

SILK MEDIATED DEFENSE BY AN ORB WEB SPIDER AGAINST PREDATORY MUD-DAUBER WASPS

by

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Summary

Stabilimenta are zigzag and spiral designs of seemingly conspicuous silk included at the centers of many spider webs. We examined the association of stabilimenta with the ability of spiders to defend themselves against predatory mud-dauber wasps. We found that *Argiope trifasciata* (Araneae, Araneidae) were significantly more likely to survive attacks by *Chalybion caeruleum* and *Sceliphron caementarium* (Hymenoptera, Sphecidae) when spiders included stabilimenta in webs. This association could not be explained by factors such as differences in sizes or conditions of spiders nor locations of webs. We suggest that stabilimenta may function to delay pursuit of spiders as they drop from webs by physically blocking wasps, camouflaging spiders or distracting attacking wasps. Stabilimenta may function in a role very similar to the retreats built by many other genera of spiders and appear to be an adaptation to reduce the predation pressure faced by spiders that have evolved foraging habits at highly exposed diurnal web sites.

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Introduction

Behavioral, morphological, and physiological defenses against predators can have large impacts upon other aspects affecting the fitness of organisms (Lima & Dill, 1990; Sih, 1994). For instance, investment in defense is often made at a cost to investment in foraging (Gilliam & Fraser, 1987; Sih, 1992; Lima & Bednekoff, 1999). Conflict between foraging and defense thus results in situations where the optimal investment in each type of behavior varies dependent upon predation risk and the physiological status of organisms. This can select for highly labile expression of defensive behaviors (Mangel & Clark, 1986; McNamara & Houston, 1986; Lima & Bednekoff, 1999). Understanding the functional consequences of variation in defensive behaviors is therefore critical to understanding how organisms confront variation in foraging-defense conflicts.

Web-building spiders are particularly fruitful models for the study of many aspects of foraging theory (Gillespie & Caraco, 1987; Higgins & Buskirk, 1992; Uetz, 1996; Pasquet *et al.*, 1999) because spider webs are easily quantifiable architectural expressions of foraging decisions (Sherman, 1994; Blackledge, 1998a). But, little is known about the defensive behaviors of web-building spiders. Many spiders rest in silk retreats next to webs or have cryptic coloration, both of which are generally accepted as important primary defenses for spiders (Cloudsley-Thompson, 1995). Orb-weaving spiders also display a suite of potential defensive behaviors that are closely tied to their web-building habits, including shaking of webs, dropping from webs, and shuttling between sides of webs (Tolbert, 1975; Cloudsley-Thompson, 1995; Rayor, 1997). But, we have a very limited understanding of the consequences of these behaviors against specific types of predators. In addition, webs themselves are defensive structures that can have important impacts upon the survivorship of spiders during attacks by predators. Silk isolates spiders from predators, signals approach of predators, and can catch or repel predators. This importance of webs in both foraging and defense means that selection on foraging and defensive behaviors can be particularly closely linked in spiders. Because of the quantifiable nature of webs, orb-weaving spiders are therefore ideal models in which to study how organisms confront foraging-defense conflict.

Several genera of orb weaving spiders include conspicuous designs of bright white silk, called stabilimenta, at the centers of webs (Edmunds, 1986;

Lubin, 1986; Eberhard, 1990). Many researchers argue that these silk designs are defensive structures because the species that build stabilimenta are highly vulnerable to visual predators (Eberhard, 1973; Scharff & Coddington, 1997), stabilimenta are more common in webs of spiders in habitats with higher predator densities (Lubin, 1975; Kerr, 1993), and the bright white silk can function as an effective aposematic signal to birds (Horton, 1980; Eisner & Nowicki, 1983; Blackledge & Wenzel, 1999). Stabilimenta have also been suggested to function as thermoregulatory devices (Humphreys, 1992), to attract prey through reflection of UV light (Craig & Bernard, 1990; Tso, 1996; Watanabe, 1999; Herberstein, 2000), to strengthen webs (Robinson & Robinson, 1973a, b), or to be non-functional reactions to stress (Nentwig & Rogg, 1988; see Blackledge & Wenzel, 1999 and Blackledge, 2000 for discussion of these alternative hypotheses). By building stabilimenta in webs, spiders also reduce their ability to forage efficiently because stabilimenta provide visual cues that insect prey use to avoid webs (Blackledge & Wenzel, 1999). Therefore, hungrier spiders are less likely to build stabilimenta (Blackledge, 1998a). The importance of this cost to the fitness of spiders is evident in the evolution of the reflectance properties of stabilimentum silk. Unlike more primitive silks, stabilimentum silk has a relatively inconspicuous coloration to insects, which likely reduces the overall visibility of stabilimenta to insect prey (Blackledge, 1998b; Blackledge & Wenzel, 2000).

Variation in stabilimentum-building behaviors can thus be understood through conflict from selective pressures from investment in foraging and defense (Blackledge, 1998a; Blackledge & Wenzel, 1999). But, the only studies on the defensive benefits of stabilimenta have been performed on adult *Argiope* spp. or other large orb-weaving spiders that build webs in extremely exposed areas. Most stabilimentum-building spiders are smaller and locate webs in sites that are less conspicuous such as in thick grasses, overhanging banks, and tree buttresses (Eberhard, 1973, 1990). These webs are relatively protected from flying birds and bird predation so that the function of stabilimenta as aposematic signals to birds is likely to be relatively unimportant for many stabilimentum-building spiders. Thus, it is unclear what defensive benefits would offset the cost to foraging success that stabilimenta have in these spiders.

All stabilimentum-building spiders are potentially vulnerable to predatory wasps. Even relatively large adult female *Argiope aurantia* are captured by some pompilids (p. 270; Krombein, 1952). Many species of mud-dauber

wasps prey exclusively upon spiders, capturing spiders and depositing the spiders in mud nests where the spiders serve as food for developing wasp larvae (Bohart & Menke, 1976; Krombein *et al.*, 1979). Sphecid wasps are ubiquitous predators of spiders (Coville, 1987) and wasps can account for more than 90% of predation suffered by spiders (Rayor, 1997). Wasps are visually hunting predators and stabilimenta can greatly affect the visual properties of webs and spiders (Craig & Bernard, 1990; Blackledge, 1998b; Blackledge & Wenzel, 1999). So it seems possible that stabilimentum-building could be an important behavioral defense against these wasps. We examined the hypothesis that stabilimenta function as defenses against predatory mud-dauber wasps (Hymenoptera: Sphecidae). We measured the association between stabilimenta in spider webs of immature *Argiope trifasciata* (Araneae: Araneidae) and predation by two mud-dauber wasps, *Chalybion caeruleum* and *Sceliphron caementarium* (Hymenoptera: Sphecidae).

Materials and methods

Enclosures

We observed the predatory interactions of wasps and spiders in three outdoor field enclosures between 28-Jul and 11-Sep 1999. Each enclosure consisted of nylon screen suspended over a wood frame ($3.8 \times 2.3 \times 2.0$ m). The bottom edge of the screen was covered with bark mulch and pebbles to prevent wasps from crawling under the enclosure. Enclosures were located in a field at the Rothenbuhler Honeybee Laboratory, Ohio State University, and contained a variety of vegetation, mostly grasses (Poaceae) and thistle (Asteraceae). The structure of the vegetation was similar to that where *A. trifasciata* were collected and wild *A. trifasciata* occurred in the field surrounding the enclosures. Each enclosure contained a plastic pan ($20 \times 30 \times 10$ cm) filled with mud from the same pond where the *S. caementarium*, used in our experiment, collected mud for nest building. Pans were partially filled with water and tilted to provide gradients from dry to completely saturated. We glued mud *S. caementarium* nests to wooden boards along the tops of the enclosures because *Chalybion* only nests in abandoned *Sceliphron* nests (Rau, 1928). Hummingbird feeders, containing 1 : 1 honey : water mixtures were placed in each enclosure as nectar sources for wasps and the honeywater was changed every two days to prevent fermentation (see Blackledge & Pickett, 2000 for more details).

The wasps

We collected adult female sphecid wasps, *C. caeruleum* and *S. caementarium*, from an old farm in Dublin, OH between Jul-Aug 1999. Both species of wasps are common predators of orb-weaving spiders, including *Argiope* spp., in mid to late summer (Krombein *et al.*, 1979; Blackledge & Pickett, 2000). Both species hunt and nest in the same areas but differ in the behaviors used to attack spiders. *S. caementarium* usually captures *Argiope* after spiders have

dropped from webs, by pursuing spiders into the vegetation below webs. While *C. caeruleum* also hunts in this manner, *Chalybion* often lands in webs and vibrates the silk in a form of aggressive mimicry that can lure spiders to them (Blackledge & Pickett, 2000).

Wasps were individually marked with paint prior to being released into the enclosures. Initially, one of the three enclosures was randomly selected to contain *C. caeruleum*, one to contain *S. caementarium*, and the third to contain no wasps, instead serving as a control. On 18-Aug we added *S. caementarium* to the control enclosure. Although we provisioned each cage with multiple wasps, most wasps escaped or died before building nests and hunting spiders. Thus, two enclosures contained a single female *S. caementarium* each and the third enclosure contained two female *C. caeruleum* for which we obtained data on their hunting of spiders.

The spiders

Blackledge and Wenzel (1999) randomly cut stabilimenta out of webs to allow a manipulative field study of the effect of stabilimenta on prey capture by spiders. We were unable to use this methodology because mud-dauber wasps often attack spiders through the centers of webs. Instead, *A. trifasciata* only include stabilimenta in about 50% of their webs (Blackledge, 1998a; Tso, 1999). Therefore, we were able to use this natural variation to examine differences in capture of spiders in webs with and without stabilimenta. *A. trifasciata* were collected from roadsides around Franklin Co., Ohio, individually marked with colored ink (Pigma Micron pens) on the thorax or abdomen, and weighed to the nearest g. Prior to the start of the experiment, 10-20 *A. trifasciata* were released into each enclosure. Very young *A. trifasciata* build disk shaped stabilimenta and gradually shift to a linear form of stabilimentum as spiders mature. But, all of the spiders in our study were of similar enough maturity that they built exclusively linear stabilimenta. We also excluded from the analysis all spiders that were larger than or smaller than the range of spiders actually captured by wasps during the experiment. Thus, all individuals for whom data are provided were of a similar size and age class, likely within one instar of one another.

Natural web trials

We surveyed each enclosure for *A. trifasciata*, every morning between 0700 and 0900 hr, before wasps began hunting. We recorded the presence of each spider, web, and if that web contained a stabilimentum. We marked the position of each web by laying a numbered nail beneath the web. Because stabilimenta were much less common in webs built deep within the grass, we also classified webs as 'exposed' or 'covered' within the vegetation. Exposed webs were defined as webs where the bridge thread (top of the web) was at or above the average level of grass (*i.e.* attached to emergent grass stems, thistle, or the enclosure itself, or else located within gaps in the vegetation) while covered webs were suspended entirely below the grass canopy. Although somewhat arbitrary, this distinction should not have biased the study because exposure of webs was determined prior to predation for each day. Each evening between 1900 and 2100 hr, after hunting ceased, we again assayed enclosures, recording presence or absence of spiders in webs.

We examined the association of stabilimenta and wasp predation in two ways. We measured the 'known' rate of predation of spiders for which we could unambiguously classify them as alive or dead at the end of each day. Spiders were classified as alive if they were

present in the enclosure when assayed in the evening or if they were found alive on a subsequent day of the experiment. We excavated the nest cells of wasps one to five days after the cells had been filled with spiders and sealed with mud by the wasps. Therefore, a spider was classified as dead either if its capture was observed directly or the spider's web was vacant and its body was found within a wasp nest cell that had been closed on that same day. We then used a *G*-test to examine the null hypothesis that the proportion of spiders known to be captured from webs containing stabilimenta was the same as that predicted by the proportion of spiders known to be captured from webs that lacked stabilimenta.

We also measured the inferred rate of capture for a larger group of spiders. Undisturbed *Argiope* spp. never leave their webs during the day and do not change sites until the spiders remove their webs just prior to dawn (Enders, 1976; Horton & Wise, 1983; Blackledge & Pickett, 2000). Therefore, we 'inferred' probable capture of a spider when three conditions were met. (1) A web occupied in the morning was found to be vacant at the end of the day. (2) That web was vacant (*i.e.* not removed by the spider) or a different spider occupied that web site on the next day. (3) The original web builder was never found again within the enclosure. We again used a *G*-test to compare the proportion of spiders inferred to have been captured in webs containing stabilimenta versus the expectation that it would be the same as in webs that did not contain stabilimenta. We included this data set because not all spiders excavated from nests could be identified, some spiders were captured without being provisioned in nests (see Blackledge & Pickett, 2000) and because it was analogous to data dealt with by field researchers who normally cannot directly observe predation events.

For both the known and inferred predation sets, we examined survivorship of spiders on the first day for which they built webs. We also include separate analyses of survivorship of spiders on their second and subsequent 'web days', to prevent pseudoreplication.

Individual observations

We examined directly the effect of stabilimenta on success of individual predation attempts by *C. caeruleum* on *A. trifasciata*. We allowed spiders to build webs within standardized 35 × 35 × 10 cm wooden frames overnight (described in Blackledge & Pickett, 2000). Then one to three frames were placed within the *C. caeruleum* enclosure and observed until a wasp attacked a spider and the spider was either captured or escaped predation. By using standardized wood frames, this technique allowed us to control for any effects of web height, location, substrates to which webs were attached, and exposure of webs. It also allowed us to determine if differences in capture of spiders with and without stabilimenta in the natural web trials were due to differences in the probability of spiders being attacked or due to differences in survivorship of spiders once attacked. We used a *G*-test to compare the proportion of spiders captured that had stabilimenta in webs versus those that did not have stabilimenta in webs. Because we directly observed all attacks, we also compared differences in the predatory tactics of *C. caeruleum* when confronted with webs that did and did not have stabilimenta, as well as differences in the defensive behaviors of *A. trifasciata*.

Results

Stabilimentum variation in natural web trials

Stabilimenta were more common in first day webs built in exposed sites than in first day webs located in covered sites (Table 1). Spiders that built stabilimenta in their first webs also tended to be heavier than spiders that did not build stabilimenta (Table 2), though this difference was only statistically significant for the *Chalybion* enclosure (Table 3).

Wasp predation in natural web trials

Sceliphron

We excluded all webs that were classified as being covered because only one inferred predation event, and no known predation, involved spiders in covered webs in the first *Sceliphron* enclosure (the second enclosure had no webs classified as covered). Yet, webs built deep in the grass, where

TABLE 1. Association of vegetative cover and presence of stabilimenta in webs of *Argiope trifasciata*

	% webs containing stabilimenta (<i>N</i>)		
	Exposed	Covered	<i>p</i>
<i>Sceliphron</i> — enclosure 1	0.77 (48)	0.57 (7)	< 0.005
— enclosure 2	0.52 (27)	—	—
<i>Chalybion</i>	0.68 (68)	0.28 (18)	< 0.001

Exposed webs were built in sites such that the top bridge threads of the orbs were at or above the canopy level of the grass. Covered webs were entirely below the canopy of grass. *p*-values are from *G*-tests (*df* = 1) comparing the number of exposed webs with and without stabilimenta to that predicted by the distribution of stabilimenta in covered webs.

TABLE 2. Relationship between mass of spiders and presence of stabilimenta in the first webs built

	Mass (mg) ± SE (<i>N</i>)	
	Stabilimentum	No stabilimentum
<i>Sceliphron</i> — enclosure 1	34 ± 3 (19)	28 ± 4 (7)
— enclosure 2	39 ± 3 (9)	41 ± 3 (11)
<i>Chalybion</i>	49 ± 2 (46)	35 ± 3 (22)

TABLE 3. Two-way ANOVAs examining mass of spiders as related to presence of stabilimenta in webs and capture of spiders by wasps

		<i>F</i>	df	<i>p</i>
<i>Sceliphron</i> (enclosure 1)	Captured?	0.60	1,19	0.45
	Stabilimentum?	2.98	1,19	0.10
	Interaction	3.51	1,19	0.08
<i>Sceliphron</i> (enclosure 2)	Captured?	0.01	1,16	0.94
	Stabilimentum?	2.99	1,16	0.10
	Interaction	0.57	1,16	0.46
<i>Chalybion</i>	Captured?	0.52	1,63	0.47
	Stabilimentum?	12.68	1,63	0.01*
	Interaction	2.95	1,63	0.09

wasps were less likely to hunt, contained significantly fewer stabilimenta. Therefore, there was an *a priori* bias toward wasps encountering spiders in webs containing stabilimenta, regardless of any potential effect of the stabilimentum itself.

On their first web day, both the known and inferred rate of capture of *A. trifasciata* by *Sceliphron* were higher for spiders in webs that lacked stabilimenta compared to spiders in webs that contained stabilimenta (Table 4). This difference was significant for all comparisons except the inferred rate of capture for the second *Sceliphron* enclosure (*G*-test, *df* = 1, *p* < 0.05). There was also a tendency for spiders in webs without stabilimenta to be captured more often on their second day of web building (Table 5). No comparisons were made for third or later days of web building because very few spiders survived and built webs for three or more days.

Chalybion

Chalybion captured spiders in both exposed and covered web sites so we present both sets of data. We were unable to obtain a meaningful measure of known predation because we were able to recognize the identities of only six spiders excavated from nests. The inferred predation rate was significantly higher for spiders in exposed first day webs that lacked stabilimenta compared to those containing stabilimenta (Table 4; *G*-test, *df* = 1, *p* < 0.001). Inferred predation was also higher for spiders in covered first day webs that lacked stabilimenta (Table 4), though a statistical comparison was not made due to the extreme skew of the data. There was also a tendency for spiders,

TABLE 4. *Capture of spiders by predatory wasps*

	% spiders captured-known (<i>N</i>)			% spiders captured-inferred (<i>N</i>)		
	Stabilimentum	No stabilimentum	<i>p</i>	Stabilimentum	No stabilimentum	<i>p</i>
<i>Sceliphron</i>						
Enclosure 1	0.30 (37)	0.45 (11)	< 0.05	0.46 (37)	0.72 (11)	< 0.001
Enclosure 2	0.21 (14)	0.46 (13)	< 0.05	0.36 (14)	0.54 (13)	NS
<i>Chalybion</i>						
-exposed				0.13 (46)	0.23 (22)	< 0.001
-covered				0.00 (5)	0.38 (13)	**

Parentheses indicate the number of first day webs built by spiders. *p*-values are from *G*-tests (*df* = 1) comparing the number of spiders that survived and the number of spiders that were captured in webs containing stabilimenta compared to that predicted by survival of spiders in webs without stabilimenta. See Materials and methods for explanation of known/inferred predation and covered/exposed webs. ** no test conducted due to the extreme skew of the data.

TABLE 5. *Capture of spiders that survived one day of predation by predatory wasps*

	% spiders captured (<i>N</i>)	
	Stabilimentum	No stabilimentum
<i>Sceliphron</i>		
Enclosure 1 2 nd web	0.33 (12)	1.00 (2)
Enclosure 2 2 nd web	0.00 (8)	**
<i>Chalybion</i>		
2 nd web	0.18 (28)	0.30 (33)
3 rd web	0.00 (14)	0.33 (15)

** All spiders were in exposed webs containing stabilimenta and none were captured.

which had survived their first web day, to be captured more often on subsequent web days if their webs lacked stabilimenta (Table 5).

Individual observations

Individual *A. trifasciata* that built webs in standardized wooden frames were 36% less likely to be captured by *C. caeruleum* when spiders were in webs that contained stabilimenta compared to spiders in webs that lacked stabilimenta (Table 6; *G*-test, *df* = 1, *p* < 0.005). The defensive

TABLE 6. *Behavioral interactions for single predation attempts by Chalybion caeruleum on Argiope trifasciata that had built webs in standardized wooden frames*

	Stabilimentum ($N = 19$)	No stabilimentum ($N = 19$)
% spiders captured	0.32	0.68
At web hub	0.17	0.18
In web periphery	0.50	0.73*
On ground	0.33	0.00*
Aggressive mimicry by wasp	0.42	0.53
Spider responds to mimicry	0.21	0.42
Spider defensive behaviors		
Runs to edge of web	0.35	0.39
Drops from web	0.47	0.47
Runs away from web	0.13	0.06

* $p < 0.01$ (binomial comparison), all other comparison NS at $p < 0.05$.

behaviors of spiders against wasps did not differ in relation to the presence of stabilimenta in webs (Table 6). But, of those spiders that were captured, wasps were more likely to capture spiders while still in webs if the webs lacked stabilimenta (Table 6). Whereas wasps usually captured spiders from webs that contained stabilimenta only after the spiders had dropped out of their webs (Table 6).

Discussion

We found that mud-dauber wasps were 10-38% less likely to capture spiders that included stabilimenta in webs compared to spiders that did not have stabilimenta (Table 4). Spiders that escaped predation on their first web day were still more likely to be captured on subsequent web-building days if they did not include stabilimenta in webs (Table 5). In single predatory attempts, wasps were also 36% more likely to capture spiders that had not included stabilimenta in webs. Stabilimentum-building has long been proposed to be a defensive behavior. Several studies have produced evidence that these conspicuous (to humans) white swaths of silk act as aposematic signals to birds, preventing damage to webs or predation of spiders (Horton, 1980; Eisner & Nowicki, 1983; Blackledge & Wenzel, 1999). But, our

data suggest that stabilimenta may also function as defenses against wasps. Spider-hunting wasps are active, visually oriented predators that cue in on the movement of spiders (Blackledge & Pickett, 2000) or the contrast of spiders against the background (Eberhard, 1970). Sphecid wasps are very common; suggesting that predation by wasps may be a major selective influence on the evolution of spider web building. Because stabilimenta can significantly alter the visibility of webs and spiders, stabilimenta may be responsible for mediating the differences in survivorship of wasp attacks found in our study. This correlation begs two important questions. What alternative hypotheses may account for the significant association between stabilimenta and the ability of spiders to avoid capture by predatory wasps? How might stabilimenta function as defenses against wasp predators?

Although the association that we found between stabilimenta in webs and decreased success of predatory attacks by wasps was strong and consistent, there are several potential alternative explanations that could account for this pattern. Building of stabilimenta is closely linked to the foraging success of spiders and spiders are more likely to build stabilimenta when they catch more prey (Blackledge, 1998a; Herberstein *et al.*, 2000). Thus, spiders that build stabilimenta tend to be heavier (Table 2) and are likely to have higher energetic reserves than spiders that do not have stabilimenta in their webs. Size of spiders can be an important determinant of prey selection by wasps (Rayor, 1997). In this study, we only considered spiders that were within the size range of *Argiope* captured by wasps and all spiders were also of relatively similar instars. Although there was a tendency for spiders without stabilimenta in webs to be lighter and therefore smaller than spiders that built stabilimenta (Table 2), this difference was only significant in the *Chalybion* enclosure and was still independent of the probability of spiders being captured (Table 3). Thus, selection for spider prey of specific sizes, within the variation considered by our study, is unlikely to account for the differences in capture that we found. Spiders without stabilimenta may have had lower energetic reserves so that they were more likely to react as though wasps were potential prey, rather than predators, thereby increasing the probability that spiders were captured. There was a tendency for spiders without stabilimenta to respond more often to potential aggressive mimicry by *Chalybion*, supporting this alternative hypothesis (Table 6). But, this difference was not significant and is therefore unlikely to account for the highly significant association that we found between presence of

stabilimenta in webs and avoidance of capture by wasps. Finally, spiders that build stabilimenta locate their webs in more exposed microhabitats (Table 1). But, both *Chalybion* and *Sceliphron* spent most of their time hunting among these more exposed webs and we restricted our analyses between covered and exposed webs so that the higher capture of spiders from webs without stabilimenta cannot be explained by differences in locations of webs. Thus, the differences that we found in capture of spiders with and without stabilimenta are likely due to an effect of the stabilimenta *per se*, rather than some other factor associated with the inclusion of stabilimenta in webs.

The large size and shape of stabilimenta increase the overall visibility of webs to insects and can reduce the prey capture of spiders that include stabilimenta in webs (Blackledge & Wenzel, 1999). But, this conspicuousness of stabilimenta to insect prey is reduced by the spectral properties of the silk used to construct stabilimenta because the silk provides relatively poor color contrast against natural backgrounds unlike other, more primitive silks (Blackledge, 1998b; Blackledge & Wenzel, 2000). The few species of mud-dauber wasps studied share visual systems similar to those of many of the insect prey of spiders (Peitsch *et al.*, 1992). This suggests that, while stabilimenta can provide some visually distinguishable cues to wasps (Blackledge & Wenzel, 1999), detection of stabilimenta would not be based primarily upon color contrast (Blackledge & Wenzel, 2000). Thus, wasps are unlikely to use stabilimenta as conspicuous cues to locate spider prey. This is also supported by the higher rate of predation suffered by spiders without stabilimenta in our study. In addition, this means that stabilimenta are unlikely to function defensively as aposematic signals to wasps, as stabilimenta can to birds (Horton, 1980; Blackledge & Wenzel, 1999).

The sequence of potential behavioral interactions in the capture of spiders by wasps can consist of up to three phases. (1) An initial attempt at capture of the spider. This may be a direct attack on the spider at the center of the web. Less direct attacks by *Sceliphron* are often initiated after the wasp touches some portion of the web, perhaps eliciting movement by the spider. *Chalybion* often initiates indirect attacks when it lands in the capture area or frame of a web and plucks the silk using its middle legs, which can lure the spider to the wasp (Blackledge & Pickett, 2000). (2) A subsequent chase through the web as the spider either runs to the top of the web toward the vegetation to which the frame of the web is attached or drops down the web to

the substrate underneath. (3) Finally, a continuation of the chase through the vegetation, potentially covering more than 0.5 m and lasting for more than one minute. Examining this sequence of behaviors, the strongest difference in captures of spiders with and without stabilimenta was between spiders that had already moved from the centers of webs, either running through or dropping from webs (Table 6). There was no significant difference in the direct capture of spiders at the centers of webs (Table 6), but many more spiders in webs without stabilimenta were captured while running from or dropping from the centers of webs than were spiders in webs containing stabilimenta. The speed with which spiders drop from webs when attacked by wasps is a critical factor determining survival of attacks (Rayor, 1997) and the observation that *A. trifasciata* in webs containing stabilimenta were captured later in the behavioral sequence of dropping from webs (*i.e.* on the ground rather than still in the web) suggests that stabilimenta may increase the success of this important defensive behavior.

There are at least three hypotheses for ways in which stabilimenta could enhance defensive dropping behaviors. (1) Stabilimenta could physically block attacks by wasps, allowing more time for spiders to escape. (2) The silk could camouflage spiders, delaying attacks by wasps. (3) Stabilimenta could startle or distract wasps as wasps attack spiders. We did observe several instances where wasps were blocked from stinging or biting spiders by the physical presence of stabilimenta and this would clearly give spiders extra time to drop from webs. But, linear stabilimenta built by *A. trifasciata* are typically built so that the stabilimenta are positioned in webs at the edges of the bodies of spiders (or even the distal tips of legs in other stabilimentum-building species), rather than being physically in front of the bodies of spiders where stabilimenta could best block attacks. Therefore, physical blocking of attacks is not by itself a fully adequate explanation for how stabilimenta defend spiders against wasps. Both the camouflage and distraction hypotheses would also result in delayed pursuit of spiders. But, if stabilimenta primarily defended spiders against wasps by camouflaging spiders then it would be expected that the rate of capture of spiders through direct attacks at the centers of webs would also be very much reduced by stabilimenta. We found no such difference, although the proportion of captures at web centers was small enough that our sample size may have been too small to detect such a difference. Nevertheless, this suggests that stabilimenta could be thought of most appropriately as visual distractions

that impede the ability of wasps to effectively pursue spiders out of webs. More data are necessary to elucidate the precise mechanisms by which stabilimenta protect spiders against their wasp predators and this will clearly be a fruitful area for future research.

Our data suggest that stabilimenta are important primary defenses against predatory wasps for orb-weaving spiders. Most orb web spiders are nocturnal and hide from predators during the day. Many of the remaining species of spiders that have orb webs during daylight typically rest off of webs in silk or leaf retreats where they are also protected both visually and physically from wasps. However, a few genera of spiders such as *Argiope*, *Cyclosa*, *Micrathena* and some Uloborids will rest at the centers of orb webs during the day. This presumably allows these spiders to respond more quickly to prey in their webs but also exposes these spiders visually to hunting wasps. Virtually all of these diurnal, hub-dwelling spiders are known to at least occasionally build stabilimenta (Eberhard, 1973; Edmunds, 1986; Scharff & Coddington, 1997), with *Leucauge* being one of the only common genera to not do so.

Stabilimentum-building can be understood as a complex behavior whose variation is affected by foraging-defense conflict at many different levels. Evolutionarily there is strong selection for spiders to exploit insect prey resources available during daylight and, by hunting at the centers of webs, to maximize responsiveness to prey. But, these factors increase exposure of spiders to their own, visually hunting predators. Behaviorally, spiders such as *Argiope* can build webs in more exposed microhabitats with high levels of flying insects. Stabilimenta are only built by hub-foraging, diurnal species of spiders and are often more common in more exposed webs (Table 1; Eberhard, 1973), again situations where spiders are exploiting high levels of prey at a high risk of capture by visually hunting predators. Previous research demonstrates the utility of stabilimenta as visual defenses against birds (Horton, 1980; Blackledge & Wenzel, 1999) and our study suggests that stabilimenta are also effective against wasps. Thus, stabilimenta may have evolved as adaptations that reduce risk of predation for spiders that forage under these particularly favorable conditions. Yet, the building of stabilimenta has its own cost to prey capture because stabilimenta provide visual cues used by insects to avoid webs (Blackledge & Wenzel, 1999). This cost should of course be less than the benefits of foraging in diurnal, exposed web sites to allow the persistence of stabilimentum-building. Indeed, the

cost of stabilimenta to prey capture is reduced by the color properties of the silk used by spiders to build stabilimenta because stabilimentum silk has a much poorer color contrast with natural backgrounds than do other silks (Blackledge, 1998b; Blackledge & Wenzel, 2000). Finally, individual spiders react to this conflict between predation risk and prey capture by varying their building of stabilimenta. Most spiders include stabilimenta in about 30-70% of webs. Spiders actively decide whether or not to build stabilimenta by using their level of foraging success, building stabilimenta with a higher frequency as spiders catch more prey (Blackledge, 1998a; Herberstein *et al.*, 2000).

Our study found that spiders that include stabilimenta in their webs are less likely to be captured by two species of sphecid wasps. These data support the hypothesis that stabilimenta function as defenses against wasps, perhaps by distracting attacking wasps or by camouflaging spiders. Because spider-hunting wasps are ubiquitous threats to web-building spiders, this potential defensive function of stabilimenta could provide a common selective factor for the repeated evolution of stabilimentum-building in three families of orb-weaving spiders, when species forage in situations with high risk of capture by visually hunting predators.

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