

Do stabilimenta in orb webs attract prey or defend spiders?

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Orb-weaving spiders are ideal organisms for the study of conflict between behavioral investments in foraging and defense because their webs provide physical manifestations of those investments. We examined the impact of including stabilimenta, designs of bright-white noncapture silk, at the center of orb webs for foraging and defense in *Argiope aurantia*. Our findings suggest that stabilimentum building is a defensive behavior, supporting the “web advertisement” hypothesis that the high visibility of stabilimenta can prevent birds from flying through webs. Yet, spiders often do not include stabilimenta in their webs, indicating that a serious cost is associated with them. We also show, through comparison of paired webs with and without stabilimenta, that stabilimenta reduce the prey capture success of spiders by almost 30%. This demonstrates the potential impact that defensive behaviors of spiders can have on their foraging success and suggests that much of the variation in stabilimenta may be accounted for by a cost–benefit trade-off made when including stabilimenta in webs. *Key words*: aposematic signal, *Argiope*, foraging–defense trade-offs, predator–prey, silk, spider webs. [*Behav Ecol* 10:372–376 (1999)]

Conflict between foraging and predator avoidance can have a profound impact on the behavior of organisms (Lima and Dill, 1990; Sih, 1980; Stephens and Krebs, 1986). Animals may forage in lower energy patches that have reduced risks of predation (Gilliam and Fraser, 1987; Holomuzki, 1986; Lima, 1985; Lima et al., 1985) or engage in defensive behaviors that reduce their foraging efficiency within patches, such as vigilance or hiding (Rothley et al., 1997; Schmitz et al., 1997; Sih et al., 1992; Skelly, 1995). Ultimately, this conflict results in a suite of foraging and defense strategies, each of which may be selectively advantageous in different environments. This may lead to selection for the ability of organisms to actively manipulate the trade-offs they make in changing environments (Rothley et al., 1997; Turner, 1997). Before the adaptive value of varying strategies in different environments can be studied, it is essential to identify the costs and benefits of the behaviors when organisms adopt those strategies.

Orb-weaving spiders provide an ideal model for the study of conflict between behavioral investment in foraging and defense because their webs are physical manifestations of their behaviors. The orb web is clearly a tool used in foraging (Eberhard, 1990), but the sticky silk and additional silk structures such as barrier webs can also serve as defenses against predators (Cloudsley-Thompson, 1997; Edmunds and Edmunds, 1986; Higgins, 1992; Rayor and Uetz, 1990; Tolbert, 1975). Unlike the transient behavioral trade-offs between foraging and defense made by animals engaging in vigilance or hiding, making a web is unique because the trade-off it represents is constant over the course of a single day. Yet spiders can alter that investment between days when webs are rebuilt. Stabilimenta are conspicuous lines or spirals of silk, included by many spiders at the center of their otherwise cryptic webs. They provide an example of how extreme variability in investment can occlude the functional role of web structures because their high degree of variation in shape and frequency often seems incompatible with existing functional hypotheses

(Blackledge, 1998a; Eberhard, 1990). We examine the functional role of stabilimenta in webs and how predator–prey conflict can explain their variability.

The reflectance of ultraviolet (UV) light by stabilimenta has been used to argue that they attract prey to webs (Craig, 1991, 1994b; Craig and Bernard, 1990; Elgar et al., 1996; Hauber, 1998; Tso, 1996, 1998a,b). Craig and Bernard (1990) and Tso (1996, 1998b) used correlations between high prey capture and presence of stabilimenta in webs to support this hypothesis. But Blackledge (1998b) demonstrated that high prey capture causes spiders to build stabilimenta more often, creating this same pattern. He proposed that spiders with low foraging success did not build stabilimenta because insects could use them to avoid webs. Furthermore, a consideration of the reflective properties of stabilimenta across the entire insect visual spectrum, rather than only UV wavelengths, suggests that the silk is cryptic to insects, compared to more primitive silks (Blackledge, 1998a). Thus, the role of stabilimenta in the attraction or repulsion of prey to webs remains to be tested in a manipulative experiment.

Stabilimentum-building spiders are largely diurnal (Eberhard, 1973; Scharff and Coddington, 1997) and rest at the center of their webs where they are exposed to visual predators, as opposed to nocturnal spiders or those species resting in retreats (Eberhard, 1973, 1990). Horton (1980) demonstrated that stabilimenta can prevent predation by captive birds, and Eisner and Nowicki (1983) found that stabilimentum-like designs of paper reduced the rate of damage to webs, presumably from birds. Decreased frequencies of stabilimenta have also been associated with absence of bird predators in island populations of *Argiope* spp. (Kerr, 1993; Lubin, 1975). These studies suggest that one defensive function of stabilimenta is to warn birds and prevent damage to webs from accidental bird fly-through or even predation of spiders. Yet no field test of the “web advertisement” function has been conducted using webs of actual stabilimentum-building spiders and natural populations of birds.

We directly examined the effect of stabilimenta on the prey capture success of the yellow garden argiope, *A. aurantia* (Araneae: Araneidae). We also conducted the first test of the web advertisement hypothesis (Eisner and Nowicki, 1983) to use real stabilimenta and natural populations of birds. Finally, we discuss the implications of our results for a cost–benefit model to explain variation of stabilimenta.

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METHODS

Stabilimenta and prey capture

We collected adult and subadult female *A. aurantia* along a drainage culvert in Gainesville, Florida, USA, during mid-July and immediately transported them back to Ohio. This allowed us to begin the experiment before native *A. aurantia* were mature. The experiment was conducted in a field adjacent to the Rothenbulla Honeybee Laboratory at Ohio State University. The field had a vegetation structure similar to the typical habitat of *A. aurantia*, and both *A. aurantia* and *A. trifasciata* (an ecologically similar species) occurred there naturally. Approximately 200 beehives were scattered to the north, south, and west, most within a 0.5 km radius and provided a large population of visually proficient, flying insect prey.

Eight stations were haphazardly placed throughout the field. Each station consisted of a pair of square wooden frames (75×75×12 cm) with the large sides being removable plastic sheets. This allowed us to confine spiders to the stations while they built webs overnight, yet let them forage freely once the sides were removed. The two frames at each station were adjacent to one another and were oriented in the same direction, though we varied orientation haphazardly between stations. Therefore, both webs at a station experienced similar microhabitat variation.

We placed a single female *A. aurantia* in each frame, making an effort to pair similarly sized spiders. Each day on which both spiders at a site built webs, one was randomly designated as an “experimental” web and its stabilimentum was removed by using a wire heated by a small butane blowtorch to cut the two radii to which the stabilimentum was attached. The stabilimentum was then easily pulled from the web using forceps. We also performed sham removals on the other “control” web by cutting radii immediately adjacent to the stabilimentum, thus creating a similar-sized hole in the web. The random removal of stabilimenta controlled for variation in total web area, web height, and mesh size of webs, which would otherwise be important variables affecting prey capture (Eberhard, 1990; Higgins and Buskirk, 1992; Sherman, 1994).

Prey capture was observed over foraging trials lasting 3 h each, beginning between 0830 h and 1000 h. Because the trials ran into the afternoon, stabilimenta were exposed to a wide range of light conditions under which *Argiope* spp. forage (Endler, 1993). We collected all prey in webs and all prey on which spiders were actively feeding every half hour and stored the prey in ethanol for later identification. Very small prey could be consumed between collection periods so, although there is no reason to expect a bias between treatment groups, we restricted our analysis to prey larger than 3 mm. We identified prey to family under a dissecting scope after dissolving the swathing silk with chlorine bleach (Vetter et al., 1996).

Cages were kept closed outside of the foraging trials; therefore each spider was fed a single large mealworm (*Tenebrio molitor*) daily. This also helped standardize foraging motivation and size of stabilimenta (Blackledge, 1998b) between spiders. Spiders occasionally built new stabilimenta where they had been removed or over an existing one. These new stabilimenta were excised from the webs only in the experimental treatment. Any prey captured during a half-hour period in which a new stabilimentum was built were excluded from the analysis for both webs at that station.

To compare capture rates between web treatments, we categorized each station as to whether the majority of paired comparisons at that station had experimental webs catch more prey than control webs. We then used a *G* test to compare the number of stations in which experimental webs captured the

most prey, compared to control webs, in greater than 50% of the paired comparisons.

Stabilimenta and defense

To examine the interaction of birds with stabilimenta, at two sites we used setups which consisted of a dark blue plastic dish containing bird seed, surrounded by a triangular array of three frames (the same frames as described in experiment 1 above). Birds were allowed to acclimate to the setups containing empty frames before the experiment began. The west campus site was in a small field in a grassy forest clearing (approximately 15 m diam) which contained natural populations of both *A. aurantia* and *A. trifasciata*. The museum site was on a mown lawn adjacent to a bird feeder at the Museum of Biological Diversity, Ohio State University, an area which would not normally have *Argiope* spp.

For each trial, two of the three empty frames were randomly replaced, one by a frame containing a web with a stabilimentum (and sham operation as in experiment 1) and one by a frame containing a web with the stabilimentum removed. The third frame was left empty to provide birds with a “web-free” access route to the station. We conducted 12 trials at each site using webs without spiders. Then we conducted an additional eight and nine trials at the west campus and museum sites, respectively, using webs with spiders left in them. Comparison of the two sets of trials allowed us to determine whether the spider itself had any influence on avoidance of webs by birds.

Frames were put out at mid-morning and observed periodically until the first sign of bird impact, at which time the trial was ended, or until dusk if neither web was damaged. Bird impact was quite distinct from insect damage, as it consisted of destruction of entire pie-shaped sectors of the web or even collapse of part or all of the web. Occasionally both webs were damaged by the time of the first observation period and were therefore both scored as “damaged.”

Data from both sites were combined for this analysis, and the frequency with which experimental webs were damaged first was compared to that of control webs using chi-square tests. Comparisons between trials for webs containing spiders were made separately from comparisons between trials for webs without spiders.

RESULTS

Stabilimenta and prey capture

Prey capture was not normally distributed, but the mean capture rate for spiders in webs without stabilimenta was higher than that for spiders in webs containing stabilimenta (mean ± SE, 2.9±0.3 versus 2.0±0.3 prey/3-h trial; *n* = 55). Spiders in webs without stabilimenta caught the most prey in more trials than spiders in control webs, at a majority of stations (*G* = 5.603, *df* = 1, *p* < .025; Figure 1).

At least 31 families of prey were captured. The most common prey were Apidae (32%, mostly *Apis mellifera*) and Muscidae (22%, mostly *Stomoxys calcitrans*; Table 1). The capture of flies (Muscidae and Calliphoridae) was strongly influenced by stabilimenta (a 56% and 100% reduction, respectively). The reduction of capture of Apidae (40%), miscellaneous (33%), and unidentified (38%) taxa in webs containing stabilimenta were all similar to the overall reduction in prey capture of 34%.

Stabilimenta and defense

Webs without stabilimenta were damaged significantly more often than webs with stabilimenta during both the trials when

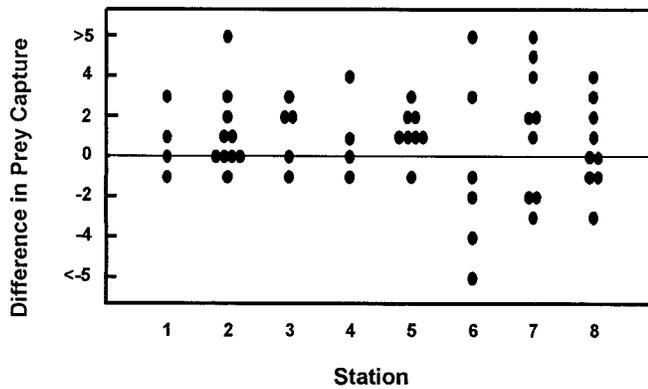


Figure 1

The distribution of differences in prey capture for 55 paired comparisons at 8 stations (difference = prey capture at webs without stabilimenta – prey capture at webs containing stabilimenta). Seven of eight stations that had webs without stabilimenta caught more prey than webs containing stabilimenta for >50% of the trials at the station ($G = 5.603$, $df = 1$, $p < .025$). The mean (\pm SE) prey capture rate over 3 h was 2.9 ± 0.3 for spiders in webs without stabilimenta and 2.0 ± 0.3 for spiders in webs with stabilimenta.

spiders were removed from the webs ($p < .001$; Table 2) and the trials when spiders were present in webs ($p < .005$; Table 2). There was no significant difference in the distribution of damage between the trials with and without spiders ($\chi^2 = 0.0985$, $df = 1$, $p > .754$).

DISCUSSION

The fitness costs of behavioral responses to predation risk can be substantial due to the reductions in foraging efficiency, alterations of patch choice, or modification of life histories which can be associated with those defensive behaviors (Lima and Dill, 1990; Schmitz et al., 1997; Scrimgeour and Culp, 1994; Sih, 1992; Skelly, 1995). Our study suggests that one function of stabilimenta is as a behavioral defense against birds because webs without stabilimenta are damaged more often by flying birds (Table 2). However, the defensive behavior of including stabilimenta in webs results in a serious reduction in the ability of *A. aurantia* to function as predators (Figure 1). Because predation pressure and prey density vary spatially and temporally, the trade-off that *A. aurantia* and similar stabilimentum-building spiders must make between the defensive benefits and foraging costs of including stabilimenta in webs may account for much of the variation seen in stabilimentum production both within and between *Argiope* spp.

Stabilimenta and prey capture

Our results contradict the hypothesis that stabilimenta attract prey to the webs of spiders (Craig and Bernard, 1990; Craig, 1994b; Hauber, 1998; Tso, 1996, 1998a,b) because we found that webs containing stabilimenta caught 34% fewer prey. Previous studies used web damage (Craig and Bernard, 1990; Hauber, 1998; Tso, 1996) or infrequent censuses (Tso, 1998b) as indices of prey interception rates and found correlations between the presence of stabilimenta in webs and high prey capture success. However, Blackledge (1998b) demonstrated that this same pattern is caused when spiders that catch more prey increase their frequency of stabilimentum construction. We controlled for this effect through direct manipulation of the presence of stabilimenta. Furthermore, we measured the

Table 1

Families of prey captured by *A. aurantia* in 55 pairs of webs, with and without stabilimenta

Taxa	No stabilimentum	Stabilimentum
Apidae	62	37
Muscidae	25	11
Calliphoridae	7	0
Halictidae	3	5
Pompilidae	3	3
Acrididae	2	3
Formicidae	0	5
Cantharidae	0	4
Pelecinidae	1	2
Pieridae	1	2
Scarabidae	1	2
Anthophoridae	3	0
Miscellaneous	18	10
Unidentified	37	23
Total	163	107

Miscellaneous taxa are those families for which fewer than three individuals were captured.

actual number of prey captured by spiders rather than inferring it from web damage. This gave us a direct measure of the effect of stabilimenta on spider foraging success. Thus, our data provide a better indication of the impact stabilimenta can have on the fitness of spiders by altering their foraging success.

One explanation for the reduction in prey capture caused by stabilimenta is that insects learn to avoid webs containing them (Craig, 1994a,b). However, all but 2 of the 31 families of prey were captured so infrequently that it is unlikely that individuals of those taxa ever encountered more than a single web. We also conducted our experiment early enough that native *A. aurantia* were not yet mature; thus prey were essentially naive to stabilimenta. Therefore, the effect of stabilimenta on prey capture we demonstrate is likely the result of first-time interactions of insects with webs, rather than a learned avoidance.

The taxa of prey captured by *A. aurantia* in our experiment is similar to that found in other studies of temperate and tropical *Argiope* spp. where Hymenoptera often constitute 50–90% of the diet of *Argiope* spp. (Brown, 1981; Horton and Wise, 1983; Howell and Ellender, 1984; McReynolds and Polis, 1987; Robinson and Robinson, 1970a), and *Apis* spp. may account for more than 15% of prey captured by *Argiope bruennichi* (Nyffeler and Breene, 1991) and *Argiope amoena* (Murakami,

Table 2

Number of days on which webs were damaged by birds

	Damaged	Not damaged
Webs without spiders		
Stabilimentum	9	15
No stabilimentum	17	7
$\chi^2 = 12.918$, $df = 1$, $p < .001$		
Webs with spiders		
Stabilimentum	7	10
No stabilimentum	12	5
$\chi^2 = 7.083$, $df = 1$, $p < .005$		

Chi-square values were computed from the expectation that webs with stabilimenta would be damaged at the same frequency as webs with no stabilimenta.

1983). However, the large percentage of Diptera captured by spiders in webs without stabilimenta is unusual (Table 1). Diptera are often less common than expected in the webs of *Argiope* spp. when compared to the diets of other co-habiting spiders (Olive, 1980) or when compared to the distribution of available prey in the environment (Bradley, 1993; Murakami, 1983). Because webs without stabilimenta caught many more flies than webs containing stabilimenta, our data suggest that at least some of the specialization on nondipteran taxa by *Argiope* spp. might be attributed to the common inclusion of stabilimenta in their webs.

Stabilimenta and defense

Our data corroborate the hypothesis that stabilimenta can function as a defense against birds (Eisner and Nowicki, 1983; Horton, 1980; Kerr, 1993; Lubin, 1975) because we found that stabilimenta can reduce the frequency of damage to webs from flying birds by 45% (Table 2). We observed several instances where house sparrows (*Passer domesticus*), carolina chickadees (*Poecile carolinensis*), and goldfinches (*Carduelis tristis*) flew toward webs with stabilimenta but abruptly halted. They then hovered briefly in front of the stabilimenta before entering the stations through open frames or flying away. Yet, we never saw birds actively avoid webs that did not contain stabilimenta. Our data also suggest that the bright black-and-yellow color pattern of *A. aurantia* does not itself function as an aposematic warning (Horton, 1980; Nentwig and Rogg 1988), at least to flying birds, because webs were damaged no less frequently in trials with spiders than in trials without spiders (Table 2).

Damage to webs in the field by birds is rare (Blackledge and Wenzel, personal observations) and alone is unlikely to account for inclusion of stabilimenta in webs, given their cost to foraging success. In addition to destroying webs, birds can be important predators of spiders (Edmunds and Edmunds, 1986; Marples, 1969). Horton (1980) demonstrated that the stabilimenta of *A. aurantia* can function as an aposematic warning to predatory blue jays (*Cyanocitta cristata*), signaling that an otherwise palatable spider was in an orb web containing irritating sticky silk. We saw no instances of predation by birds, but two *A. aurantia* disappeared during the experiment on prey capture and were likely eaten by birds. In both cases, the orb webs were almost completely destroyed with single spider legs remaining; in one case the leg was even hanging in the tattered web remains. Adult *A. aurantia* are too large to be prey for most temperate North American wasps and salticid spiders, no vertebrate predators other than birds were seen during the experiment, and *Argiope* do not normally abandon a web without first consuming it. Interestingly, one of the two spiders that disappeared was in an experimental web with the stabilimentum removed, and the other web had been excluded from the experiment because it had an abnormally short and thin stabilimentum that was barely visible to us.

Conflicts in stabilimentum building

Many spiders vary their behaviors in response to changes in predation risk and foraging success (Rayor and Uetz, 1990; Whitehouse, 1997). Tolbert (1975) has suggested that changes in stabilimentum shape as spiders mature are responses to changes in predation risk as spiders increase in size. Our study supports the hypothesis that stabilimenta can help defend spiders against birds (Eisner and Nowicki, 1983; Horton, 1980) by demonstrating that webs containing stabilimenta are 45% less likely to be damaged by flying birds. Kerr (1993) and Lubin (1975) found correlations between reduced densities

of bird predators of *Argiope* spp. and reduced frequency of stabilimentum building, suggesting that spiders can respond to variation in predation risk by modifying stabilimentum building. Yet, it can be difficult for organisms to track changes in risk of predation accurately over short periods of time (Sih, 1992). They are therefore expected to be conservative in their estimation of predation risk, and such risk cannot alone account for stabilimentum variation.

We also found that stabilimenta cause a 34% reduction in prey capture by *A. aurantia*, and Blackledge (1998b) demonstrated that *A. aurantia* and *A. trifasciata* alter their investment in stabilimenta based on variation in foraging success. Variation in foraging success can also be more reliably assessed by most organisms than can risk of predation. Thus, much of the variation in stabilimentum frequency, particularly that observed within populations, is more likely to be attributed to behavioral responses of spiders to fluctuating prey availability. This model also explains investment in stabilimenta in noncapture webs by several genera of spiders which increase the frequency of stabilimentum building just before molting or egg laying (Eberhard, 1973; Nentwig and Heimer, 1987; Robinson and Robinson, 1970b, 1973). Spiders do not feed at these times, and the costs of including stabilimenta in their nonsticky webs are therefore minimal. Future research should focus on modeling the relative contributions of predation risk and prey capture success to the control of intra- and interpopulation variation in stabilimentum production. Such study will help elucidate the importance of behavioral responses to predation risk on other aspects of the life history of spiders. Our results further support the importance of dynamic behavioral responses by organisms when they confront conflict between foraging strategies and predation risk, particularly in a variable environment.

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