orbs of immatures with 1 mm abdomens, 62.5% had at least one silk stabilimentum line (corresponding value for 71 orbs at the other sites was 10.9%); of 21 orbs of immatures with 2-4 mm abdomens, 52.4% of the Chitaria had at least one silk stabilimentum line (corresponding value for 70 orbs at other sites was 8.6%) ($\chi^2 = 25.7$ and 20.4, both df = 1, $p < 0.0001$).

The egg sacs in Chitaria had the same form and two-layer design, but some had a strikingly different color. Of 20 orbs of mature females, the outer layer of the egg sacs in 13 was rust-brown; in the other 7 it was green. All but three of these webs had more than a single sac (mean = 5.7 ± 4.1 sacs/orb), and all of the sacs in a given web were the same color. There were no sacs of intermediate color. The silk of the inner layer of sacs with a brown outer layer was more yellowish or brownish white than that seen at the other sites.

**Experimental manipulation of stabilimenta**

Experimental removal of egg sac stabilimenta in San Antonio sharply increased the frequency with which spiders built silk stabilimenta (compare Figs 6a and 7), while experimental addition of egg sacs to webs lacking egg sacs or detritus had the opposite effect (Fig. 7). The effects of removing and adding egg sacs persisted in webs built a day after the manipulation (‘second day’ in Fig. 7), indicating that the effect of web damage during manipulation was not responsible for the spiders’ responses. This lack of effect was confirmed by cutting the egg sacs free from the orb and then immediately placing them in the sticky spirals; in 17 of 18 spiders, the web built the following day had an egg sac stabilimentum but no silk stabilimentum.
Fig. 7. Results of experimental removal and addition of egg sacs. All comparisons between responses to addition and removal of egg sacs were statistically significant with $\chi^2$ tests, with the exception of the second day below the hub (bars with the same letter and number differ significantly (a indicates $p < 0.05$; c indicates $p < 0.001$).

*Cyclusa monteverde*

Each of 22 mature and penultimate females found in the field had a detritus or a detritus and egg sac stabilimentum. The spider crouched at the hub during the day (Fig. 5c), and its irregular outline and the blob-like shapes of the stabilimenta made it difficult to distinguish the spider from its stabilimentum. The first orb built in captivity by 13 mature and penultimate females had an egg sac and detritus stabilimenta but lacked a silk stabilimentum. When the egg sac and detritus stabilimenta were then removed, however, the next web of 4 of the 13 included a silk stabilimentum (Fig. 5c).
Discussion

_Egg sac stabilimenta_

Several observations suggest that the egg sac stabilimenta of _A. bifurca_ function to camouflage the spider at the hub: the protruding tufts of the silk added on the outer surface of the outer side of the egg sac resembled the dorsal bumps on the spider’s abdomen; the spider rested on the orb so that its dorsal surface was generally on the same side of the orb as the tufts on the egg sac (Fig. 3a, c); the tufts of green silk in egg sacs were relatively unimportant in providing support for the eggs, but were an apparent adornment; there was often a space between egg sacs at the center of the hub into which the spider’s body just fit (Fig. 3c); the usual crouched and the rarer extended positions assumed by the spider during the day increased the similarity of its outline to that of an egg sac (crouched position), or caused the spider’s outline to merge with that of a sac (extended position); and these constrained positions were abandoned at night (Fig. 5b). Differences in the Chitaria population were also in accord with the camouflage hypothesis: the abdomens of adult females more often had brown colors, and their egg sacs were often covered with brown rather than green silk. Similar arguments can be made for detritus stabilimenta as camouflage devices, with respect to spider colors (brown abdomen matches generally brown colors of bits of dried vegetation), the spaces left at the hub into which the spider’s body fit, and the spider’s constrained posture at the hub during the day but not at night. Perhaps the strong tendency to include shed spider cuticle in detritus stabilimenta (seen also in _C. insulana_ — McClintock & Dodson, 1999) serves as a distraction (chemical? tactile?) for predators.

Additional indications of a camouflage function are the match between the grey-green coloration of the adult female abdomen and the coloration of the egg sacs; and the change from the browner coloration of earlier instars (that matched the brown detritus stabilimenta in their webs) the green and grey colors of older adults. This ontogenetic change in the spider’s color occurred, as predicted by the camouflage hypothesis, at approximately the time when the spider began to make egg sacs. It must be noted that human perception of the colors of some objects differs from that of some potential predators such as flies and wasps, because of our lack of sensitivity to UV light. But because the possible predators of these spiders also include primates, as well as birds, and lizards, human perception of a match of the color of the spiders
and their egg sacs is probably not irrelevant with respect to defense of the spider. Further work will be needed to test the generality of possible color camouflage.

The set of traits just enumerated is not predicted by any of the other hypotheses mentioned in the Introduction. Thus, the data support the previous proposals that the egg sacs in the orbs of *A. bifurca* function to camouflage the spider.

**Silk stabilimenta**

The experimental demonstration that *A. bifurca* spiders replaced egg sac and detritus stabilimenta with silk stabilimenta, and refrained from constructing silk stabilimenta when egg sacs were available, suggest that, for the spider, egg sac and silk stabilimenta are somehow equivalent, with egg sacs and detritus being preferred when they are available. Because of the evidence that egg sac stabilimenta function to camouflage spiders at the hub, this implies that silk stabilimenta of *A. bifurca* also function as camouflage. Similar conclusions may apply for the closely related *C. monteverde*, which also sometimes replaces detritus or egg sac stabilimenta with silk stabilimenta. Marcelo Gonzaga (in prep.) has also found that silk stabilimentum construction is sometimes induced in *C. fililineata* and *C. morretes* when detritus and egg sac stabilimenta are experimentally removed.

Some of the observations reported here also argue against other possible functions of silk stabilimenta in *A. bifurca*. The swaths of silk in silk stabilimenta were in many cases not under tension and often did not connect radial lines, and are thus inappropriately designed to stabilize the web or alter tensions (Neet, 1990). In addition, webs with egg sacs would need more rather than less reinforcement to sustain the weight of the sacs, yet the addition of egg sacs reduced silk stabilimentum construction, and removal of egg sacs increased it. Neither silk lines nor discs were appropriately placed to shade spiders from the sun (Humphrey, 1992). Detritus stabilimenta only seldom contained prey (and then only dessicated prey), so the food storage function (Herberstein *et al.*, 2001) can also be discarded. Web advertisement for large, fast-moving animals such as birds, seems unlikely because of the relatively confined spaces where webs were built, such as between leaves of bromeliads. The spider’s crouched position during the day but not at night is also not explained by this hypothesis. The prey attraction hypothesis (Craig
& Bernard, 1990; Craig, 1991) was also not supported. It seems improbable that removal or addition of detritus and egg sac stabilimenta would affect the spider’s hunger level, inducing it to attempt to attract prey when it lacks egg sacs or detritus, and to abandon such attempts when it has them.

One seemingly powerful argument against the camouflage hypothesis for silk stabilimenta is that they are often highly visible. Humans hunting for spiders can use silk stabilimenta to find the otherwise much less conspicuous spiders (Eberhard, 1973), and birds and salticid spiders can also learn to associate model stabilimenta with food (Robinson & Robinson, 1970; Seah & Li, 2001). Herberstein et al. (2000) considered this to be a ‘strong argument’ against the anti-predator function. But this reasoning confounds cues that can be used with cues that are used by predators in nature. As noted previously (Eberhard, 1973), the crucial question is not whether predators have the ability to perceive stabilimenta and to learn to associate them with food, but whether such learning actually occurs in nature. A yellow flower may highly visible from a distance, but this does not mean that a yellow spider resting on the flower is not camouflaged.

The only data on whether predators in nature learn to associate silk stabilimenta with spiders favor the camouflage hypothesis. Birds in nature avoided models of silk stabilimenta when they were first exposed to them (Robinson & Robinson, 1970). Sphecid wasps captured in the field also had apparently not learned to associate silk stabilimenta with prey; when they were kept with Argiope spiders with and without silk stabilimenta, the rate of capture of spiders with stabilimenta was lower rather than higher (Blackledge & Wenzel, 2001). Naive mantids showed a preference for the side of a ‘Y’ maze with a stabilimentum (Bruce et al., 2001), but the biological significance of this preference is not clear (for instance, it is possible that this was an escape rather than a predatory response).

Most of the arguments presented here for A. bifurca are based on correlations rather than direct experiments on rates of predation. Experiments per se, however, are no guarantee of reliable conclusions, as is clear from criticisms of interpretations of previous experiments involving stabilimenta (Eberhard, 1990; Herberstein et al., 2000; Craig et al., 2001). When, as in the case of the prey attraction and camouflage hypotheses, one is dealing with effects that must be appropriately weighted and summed over many different groups of possible predators and parasites (including primates, birds, lizards, damselflies, mantids, ichneumonid and sphecid wasps, and salticid spiders
— Marples, 1969; Robinson & Robinson, 1970; Eberhard, 1973; Edmunds, 1986; Coville, 1987), as well as an even wider variety of possible insect prey (see Tso, 1996 for different effects on different prey), it is difficult to devise definitive experiments that balance effects appropriately. One advantage of using contextually flexible responses and comparisons between different life stages, as in this study, is that natural selection on the spiders can be expected to have weighted and summed these different effects the appropriate ways.

Can these observations, which suggest that silk stabilimenta function in *Allocyclosa* as camouflage devices, be generalized to silk stabilimenta in any other groups of spiders? Herberstein *et al.* (2000) argued that the repeated derivation of stabilimenta in different groups of orb-weaving spiders favors the idea that stabilimenta have different functions in different groups, and noted that the stabilimenta of *Allocyclosa* and *Cyclosa* probably evolved independently of those of other groups. But the logic of arguing that independent derivation constitutes convincing evidence against the generality of function is inconclusive: few would agree, for instance, that because flattened limbs have evolved independently in many different groups of aquatic animals, they therefore do not have the common function of increasing swimming ability.

The following points favor generalizing the conclusions that silk stabilimenta function as camouflage in *Allocyclosa* and *Cyclosa* to the much-debated function in the genus *Argiope* and several others that always build their stabilimenta near the hub: the forms of the silk stabilimenta of *Allocyclosa* and *Cyclosa* encompass the three most common designs in other groups (Herberstein *et al.*, 2000); the lines in their silk stabilimenta are loose rather than being tensed, as is true in other groups (Wiehle, 1927 on *Zosis*; Eberhard, 1973 on *Uloborus*; Shinkai & Takano, 1987 on *Zilla*); and they share with other species that produce silk stabilimenta the behavioral traits of sitting at the hub of the web during the day in a constrained position, and abandoning this position at night. Two species of *Metepeira* may also show ontogenetic changes in silk stabilimenta similar to the facultative changes documented here for *A. bifurca*: juveniles and adults without egg sacs sit at the hub, where they often make a white silk disc stabilimentum; but adults with egg sacs sit in a retreat away from the hub where they hang their egg sacs and apparently do not make silk stabilimenta (Piel, 2001). The apparent replacement of silk stabilimenta with detritus stabilimenta in a species
of *Uloborus* (Lubin, 1986) may also parallel the substitution of silk stabilimenta for egg sacs documented here.

Finally, there is a general implication of the demonstration of the apparent ease with which stabilimenta have arisen in different groups (Herberstein *et al.*, 2000) which favors the camouflage hypothesis over all others (except the shade hypothesis). There are many orb-weavers in which the spider builds a diurnal web and rests away from the hub, under a leaf or other concealing object near the hub. Under the camouflage hypothesis, a spider that rests off the web should have no need for camouflage at the hub, and should not build stabilimenta. In contrast, under the prey attraction hypothesis, for instance, spiders which rest off the web should be, if anything, more prone to evolve stabilimenta (to compensate for their presumably poorer prey capture success that results from their longer response times to attack prey in the web). The data are in clear accord with the camouflage prediction. There is not a single species known in which the spider rests off of the web and builds a silk stabilimentum: *Alpaida* (Eberhard, 1986, unpubl.; Levi, 1988); *Araneus* (Wiehle, 1928, 1929; Comstock, 1948; Robinson & Robinson, 1970; Shinkai & Takaji, 1984; Edmunds, 1986; Shinkai & Takano, 1987; Levi, 1991; W. Eberhard, unpubl.); *Chrysometa* (Levi, 1986; Eberhard, 1986, unpubl.); *Dolichognatha* (Eberhard, 1986, unpubl.); *Hingstjepeira* (Levi, 1995; W. Eberhard, unpubl.), several *Metepeira* (Comstock, 1948; Piel, 2001); *Micrepeira* (Levi, 1995), *Paraneus* (Edmunds, 1986), *Phonognatha* (McKeown, 1963; Hormiga *et al.*, 1995; W. Eberhard, unpubl.); *Spilasma* (Eberhard, 1986, unpubl.; Levi, 1995); *Yaginumia* (Shinkai & Takaji, 1984); *Zygiella* (Wiehle, 1927; Nielsen, 1931; Comstock, 1948). Marples (1969) noted the pattern predicted by the camouflage hypothesis in the genus *Uloborus*. Most species make silk stabilimenta and rest at the hub during the day, but one species, *U. gibbosus*, both lacks a silk stabilimentum and often rests on a twig at the edge (where it is ‘very inconspicuous’) (Marples, 1955).

**References**


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