

Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support of the predator-defense hypothesis

Thomas W. Schoener and David A. Spiller

Department of Zoology, University of California, Davis, CA 95616-8755, USA

Received November 14, 1991 / Accepted May 8, 1992

Summary. A variety of orb-weaving spider species construct stabilimenta, patterned areas of dense silk, typically near the hub of the orb. The adaptive significance of this construction, along with associated behaviors such as shuttling and vibrating, is much debated. *Argiope argentata* on small islands of the Bahamas frequently possess stabilimenta; we studied 397 individuals of this species to investigate possible functions of their stabilimenta, paying particular attention to predator-defense hypotheses. Cruciform stabilimenta were commoner in all size classes of spiders than discoid stabilimenta or no stabilimentum at all; discoid stabilimenta occurred mostly among intermediate size classes. Within the cruciform type, two-segmented stabilimenta were especially common among the very smallest spiders. Size of cruciform stabilimenta showed a curvilinear relation to spider body length; the fitted curve for “total segment length” had a maximum at an intermediate spider length. We argue that this relationship (among other phenomena) supports an apparently-larger-size hypothesis, whereby intermediate-sized spiders in particular appear much larger than they actually are. This could discourage predators, including those that are gape-limited such as lizards. We argue that stabilimenta in the smallest spiders, in which typically two segments are opposed, so that they more or less “line up”, serve as camouflage. When disturbed experimentally, spiders with discoid stabilimenta shuttle to the opposite side of the centrally located stabilimentum. This seems an obvious defensive behavior and occurs less frequently among spiders with cruciform stabilimenta. Large spiders vibrate more frequently than small ones, but no relation exists between vibration frequency and stabilimentum type. We argue (see also Tolbert 1975) that vibrating behavior, in which the spider can become a blur, renders its location more difficult to discern and the spider more difficult to grasp, rather than increasing apparent size.

Introduction

The widespread, sometimes very abundant, Neotropical spider *Argiope argentata* frequently has concentrated areas of white silk surrounding the hub, collectively known as the stabilimentum. Stabilimenta can take several forms and occur in a variety of species in the Araneidae and Uloboridae (Edmunds 1986). In *A. argentata*, two forms occur: (1) a *cruciform* (or linear) stabilimentum, in which one to four zig-zag segments are arranged radially around the hub (Fig. 1 a); and (2) a *discoid* stabilimentum, in which dense silk is arranged at the hub in a circular pattern (in our data 3–33 mm in diameter; Fig. 1 b). Stabilimenta of the first type especially are very characteristic, striking features, and understandably have become of considerable interest.

As for many such unusual traits, a number of hypotheses have been proposed to explain the “function” of the stabilimentum, including two that are virtually contradictory. Edmunds (1986) groups hypotheses into three classes (we modify the designation of one of them here):

1. A *predator-defense* function, whereby the spider-cum-stabilimentum resembles some object that is less likely to be seen or successfully attacked by predators than the spider itself (Hingston 1927; Bristowe 1958; Ewer 1972; Eberhard 1973; Tolbert 1975; Lubin 1975)
2. A *mechanical* function, whereby the stabilimentum either (a) supports the spider by virtue of its denser silk, perhaps especially important when molting, or (b) is used to adjust tension in the web [McCook 1889 (cited in Nentwig and Rogg 1988); Simon 1893 (cited in Edmunds 1986); Comstock 1940; Robinson and Robinson 1970, 1973; Nentwig and Rogg 1988 (but see below)];
3. A *conspicuousness* function, whereby the stabilimentum by its visibility allows birds to avoid the web, a feature mutually beneficial to both the spider and the birds (Horton 1980; Eisner and Novicki 1983).

A fourth hypothesis, somewhat related to 3, was recently proposed and supported by Craig and Bernard (1990): stabilimenta, which reflect ultraviolet light, may attract the prey of spiders.

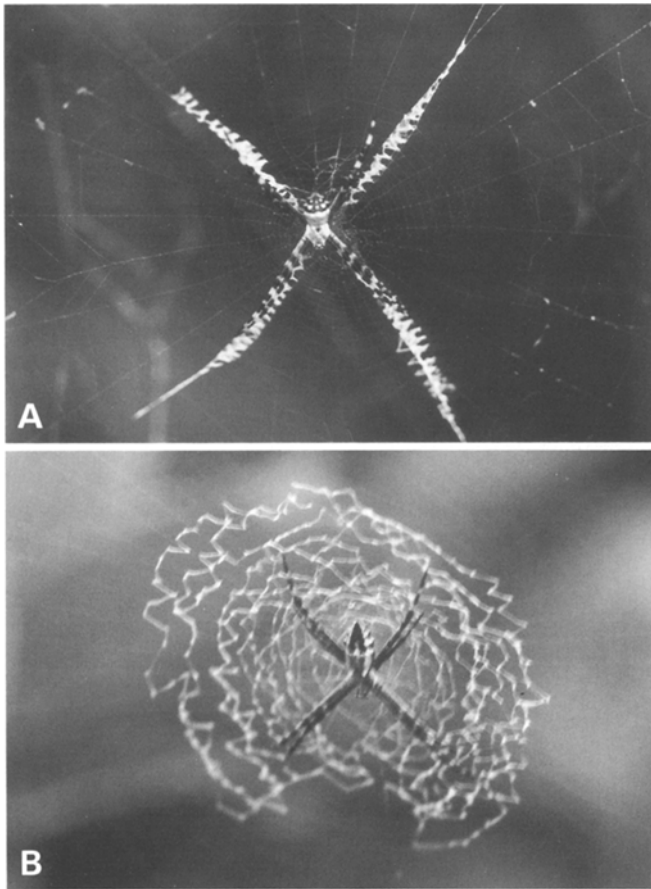


Fig. 1 A, B. Stabilimentum types in *Argiope argentata*: A cruciform; B discoid

Within the category of predator defense, concealment, confusion and an increase in apparent size have each been suggested as contributory. In observing *Argiope argentata* on very small Bahamian islands, we were especially struck by the third of these possibilities for the cruciform stabilimentum. Segments of the cruciform stabilimentum appear as extensions of pairs of spider legs, increasing the apparent size of the spider (Fig. 1 A; see also below). Population numbers of *A. argentata* on these islands show a great deal of variation that is related to the presence and absence of lizards (Schoener and Toft 1983; Toft and Schoener 1983; Schoener 1986). Such variation has also been produced experimentally (Spiller and Schoener 1988). Lizards are gape-limited predators and occur in a variety of sizes from hatchling to adult; *Anolis*, especially common in our study sites, achieve maximum body (snout-vent) lengths of about 50–60 mm, so that many of the lizards present are quite small. All this suggests that an apparently larger size (ALS) might protect spiders from attack by lizards, a possibility also suggested for attack by arthropod predators (Edmunds 1986) and which may apply to other kinds of predators as well. However, previous evaluations of this hypothesis tended to emphasize larger sizes of spiders. We will argue that a large stabilimentum would be especially favored among individuals of inter-

mediate size: the largest spiders do not need to appear larger, and the smallest spiders are physically and perhaps energetically prevented from having a very large stabilimentum. We will also argue that the ALS function cannot be the entire story. First, among cruciform stabilimenta, adding some size to a very small spider might bring it within a predator's preferred range of prey sizes; for such spiders, concealment seems a better hypothesis, especially as they tend to have only two segments in their stabilimenta.

Similarly, discoid stabilimenta also require explanation, and we will show that they are associated with a rather stereotyped behavior whereby the spider "shuttles" to the side of the orb away from the potential predator, thus causing the disc to occur between it and the predator. Again, concealment is apparently involved, as well as perhaps direct shielding of the spider from attack.

Subjects, localities and methods

Data were gathered in two sessions 3 years apart.

The purpose of the first session was to determine the relationship between spider size and stabilimentum characteristics. All individuals with orbs (including recognizable males occupying separate orbs) on about two-thirds of a larger island (671 m² vegetated area) and all of a smaller island (216 m²) were studied; the two unnamed islands are near Kemp Cay, central Exumas. The recording session was conducted on 9 May 1984, and 282 spiders were found. The following information was recorded:

1. Spider body length (chelicera to posterior abdomen)
2. Total foreleg length
3. Type of stabilimentum, if any (categories were "cruciform," "discoid," "both cruciform and discoid," and "none")
4. Maximum diameter of the disc, if present
5. Number of segments, 1–4, comprising the cruciform stabilimentum, if present (a continuous arm of the "X" that crosses the hub is counted as two segments)
6. Size of the cruciform stabilimentum, if present, defined in three ways: (a) "maximum distance," which is the larger of the two arms of the "X," including the distance (if any) from the inner tip of each segment to the center of the hub; (b) "total stabilimentum extent," which is the sum of the lengths of the two arms of the "X," including (as in measure a) the distance (if any) from the inner tip of each segment to the center of the hub; and (c) "total segment length," which is the sum of the lengths of the one to four individual segments.

The purpose of the second session was to record the kinds of defensive behavior exhibited by spiders with various types of stabilimenta and of varying sizes. The same two islands were studied as in the previous session; all spiders were used on both islands. In addition, a third, unnamed island (594 m²) in Pipe Creek, near the others, was also studied; here, mostly larger spiders (≥ 10 mm in body length) were observed, so as to gather more data on behaviors of such individuals, differentially rare on the first two islands. The session was conducted on 27 May 1987; 115 spiders (not including those used to test the method) were used in analyses below. Each spider was slowly approached dorsally with the eraser-tipped end of a pencil until a response occurred; sometimes the spider was touched lightly before such a reaction. At least five trials were performed (or fewer, if the spider left the web, either by dropping to the ground or retreating into the vegetation), and the defensive behavior was recorded for each trial. A few spiders, used in preliminary sessions to establish the method, did not conform to this protocol because we deliberately did not carry out a full five trials; these are not included in most of the analyses below. In cases in which more than five trials were performed on a given individual,

the first five trials are considered separately from the others (see below). Spiders dropping in the first trial were not included in analyses.

Mutually exclusive categories of response behavior are:

1. "runs," in which the spider flees from the hub to some other portion of the web, usually near an edge
2. "Shuttles," in which the spider slips through the web to the opposite side of the hub
3. "Leaves the web," in which the spider either drops to the ground or moves out of the web into the vegetation
4. "No movement," in which the spider holds its position in the web (and occasionally appears to attack the pencil)

We also recorded whether or not "vibrating" behavior, in which the spider shakes the web gently to vigorously (in which latter case the spider and adjacent strands become a blur), accompanied the above four categories of behavior.

Results

Frequency of stabilimentum types and relation to body size

For the 1984 data, in which all spiders encountered in given areas were recorded, 66.3% had cruciform stabilimenta (this includes incomplete as well as complete structures; see next section for breakdown), 17.4% had discoid stabilimenta, 3.9% had both of the previous types, and 12.4% had no stabilimentum. Frequency of stabilimentum type varied with body-size class (Table 1; $\chi^2 = 46.951$, $P < 0.001$, "both" excluded). The smallest sized spiders (1–2.5 mm) had mostly cruciform stabilimenta or no stabilimentum. Intermediate sizes (3–5.5 or 6–9.5 mm) had mostly cruciform stabilimenta or discoid stabilimenta; percent spiders with no stabilimenta was very low (4–5%). Largest sizes (≥ 10 mm) were similar to the smallest sizes in having mostly cruciform or no stabilimenta. The 1987 data gave similar within-size proportions, except that individuals with no stabilimentum were very rare for the largest size class (2 of 29). The largest spider with a discoid stabilimentum was 12 mm in body length, whereas the largest spider in the study was 25 mm.

The 1984 data (but not the 1987 data, because it differentially included the largest individuals on one island) can also be used to construct distribution histograms of spider size for the various stabilimentum types (we included the category "both" in the category "discoid" for this analysis). These (Fig. 2) show that most discoid stabilimenta occur among spiders of intermediate or somewhat smaller-than-intermediate size. Cruciform or no stabilimenta ("none") are found among spiders of all sizes; except for the smallest size classes, the distribution for "none" is relatively uniform. Pairwise Kolmogorov-Smirnov two-sample tests can be used to compare the histograms of Fig. 2 statistically; a two-tailed test is used, because the null hypothesis is no kind of difference between the distributions (Siegel 1956). Maximum differences in cumulative frequencies (D) and unadjusted probabilities are: (1) cruciform vs discoid: $D = 0.149$, $P = 0.265$; (2) cruciform vs none: $D = 0.277$, $P = 0.022$; (3) discoid vs none: $D = 0.355$, $P = 0.008$. A sequential Bonferroni adjustment (Rice 1989) makes comparisons 2 and 3 significant at the 5% level.

Table 1. Frequencies (percent) of stabilimentum types within various spider size classes

	Spider length (mm)			
	1.0–2.5	3–5.5	6–9.5	≥ 10
1984 data $n = 282$				
Percent cruciform	50.0	75.2	60.5	65.3
Percent discoid	13.9	16.5	28.9	4.1
Percent both	2.8	3.3	6.6	2.0
Percent none	33.3	5.0	3.9	28.6
Total n for size class	36	121	76	49
	0.5–2.5	3–5.5	6–9.5	≥ 10
1987 data $n = 134$				
Percent cruciform	56.8	72.1	52.0	79.3
Percent discoid	5.4	16.3	32.0	6.9
Percent both	2.7	11.6	16.0	6.9
Percent none	35.1	0.0	0.0	6.9
Total n for size class	37	43	25	29

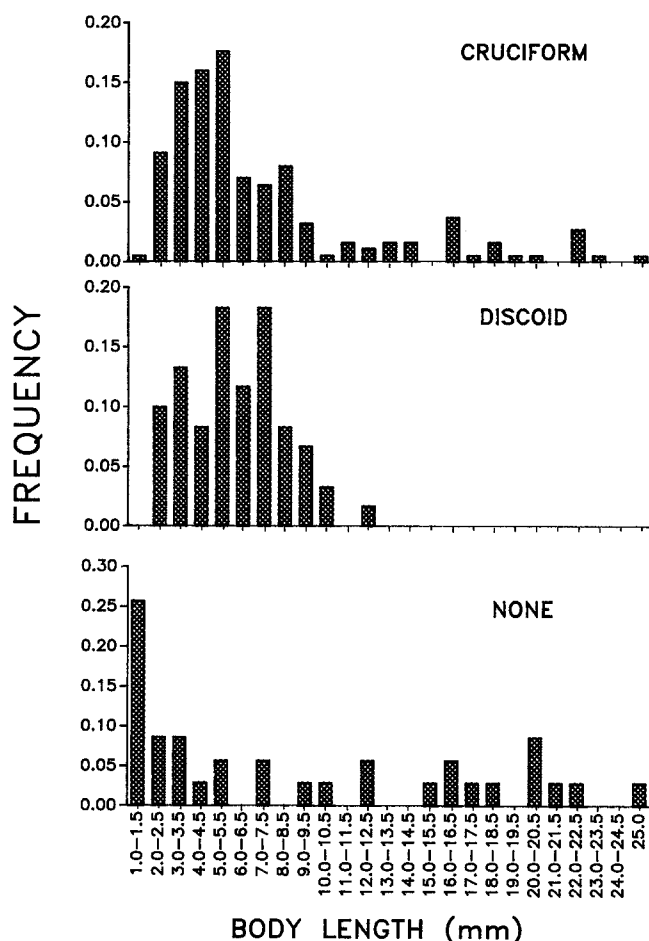


Fig. 2. Frequency distributions of spider lengths for three stabilimentum classes (1984 data); "both" included in "discoid". Sample sizes are $n = 187$ (cruciform), $n = 60$ (discoid), $n = 35$ (none)

Table 2. Frequencies of spiders within body-size classes with various numbers of segments in the cruciform stabilimentum (1984 data)

	Number of segments (%)				<i>n</i> for body-size class
	1	2	3	4	
Body length (mm)					
1–2.5	10.5	84.2	0.0	5.3	19
3–4.5	1.7	48.3	1.7	48.3	60
5–6.5	2.0	22.4	0.0	75.5	49
7–8.5	16.1	12.9	9.7	61.3	31
9–10.5	0.0	25.0	0.0	75.0	8
11–12.5	0.0	60.0	0.0	40.0	5
13–14.5	16.7	0.0	0.0	83.3	6
15–16.5	14.3	28.6	14.3	42.9	7
17–18.5	50.0	0.0	0.0	50.0	4
19–20.5	0.0	100.0	0.0	0.0	2
21–22.5	40.0	0.0	0.0	60.0	5
23–25	0.0	50.0	50.0	0.0	2
All	7.6	35.4	3.0	54.0	198
Stabilimentum type	Total number				
Only cruciform	13	67	6	101	187
Both	2	3	0	6	11
All	15	70	6	107	198

Number of segments in cruciform stabilimenta

As noted by Robinson and Robinson (1970), the so-called cruciform stabilimentum is often not perfectly cruciform, lacking one to three of the four segments characterizing the complete structure. Table 2 gives total segment counts (last row), as well as separate counts for only spiders having cruciform stabilimenta (third-to-last row), spiders additionally having a disc (second-to-last row), and spiders of varying sizes (other rows). The commonest condition (54% overall) is to have a complete stabilimentum; the next commonest (35%) is to have two of the four possible segments. No obvious difference in number of segments exists for spiders with and without discoid stabilimenta, although sample size for the former is small. In contrast, inspection of the data by size class shows that the smallest spiders (1–2.5 mm) almost never have more than two segments (18 of 19) and usually have exactly two segments (16 of 19). Four-segmented stabilimenta become the modal class for spiders 5–10.5 mm, then diminish with spider size (moderately and erratically, although sample size becomes quite small).

Relation of cruciform stabilimentum size to body size

Each of the three measures of stabilimentum size – “maximum distance,” “total stabilimentum extent,” and “total segment length” – is significantly related to the independent variable “both length” in simple regression ($P < 0.0001$ in all cases; spiders with no stabilimen-

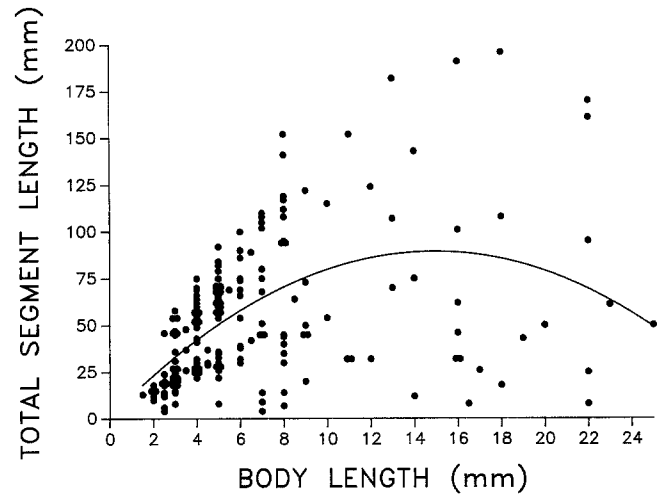


Fig. 3. Relation of total segment length to body length, cruciform stabilimenta

tum omitted). However, inspection of plots shows that the empirical relation appears curvilinear: stabilimentum size increases with body length at a decreasing rate. To test for curvilinearity statistically, we performed quadratic regression, a multiple regression with “body length” and “(body length)²” as independent variables (e.g., Sokal and Rohlf 1981). For all three measures of stabilimentum size, the regression coefficient for “body length” is significantly positive and the regression coefficient for “(body length)²” is significantly negative ($P < 0.0001$ in all cases). For the third measure, “total segment length,” the fitted curve is quite domed and has its maximum at a spider length of 14.9 mm (Fig. 3). In contrast, the first measure of stabilimentum size, “maximum distance,” has its maximum near the largest spider size (23.8 mm), whereas the second measure is intermediate, at 18.7 mm. For the third measure we also performed quadratic regression in which all spiders without stabilimenta of any kind (i.e. with the dependent variable equal to zero) were included; regression coefficients were similar ($P < 0.0001$ for both coefficients). Finally, because of the result that segment number is especially small for the smallest spiders, and perhaps for the largest spiders (last section), we tried “mean segment length” (measure 3 divided by “number of segments”) and its analogue for measure 2 as dependent variables; this attempts to eliminate the contribution of segment number to the results. Relationships were still very significantly curvilinear (all P values < 0.0001), although that for measure 2 did not decline over any portion of the plot.

We considered the possibility that leg length might be a better measure of spider size, or at least a more appropriate one for testing the ALS hypothesis, given a spider’s positioning, than body length. However, despite the possibility that legs might be differentially bent between individuals, the Pearson correlation between leg and body length was 0.986, demanding no additional analysis.

Association of defensive behavior and stabilimentum type

Excluding cases in which the spider drops at the first trial or does not move during the entire session, we compared the relative frequency of shuttle and run behavior for spiders of various stabilimentum types in three ways.

First, we used the modal type of behavior calculated for each individual. Compilations included either (1: Table 3A) only spiders involved in at least five “successful” trials (i.e. those in which the spider did not leave

Table 3. Relation of defensive behavior and stabilimentum type. Values listed are numbers of individuals. χ^2 (I) is cruciform vs discoid; χ^2 (II) is cruciform + none vs discoid + both.

A. Modal behavior – excluding spiders that left the web before 5 trials and spiders in “preliminary sessions”

	Stabilimentum type			
	Cruciform	Discoid	Both	None
Shuttle	12	12	2	1
Run	31	4	3	5
Shuttle/run	0	0	0	0
No movement	2	0	0	0

χ^2 (I)=10.717, $P=0.001$; χ^2 (II)=9.994, $P=0.002$

B. Modal behavior – including spiders that left the web before 5 trials, excluding spiders in “preliminary sessions”

	Stabilimentum type			
	Cruciform	Discoid	Both	None
Shuttle	14	12	2	1
Run	54	6	4	8
Shuttle/run	1	0	1	0
No movement	2	0	0	0

χ^2 (I)=14.327, $P<0.0005$; χ^2 (II)=13.494, $P<0.0005$

C. First observation – all spiders

	Stabilimentum type			
	Cruciform	Discoid	Both	None
Shuttle	17	9	3	3
Run	64	8	6	10
Shuttle/run	0	0	0	0
No movement	3	1	0	0

χ^2 (I)=7.360, $P=0.007$; χ^2 (II)=6.445, $P=0.011$

D. Presence of any shuttling during first five trials – excluding spiders that left the web before 5 trials and spiders in “preliminary sessions”

	Stabilimentum type			
	Cruciform	Discoid	Both	None
Yes	29	14	5	3
No	16	2	0	3

χ^2 (I)=3.016, $P=0.082$; χ^2 (II)=5.537, $P=0.012$

the web), in which case the more prevalent of the first five responses is considered the modal type, or (2: Table 3B) spiders in (1), plus spiders leaving the web before five successful trials could be performed, in which latter case the mode is taken over however many trials could be applied before the spider departed. In both cases individuals with discoid stabilimenta modally shuttled more than ran, and vice versa for individuals with cruciform stabilimenta. Individuals with no stabilimenta ran most frequently of the four stabilimentum types.

Second, we used response in the first trial only [Table 3C; note this increases sample size, as spiders in “preliminary sessions” (see Methods) could be used]. Results were similar to those for the first measure, except that differences were not as strong.

Third, we classified individuals according to whether they ever shuttled during the first five observations or never shuttled (Table 3D). (Only two individuals did not shuttle during the first five trials but shuttled later.) For all types except spiders without stabilimenta, “ever shuttling” was commoner than “never shuttling.” However, spiders with discoid stabilimenta had a higher percentage “ever shuttling” than those without discoid stabilimenta.

Eight 2×2 contingency tables were constructed to evaluate various aspects of these results statistically. The first four contrast spiders with cruciform stabilimenta and those with discoid stabilimenta; the second four contrast spiders with cruciform or no stabilimenta and spiders with discoid or both types of stabilimenta. For each of these groups of four, χ^2 values are computed from data in Table 3, A–D, first two rows only. Three χ^2 values are significant at or better than the 0.001 level, one at the 0.002 level, and three at about the 0.01 level, while one has $P=0.08$ (all 2-tailed tests). Homogeneity is rejected in 7 of 8 comparisons [whether a sequential Bonferroni correction for multiple comparisons (Rice 1989) is applied or not]. Use of G (Sokal and Rohlf 1981) instead of χ^2 gave nearly identical values and did not change significance judgments at the 5% level.

Although spiders with cruciform stabilimenta tended to leave the web more frequently during a session, no significant relation was found between stabilimentum type and this behavior (first type of contrast $\chi^2=2.454$, $P=0.117$; second type of contrast $\chi^2=1.096$, $P=0.295$).

Bearing in mind that larger spider sizes were differentially sampled, we can examine the relationship of modal behavior (shuttles vs runs; spiders leaving the web included) and spider size by comparing the frequency of the two types of behavior separately within each size class. We do this only for spiders with cruciform stabilimenta, as other stabilimenta classes are much less numerous (Fig. 4). Running is preponderant over shuttling for most sizes, but perhaps especially the largest ones – to see this descriptively (not statistically), note proportions within each size class. To evaluate homogeneity within size classes statistically, we split combined data at the median spider size (≤ 5 mm vs > 5 mm) and did a 2×2 χ^2 -test (two-tailed). Large spiders had running as the modal behavior in 87.1% of individuals, as compared to 73.0% for small spiders. This gives a χ^2 of

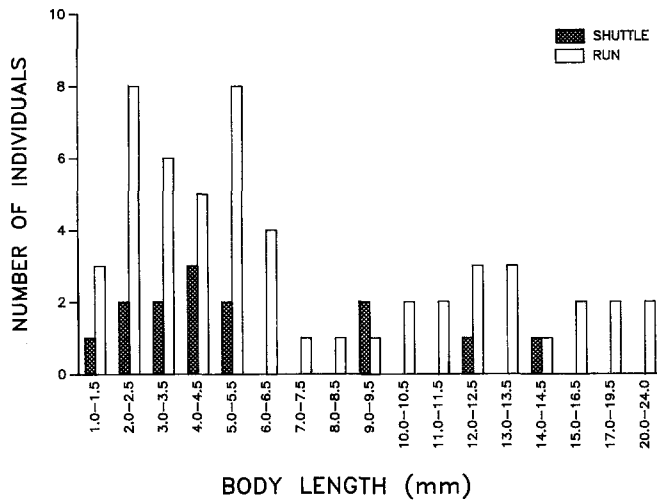


Fig. 4. Frequency of “shuttle” (shaded bars) vs “run” (open bars) modal behavior as a function of body length. Spiders leaving the web before five trials included. Cruciform stabilimenta only, $n = 68$ (ties not counted)

2.058, not significant at the 5% level ($P = 0.151$; note, however, that the median size and proportions especially within the “large” category might have been different if we had sampled all the spiders present). We also observed that, while size classes of spiders with discoid stabilimenta often had “shuttle” as the modal response, spiders with stabilimentum types other than discoid almost never did if they were larger than the largest spiders with discoid stabilimenta (12 mm).

Relation of vibrating behavior to stabilimentum type and spider size

No matter what the analysis, we found no or little association of stabilimentum type and presence of vibrating behavior (Table 4). Using responses in the first five trials only, a 2×2 χ^2 -test for the commonest two stabilimentum categories gave no significant differences, whether only spiders not leaving the web (and therefore observed five times) or all spiders were used ($\chi^2 = 0.854$, $P = 0.356$; $\chi^2 = 1.580$, $P = 0.209$; respectively). [We evaluated whether adding spiders that left the web might bias results (because individuals that would have eventually vibrated departed first) by calculating for all spiders (first five trials) the fraction of “all spiders that eventually vibrated” that vibrated by the i th trial: 58% of such spiders vibrated by the first trial and 81% by the second. In our protocol (see above) all of the spiders leaving the web were observed at least once before leaving, and 58% were observed at least twice. Hence, bias should be minimal.] Only three spiders did not vibrate during the first five trials but vibrated in subsequent trials; if these are added, tests are still not significant ($\chi^2 = 1.422$, $P = 0.233$; $\chi^2 = 2.085$, $P = 0.149$). If spiders with both types of stabilimenta are added to spiders with discoid stabilimenta only (which they resemble in response), and spiders ever vibrating are considered (i.e., including the above-mentioned three individuals), a contingency table

Table 4. Relation of vibrating behavior to stabilimentum type^a

	Number of cases (spiders never leaving the web/all spiders)			
	Cruciform stabilimentum	Discoid stabilimentum	Both stabilimenta	No stabilimentum
Vibrated	17/27	4/4	1/2	1/2
Did not vibrate	28/44	12/14	4/5	5/7

^a responses in first five trials only

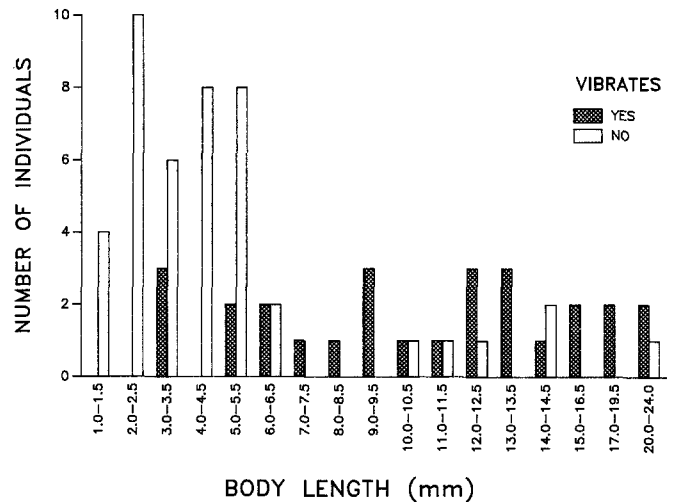


Fig. 5. Frequency of ever vibrating (shaded bars) vs not vibrating (open bars) (during the first five trials) as a function of body length. Spiders leaving the web before five trials included. Cruciform stabilimenta only, $n = 71$

using only spiders with at least five trials is still not significant at the 0.05 level ($\chi^2 = 2.209$, $P = 0.137$). If spiders with no stabilimenta are compared to all others in a 2×2 table, no significant difference is obtained ($\chi^2 = 0.723$, $P = 0.395$). One-tailed tests may be justified for some of these comparisons, but even with such tests, the 5% significance level is never attained.

Frequency distributions for size constructed as before suggest that the relation of vibrating behavior to size is stronger than the corresponding relation to stabilimentum type (Fig. 5). We evaluated this relation statistically, as in the last section (with similar cautions), using spiders with cruciform stabilimenta only, and splitting the data at an overall median size (again 5 mm). Of large spiders 66.7% vibrated, whereas only 13.2% of small spiders did. This difference in proportion is highly significant ($\chi^2 = 21.458$, $P < 0.001$).

Discussion

We now evaluate the evidence from our study supporting and not supporting the predator-defense hypothesis for the function of stabilimenta in *Argiope argentata*. Implications for Edmunds's two other major hypotheses will also be discussed; because the Craig and Bernard (1990) hypothesis is somewhat similar to Edmunds's third hy-

pothesis, its implications may be similar as well. Eight characteristics of stabilimenta and associated behavior will be considered in turn.

1. *Stabilimenta are common among spiders of small Bahamian islands.* The predator-defense hypothesis requires that predators be a major feature of the spider's environment. On small Bahamian islands lizards are major predators of orb spiders. We have shown both by comparative studies (Schoener and Toft 1983; Toft and Schoener 1983; Schoener 1991) and direct experimentation (Schoener and Spiller 1987a; Spiller and Schoener 1988) that lizards exert a major impact on orb-spider populations. In particular, *Argiope argentata* is one of the two species showing the greatest "lizard effect" in comparative surveys, islands with lizards being inhabited by many fewer *Argiope* for a given island size than islands without lizards. *Argiope* is never extremely abundant on a lizard island, whereas it can show explosive population growth in the absence of lizards. Although *Argiope* was not common in the plots we used to investigate the effect of lizards experimentally, lizard removal affected *Argiope* proportionately about as much as the other species of orb spiders present. Thus lizards would seem to be a major predator of *Argiope* (a large wasp has also been observed to attack *Argiope* in this system, and other arthropods as well as other vertebrates, e.g. birds, may do likewise).

We do not have information on the sizes of *Argiope* eaten by various sizes of lizards, but *Anolis* lizards, those most common on our study islands, are gape-limited predators that generally show a strong intraspecific relation (and often an interspecific relation) of prey size to head size (Pacala and Roughgarden 1985; Schoener 1967, 1968; Schoener and Gorman 1968; but see Floyd and Jenssen 1983). Smaller size classes of *Anolis* in the Bahamas, to which most lizards belong (Schoener and Schoener 1980), rarely take prey as large as 20–25 mm, the largest sizes of *Argiope argentata* [see data on Bimini *Anolis sagrei*, *A. distichus*, and *A. carolinensis*, females and juveniles, in Schoener (1968, Figs. 1, 2, and 4) and data on Exumas anoles in Spiller and Schoener (1990, Fig. 1)]. Differential harmfulness of the larger spiders to potential predators, or the appearance of such harm, could also affect spider sizes eaten and may reinforce the apparently-larger-size (ALS) hypothesis. Moreover, larger spiders may be less vulnerable to lizard predators because their webs are larger, so a lizard must jump farther to capture the spider; this may also affect the size and presence of the stabilimentum.

Commonness of lizards in our Bahamas system may, in addition to differences in the size classes studied, explain the commonness of our spiders having stabilimenta as compared to Panama sites – 87.6% (1984 data) for all Bahamas spiders vs 34.6% (Robinson and Robinson 1970) or 33.2% (Nentwig and Rogg 1988) for Panama adults only (note we do not distinguish adults in our study); or versus 54.8% for Panama juveniles and 26.2% for Panama subadults (Nentwig and Rogg 1988). Data of Marples (1969) for *A. argentata* (sizes unspecified) around Kingston, Jamaica, are more similar to ours: 75.4% (no repeated observations) or 84.8% (including

repeated observations on given individuals) had stabilimenta. However, all our data were obtained from islands without lizards. Because the study islands are surrounded by much larger islands that invariably have lizards, immigration from islands with lizards must be very common (see also Schoener and Spiller 1987b), so that gene flow is probably quite high. However, this situation does demonstrate that if lizards are the major predators, stabilimenta are not behaviorally flexible responses to their presence. In partial contrast, Lubin (1975) found stabilimenta in two Galápagos populations of *A. argentata* to be more frequent on that island with more predatory bird species.

An argument similar to the preceding can be made for the conspicuousness hypothesis; however, insectivorous birds, that predator toward which the advertisement is supposed mainly to be directed, breed on fewer islands in our system than do lizards (although birds may casually visit all islands, and the hypothesis may apply to lizards).

Commonness of stabilimenta on our islands could support a mechanical function, if the strong winds that frequently affect the islands make support or adjustment more desirable (but see Lubin 1975).

2. *All measures of absolute cruciform stabilimentum size show a curvilinear relation to spider size, increasing at a decreasing rate; the fitted curve for "total segment length" has its greatest values at intermediate spider sizes.* This characteristic provides major support for the ALS hypothesis: the largest spiders do not need to appear much larger still, and the smallest spiders cannot appear large no matter what they do, because of the small sizes of their webs and bodies, as well as perhaps energetic constraints on the production of the necessary dense silk. The fact that measures of stabilimentum size that include the gap (if present) between a segment and the web center (measures 1 and 2) are less domed indicates that such gaps tend to be disproportionately large in the larger spiders, perhaps because such spiders are quite robust and gain little from appearing larger still.

The ALS argument assumes that the largest spiders are less likely to be attacked than intermediate-sized spiders, an assumption for which we have no direct evidence but some indirect evidence (see 1 above on lizard diets). For small spiders, however, the additional apparent size they would gain could take them into the range of the most preferred size classes, i.e., those providing the highest potential energy that can still be easily swallowed, as in optimal foraging models (e.g. Schoener 1969). For such small spiders, the cruciform stabilimentum may serve an entirely different function, i.e., direct camouflage. Recall that in the smallest spider size-class, stabilimenta with two segments were differentially more common [Table 2; a similar result was obtained for *Argiope flavipalpis* in Ghana by Ewer (1972)]. The apparently continuous outline of a linear stabilimentum (i.e., the two segments are opposed so that they lie along a more-or-less straight line) could conceal a spider situated on a segment or between segments. For example, in some *Cyclosa* the spider positions itself at one end of the feces-studded linear stabilimentum, so that the

hub appears to contain some elongated plant part. In fact, all 70 stabilimenta we observed (in 1984) with two segments are linear except those of two relatively large (16 mm, 19 mm) spiders; thus all small spiders with two segments have linear stabilimenta. The differential presence of incomplete stabilimenta for small spiders may contribute toward the left-hand rise of the relation for total segment length in Fig. 3; however, the relation of mean segment length to body size is still very significantly curved (see Results). Finally, at certain intermediate spider sizes, the full cruciform stabilimentum, because of its resemblance to a much larger spider than the occupant, may distract a predator, allowing the occupant to escape; this is consistent with the tendency (albeit not quite statistically significant) for spiders with cruciform stabilimenta to drop or otherwise to leave the web more frequently when disturbed than do spiders with discoid stabilimenta.

The curvilinear relation of stabilimentum size to body size may favor a particular version of the mechanical hypothesis, that in which the stabilimentum serves to support the spider. Robison and Robison (1973) report that immature *Nephila clavipes*, among other species, construct a stabilimentum in "skeleton webs"; they believe support for molting is the most likely function. A molting function could contribute toward the tendency of immature *Argiope* to have the largest stabilimenta in our system: the largest (i.e., adult female) spiders do not molt, and the larger a molting spider, the more support is needed. However, this function alone is not sufficient to explain our data, because adults often have stabilimenta. Moreover, *Argiope* is able to molt without a stabilimentum (Nentwig and Rogg 1988), although having one could increase survivorship.

The curvilinear relation of stabilimentum size to body size could support a conspicuousness function, if a threshold exists above which a web is "conspicuous enough." As for the pure ALS hypothesis (i.e., without the additional camouflage function), constraints on stabilimentum size for the smallest spiders must be argued to exist.

3. *Stabilimenta of all types are more likely to be found among intermediate-sized spiders than among the smallest or largest spiders.* This presence/absence pattern of stabilimenta (Table 1) provides a similar kind of support for ALS as the results just discussed in section 2: an argument for a smaller cruciform stabilimentum logically extends to an argument for no stabilimentum at all (see section 5 for the argument for the discoid stabilimentum). Robison and Robison (1970) view the frequent absence of any stabilimentum in their field system as a serious argument against a predator-defense hypothesis; they argue (B. Robison and M. Robison 1978) that this is further supported by the lesser frequency of cruciform stabilimenta under confined laboratory conditions except when molting. As discussed above (section 1), however, we found a much smaller percentage of spiders without stabilimenta than even for their field system. Moreover, as we said above (section 2), ALS predicts that the largest spiders should not have as large a stabilimentum as intermediate sized spiders;

having no stabilimentum is consistent with this expectation. Finally, the spider *Nephila clavipes*, which in the Bahamas reaches an even larger size than *A. argentata*, rarely has stabilimenta in perfect webs, and then only in immatures (Robison and Robison 1973); these characteristics would support ALS were stabilimenta to function in defense in this species.

Implications for the mechanical and conspicuousness hypotheses are similar to those of the last section (2).

4. *Cruciform stabilimenta are often "incomplete," i.e., one or more of the four segments are missing.* Robison and Robison (1970) consider this fact very damaging to the predator-defense hypothesis. If the function of the stabilimentum were mostly to confuse the predator, Ewer (1972) and Eberhard (1973) point out that irregular incompleteness would not be a disadvantage. For one form of the predator-defense hypothesis, ALS, we agree incompleteness could present a problem if four segments were necessary for a significant advantage, this in part depending on perceptual properties of the predators. However, spiders in our study showed a substantially higher percentage of complete stabilimenta than that reported for Panama *A. argentata*. Among the (adult) webs with (non-aberrant) cruciform stabilimenta studied by Robison and Robison (1970), 54.5%, 30.1%, 6.4% and 9.0% had 1, 2, 3 and 4 segments, respectively. The figures for adults studied by Nentwig and Rogg (1988) are similar: 61.4, 23.2, 7.2 and 8.1%. Juveniles studied by Nentwig and Rogg (1988) had a greater fraction of 2-segmented stabilimenta, but still very few 3- or 4-segmented stabilimenta (35.5, 58.8, 1.4 and 4.3%, respectively); their subadults were more-or-less intermediate. The same figures for our webs (1984 data, all individuals, cruciform only) were 7.0, 35.8, 3.2 and 54.0%; even the largest spider sizes we studied did not have as low a percentage of complete stabilimenta [Table 2; see also Marples (1969, Table 3) for data similar to ours]. Moreover, as argued above (section 2), concealment of small spiders may be aided, or at least not harmed, by incomplete stabilimenta.

As Robison and Robison (1970) argue, incomplete stabilimenta may be quite consistent with the tension-adjustment version of the mechanical hypothesis, if different portions of the web needed adjustment upon each reconstruction.

The significance of incomplete stabilimenta for the conspicuousness hypothesis is similar to that for the ALS hypothesis, as the fewer the segments the less visible would be the web. For conspicuousness, however, it is perhaps more plausible that any kind of stabilimentum would confer a significant advantage.

5. *Spiders having discoid stabilimenta show a differentially high proportion of shuttling behavior. The discoid stabilimentum is a major alternative to a cruciform stabilimentum among intermediate-sized spiders.* Discoid stabilimenta were commonest among intermediate-sized spiders and did not occur for spiders larger than 12 mm; this cutoff is similar to findings of B. Robison and M. Robison (1978). Spiders having discoid stabilimenta are more likely than others to shuttle to the opposite

side of the orb when disturbed; similar characterizations on a species-by-species basis are reported by Edmunds [1986; see especially Robinson and Robinson (1970), Tolbert (1975)] for various *Argiope* species, including *A. argentata*. The shuttling behavior is an extremely quick, surprisingly agile and almost graceful movement. It could function to protect the spider both by placing thick webbing between it and a predator, thereby shielding the spider, as well as by concealing the spider from view. [A "sunshield" function has also been suggested by M. Robinson and B. Robinson (1978)]. The association of shuttling behavior with presence of a discoid stabilimentum provides very strong support for the predator-defense hypothesis.

The frequent presence of the discoid alternative for spiders of intermediate size [Table 1; see also Ewer (1972)], with its attendant behavior, suggests that such spiders "require" protection, perhaps more than extreme (or at least larger) sizes. Furthermore, the fitted curvilinear function of Fig. 3 relating cruciform stabilimentum length to body length declines over most of the range of lengths of those spiders that never have discoid stabilimenta. Additionally, discoid stabilimenta could conceivably be abandoned in favor of cruciform stabilimenta, or no stabilimentum at all, in part because of the impracticality of constructing dense silken structures large enough to conceal the largest spiders.

Spiders without discoid stabilimenta do, however, sometimes shuttle (e.g. Fig. 4). Especially for small spiders, a cruciform stabilimentum extending continuously through the center, or with the sheet-like matted silk sometimes found at the center between segments, could function to conceal and shield in a similar way to a discoid stabilimentum.

Differential frequency of the discoid stabilimentum between spider sizes does not relate to mechanical or conspicuousness hypotheses in any way obvious to us; presence of a discoid stabilimentum, of course, would increase conspicuousness (e.g., Eisner and Novicki 1983). The association of shuttling behavior with discoid stabilimenta would seem entirely unrelated to mechanical or conspicuousness hypotheses.

6. *Spiders often line up, with adjacent legs adpressed in pairs, so that one or more pairs of legs are collinear with a cruciform stabilimentum segment and the others are close to collinear.* We have no precise measure of this tendency, but Fig. 1a illustrates a fairly typical case. As pairs of legs are not always quite collinear with segments of the stabilimentum (e.g., Fig. 1a), the plausibility of this argument depends upon how close to perfect an adaptation is expected to be; we are more impressed by the nearness to collinearity than the imperfection of the behavior. Furthermore, the cruciform attitude of the spider (in which four pairs of adpressed legs, not eight separated legs, are the conspicuous feature), itself prima facie evidence, is according to Robinson and Robinson (1970) only adopted during the day (they believe this favors "leg concealment" as a function).

Because the mechanical argument has little theoretical development as yet, it is hard to evaluate with respect to the above behaviors; possibly the position of the

spider's legs is consistent with both a support function and an adjustment function.

Depending on the perceptual properties of predators, the conspicuousness hypothesis could be either supported or not by the spider's alignment. An aligned spider may reinforce the cruciform image of the stabilimentum, making the total more conspicuous. On the other hand, the full extent of the web might be better indicated by a misaligned spider (and indeed, by a more dispersed stabilimentum).

7. *The zig-zag patterning of the cruciform stabilimentum resembles the striped legs of spiders, making the spider appear larger.* Here we are in apparently complete disagreement with Robinson and Robinson (1970), who argue (against Hingston 1927) that there is a contrast between the legs and the stabilimentum. Ours would be an extremely difficult claim to back up with some kind of precise measurement, and we can only offer Fig. 1a as a plausibility argument: to us, the alternation of light and dark of the zig-zag stabilimentum segment is similar to the alternation of light and dark on the leg. Of course, perceptual properties of the predators may be very different from ours, but it is not obvious how else the stabilimentum could be arranged to make it look *more* like a striped, solid object.

It is possible that a sufficiently well-developed theory would explain how the zig-zag elements relate to adjustment and/or support, and so be evidence for a mechanical hypothesis.

Both the zig-zag patterning and striped legs could be deemed conspicuous and so at least be consistent with a conspicuousness function for the stabilimentum.

8. *Vibrating behavior for spiders with cruciform stabilimenta is commoner for large than small spiders; no significant relation of vibrating behavior to stabilimentum type exists.* Our second result here can be compared with those of Edmunds (1986) and Tolbert (1975), who report that spider species with a higher proportion of stabilimenta or more extensive stabilimenta vibrated more often. Although we had only nine individuals without stabilimenta, in conformity with the general size trend, the seven that did not vibrate were all very small (0.5–1 mm), whereas the two vibrating spiders were both large (13, 15 mm).

Vibrating behavior has been argued to increase apparent size of the spider (Edmunds 1986). Were this to be so, our finding would contradict the ALS hypothesis, because ALS assumes that the largest spiders are less in need of increasing apparent size than are intermediate-sized spiders (unless, of course, vibrating is the principal reason why they are less in need). We suggest vibrating behavior functions to render the exact location of the spider more difficult to discern, and the spider more difficult to grasp, both reducing the likelihood of a successful predator attack (see also Tolbert 1975). Additionally, especially for arthropod predators, vibration may serve as a "scare" or "startle" tactic.

Vibrating behavior has no obvious implication for a mechanical hypothesis. Whether or not it supports assumptions of the conspicuousness hypothesis depends

on whether or not vibrating behavior renders the spider more or less visible.

In conclusion, most of the eight characteristics reviewed above support or are at least consistent with the predator-defense hypothesis. This is in agreement with that function concluded in the more general treatments of Edmunds (1986) and Eberhard (1990) to apply to the majority of cases. In addition, many characteristics support the ALS version of that hypothesis, while a few are hard to account for with a mechanical or conspicuousness hypothesis. However, our analysis is restricted to certain *Argiope argentata*, and other hypotheses may be required for other species, e.g. the stabilimentum of immature *Nephila clavipes* (Robinson and Robinson 1973) discussed above. Moreover, stabilimenta vary in kind within *Argiope argentata*, and these must function in at least somewhat different ways. Even the cruciform stabilimentum is likely to function differently depending on spider size. Finally, Nentwig and Rogg (1988) suggested "stress" rather than some adaptive reason for stabilimentum occurrence; they view the stabilimentum as perhaps originally evolved to facilitate molting but no longer necessary in that regard.

Further progress in this general area would be aided by development of a more detailed mechanical theory and by additional experimentation of all kinds, including that using potential predators.

Acknowledgements. Supported by grants from the United States National Science Foundation. The reviewers and the editor made helpful comments.

References

- Bristowe WS (1958) The world of spiders. Collins, London
- Comstock JH (1940) The spider book (Revision of 1912 edition), Comstock Publishing, New York
- Craig C, Bernard GD (1990) Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* 71: 616–623
- Eberhard WG (1973) Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. *J Zool London* 171: 367–384
- Eberhard WG (1990) Function and phylogeny of spider webs. *Annu Rev Ecol Syst* 21: 341–372
- Edmunds J (1986) The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in West Africa, with a discussion of the function of stabilimenta. In: Eberhard WG, Lubin YD, Robinson BC (eds) Proceedings of the ninth international congress of arachnology, Panama, 1983, Smithsonian Press, Washington, pp 61–72
- Eisner T, Nowicki S (1983) Spider web protection through visual advertisement: role of the stabilimentum. *Science* 219: 185–187
- Ewer RF (1972) The devices in the web of the West African spider *Argiope flavipalpis*. *J Nat Hist* 6: 159–167
- Floyd HG, Jenssen TA (1983) Food habits of the Jamaican lizard, *Anolis opalinus*: resource partitioning and seasonal effects examined. *Copeia* 1983: 319–331
- Hingston RWG (1927) Protective devices in spiders' snares, with a description of seven new species of orb-weaving spiders. *Proc Zool Soc London* 1927: 259–293
- Horton CC (1980) A defensive function for the stabilimenta of two orb weaving spiders (Araneae, Araneidae). *Psyche* 87: 13–20
- Lubin YD (1975) Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae, Araneidae) on Daphne and Santa Cruz Islands, Galápagos. *J Arachnol* 2: 119–126
- Marples BJ (1969) Observations on decorated webs. *Bull Brit Arach Soc* 1: 13–18
- McCook HC (1889) American spiders and their spinning work. Philadelphia, Academy of Natural Sciences
- Nentwig W, Rogg H (1988) The cross stabilimentum of *Argiope argentata* (Araneae: Araneidae) – nonfunctional or a nonspecific stress reaction? *Zool Anz* 221: 248–266
- Pacala S, Roughgarden J (1985) Field experiments with *Anolis* lizards in the Lesser Antilles. *Ecology* 66: 129–141
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43: 223–225
- Robinson B, Robinson MH (1978) Developmental studies of *Argiope argentata* (Fabricius) and *Argiope aemula* (Walckenaer). *Symp Zool Soc London* 42: 31–40
- Robinson MH, Robinson B (1970) The stabilimentum of the orb web spider, *Argiope argentata*: an improbable defence against predators. *Can Entomol* 102: 641–655
- Robinson MH, Robinson B (1973) The stabilimentum of *Nephila clavipes* and the origins of stabilimentum-building in araneids. *Psyche* 80: 277–288
- Robinson MH, Robinson B (1978) Thermoregulation in orb-web spiders: new description of thermoregulatory postures and experiments on the effects of posture and coloration. *Zool J Linn Soc* 64: 87–102
- Schoener TW (1967) The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155: 474–477
- Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726
- Schoener TW (1969) Models of optimal size for solitary predators. *Am Nat* 103: 277–313
- Schoener TW (1986) Patterns in terrestrial vertebrate versus arthropod communities: do systematic differences in regularity exist? In: Diamond J, Case TJ (eds) Community ecology. Harper & Row, New York, pp 556–586
- Schoener TW (1991) Extinction and the nature of the metapopulation: a case system. *Acta Oecol* 12: 53–75
- Schoener TW, Gorman GC (1968) Some niche differences among three species of Lesser Antillean anoles. *Ecology* 49: 819–830
- Schoener TW, Schoener A (1980) Densities, sex ratios and population structure in four species of Bahamian *Anolis* lizards. *J Anim Ecol* 49: 19–53
- Schoener TW, Spiller DA (1987a) Effect of lizards on spider populations: manipulative reconstruction of a natural experiment. *Science* 236: 949–952
- Schoener TW, Spiller DA (1987b) High population persistence in a system with high turnover. *Nature* 330: 474–477
- Schoener TW, Toft CA (1983) Spider populations: extraordinarily high densities on islands without top predators. *Science* 219: 1353–1355
- Siegel S (1956) Nonparametric statistics. McGraw-Hill, New York
- Simon E (1893) Histoire naturelle des araignées. Vol 1. Roret, Paris
- Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. WH Freeman, San Francisco
- Spiller DA, Schoener TW (1988) An experimental study of the effect of lizards on web-spider communities. *Ecol Monogr* 58: 57–77
- Spiller DA, Schoener TW (1990) Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* 83: 150–161
- Toft CA, Schoener TW (1983) Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos* 41: 411–426
- Tolbert WW (1975) Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *Psyche* 82: 29–52