Spider Web Protection Through Visual Advertisement: Role of the Stabilimentum

Abstract. *The conspicuous white silken adornments known as stabilimenta, which are commonly found in the orb webs of some spiders, appear to be protective devices that warn birds of the presence of webs in their flight path. Webs endowed with artificial equivalents of stabilimenta tended to survive intact the early morning period when birds are on the wing; unmarked webs showed a high incidence of destruction.*

Biologists have long been puzzled by the function of the so-called stabilimenta in the orb webs of certain spiders (*1*). Consisting of loosely spun bands or patches of white silk laid out across the center of the web, stabilimenta make the orbs more conspicuous, often allowing the webs to be detected from a distance by the human eye. Stabilimenta take on different forms. Some are laid out in the pattern of an X, others in a vertical strand, and still others in a quasi-circular patch (Fig. 1, A to F).

Stabilimenta are produced by spiders of the two major families of orb weavers, Araneidae and Uloboridae (*2*), but only by species that spin durable webs persisting through the daytime. Spiders that spin in the evening and take their webs down at dawn do not add stabilimenta to the orbs. This suggests that stabilimenta are visual markers that are apparent in the daytime and serve as deterrents to potentially destructive, visually oriented animals such as birds, which might otherwise tear through the webs in flight. While it is of obvious benefit to spiders to protect their webs against needless destruction, birds themselves could profit from heeding the warnings implicit in the markers, since flying into webs could have a startling effect as well as leave the birds contaminated with the web's sticky threads. We present experimental evidence indicating that web stabilimenta contribute significantly to daytime web durability.

Casual observation by one of us (T.E.) on Barro Colorado Island, Panamá, and Islamorada Key, Florida, had shown that birds on the wing may take short-range evasive action when approaching spider webs. On several occasions unidentified birds that were hunting aerial insects were seen to change flight direction abruptly and to fly up and over webs just before making actual contact with the orbs. The spiders, which were abundant at both sites, with webs that spanned many of the lower flight paths in the area, were species of *Argiope*, which add conspicuous stabilimenta to their webs (*3*).

In order to test for the diurnal web-preserving capacity of visual web markers, a comparison was made of the durability of 30 natural webs without stabilimenta that served as controls (Fig. 1G) and 30 comparable webs that were adorned with artificial equivalents of stabilimenta. The webs used in the test were mostly those of spiders that construct webs at night and take them down at dawn (Table 1) (*4*). In order to expose the webs in the daytime, the spiders were removed from the webs before 2 a.m. and after they had completed web construction. The experimental webs were marked with adornments immedi-

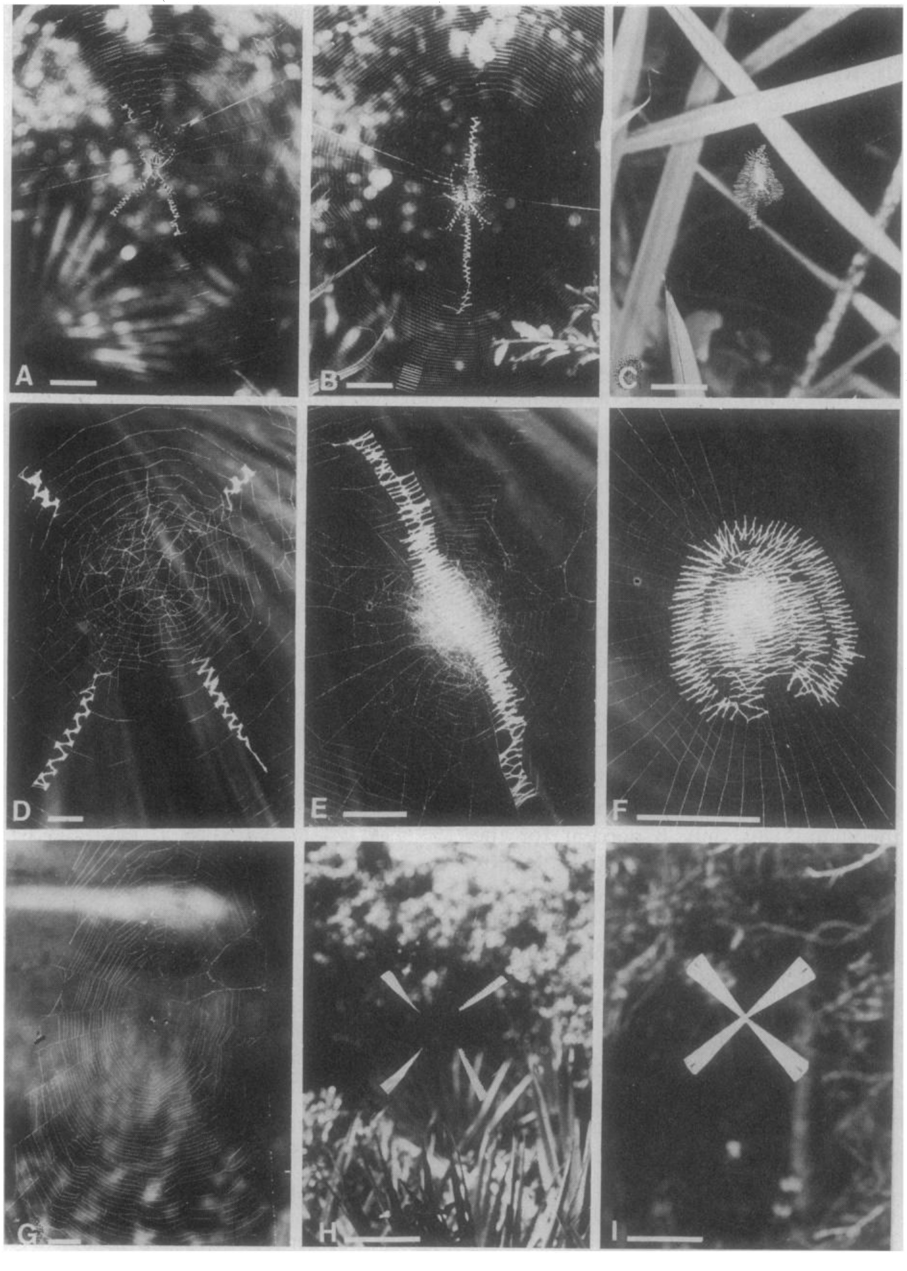

Fig. 1. (A to F) Webs and enlarged views of stabilimenta of three orb-weaving spiders: *Argiope florida* (A and D); *Argiope aurantia*, mature (B and E); *Argiope aurantia*, juvenile (C and F). (G) Web of a nocturnal spider (probably *Eriophora ravilla*) that does not weave stabilimenta; such webs are usually taken down by the spider at dawn; in our experiments they tended to be destroyed if left exposed in daytime. (H and I) Artificial stabilimenta used in our experiments were either applied to the web (H) or suspended by threads immediately beside the web (I). Scale bars: (A to C) 3 cm; (D to F) 1 cm; and (G to I) 5 cm.

Table 1. Source, treatment, and number of webs used in the web persistence experiment (Fig. 2).

Spider	Number of webs		
	No stabilimentum	Stabilimentum added	
		On web	Beside web
Acacesia hamata	5	4	
Eriophora ravilla	12	6	3
Eustala sp.	1	3	1
Eustala cepina	4	1	1
Eustala emertoni		2	
Neoscona domiciliorum	8	9	
Total	30	25	5

ately after removal of the spiders. On 25 of these webs the markers consisted of four triangular strips of white paper laid out to form the arms of an X and attached directly to the web's viscid threads (Fig. 1H). On the remaining five webs the marker was a rigid white X (*4*) placed in close parallel to the center of the web and suspended by four black threads tied to adjacent shrubbery (Fig. 1I). By this latter arrangement the webs were provided with markers without being physically loaded. The X-shaped markers were roughly imitative of the stabilimentum of *Argiope florida*, one of the dominant spiders at our study site (*5*).

The test webs were checked just before dawn (6 a.m.) and at 2-hour intervals thereafter until noon. Webs were scored as "intact," "damaged" (if at least half of the supporting radial threads were broken, but the web was still in place), or "destroyed" (completely gone or consisting of loose dangling fragments only). Webs that showed only occasional small perforations were rated as intact (*6*).

The results were clear-cut (Fig. 2). During the dark period before 6 a.m. the marked and unmarked webs showed about equal persistence (85 and 87 percent, respectively; $P = .50$) (*7, 8*); after dawn only the marked webs tended to endure (*9*). By noon more than 60 percent of the marked webs were still intact; the figure was only 8 percent for the unmarked controls ($P < .001$). Results with the two types of marked webs did not differ significantly ($P > .20$) and were therefore combined. Web durability was therefore due to the presence of the visual markers and not to the strengthening of the directly marked webs effected by incorporation of the paper strips into the fabric of the web.

We predicted that if flying birds were responsible for the destruction of unmarked webs, we should be able to witness early morning bird-web encounters at our study site at the rate of 0.24 encounter per hour of web observation (*10*). Webs were observed for a total of 7.5 hours (*11*), and one such encounter was witnessed. The bird, a rufous-sided towhee (*Pipilo erythrophthalmus*), faltered momentarily upon hitting the web and dropped conspicuously in its flying trajectory, but proceeded without alighting and vanished from sight. The web (of *Eriophora ravilla*, 1.5-m web diameter) was totally ripped away.

Although we conclude from these data that spider stabilimenta serve as visual advertisements of webs, we do not mean to imply that flying birds are the only animals potentially forewarned by the markers. Larger ambulatory mammals might also be deterred, to the obvious benefit of the spiders (*12*). Even larger insects might at times react visually to spider webs. We have on several occasions seen butterflies (heliconiids in Panamá; papilionids and the danaid *Danaus gilippus* in Florida) change direction abruptly in front of *Argiope* webs and fly upward and past the orbs. The warning may result in occasional prey loss to a spider, but the detriment may be less severe than total web destruction. A spider invests more than time and spinning energy in the construction of its web. The proteinaceous silk is itself a resource, which the spider ordinarily ingests when it takes down its web (*13*), and which it may irretrievably lose when the web is torn away by a vertebrate.

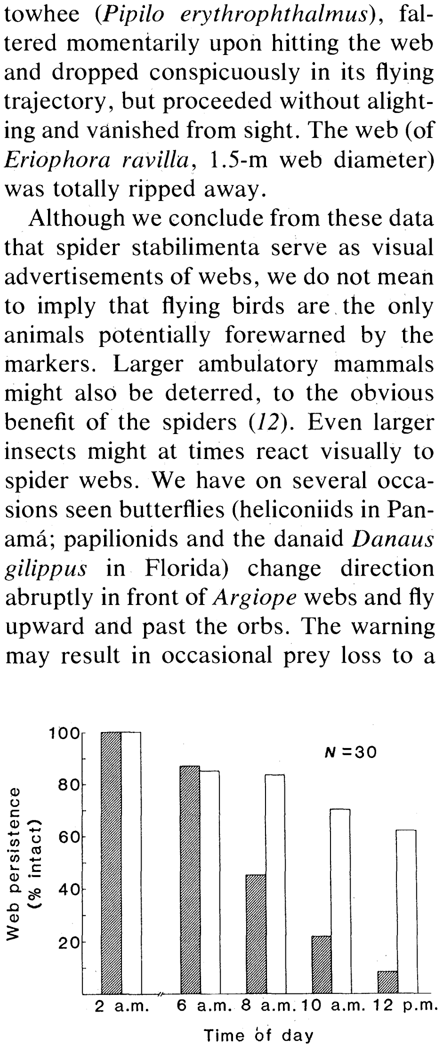

Fig. 2. Web persistence (percentage of intact webs) at various times of day. Open bars represent experimental webs with artificial stabilimenta; data for those with markers directly applied ($N = 25$) and those suspended beside webs ($N = 5$) were combined. Hatched bars represent unadorned control webs. Damaged (as opposed to destroyed) webs are rated as half intact; hence, the percentage of intact webs = $[(\text{number intact} + 1/2 \text{ number damaged})/N] \times 100$. Sunrise was approximately 7:15 a.m., with first light at 6:30 a.m. eastern daylight time.

By calling attention to a web, a stabilimentum could also operate to the detriment of a spider by attracting unwelcome visitors to the web. Robinson and Robinson (*14*), on the basis of tests with model stabilimenta, conclude that birds might use the markers as aids to prey location. On the other hand, tests by Horton (*2*) suggest that blue jays (*Cyanocitta cristata*) may learn to shun contact with webs, prefer spiders as prey when these are out of webs, and may recognize webs on the basis of stabilimental markers. Attraction might still be detrimental in the case of certain predatory wasps (*15*), which could cue in on stabilimenta in their search for the orb-weaving spiders that they use to provision their nest cells.

Numerous functions have been suggested for stabilimenta (*1, 14, 16, 17*), most without supporting evidence. Some simple tests showed that removal of stabilimenta does not impair the spider's ability to capture its prey. By use of hot needles we singed away the stabilimenta in four orbs of *A. florida*, taking care not to transect any of the structural strands of the webs. Insects that we subsequently dropped into the orbs were all instantly located by the spiders, which pounced on them, spun them in, and proceeded to feed on them. Furthermore, none of the spiders' normal defensive behaviors (web shaking, moving across the hub from one side of the orb to the other, or dropping to the ground), which we elicited by poking the spiders, seemed to be affected by the removal of the stabilimenta.

There is one abundant well-known New World spider, *Nephila clavipes*, that constructs diurnal webs ordinarily devoid of stabilimenta. The orbs of *Nephila* are nonetheless relatively conspicuous in daytime, because the strands of its viscid silk are yellow (*17*). We suggest that the yellow coloration serves specifically for web advertisement, in the same adaptive context as advertisement by stabilimenta.

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References and Notes

1. M. H. Robinson and B. C. Robinson, *Psyche* **80**, 277 (1973).
2. C. C. Horton, *ibid.* **87**, 13 (1980).
3. H. W. Levi, *Bull. Mus. Comp. Zool. Harv. Univ.* **136**, 319 (1968).
4. The X was cut from stiff white plastic and had arms roughly matching the triangular paper markers.
5. The study was conducted at the Archbold Biological Station, Lake Placid, Highlands County, Florida, a relatively undisturbed, sandy, scrub oak–palmetto, highlands habitat. *Argiope aurantia*, with a vertical-band or patch stabilimentum (Fig. 1, E and F), was also abundant at the site. We made our observations from 12 to 20 August 1981.
6. We attribute such perforations to damage inflicted by larger insects that flew through the web or by others that worked themselves loose after entrapment.
7. Of the total of 60 webs (marked and unmarked), seven were destroyed and three were damaged by 6 a.m. Destruction during the night might have been caused by bats, flying squirrels, gusting wind, or large beetles or moths. Because of the invisibility at night of our markers, the comparable incidence of destruction in the marked and unmarked webs in the period before 6 a.m. was to be expected.
8. These and subsequent statistics are based on 3 by 2 chi-square contingency tests comparing marked and unmarked webs for the three categories: intact, damaged, and destroyed.
9. Scores by noon (intact, damaged, and destroyed) were as follows: 2, 1, and 27 for unmarked webs; and 14, 9, and 7 for marked webs (both types combined).
10. Calculation based on the fact that of the 27 unmarked webs that were intact at 6 a.m., 13 underwent damage or destruction by 8 a.m.
11. Observations were made from 6:30 to 8:00 a.m. on each of five unmarked webs, by four observers who were partially concealed, 7 to 10 m from the webs.
12. Because they are scarce, such mammals could not have been a major factor at our study site.
13. P. N. Witt, C. F. Reed, D. B. Peakall, *A Spider's Web: Problems in Regulatory Biology* (Springer-Verlag, New York, 1968).
14. M. H. Robinson and B. C. Robinson, *Can. Entomol.* **102**, 641 (1970).
15. M. H. Muma and W. F. Jeffers, *Ann. Ent. Soc. Am.* **38**, 245 (1945).
16. R. F. Ewer, *J. Nat. Hist.* **6**, 159 (1972); R. W. G. Hingston, *Proc. Zool. Soc. Lond.* **18**, 259 (1927); J. H. Marson, *ibid.* **117**, 219 (1947); W. W. Tolbert, *Psyche* **82**, 29 (1975).
17. J. H. Comstock, *Spider Book*, revised by W. J. Gertsch (Doubleday, Garden City, N.Y., 1940).
18. We thank H. W. Levi for identifying the spiders, D. Aneshansley for statistical advice, D. Dussourd and M. Malarcher for assistance with observations, the staff of the Archbold Biological Station for hospitality during our stay in the field, and an anonymous reviewer for helpful comments. Study supported in part by NIH grant AI-02908. Paper No. 71 of the series *Defense Mechanisms of Anthropods.*

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Adaptation of Fruit Morphology to Dispersal Agents in a Neotropical Forest

Abstract. *Two-thirds of 258 fruit species from Peruvian tropical forest belong to one of two classes: large orange, yellow, brown, or green fruits with a husk; or small red, black, white, blue, purple, or mixed-color fruits without a husk. The characteristics of the two fruit classes match the size, visual ability, and jaw morphology of mammals and birds, respectively, and the animals also prefer to eat one class of fruits. Thus, most plants in this forest seem to be adapted to seed dispersal by either of two distinct broad arrays of animal taxa.*

The intricate morphological adaptations of flowers to their pollinators are considered strong evidence for coevolution, but similarly clear adaptations of fruit morphology to one or a few disperser species are scarce (*1*). Yet it has long been known that various animal groups—ants, birds, bats—feed preferentially on fruits with distinctive disperser-correlated combinations of size, color, and construction (*2*). These disperser-specific morphologies (syndromes) are thought to indicate generalized evolutionary adaptation by plants to dispersers (*2, 3*). This evidence for adaptation has two difficulties. First, it is based on compilations of nonsystematic accounts of fruit-eating by animals from many localities and habitats (*4*). If only the more obvious examples of fruit-disperser correspondence were published, the derived correlations would be biased or exaggerated. Second, even if the observed correlations are accurate, they may represent only a small fraction of the fruit species that occur in one locality. Existing evidence does not rule out the possibility that a large proportion of plants in a community are morphologically poorly matched with their dispersers (*5*). Based on an extensive systematic analysis of fruit morphology from a single tropical forest, I show that a substantial majority of plant species have fruits of one of two distinct types corresponding to birds and mammals as major dispersers.

All the plant species with fleshy fruits known to have fruited between September 1980 and December 1981 were systematically collected and described in a tropical moist forest (*6*) at the Cocha Cashu Biological Station in the Manu National Park, Peru (71°22′W, 11°52′S). These 258 species represent approximately a quarter of the known plant diversity in the study area, and over half the genera with fleshy fruits (*7*). Potential disperser taxa in the study area include ants, fish, lizards, birds, bats, monkeys, and other mammals. Because primates were especially well studied in the area, fruits eaten by monkeys might have been more thoroughly sampled. I tried to counteract this possible bias by searching for all fruits produced in the study area.

For each fruit I recorded color (*8*), size, and presence or absence of a husk. Protected fruits were defined as those in which the ripe pulp is covered by a husk—a distinct stiff layer that is not nutritious and presents a barrier to feeding or digestion. Fruits with flexible skins less than 10 percent as thick as the smallest external fruit dimension were considered unprotected (for example, oranges are protected and cherries are not).

The species of many genera varied little with respect to the characters analyzed, yet virtually no family showed similar uniformity among component genera. Thus I considered the genus as the smallest independent unit of morphological classification. In the following analysis, I counted each nonvariable genus as only one form, assigning to it the morphology of its component species. Genera with appreciable variability of color or construction among species were assigned to two or more morphological forms as appropriate.

For the nonvariable genera, the frequency of protected fruit forms shows a statistically significant variation by color (Fig. 1) (*9, 10*). Almost every color category can be objectively assigned to one of two distinct sets, according to the percentage of protected fruits (*11*). Type A fruits, with few protected genera, contain red, white, black, and mixed colors, whereas type B fruits, with mostly protected genera, are orange, brown, yellow, or green. The blue and purple color category could be included in either type, but is most similar to type A (*12*), and is included in it for further analysis.

The same statistically significant asso-

Table 1. The distribution of fruit forms (N = 172) among all possible combinations of three dichotomous characters. There is a statistically significant association among the three characters and also among each pair of characters (*22*). Numbers in parentheses are values expected assuming joint independence of characters.

Size	Set A colors		Set B colors	
	Protected	Unprotected	Protected	Unprotected
≤ 14 mm	5 (17.3)	70 (33.0)	10 (14.3)	7 (27.4)
> 14 mm	6 (15.0)	13 (28.7)	38 (12.4)	23 (23.8)