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STABILIMENTA IN SPIDER WEBS:

PREDATOR-PREY CONFLICT AND SENSORY DRIVE

DISSERTATION

Presented in Partial Fulfillment of the Requirements for

the Degree Doctor of Philosophy in the Graduate

School of The Ohio State University

By

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*****

The Ohio State University
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ABSTRACT

Orb-weaving spiders are dominant predators in terrestrial ecosystems and depend upon the near invisibility of webs for prey capture. But, several genera include conspicuous zigzags of bright white silk, called stabilimenta, in otherwise cryptic webs. Stabilimentum-building provides an opportunity for study of basic ecological and evolutionary issues such as evolution of convergent behaviors, predator-prey dynamics, and signal evolution.

I examined the ecology of stabilimentum building, emphasizing variability in expression of stabilimenta and evolution of spider silk coloration, using *Argiope aurantia* and *A. trifasciata* (Araneae, Araneidae). Stabilimenta are defensive structures that protect spiders against predatory mud-dauber wasps. Juvenile *A. trifasciata* are 40% less likely to be captured by wasps when in webs that contain stabilimenta and increase stabilimentum-building by 40% when wasps are hunting. Stabilimenta also protect adult *A. aurantia* from flying birds, which are 45% less likely to damage webs containing stabilimenta. But, stabilimenta cost *Argiope* prey capture, as webs containing stabilimenta catch 34% fewer prey than do webs with stabilimenta removed. Variation in frequency of stabilimenta can be explained by this conflict between the defensive benefits of stabilimenta and their cost to capture of prey. Foraging success is a proximate
regulator of this predator-prey conflict because spiders that catch fewer prey decrease investments in stabilimenta, building stabilimenta 40% smaller and up to 60% less frequently. Conflict between visibility of stabilimenta to predators and to prey may also have been important in the evolution of silk color. In training experiments, 60% of honeybees learned to find sucrose rewards at “primitive” tarantula silk targets, which have conspicuous ultraviolet reflective peaks. But no honeybee learned to use stabilimentum silk, indicating that the ultraviolet + blue + green reflectance of stabilimentum silk is cryptic. This removes a critical cue, background color contrast, that insects could use to see and avoid stabilimenta, reducing the cost of stabilimenta to foraging. This suggests that spider silk color properties have evolved through sensory drive via selection from visual physiologies of insect prey.
Dedicated to my parents
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INTRODUCTION

Several genera of orb-weaving spiders include conspicuous designs of bright white silk in their otherwise cryptic webs. These designs include zigzag lines, crosses, or spirals of silk and are historically termed stabilimenta. Stabilimentum-building provides a wealth of opportunity for the study of basic ecological and evolutionary issues such as the evolution of convergent behaviors, predator-prey dynamics, and signal evolution. It also provides an opportunity to study how spiders perceive and react to their environment. Little empirical work has been conducted on stabilimenta and study has been largely confined to Argiope argentata, with a few authors also examining Cyclosa or Uloborus. Thus, there is a great need for study of a wider variety of taxa. No theory of the function and evolution of stabilimenta will be complete unless it can adequately account for the enormous variation in stabilimentum-building behavior. Most spiders that build stabilimenta include them in only 30-70% of webs and will often build incomplete designs or change the shape of stabilimenta from web to web.

This dissertation examines the ecology of stabilimentum building and its evolutionary implications using two common temperate spiders, Argiope aurantia and A. trifasciata (Araneae, Araneidae), as model organisms. I use Chapter 1 to review the literature on stabilimenta, providing a comprehensive list of the spiders that build
stabilimenta and reviewing the hypotheses proposed for the function of stabilimenta. In Chapter 2, I explore how foraging success acts as a proximate regulator of stabilimentum variability, explaining intra-individual variation. Chapter 3 then provides controlled tests of the prey attraction and web advertisement hypotheses, and places the stabilimentum variability, examined in Chapter 2, in the context of a predator-prey conflict model. I use Chapter 4 to develop a new hypothesis on the evolution of stabilimentum silk coloration under this predator-prey conflict -- that stabilimentum silk has evolved a cryptic coloration to insect prey, reducing the costs associated with stabilimenta. Chapter 5 then illustrates an empirical test of the cryptic silk hypothesis. In Chapter 6, I develop a protocol to explore the predatory behavior of wasps that hunt stabilimentum building spiders and compare the predatory tactics of two common sphicid predators of Argiope. Chapter 7 then uses that protocol to test the effect of stabilimenta on wasp predation, examining the implications of the cryptic silk hypothesis and predatory wasps for the camouflage and predator confusion hypotheses of stabilimentum function.
CHAPTER 1

THE BIOLOGY OF STABILIMENTUM DECORATIONS IN SPIDER WEBS

Spiders are common, ecologically important, predators in most terrestrial ecosystems (Moulder & Reichle 1972; Turnbull 1973; Uetz 1992; Wise 1993) and their predatory behavior is epitomized by the orb-weavers. Their elegant and efficient orb shaped webs depend upon almost complete invisibility of the silk to snare insects out of the air (Olive 1980; Rypstra 1982; Craig 1986, 1988; Uetz 1990). So it is little wonder that biologists have long been fascinated by spiders that add seemingly conspicuous designs of bright white silk, called stabilimenta, to their otherwise cryptic webs. In addition to igniting more than a century of debate about their function, stabilimenta provide an important model to examine predator-prey interactions and the evolution of animal signaling and sensory systems. This chapter is an attempt to summarize the diverse body of literature about stabilimenta, to form a consensus as to the function of stabilimenta, and to explore the implications of stabilimentum-building for our understanding of predator-prey dynamics and signal evolution.

The term stabilimentum was first coined by Simon (1895) to refer to the ribbon-like zigzags of silk that Argiope place in the centers of webs. As the name implies, Simon thought that these designs stabilized webs mechanically. But a century of debate has
produced many alternative hypotheses. In addition, the term stabilimentum has been used by many authors to include a variety of silk and detritus structures in spider webs that may share few similarities in their construction and function. The only common characteristic seems to be that stabilimenta are structures that are added to orb webs, in addition to the frame threads, radii, and capture spirals, which characterize webs themselves. The pattern of the stabilimentum built is often species specific (Hingston 1929; Lubin 1986; Nentwig & Heimer 1987) and many authors have cataloged different types of designs. Hingston (1927) defined 22 devices (stabilimenta) in spider webs. But, as many of these categories shared architectural elements and are thus likely intermediates between one another, I will consider seven broad classes of stabilimenta (Table 1); 1) lines or crosses of silk, 2) circular designs of silk, 3) solid disks of silk, 4) silk tufts, 5) egg sacs, 6) detritus, and 7) leaves.

1) Linear silk designs are the best known and studied type of stabilimentum. They are typically built within the inner hub and free zone areas of webs but may extend slightly into the sticky capture zones, particularly in Cyclosa. Linear stabilimenta consist of either vertical lines (Fig. 1.1) or x-shaped crosses, cruciate designs, built at approximately 30° off the longitudinal, or vertical, axes of webs (Fig. 1.2). Linear silk stabilimenta often have gaps in their centers, where spiders rest while hunting on webs. Occasionally horizontal, or lateral, lines are built (Cyclosa insulana - McClintock & Dodson 1999). The horizontal orb web of Uloborus filifaciens includes both longitudinal and lateral lines rather than the more typical x-shaped design (Hingston 1927). Argiope
*catenulata* includes the lower portion of a cross in the bottom of its hub and the upper portion of a vertical line in the top of its hub (Hingston 1927, 1929).

2) Circular stabilimenta can consist of a single spiral of silk that may be fairly regular in shape or meander across the web hub (Fig. 1.3; *Cyclosa* and *Uloborus*). A circular stabilimentum may also be formed by concentric loops of silk (Fig. 1.4; *Argiope*, *Uloborus*), which I distinguish from the solid disk "type" of stabilimentum described below because it is made from distinct ribbons of silk. Most genera that build circular stabilimenta also built linear designs at some point in their development. Spirals or concentric loops are commonly built by young *Argiope* and *Uloborus* that then build exclusively linear forms as adults (Eberhard 1973; Edmunds 1986; Nentwig & Heimer 1987). Some *Cylcosa* built spiral stabilimenta as adults (Marson 1947a) and some spiders commonly switch between spiral and linear stabilimenta, even within the adult instar, such as *A. savignyi* (Edmunds 1986) and *Octonoba* (Watanabe 1999a).

3) Solid disks of silk (Fig. 1.5) are built by both adult and juvenile spiders. In *A. aurantia* the disk is included with a vertical line silk stabilimentum. The disks are made of amorphous fluffy silk and are constructed with movements similar to those used to build linear stabilimenta (Blackledge 1998a). But, in *Neogea* these disks are made of solid parchment like silk (Humphreys 1992).

4) A variety of spiders include either a mesh of extremely fine silk dots in webs (particularly in the juvenile webs of some uloborids - Lubin 1986) or else disperse...
several fluffy silk flocculations on the frame threads and radii of webs (Fig. 1.6). Unlike other types of stabilimenta, which are added to webs after all other structural elements are complete, tufts and dots are added to individual threads as the threads are spun during the web building process (Marples 1969; Muma 1971). Stabilimentum tufts should not be confused with flocculations created by threads that bunch together after being severed during web construction.

5) Many spiders suspend their eggs sacs in specially made scaffolds of webbing or in their own tangle webs (Lubin 1986; Hieber 1992). But some orb weavers incorporate egg sacs into stabilimenta in the hubs of webs (Fig. 1.7). Egg sacs are suspended in webs along the same vertical or longitudinal axis as linear silk stabilimenta and both may sometimes occur together. In many instances, the coloration of spiders and their egg sacs are closely matched (Hingston 1927; Comstock 1940).

6) Detritus consisting of prey remains, exuviae, dust, plant remains and other debris are often incorporated into linear stabilimenta (Fig. 1.8). Detritus is also deposited around egg sacs, may form "false hubs" in the sticky spirals of webs, or even resemble "false spiders" (Bristowe 1941; Cloudsley-Thompson 1980). Detritus stabilimenta are often built on top of silk stabilimenta, particularly by Cyclosa. But, Rovner (1979) demonstrated that C. turbinata still built vertical detritus stabilimenta after their webs were rotated 90°, thereby altering the vertical orientation of the original silk stabilimenta. Rovner argued that detrital stabilimenta were oriented independently from the original silk stabilimenta and that the two types of stabilimenta were therefore different.
components in webs. Detritus is also included in other types of webs such as the tangle webs built by *Latrodectus* where it can both conceal spiders from predators and assist in thermoregulation by shading spiders (Konigswald *et al.* 1990).

8) A few spiders place whole leaves in the centers of webs. *Phonognatha* will select a leaf from the forest floor and then carry it to the web where it is carefully curled into a retreat (Fig. 1.9). Other spiders, such as *Arachnura*, rest below leaves placed in their webs. Some spiders such as *Metepeira* include rolled leaves and other debris, which function as retreats, in tangles of silk adjacent to their orbs webs (Levi 1977a). While leaves are not typically considered to be stabilimenta, I have included them here to allow for a consistent definition of what "stabilimentum" means. But, this is a very different type of behavior from most other types of stabilimenta and likely has important consequences for how webs are loaded and how vibrations are transmitted through webs, compared with silk stabilimenta. Unlike the other forms of stabilimenta described herein, there is little controversy that leaves function simply as a means to allow spiders to rest in safe, sheltered microhabitats (Levi 1977b; Cloudsley-Thompson 1995), while remaining at the center of webs, where spiders can sense and attack prey most efficiently (Masters & Moffat 1983). Several spiders also position webs so that sticks run through the hubs of webs. These spiders then rest closely appressed to the sticks, making the spiders quite difficult to discern (Bristowe 1941; Cloudsley-Thompson 1980; Peters 1995). *Uloborus plumipes* often incorporates sticks into webs but will build linear silk stabilimenta when they do not have sticks (Kullman 1972), suggesting that it is not so far
fetched to consider sticks or leaves to be functionally similar to the more traditional silk stabilimentum.

The variety of structures that may be termed stabilimenta hints at the high homoplasy of this behavior when examined phylogenetically. Even if we restrict our definition of stabilimenta to include only linear and circular designs of silk, stabilimenta are built by at least 16 genera of spiders, primarily in the Araneidae and Uloboridae but also in the Tetragnathidae (Table 1). In some genera such as *Argiope*, *Cyclosa*, and *Uloborus* virtually every species for which data are available is known to include silk stabilimenta in some webs. Phylogenetic analysis suggests at least 9 origins of this behavior in the Araneoidea (Scharff & Coddington 1997). More important, their analysis demonstrates a very strong correlation between stabilimentum-building behavior and taxa that rest at the center of webs during daylight (Scharff & Coddington 1997: see also Eberhard 1973; Edmunds 1986). This correlation suggests that stabilimenta have a common (or at least similar) function across taxa and that the function of stabilimenta is related to the exposure to daylight of these spiders, compared with retreat dwelling or nocturnal taxa. This assertion is further supported by the behavior of *Uloborus gibbosus*, which is unusual for the genus because it does not rest at the web hub and also does not build a stabilimentum (Marples 1969). Despite this ecological commonality across stabilimentum-building taxa, at least 10 hypotheses have been proposed for the function of stabilimenta (Table 1.2). All of them have been proposed with particular reference to linear, cruciate, and circular silk stabilimenta. The evidence for and against each hypothesis is discussed below.
Strengthen webs or molting platforms. Stabilimenta may adjust tensions in webs, strengthening webs by altering tensions of radii at hubs (McCook 1889; Simon 1895; Rabaud 1932; Comstock 1940; Tilquin 1942; Gertsch 1949). Stabilimenta are attached to webs after all other elements are completed, suggesting that stabilimenta could be final adjustments to the tensions in threads. Silk stabilimenta are built more frequently by many taxa around the time that they molt (Nentwig & Rogg 1988). Nephila clavipes and N. maculata only include stabilimenta in molt webs (Robinson & Robinson 1973a, 1973b). Thus, molt webs that contain stabilimenta may provide particularly stable environments for ecdysis. The tensions of radial threads in Octonoba sybotides webs are higher in webs containing spiral silk stabilimenta, built by food-limited spiders, than that of radial threads in webs containing linear silk stabilimenta, built by well-fed spiders (Watanabe 1999a, unpubl.). This difference in tensions causes webs with spiral stabilimenta to transmit the vibrations of smaller prey, allowing hungry spiders to attack a wider breadth of prey (Watanabe unpubl.) Finally, Neet (1990) found that spiral silk stabilimenta were included in Cyclosa insulana webs more frequently after windy days, and suggested that spiders use spiral stabilimenta to stabilize webs.

However, the silk used to construct Argiope and Uloborus stabilimenta is relatively loose and unstressed and therefore could not greatly affect web tension (Hingston 1927; Eberhard 1973; Edmunds 1986; Peters 1993). The propensity of spiders to include stabilimenta in webs near or during molts could instead reflect the greater vulnerability of these spiders to predators, if stabilimenta function defensively (see below). Furthermore, stabilimentum-building spiders can molt in webs that do not contain stabilimenta (Nentwig & Rogg 1988) and, Nephila edulis, unlike other Nephila,
never includes stabilimenta in molting platforms, instead building stabilimenta only in capture webs (Austin & Anderson 1978). The results of Watanabe (unpubl.) are provocative, and do show a correlation between form of stabilimenta and differences in web tension. But, it is possible that the tensions of webs were finalized by adjustments to web hubs prior to the addition of any stabilimentum (Watanabe unpubl.), as is done by spiders that do not build stabilimenta. While Neet (1990) found an increase in the frequency of spiral stabilimenta after windy days, he did not find a difference in stabilimentum frequencies between populations in exposed and unexposed localities, as expected if stabilimenta functioned to stabilize webs. Finally, there is no clear selective pressure associated with web tension that could explain the repeated evolution of stabilimenta in only diurnal, hub-dwelling spiders and not also nocturnal hub-dwelling spiders, whose body weights would load webs similarly. Finally, the mechanical factors determining tensions of threads in vertical ecribellate (e.g. Argiope and Cyclosa) and horizontal cribellate (e.g. uloborids) webs can be quite different (Vollrath & Edmunds 1989; Köhler & Vollrath 1995; Bond & Opell 1998) yet both types of webs include similar looking stabilimenta.

*Deposits of excess silk.* Some silk glands, such as the aggregate and flagelliform glands that produce the sticky spirals of Araneid webs, limit web construction (Eberhard 1988) and are likely emptied completely during web construction. But, the glands used to spin silk stabilimenta are not emptied during web building and stabilimenta may simply be convenient ways to remove that excess silk (Wiehle 1928 in Eberhard 1973; Peters 1993). Peters (1995) found that *Polenecia producta*, an uloborid which builds derived
orbs completely lacking in sticky spirals, places stabilimentum-like deposits of silk on the branches that these spiders orient through the centers of their webs.

It is unclear what would be the adaptive advantage of depositing excess silk. More important, the stabilimentum of *Argiope* is composed entirely of aciniform gland silk (Peters 1982 in Foelix 1996; Peters 1993) and that of *Uloborus* includes aciniform gland silk (Peters 1993). Both of these genera use aciniform gland silk to wrap their prey (Foelix 1996). It is seems unlikely that spiders would need to empty the aciniform gland immediately before they begin to forage. Also, during an experiment that involved cutting stabilimenta from webs, some *A. aurantia* immediately built new stabilimenta one or more times (Blackledge & Wenzel 1999) indicating that spiders likely had not emptied their aciniform glands. Finally, the silk deposited by *P. producta* includes at least six different types of silk, unlike stabilimenta.

"Love paths". Stabilimenta may be sexual signals, which guide males to females in webs (Crome & Crome 1961; Junghans 1924 in Nentwig & Rogg 1988). *Philoponella herediae* includes stablimentum silk on vertical lines that extend into a complex vegetative substrate below its web. Opell (1987) suggested that the stablimentum silk may act as a tactile cue signaling presence of the web to wandering males (see also Bradoo 1985).

There is simply no documented evidence to support an hypothesis of sexual signaling. Male orb-weaving spiders typically do not use visual cues when searching for females and males will cut the silk in webs to produce isolated mating threads where
copulation takes place (Robinson & Robinson 1980; Foelix 1996), so that stabilimenta are also unlikely to affect vibratory courtship. While stabilimenta could theoretically function to transmit pheremones, as do silk draglines (Tietjen & Rovner 1982), there is no evidence to support this hypothesis. More important, this would be at best an incomplete explanation because both immature and already mated females as well as males build stabilimenta (e.g. Marson 1947b; Eberhard 1973; Robinson & Robinson 1978; Nentwig & Rogg 1988; Cushing & Opell 1990). Like the above hypotheses, sexual signaling does not explain why stabilimenta are not built by nocturnal or retreat dwelling spiders, both of which also need to attract mates.

**Thermoregulation.** The diurnal habits of stabilimentum-building spiders expose them to greater thermal stress than that experienced by spiders in retreats. Stabilimenta could act as sun shields that reduce thermal stress (Robinson & Robinson 1974; Humphreys 1993), much as can retreats in other web dwelling spiders (Humphreys 1974; Riechert & Tracy 1975; Königswald et al. 1990). Humphreys (1992) demonstrated that the solid disk stabilimenta built by *Neogea egregia* create shaded microclimates that *N. egregia* moves into during the hottest times of day, cooling the spiders by 1.8°C. Some studies have also found that stabilimenta are more common or larger in webs built in more exposed sites (Marson 1947b; Eberhard 1973; Blackledge & Wenzel submit.; Chapter 7).

Linear and cruciate stabilimenta do not provide any appreciable shade to spiders and do not produce cooler microclimates (Nentwig & Heimer 1987). While circular stabilimenta can provide shade, many of the spiders that build them, particularly uloborids, locate webs in highly sheltered microhabitats, such as in thick grass, sheltered
banks, and tree buttresses (Muma & Gertsch 1964; Lubin 1986). Thus, the shade produced by stabilimenta in these habitats is unlikely to be of significant adaptive value. Elgar et al. (1996) found stabilimenta to be more common in shaded environments, leaving unclear the relationship between stabilimenta and exposure of webs. In summary, solid disk stabilimenta may act as sun shields in some spiders (Humphreys 1992), but such a function cannot account for the repeated evolution of stabilimenta in shade dwelling taxa nor for the occurrence of linear and cruciform stabilimentum designs.

**Prey attraction.** Stabilimenta may provide visual signals or cues that attract insects to webs (Gertsch 1949; Ewer 1972; Elgar et al. 1996), much as some other spiders use chemical cues (Tietjen et al. 1987; Yeargan 1994). This hypothesis began to gain strong favor after an innovative study by Craig & Bernard (1990) in which they examined the spectral color properties of stabilimentum silk, along with other spider silks (see also Craig et al. 1994; Bond & Opell 1997; Craig 1997). They found that primitive spider silks reflect large amounts of ultraviolet (UV) light and that stabilimentum silk retains this UV reflectance, whereas other silks in Araneid orb webs reflect very low amounts of UV. Because UV light is an important component of insect navigation (Goldsmith 1961; Wehner 1981) and floral signals (Menzel & Shmida 1993; Chittka et al. 1994; Kevan et al. 1996), Craig & Bernard (1990) reasoned that stabilimenta, or "web decorations", could attract prey to webs (Craig 1995; Kiltie 1996). In experimental choice chambers, *Drosophila* fly toward chambers that are illuminated by full spectrum (UV+white) light in preference to chambers illuminated by UV-minus (human white only) light when both chambers contain either high UV reflecting webs (Craig & Bernard 1990) or low UV-
reflecting webs that also contain UV reflecting stabilimenta (Watanabe 1999b). Several studies have found correlations between the presence of stabilimenta in webs and high levels of insect interception in *Argiope argentata*, *A. trifasciata*, *Cyclosa conica*, and *Octonoba sybotides* (Craig & Bernard 1990; Tso 1996, 1998a; Watanabe 1999b). The number of linear silk bands in stabilimenta has also been correlated with increased prey capture in *Argiope keyserlingi* (Herberstein unpubl.). Hauber (1998) failed to find an association between stabilimenta and prey capture in *Argiope appensa* but noted that webs containing stabilimenta were smaller. This suggests that spiders may employ two different foraging strategies, one with small but highly attractive webs and the other with larger, more generalized, webs (Hauber 1998; Herberstein et al. 2000). Finally, sticky traps containing stabilimenta, which were collected from webs using acetate frames, intercepted more insects than did traps without stabilimenta (Tso 1998b).

Attraction of insects to UV reflecting silk has been suggested to be a contributing factor to the evolution of group foraging by spiders (Craig 1991). Even the bodies of spiders, which may reflect UV light, have been hypothesized to attract prey to webs (Craig & Ebert 1994). One interesting implication of the high visibility of stabilimenta to insect prey is that insects could potentially learn to use stabilimenta as visual cues to avoid webs. Thus, spiders may vary the shape of stabilimenta, particularly the number of arms in linear cruciate designs, to prevent insects from learning to avoid webs (Craig 1994a).

Despite the recent emphasis on the prey attraction hypothesis, there are several serious challenges to it. While prey attraction is consistent with the diurnal nature of stabilimentum building taxa, there is no obvious explanation for why diurnal, but retreat-
dwelling spiders, such as *Araneus*, *Metepeira*, and *Zygiella* do not build stabilimenta. Any diurnal spider would certainly benefit from visual attraction of prey, yet those spiders that rest in retreats do not build stabilimenta. Choice chamber experiments demonstrate only that insects fly toward sources of maximum photic stimulation in an isolated environment that is unlike the complex vegetative habitat where insect navigation evolved and where spiders build webs. For instance, phototaxis is a wavelength dependent behavior that involves a response to overall gradients of UV light across the sky and not to pinpoint sources of less intense, reflected UV light (Wehner 1981; Menzel & Greggers 1985). Although some studies have failed to find an effect of foraging success on stabilimentum building (Eberhard 1973; Nentwig & Rogg 1988; Tso 1999), other studies demonstrate that *Argiope aurantia*, *A. keyserlingi*, and *A. trifasciata* build larger and more frequent stabilimenta when they catch more prey (Blackledge 1998a; Herberstein et al. 2000). This means that correlations between prey capture and presence of stabilimenta in webs may be caused by high prey capture influencing the inclusion of stabilimenta in webs rather than the reverse (Blackledge 1998a). Furthermore, a stabilimentum represents a relatively small investment of silk so that it is unclear why a hungry spider would be less likely to build a stabilimentum if it would attract prey to the web (Blackledge 1998a; but see Herberstein et al. 2000). In a direct test of the prey attraction hypothesis, Blackledge and Wenzel (1999) paired *A. aurantia* webs at individual sites in the field, randomly selected one of the pair to have its stabilimentum removed, and performed a sham removal on the other web. This allowed them to control for the effects of previous foraging success (Blackledge 1998a), site quality differences (Janetos 1986), and architectural differences between webs with and
without stabilimenta (Hauber 1998; Herberstein et al. 2000). They found that stabilimenta actually cost spiders a 30% reduction in prey capture (Blackledge 1998b; Blackledge & Wenzel 1999). A final argument against the prey attraction hypothesis is that stabilimenta are often more common and larger in molting webs that do not contain sticky silk and do not act as prey capture devices (Ewer 1972; Robinson & Robinson 1973a, 1973b; Nentwig & Rogg 1988).

Recently, the critical issue of conspicuousness of stabilimentum silk to insects has been examined more thoroughly. Although stabilimenta reflect UV light, they also reflect large amounts of blue and green light, which means that stabilimenta have a flat, achromatic coloration to insects. Such achromatic objects blend with the background, as viewed by insects, and are considered to be cryptic (Chittka et al. 1994; Kevan et al. 1996; Blackledge 1998b). This crypsis of stabilimentum silk has since been empirically demonstrated in an experiment where honeybees were trained to associate “flowers” made of spider silk with nectar rewards. Bees could learn to find flowers made from primitive tarantula silk, which has a UV reflective peak. But, bees could not learn to find flowers made from stabilimentum silk, because its UV+blue+green reflectance gave poor color contrast against the natural grass background where the experiment took place (Blackledge & Wenzel 2000). The reflectance of stabilimentum silk is much more intense than that of most natural backgrounds yet the silk is still relatively inconspicuous because insects do not differences in brightness for color comparisons (Chittka et al. 1992; Giurfa et al. 1995a; Blackledge 1998b). These results are similar to those of classic bee training experiments using white+UV paper signals, which could not be used as obvious visual signals by bees (von Frisch 1950).
The stabilimentum as a defense.

The most often cited function for stabilimenta is that of defenses against visually hunting predators such as birds or wasps (see Eberhard 1990). This stems from the tight correlation between diurnal, hub dwelling habits and the building of stabilimenta because spiders resting on their webs in daylight are particularly exposed to visually hunting predators. Defensive hypotheses are also consistent with the frequent building of larger than normal stabilimenta by molting spiders because molting spiders are especially vulnerable to predators. Studies have also shown correlations between increased frequencies of stabilimenta and presence of avian predators in island populations of *Argiope* (Lubin 1975; Kerr 1993). Yet, there are several different hypothesized ways in which stabilimenta could defend spiders (examined below).

Camouflage/hide spiders. Stabilimenta may provide camouflage for spiders or in some cases physically hide spiders from predators (Hingston 1927; Marson 1947a,b; Marples 1969; Ewer 1972; Eberhard 1973; Lubin 1975, 1986; Tolbert 1975; Robinson & Robinson 1978; Neet 1990; Schoener & Spiller 1992). Most of the support for this hypothesis is largely circumstantial and consists of human perceptions of the conspicuousness of spiders and stabilimenta. The coloration of many spiders blends well with that of their stabilimenta, to the human eye. Spiders such as *Cyclosa* have the same mottled brown color as their debris stabilimenta while *Argiope*, particularly juveniles, often have silvery hairs on their dorsum that blend with the bright white silk of their stabilimenta. There are many anecdotal accounts of such spiders being almost impossible to discern from their stabilimenta (e.g. Marples & Marples 1937; Bristowe 1941; Marson
1947a; Eberhard 1973; Edmunds 1986; Lubin 1986). Some *Cyclosa* change from a silvery to brown coloration as they develop and this is accompanied by a change from largely silk to largely debris stabilimenta in webs (*i.e.* light to dark colored designs; Bristowe 1941; Marson 1947a). *Argiope catenulata* builds an unusual stabilimentum consisting of a single vertical linear silk zigzag above the spider and two diagonal silk zigzag lines below the spider. Hingston (1927) argues that the coloration of *A. catenulata*, which has one longitudinal and two lateral silver bands, is specifically adapted to blend with this unique stabilimentum design. The resting postures of spiders in webs are highly stereotyped (Opell & Eberhard 1984) and have been suggested to be essential clues to the camouflage function of stabilimenta. Uloborids, which build linear stabilimenta, rest in small gaps in the stabilimenta with their legs tightly appressed to the designs (Fig. 1.1) while *Argiope*, which build cruciate stabilimenta, hold their legs in tight alignment with their x-shaped designs (Fig. 1.2; Hingston 1927; Ewer 1972; Eberhard 1973; Robinson & Robinson 1974). Interestingly, these spiders will relax the position of their legs after sunset, when visual predators are presumably no longer hunting. Even species with stabilimenta unlike those of closely related taxa keep their legs aligned with their unique designs during daylight, such as *A. catenulata* with its tripartite design or *U. cruciferiens*, an uloborid with a cruciate design (Hingston 1927). A camouflage function is particularly likely for debris stabilimenta as some *Cyclosa* and Gasteracanthines even build decoy spider bodies or web hubs (Hingston 1927; Cloudsley-Thompson 1980). Disk stabilimenta may also hide spiders physically by providing an opaque surface that spiders can move behind when attacked (Tolbert 1975). Some spiders are more likely to build stabilimenta in more exposed web sites, which may
be a response to the increased vulnerability of these spiders to visual predators (Eberhard 1973; Blackledge & Wenzel submit.; Chapter 7). The only experimental evidence for a camouflage function comes from a study of sphecid wasp predation on juvenile *A. trifasciata*. Blackledge and Wenzel (submit.; see also Chapter 7) found that linear stabilimenta were associated with a significant decrease in the probability that spiders were captured by wasps. They suggested that stabilimenta may provide enough camouflage to allow spiders extra time to drop safely from webs when attacked.

In general, the camouflage hypothesis is supported by much circumstantial evidence and little empirical support (but see Blackledge & Wenzel submit, and Chapter 7). However, this is due mostly to a lack of experimentation *per se*. Robinson and Robinson (1970a) argued strongly against the camouflage hypothesis because they considered silk stabilimenta to be conspicuous cues that predators could learn to associate with spider prey. They found that birds learned to use artificial stabilimenta to find cricket prey. Yet, they had to present prey at high levels for learning to occur and, because birds had to learn to use stabilimenta, their experiment demonstrated that such use of stabilimenta as cues in prey location was not already present in wild birds. This is itself an argument that avian predators do not ordinarily use stabilimenta to locate prey. Furthermore, although the conspicuousness of silk stabilimenta to humans is indisputable, it is the contrast of spiders against stabilimenta, and stabilimenta against backgrounds, that are important in determining whether or not stabilimenta act as camouflage (Eberhard 1973). And, at least to insect predators, stabilimenta may appear quite inconspicuous (Blackledge 1998b; Blackledge & Wenzel 2000, submit.; Chapter 7). In at least a few instances spiders may also contrast, to the human eye, with their
stabilimenta, such as dark colored *Neogea egregia* on white silk disks (Humphreys 1992). Finally, while the resting postures of spiders seem to be behaviorally adapted to blend with stabilimenta, the importance of spiders aligning their legs with stabilimenta is not absolute. *Argiope* that build vertical-line stabilimenta, such as *A. aurantia*, *A. bruennichi*, and *A. trifasciata*, do not rest with their legs aligned with stabilimenta.

**Predator confusion.** The bright silk of stabilimenta may increase the probability of spiders surviving attacks by startling or confusing predators (Marples 1969). Many spiders vibrate or pump their webs when disturbed, causing the outlines of spiders and stabilimenta to blur (Cloudsley-Thompson 1995). This may make it more difficult for predators to attack spiders (Tolbert 1975; Schoener & Spiller 1993). Also, the bright silk of stabilimenta may simply draw the attention of attacking predators away from spiders (Hingston 1927; Bristowe 1941). Blackledge and Wenzel (submit.; see also Chapter 7) suggested that confusion may be a second contributing factor to the higher rates of survival of spiders with stabilimenta in their wasp predation experiment. Finally, salticid spiders will attack wrapped prey bundles in webs in preference to *Argiope* (Robinson & Valerio 1977), suggesting that detrital stabilimenta could act as similar “decoys”. There has been little direct criticism of the predator confusion hypothesis and more empirical tests are needed.

**Web advertisement.** Because stabilimenta can be so much more conspicuous than the rest of webs, they could act as warnings to potential predators, flying birds, or insects that are too large to be captured (Ewer 1972). The sticky silk of webs can be dangerous to many
predators such as wasps and small lizards (Edmunds & Edmunds 1986; Cloudsley-Thompson 1995; Rayor 1997), and it is an irritant to birds, which may spend up to an hour grooming after sticky silk adheres to their feathers (Horton 1980; Eisner & Nowicki 1983). Thus, stabilimenta may function as aposematic signals. Horton (1980) performed the first test of this hypothesis using captive blue jays (Cyanocilla cristata). He demonstrated that blue jays learned to prey preferentially upon spiders in non-sticky silk scaffolding over spiders in webs with complete sticky silk spirals, and most especially spiders in webs which also contained stabilimenta. Eisner and Nowicki (1983) placed artificial stabilimenta in webs and found that the webs survived early morning hours better than webs without stabilimenta, suggesting that stabilimenta protect webs from flying birds. These results have since been replicated using real stabilimenta in the webs of A. aurantia (Blackledge & Wenzel 1999). Finally, Lubin (1975) and Kerr (1993) found that stabilimenta are more common in populations of spiders where bird predators are present.

These studies clearly demonstrate that web advertisement by stabilimenta can be beneficial to spiders. However, these studies do not address how important such a function is to the overall fitness of spiders. Because bird "fly-through" is probably rare, preventing it may not offset the cost of signaling presence of webs if insect prey detect stabilimenta (Blackledge & Wenzel 1999). This suggests that web advertisement alone cannot account for the repeated evolution of stabilimenta. Furthermore, many taxa that build stabilimenta do so in relatively sheltered areas such as deep in tall grass or around tree buttresses, where birds are unlikely to fly into webs (Eberhard 1990). While preventing predation by birds is undoubtedly more important than preventing birds from
flying through webs (Blackledge & Wenzel 1999), protection from avian predators is likely to be relatively unimportant for any but the most exposed stabilimentum-building spiders, such as *Argiope* and *Cyclosa*. Testing an assumption of the web advertisement hypothesis, McClintock and Dodson (1999) predicted that *Cyclosa insulana* would change the orientation of linear stabilimenta (vertical versus horizontal) to contrast better with the background after webs were disturbed. They did not find the predicted effect.

**Apparent size hypothesis.** Because the legs of spiders that build cruciate silk stabilimenta are closely aligned with the designs, cruciate silk stabilimenta may appear as extensions of the legs of spiders thereby increasing the apparent size of spiders to gape-limited predators (Tolbert 1975). Cruciate stabilimenta are most common in intermediate sized *A. argentata*. Schoener and Spiller (1992) argue that spiders of intermediate size benefit from cruciate stabilimenta by appearing larger than the maximum size of prey attacked by *Anolis* lizards. Very small spiders do not build cruciate stabilimenta because these stabilimenta could increase the apparent size of spiders into the range preferred by lizards, while adult spiders are already larger than the maximum prey size (Schoener & Spiller 1992).

This hypothesis has yet to be tested empirically. The apparent size hypothesis is likely to apply only to cruciate stabilimenta because other stabilimentum shapes obliterate, rather than potentially increase, the outlines of spiders. But, Edmunds (1986) suggests that even linear silk stabilimenta enhance the apparent size of spiders when spiders vibrate webs.
Non-functional. Finally, the wealth of studies with contradictory findings and the lack of a clear over-riding influence of many environmental parameters on stabilimentum-building have led some to suggest that stabilimenta are non-functional vestiges (Rabaud 1932; Gertsch 1949; Reed et al. 1969) or reactions to stress (Nentwig & Heimer 1987; Nentwig & Rogg 1988).

An inability to pinpoint a function due to a lack of empirically based research should not be taken as an argument for lack of function. Also, the tight ecological correlation between evolution of stabilimenta and diurnal, hub-resting habits argues for a convergent function (e.g. Coddington 1994). Finally, the cost to capture of prey caused by stabilimenta would provide strong selection against the building of stabilimenta, if they had no selective benefit (Blackledge & Wenzel 1999).

Summary

Most hypotheses about the adaptive value of stabilimenta have limited circumstantial support and no empirical support, though the later is usually due to a lack of study rather than experimental refutation. Of the two hypotheses that have received serious empirical attention (prey attraction and predator defense), the weight of evidence argues against the prey attraction hypothesis. However, there is little evidence arguing against defensive functions (Eberhard 1973), particularly those of camouflaging spiders or confusing attacking predators. More important, there are several studies that provide direct evidence for defensive functions (Horton 1980; Eisner & Nowicki 1983; Blackledge & Wenzel 1999, submit; Chapter 7). Perhaps solid disk stabilimenta may also have a thermoregulatory function (Humphreys 1992, 1993), but this is likely a secondary
function because of its limited application to only solid disk stabilimenta in only a few species (e.g. argiopids that build webs in highly exposed habitats). So, it seems likely that most types of stabilimenta in most taxa function defensively, although the precise fitness advantages are likely to vary with the age of spiders, type of stabilimenta, and microhabitats in which webs are built. More well-controlled experimentation is needed to test this conclusion rigorously.

Convergence and stabilimenta

The repeated evolution of stabilimentum-building under the same ecological context of diurnal, non-retreat dwelling taxa suggests that stabilimenta are meeting the same evolutionary challenge in all of these spiders. If so, then the variation in stabilimentum form and frequency, both within individuals and populations as well as between species begets an important question. Have different taxa converged upon similar solutions to the same ecological problem using different behavioral pathways? Or, is stabilimentum building a homologous behavioral algorithm for which the expression is repeatedly evolving across many taxa?

There are several lines of evidence that suggest that the independent derivations of stabilimentum building actually represent different approaches to the same ecological problem (i.e. producing a structure at the centers of webs that defends against visual predators, perhaps analogous to retreats). This is because different taxa of spiders will construct superficially similar looking silk stabilimenta, but by using different behaviors. For instance, *Uloborus* uses silk from both the aciniform and piriform glands to make stabilimenta while *Argiope* uses silk from only the aciniform gland (Peters 1993).

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Second, *Cyclosa, Uloborus* and *Nephila* begin constructing linear silk stabilimenta from hubs toward the outside of webs (Marples 1937; Eberhard 1973; Higgins 1990) while *Argiope* begins at the outside and finishes at the hub (Robinson & Robinson 1970a; Edmunds 1986, pers. obs.). Third, *Uloborus* uses its fourth pair of legs to pull silk from its abdomen when making stabilimenta (Eberhard 1973) while *Argiope* keeps all legs on the orb web, using only movements of the abdomen to build stabilimenta (Edmunds 1986, pers. obs.). Finally, the detailed structure of stabilimenta can be quite different.

Linear stabilimenta of *Uloborus* and *Cyclosa* are thick bands of amorphous silk while the linear stabilimenta of *Argiope* consist of more or less distinct zigzags.

**Conclusions**

The extreme variability in form and frequency of stabilimenta has long confounded attempts to explain their function. Thus, a variety of functional roles have been proposed for stabilimenta. A defensive hypothesis is most consistent with the ecological similarities across stabilimentum-building taxa (*i.e.* spiders that rest at the centers of webs during daylight where they are exposed to visual predators). There is little evidence to argue against a defensive function and several studies have found empirical support for the camouflage, predator confusion and web advertisement defensive hypotheses (Horton 1980; Eisner & Nowicki 1983; Blackledge & Wenzel 1999, submit.; Chapter 7). The prey attraction hypothesis has also received much empirical support but does not explain the ecological similarities across stabilimentum-building taxa. Also, a direct comparison of prey capture in *A. aurantia* demonstrates that stabilimenta can cause a reduction in prey capture (Blackledge & Wenzel 1999). Finally,
examining the visibility to insects of stabilimentum silk versus other spider silk shows that stabilimentum silk is cryptic, rather than attractive to insects (Blackledge 1998b; Blackledge & Wenzel 2000).
Figure 1.1: Linear silk stabilimentum. Most spiders rest with their legs closely appressed to the axes of the designs, although *Argiope* that build vertical lines do not.
Figure 1.2: Cruciate silk stabilimentum. Although spiders sometimes build complete designs, it is more common for them to build only one or two arms of the stabilimentum.
Figure 1.3: Circular silk stabilimentum. Uloborids and *Cyclosa* build circular stabilimenta out of single spirals of silk. The spirals can sometimes be quite irregular, meandering across the hubs of the webs.
Figure 1.4: Concentric circular silk stabilimentum. Argiope construct circular stabilimenta out of concentric loops of zigzagging silk.
Figure 1.5: Solid disk stabilimentum. The spider cannot be seen when on the opposite side of a solid disk stabilimentum.
Figure 1.6: Silk flocculations. Gasteracanthines include fluffy puffs of silk along the radii and frame threads of webs. Juvenile uloborids include a mesh-like array of fine silk dots in their webs.
Figure 1.7: Egg sac stabilimentum. Egg sacs are often included in orb webs. Notice that the egg sacs are similar in size and shape to the spider and that the spider rests in alignment with the stabilimentum. The legs of the spider are also drawn in, closely appressed to its body.
Figure 1.8: Detritus stabilimentum. Detritus stabilimenta may be built on top of a linear silk stabilimentum or placed in a web that contains no other stabilimentum. Materials used to construct detritus stabilimenta include exuviae, prey remains, plant materials, and any other small debris blown into webs. The debris is reused when a new web is built.
Figure 1.9: Whole leaf. *Phonognatha* will fold a leaf into a retreat at the center of its web, which the spider rests within. Other spiders, such as *Arachnura*, will sometimes place entire leaves in the hubs of their webs and will rest below the leaves.
Table 1.1: Genera of stabilimentum-building spiders and the types of stabilimenta that they are known to construct. a.) Stabilimentum building behavior not described for this genus but inferred from phylogenetic analysis (Scharff & Coddington 1997). b.) Listed as building stabilimenta in Scharff & Coddington (1997) but unable to verify.

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<td>Phonognatha</td>
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<td>12, 33</td>
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</table>

Table 1.1 (continued)
Table 1.2: Hypotheses for the function of stabilimenta in spider webs.
<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Evidence in Support</th>
<th>Evidence in Criticism</th>
</tr>
</thead>
<tbody>
<tr>
<td>strengthen webs or provide molting platform</td>
<td>-spiral stabilimenta are built more after windy days (Neet 1990)</td>
<td>-silk is unstressed and loosely attached to webs (Eberhard 1973; Edmunds 1986; Peters 1993)</td>
</tr>
<tr>
<td></td>
<td>-found in only molt webs of <em>N. clavipes</em> &amp; <em>N. maculata</em> (Robinson &amp; Robinson 1973a, 1973b)</td>
<td>-found in only capture webs of <em>N. edulis</em> (Austin &amp; Anderson 1978)</td>
</tr>
<tr>
<td></td>
<td>-different types of stabilimenta are associated with different web tensions in Octonoba (Watanabe unpubl.)</td>
<td>-molting can occur in webs without stabilimenta (Nentwig &amp; Rogg 1988)</td>
</tr>
<tr>
<td>deposit of excess silk (Wiehle 1928; Peters 1993)</td>
<td>-<em>Polenecia</em> deposits stabilimentum-like silk when making web (Peters 1995)</td>
<td>-stabilimentum silk produced from aciniform gland that also produces silk for wrapping prey (Peters 1993)</td>
</tr>
<tr>
<td>&quot;love path&quot; to guide males to female (Junghans 1924; Crome &amp; Crome 1961)</td>
<td><em>Philoponella heredia</em> includes stabilimentum silk on vertical web elements that protrude into dense vegetation and may provide tactile cue to males (Opell 1987)</td>
<td>-multiple stabilimenta can be built indicating there is still silk in aciniform gland (Blackledge &amp; Wenzel 1999)</td>
</tr>
<tr>
<td>thermoregulation (Robinson &amp; Robinson 1974; Humphreys 1993)</td>
<td>-juvenile <em>Neogea egregia</em> were 1.8°C cooler on the shaded side of disk stabilimenta and moved under them during periods of thermal stress (Humphreys 1992)</td>
<td>-cruciform stabilimenta produce no temperature differential (Nentwig &amp; Heimer 1987)</td>
</tr>
<tr>
<td></td>
<td>-consistent with pattern of diurnal spiders at web hub</td>
<td>-can be more common or thicker in webs in shady sites (Elgar et al. 1996 but see Marson 1947b; Eberhard 1973)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-uloborids build webs in shaded locations (Muma &amp; Gertsch 1964; Lubin 1986)</td>
</tr>
</tbody>
</table>

(Continued on pg. 42)
### Table 1.2 (continued)


- silk reflects UV light (Craig & Bernard 1990; Craig et al. 1994; Watanabe 1999b)
- increased web damage or prey capture is correlated with presence of stabilimenta in webs (Craig & Bernard 1990; Hauber 1998; Herberstein unpubl.; Tso 1996, 1998a; Watanabe 1999b)
- sticky traps with stabilimenta catch more (Tso 1998b)
- bodies of spiders also reflect UV (Craig & Ebert 1994)

hungry spiders are less likely to build stabilimenta (Blackledge 1998a; Herberstein et al. 2000)
- correlation between stabilimenta and prey capture could be caused by foraging success influencing decisions to build stabilimenta (Blackledge 1998a)
- webs with stabilimenta removed catch more prey than webs containing stabilimenta (Blackledge & Wenzel 1999)

- UV+white color of silk may be cryptic to common insect prey (Chittka et al. 1994; Kevan et al. 1996; Blackledge 1998b; Blackledge & Wenzel 2000)
- no diurnal retreat dwelling spider builds stabilimenta, but they would benefit from prey attracted to webs

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camouflage or hide spiders (Marson 1947a; Marples 1969; Lubin 1975; 1986; Tolbert 1975; Robinson & Robinson 1978; Schoener & Spiller 1992; Neet 1990)

- diurnal, hub hunting spiders are highly vulnerable to visual predators
- spiders closely align legs with stabilimenta (Hingston 1927; Eberhard 1973; Ewer 1972)
- change from white silk to darker debris stabilimenta accompanies color change of spiders (Marson 1947a)
- sphecid wasps capture higher proportion of spiders without stabilimenta (Blackledge & Wenzel submit.; Chapter 7)

- birds can learn to use artificial stabilimenta to find prey (Robinson & Robinson 1970a)
- silk stabilimenta per se are bright white to humans

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(Continued on pg. 43)
predator confusion (Hingston 1927; Marples 1969; Tolbert 1975; Schoener & Spiller 1992)
- sphecid wasps capture higher proportion of spiders without stabilimenta (Blackledge & Wenzel submit. Chapter 7)
- shaking of webs is associated with stabilimenta and blurs outlines of spiders (Tolbert 1975; Edmunds 1986)
- salticids attack wrapped prey in webs (similar to "decoy" stabilimenta) before attacking Argiope (Robinson & Valerio 1977)
- there has been no empirical test of the predator confusion hypothesis

web advertisement (Ewer 1972)
- captive birds preferentially prey upon spiders in webs without stabilimenta (Horton 1980)
- webs with real (Blackledge & Wenzel 1999) or artificial (Eisner & Nowicki 1983) stabilimenta are damaged less often by birds
- stabilimenta are more common on islands with insectivorous bird predators (Lubin 1975; Kerr 1993)
- birds can learn to use artificial stabilimenta to find prey (Robinson & Robinson 1970a)
- *Cyclosa* do not change orientation of stabilimenta to contrast with background after webs are damaged (McClintock & Dodson 1999)

increase apparent size of spiders to predators
- stabilimenta are more common among intermediate size classes of spiders which would most benefit from an apparent increase in size (Schoener & Spiller 1992)
- pumping of webs blurs and enlarges outline of spiders (Tolbert 1975; Edmunds 1986)
- there has been no empirical test of the apparent size hypothesis

non-functional, vestigial, or reaction to stress (Rabaud 1932; Gertsch 1949; Reed et al. 1969)
- variability in form, frequency, and environmental control of stabilimenta is difficult to explain (Nentwig & Heimer 1997)
- stabilimenta cost spiders prey (Blackledge & Wenzel 1999) and this cost would select against expression of a non-functional structure

Table 1.2 (continued)
CHAPTER 2

STABILIMENTUM VARIATION AND FORAGING SUCCESS IN *ARGIOPE AURANTIA* AND *ARGIOPE TRIFASCIATA* (ARANEAE, ARANEIDAE)

Stabilimenta are conspicuous designs of white silk included in the otherwise cryptic orb webs of several genera of orb weaving spiders. Stabilimenta are highly variable in shape, including spiral disks, crosses or vertical lines, and are often incomplete (Hingston 1927; Eberhard 1973). Detritus or egg sacs included in orb webs are also sometimes termed stabilimenta (Eberhard 1990), but these structures are not discussed herein.

Many functions have been proposed for stabilimenta, though evidence is lacking for most. They were initially thought to mechanically stabilize orb webs (McCook 1889; Simon 1895; Robinson & Robinson 1970a). Yet, the silk stabilimenta are built from is too loosely attached to webs to affect them mechanically (Eberhard 1973; Foelix in Edmunds 1986). Other early hypotheses suggested that stabilimenta functioned as "love paths" to guide male spiders to females (Wolfram in Eberhard 1973) or as deposits of excess or reserve prey swathing silk (Vinson in Eberhard 1973). Yet, stabilimenta are common in webs of juvenile spiders, built long before sexual maturity (Eberhard 1973;
Edmunds 1986). And, it is unlikely that stabilimenta are reserve swathing silk because the silks are structurally different (Eberhard 1973) and stabilimenta are often included in molting webs, which do not contain the sticky silk necessary for prey capture (Robinson & Robinson, 1973a). A thermoregulatory, sun shading, function has been suggested for disk shaped stabilimenta in *Neogea* sp. (Humphreys 1992) but is unlikely for linear designs which often don't occlude the bodies of spiders (Nentwig & Heimer 1987).

Stabilimentum production has evolved many times in the Araneidae but is found only among spiders that rest at the hubs of their webs in daylight (Eberhard 1973; Scharff & Coddington 1997). Stabilimenta are therefore thought to function as visual signals used in either predator defense or attraction of prey. The designs may camouflage spiders (Eberhard 1973; Edmunds 1986), startle predators (Tolbert 1975; Schoener & Spiller 1992), or even serve as aposematic warnings to flying birds or large insects (Ewer 1972; Eisner & Nowicki 1983; Kerr 1993). Prey may be attracted to the webs of spiders by UV light reflected off the stabilimenta (Craig & Bernard 1990; Tso 1996).

Both classes of functional hypotheses have had difficulty accounting for the great amount of variation in shape and frequency of stabilimenta (Eberhard 1990). Within a species, individual spiders vary in how often they build these designs (Eberhard 1973; Edmunds, 1986). Spiders may also produce several different types of designs over their lifetime and often include incomplete designs in their webs (Ewer 1972; Edmunds 1986; Nentwig & Rogg 1988). Some of this variability has been correlated with the maturation of spiders (Ewer 1972; Robinson & Robinson 1973a; Edmunds 1986; Nentwig & Rogg 1988). Yet, few correlations between stabilimentum construction and environmental parameters have been demonstrated (Edmunds 1986; Nentwig & Rogg 1988).
Hypotheses for a prey attraction or predator defense function for *Argiope* stabilimenta generate mutually exclusive predictions about the effect of foraging success on stabilimentum variation, based upon the trade-offs that spiders must make between foraging and defense. Many species of orb weaving spiders increase their foraging effort, when starved, through an increase in the capture area of their webs (Higgins & Buskirk 1992; Pasquet *et al.* 1994; Sherman 1994). It has been argued that webs with more stabilimentum silk should catch more prey (Craig & Bernard 1990) and that *Argiope aetherea* adjusts the amount of silk in stabilimenta to increase insect attraction in dim habitats (Elgar *et al.* 1996). Therefore, an increase in stabilimentum size and frequency in the webs of starved spiders seems likely if these designs are prey attractants, particularly if stabilimenta are cheap to build. At the same time, these highly visible structures could also attract predators to webs. Pompilid and sphecid wasps as well as salticid spiders are important predators of orb weaving spiders (Tolbert 1975; Hoffmaster 1982; Coville 1987) and are likely to have visual pigments similar to the arthropod prey of *Argiope* (Chittka 1996). Furthermore, vertebrate predators such as birds can perceive and utilize the UV light (Bleiweiss 1994; Derim-Oglu & Maximov 1994) thought to be so crucial to attraction of prey. Birds can also associate artificial stabilimenta with potential prey (Robinson & Robinson 1970a). Thus, if stabilimenta are prey attractants then satiated spiders are likely to decrease investment in them to avoid increased predation risk. Alternatively, if stabilimenta function as predator defense mechanisms, then starved spiders would be expected to build them less often, particularly if stabilimenta are energetically costly. The silk in stabilimenta could be calorically expensive. More likely, a highly visible stabilimentum designed to advertise webs to predators may also help
prey avoid webs. Web visibility has been demonstrated to be a very important factor in prey capture success (Craig & Freeman 1991; Olive 1980) and there is evidence that Araneid orb webs have evolved to be visually cryptic (Craig 1986, 1988; Craig et al. 1994). Craig (1994a) has argued that variation in stabilimenta in *A. argentata* functions to prevent some prey from learning to avoid webs. Thus, satiated spiders would be more likely to include conspicuous defensive structures in their webs.

If stabilimenta are prey attractants, spiders experiencing poor foraging success should invest more in them despite a probable increased risk of predation. Alternatively, if stabilimenta are defensive structures, then spiders experiencing good foraging success should invest more in them despite a probable decrease in prey capture. Such trade-offs between foraging success and predation risk may already made by juvenile *Argiope* when they include a non-sticky silk barrier around their web. While the barrier may physically deter predators, it may also inhibit prey from reaching the web (Tolbert 1975; but see Higgins 1992). Foraging-defense trade-offs are also well documented in colonial orb weaving spiders (Rayor & Uetz 1990; Uetz & Hieber 1997).

While these predictions have not been explicitly tested, Eberhard (1973) and Nentwig and Rogg (1988) found no influence of short-term fluctuations in the foraging success of *Uloborus diversus* or *Argiope argentata* on stabilimentum frequency. But, neither study examined the effect on stabilimenta of differences in the foraging success between spiders, which could easily result from variation in prey abundance between web sites (Craig 1989).

In this study, I examine the effect of longer-term differences between groups of spiders in the amount of prey captured and of variance in capture rate on the frequency of
inclusion and size of stabilimenta in the webs of the yellow garden argiope Argiope aurantia Lucas and the banded argiope Argiope trifasciata (Forskal).

Methods

All of the spiders used in this experiment were collected on 30 August 1996 from a prairie reserve at the Marion campus of The Ohio State University (latitude 40° 34', longitude 83° 05'). Argiope aurantia and A. trifasciata are common as adults in old fields of Ohio in late summer and early autumn. Both species build disk stabilimenta when juveniles and vertical line stabilimenta as mature adults. After collection, all spiders were starved for five days to allow them to evacuate their guts (Nakamura 1987). Spiders were weighed to the nearest mg on a Mettler PM400 balance before and after the experiment.

Twenty-eight female A. aurantia and ten female A. trifasciata were used in the experiment. All were mature except for one of the High Prey A. trifasciata which molted to maturity on the fourth day of the experiment. Argiope aurantia were housed in wooden cages (35 x 35 x 10cm) covered with clear plastic sheeting on the top, front and back. Screen sides provided ventilation. Wooden rods, 35cm in height, at either end of the cage were connected at the top by a thread to provide web attachment sites. Argiope trifasciata were housed in metal cages (45 x 45 x 8cm) with plexi-glass fronts and backs. Here, the screen top and sides provided continuous web building substrates. The experiment was conducted in a southeast room of the OSU Insectary greenhouse where vents maintained temperature near outdoor levels. Light intensity was not homogeneous throughout the room. Therefore, A. aurantia cages for each of the two feeding treatments were placed alternately on shelves around the room, with A. trifasciata cages mixed
among them, so that both species and all treatments were subjected to similar variation in light. All spiders were sprayed with a fine mist of water every day.

Feeding treatments

Individuals of both species were randomly assigned to either a High Prey or a Low Prey treatment (15 *A. aurantia* and 4 *A. trifasciata* were in the High Prey treatments). Prey were placed directly in the capture area of webs. If a spider had not built a web, prey was instead offered to it by gently rubbing the larva against the chelicerae of the spider until accepted or until 90s elapsed. High Prey spiders were offered one large *Tenebrio molitor* larva (13.3 ± 1.0mg) daily for the entire 27 days of the experiment. Low Prey spiders were offered approximately one-third this amount, in two sequential feeding regimes.

All Low Prey spiders were included first in a high variance regime and then in a low variance regime. During the high variance regime, frequency of prey capture was altered. Low Prey spiders were offered the same size of larvae as High Prey spiders, but one-third as often. They received one large *T. molitor* larva (13.3 ± 1.0mg) every three days for the 13 days of the high variance regime. Then size of prey was manipulated in the low variance regime. Low Prey spiders were now offered smaller prey than the High Prey spiders, but at the same rate, for the final 14 days of the experiment. In the low variance regime one small *T. molitor* larvae (3.6 ± 0.8mg) was offered to each Low Prey spider daily. This change in feeding regime allowed me to determine if prey size or variance of capture rate had a confounding influence.
Data collection

I used calipers to measure, to the nearest mm, the maximum height and width of each web, from outermost sticky spiral, and the maximum height and width of the free zone, from innermost sticky spiral (Fig. 2.1). Overall web area and free zone area were estimated using the formula: area = π * 0.5(height) * 0.5(width). Capture area of the web was then computed as: capture area = web area - free zone area.

Stabilimenta consisted of either a single lower vertical arm or both a lower and an upper vertical arm. I measured the length of each arm to the nearest mm with calipers. Stabilimenta were generally contained within two adjacent radii which diverged from the centers of webs (Fig. 2.1). Therefore, stabilimentum width was highly dependent upon stabilimentum length and I did not include width in the analysis.

Spiders often did not build new webs every day, although data were only collected from new webs. If a spider remained in an old web for two days, several radii were broken to collapse the web and encourage rebuilding. I occasionally damaged webs during data collection. This prevented complete data collection for five *A. trifasciata* orb webs.

Web collection

I collected nineteen *A. aurantia* laboratory webs on the final four days of the experiment and weighed them to compare how much silk was invested in stabilimenta and webs. *Argiope aurantia* characteristically filled in the hubs of its orb web with an amorphous shield of white silk that was laid down just prior to the stabilimentum, with similar movements of the abdomen. I assumed that the hub silk was homologous to that
in the stabilimentum itself. I cut out the hub and stabilimentum using forceps heated in a clean blue flame and wrapped them around a small, pre-weighed piece of nylon fishing line. Finally, I cut the orb web from the frame and wrapped it around a second piece of pre-weighed fishing line. Because the sticky silk of webs absorbed water, all samples were dried at 50°C for at least 48 hrs before being weighed, to the nearest μg, on a Mettler UMT2 balance. Although dehydration of the nylon line was minuscule, I dried and weighed twelve additional pieces of fishing line to obtain a correction factor for dehydration of the nylon itself.

Data analysis

All comparisons of web and stabilimentum measurements between treatments were made separately for the two species.

I compared the frequency with which spiders built stabilimenta between treatments using contingency tests. Each spider was classified as to whether it built stabilimenta more or less often than the mean frequency of all spiders. I then used a Chi-square goodness of fit test to compare the distribution of spiders above and below that overall mean.

Stabilimentum length was normally distributed and I compared it between treatments using nested ANOVAs (Sokal & Rohlf 1981). The multiple stabilimenta built by individual spiders were nested within treatment to avoid pseudo-replication. Many web parameters were not normally distributed so nested ANOVAs could not be performed. Instead, I examined all web parameters using t-tests to compare the means of each spider, thereby preventing pseudo-replication.
I examined the effect of prey variance regime within the Low Prey treatment by using Wilcoxon Signed Rank tests to compare the means for each spider between the high variance and low variance regimes.

Results

Initial spider mass was similar between treatments for *A. aurantia* (High Prey = 542.4 ± 62.7mg, Low Prey = 440.7 ± 66.0mg; t=1.11, P>0.25) and mass did not change significantly over the experiment for either High Prey treatment (t=0.771, P>0.45) or Low Prey treatment (t=1.471, P>0.16). *Argiope aurantia* produced egg sacs throughout the experiment (High Prey n = 8, Low Prey n = 7). *Argiope trifasciata* initial mass was similar between treatments (t=0.28, P>0.75) but mass increased significantly in both the High Prey treatment (initial = 181.7 ± 30.6mg, final = 420.3 ± 66.4mg; t=3.67, P<0.05) and Low Prey treatment (initial = 192.3 ± 22.7mg, final = 400.3 ± 54.3mg; t=4.86, P<0.005). However, there was no significant difference between treatments in the increase (t=0.412, P>0.65). Egg sacs were produced by *A. trifasciata* only on the last eight days of the experiment (High Prey n = 4, Low Prey n = 1).

Effect of variance regime

Low Prey treatment webs and stabilimenta were relatively similar between prey variance regimes, for both species. Wilcoxon Signed Rank tests revealed that *A. aurantia* built significantly longer free zones during the low variance regime (P<0.05; 105.8 ± 2.3mm vs. 98.3 ± 2.5mm). They also built longer lower stabilimentum arms during the low variance regime (P<0.05; 31.8 ± 1.0mm vs. 28.6 ± 1.5mm). *Argiope trifasciata* orb
webs were significantly wider in the low variance regime (P<0.05; 296.1 ± 8.3mm vs. 268.9 ± 10.8mm). For each of these three parameters, the mean of both regimes and the Low Prey treatment mean itself were consistently all higher or all lower than the mean of the High Prey treatment.

Effect of prey treatment

Lower and upper stabilimentum arms were significantly shorter in Low Prey treatment orb webs for both *A. aurantia* (Table 2.1) and *A. trifasciata* (Table 2.2). *Argiope trifasciata* webs included both stabilimentum arms significantly less often in the Low Prey treatment than in the High Prey treatment (Table 2.2). All of the High Prey *A. trifasciata* built both stabilimentum arms more often than average. While all Low Prey treatment *A. trifasciata* built the upper stabilimentum arm less often than average, and all but one built the lower arm less often than average. Chi-square tests could not be conducted because of the empty cells and P-values were instead calculated as the probability of these skewed distributions occurring by chance (i.e. that these distributions would occur if every spider had a 50% chance of building stabilimenta more often than average).

Prey treatment had little effect on the webs of either *A. aurantia* (Table 2.3) or *A. trifasciata* (Table 2.4). Except that Low Prey *A. aurantia* built significantly shorter free zones (P<0.025) and consequently had significantly smaller free zone areas (P<0.05).
Stabilimentum and web mass

Web mass was $1,404 \pm 632 \mu g$ while the mass of the stabilimentum and hub together was $304 \pm 210 \mu g$. The hub and stabilimentum of an additional three webs were collected and were of equal mass ($111 \pm 23 \mu g$ and $111 \pm 30 \mu g$ respectively). Thus, stabilimenta alone accounted for approximately 10% of the dry mass of silk in webs that included them.

Discussion

My study demonstrates that the foraging success of *Argiope* has a significant effect on stabilimentum building. Well-fed *A. trifasciata* included stabilimenta in their webs more often than hungrier spiders. Both *A. aurantia* and *A. trifasciata* built larger stabilimenta when well-fed. These results agree with the predictions of the predator defense hypothesis but do not support those of the prey attraction hypothesis.

Feeding treatments were chosen to approximate moderate variation in foraging success of temperate *Argiope* spp. Change in spider mass did not differ between feeding treatments for either species and both *A. aurantia* treatments produced similar numbers of egg sacs. (*Argiope trifasciata* produced egg sacs too late in the experiment for real comparison.) Therefore, web and stabilimentum differences were likely the result of relatively minor variation in foraging success rather than traumatic starvation of Low Prey spiders. While several studies have catalogued the prey caught by *Argiope*, few have examined the average daily consumption rate of *Argiope* in the field. Olive (1980) estimated the dry weight of prey captured by *A. trifasciata* to be 0.73mg/hr (this extrapolates to 10.2mg/day, assuming a 14hr day) with a capture rate of 0.65 prey/hr (9.1
prey/day, assuming a 14hr day). Tso (1996) estimated a capture rate of one to two prey per day for *A. trifasciata*. While Horton and Wise (1983) found between 21-23% of *A. aurantia* webs and 13-19% *A. trifasciata* contained prey when surveyed. Brown (1981) also found that *A. aurantia* contained an average of 0.6-1.3 prey/web and *A. trifasciata* 0.5-1.1 prey/web. Prey capture rates tend to be higher in tropical species of *Argiope* (Robinson & Robinson 1970b; Craig & Bernard 1990).

Two previous studies had found no immediate effect of feeding on stabilimentum frequency in the orb webs of *U. diversus* (Eberhard 1973) and *A. argentata* (Nentwig & Rogg 1988) over three to five day periods of starvation. But *Argiope* are sit-and-wait predators and may not alter stabilimenta based on foraging success over such a short time. In this study, the short-term foraging success of Low Prey treatment spiders changed between prey variance regimes but this did not result in large changes in web or stabilimentum parameters. Along with Eberhard (1973) and Nentwig and Rogg (1988), this suggests that stabilimentum building by spiders is not strongly affected by daily fluctuations in prey capture.

Many Araneoid spiders will construct larger webs or increase the capture areas of their webs during times of low prey capture success (Higgins & Buskirk 1992; Pasquet *et al.* 1994; Sherman 1994). Neither *A. aurantia* nor *A. trifasciata* had significantly larger overall web areas or capture areas in the Low Prey treatments (Table 2.3 and 2.4). This may have been due to confinement of spiders in cages smaller than their maximum possible web size. However, the decrease in free zone area by Low Prey *A. aurantia* is consistent with a pattern of increased foraging effort by spiders suffering reduced prey capture (Higgins & Buskirk 1992; Sherman 1994; but see Witt 1963).
There is little reason to believe that an orb web structurally determines, *a priori*, stabilimentum length. Stabilimentum arms could extend beyond free zones into the capture areas of webs, but often stopped far short of the first sticky spirals. Also, stabilimentum silk is produced by the aciniform glands while web silks are produced by the aggregate, ampullate, and flagelliform glands (Foelix 1996). Finally, the frequency and overall size of stabilimenta were strongly affected by biomass of prey captured (Tables 2.1 and 2.2) while webs were relatively homogeneous (Tables 2.3 and 2.4).

There are many other potential influences on stabilimentum variation. Changes in form, particularly from disk shapes to linear designs, are well correlated with maturation in many species of spiders (Eberhard 1973; Edmunds 1986). Molting and sexual receptivity can be correlated with an increased frequency of stabilimenta (Nentwig & Heimer 1987; Robinson & Robinson 1973a). But this study suggests that some of the variation in size and frequency of stabilimenta within populations of orb-weaving spiders is caused by variation in the foraging success of those spiders. This has important implications for the study of stabilimentum function.

The prey attraction hypothesis has been supported by field studies that have demonstrated correlations between prey capture success and the presence of stabilimenta (Craig & Bernard 1990; Tso 1996). However, this study indicates that foraging success influences stabilimentum form and frequency. Those correlations may have been caused by an increase in stabilimentum building due to successful foraging rather than an increase in prey capture due to attractiveness of stabilimenta. Craig & Bernard (1990) and Tso (1996) used natural variation in stabilimenta in their comparisons of decorated and undecorated webs. Thus, both studies contained an *a priori* bias toward
demonstrating correlations between foraging success and stabilimentum presence. Even
the restriction of comparisons to capture rate differences between webs at the same site
(Tso 1996) may not adequately control for this effect if prey abundance varies temporally
or if different spiders with different foraging histories sequentially build webs at the same
site. Comparison of insect interception rates between stabilimentum-containing webs and
webs where the stabilimenta have been artificially removed would eliminate this
influence of past foraging success and provide a clearer test of the prey attraction
hypothesis. While Craig & Bernard (1990) did remove existing stabilimenta from some
webs, their analysis combined those webs with an unspecified number of webs that
naturally did not include stabilimenta, making it difficult to interpret their results.

More important, my study directly tests the mutually exclusive predictions
generated by the predator defense and prey attraction hypotheses. It demonstrates that
starved *Argiope* put less effort into the production of stabilimenta than do well-fed
spiders. Both *A. aurantia* and *A. trifasciata* build stabilimentum arms that are 10% to
40% shorter when fed less. *Argiope trifasciata* reduces stabilimentum frequency by as
much as 60% when offered less prey. These reductions occur even though stabilimenta
appear to be relatively inexpensive to build, accounting for only 10% of the silk in webs.
It is difficult to believe that a structure that attracts prey and is energetically inexpensive
would be less common and smaller in the webs of starved spiders. Conversely, the
pattern reported here is expected if linear stabilimenta serve as a predator defense
mechanism, particularly if prey are able to use stabilimenta to avoid webs. This
possibility must be more closely examined.
Figure 2.1: A stylized orb-web containing a stabilimentum (S) consisting of both a lower and an upper arm. The capture area (C) is that portion of the orb-web covered by sticky spirals. The free zone (F) is the inner portion of the orb web and contains no sticky spirals. *Argiope aurantia* and *Argiope trifasciata* both rest at the center of the free zones of their webs during daylight.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>HP (N=15)</th>
<th>LP (N=13)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Arm - freq.</td>
<td>0.59±0.05 N_w=111</td>
<td>0.56±0.04 N_w=132</td>
<td>&lt;0.100</td>
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<tr>
<td>Length (mm)</td>
<td>23.8±1.1 n=65</td>
<td>20.1±1.02 n=74</td>
<td>&lt;0.010</td>
</tr>
<tr>
<td>Lower Arm - freq.</td>
<td>0.87±0.03 N_w=111</td>
<td>0.88±0.03 N_w=132</td>
<td>&lt;0.100</td>
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<td>Length (mm)</td>
<td>38.0±1.2 n=97</td>
<td>30.5±0.8 n=116</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 2.1: Mean (±SE) stabilimentum parameters for High Prey (HP) and Low Prey (LP) *Argiope aurantia*. P-values are from Nested ANOVAs comparing the treatments, except for stabilimentum arm frequencies where P-values are from χ² tests comparing the number of spiders that built a stabilimentum arm more or less often than the average of the treatments combined (a null hypothesis of no difference). N is the number of spiders in a treatment and N_w is the total number of webs built in a treatment. n is the number of webs containing the appropriate stabilimentum arm.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>HP (N=4)</th>
<th>LP (N=6)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Arm - freq.</td>
<td>0.75±0.05 N_w=65</td>
<td>0.16±0.04 N_w=88</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>17.8±1.5 n=49</td>
<td>10.8±1.7 n=14</td>
<td>&lt;0.050</td>
</tr>
<tr>
<td>Lower Arm - freq.</td>
<td>0.88±0.04 N_w=65</td>
<td>0.63±0.05 N_w=88</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>32.4±1.7 n=57</td>
<td>24.0±1.4 n=55</td>
<td>&lt;0.025</td>
</tr>
</tbody>
</table>

Table 2.2: Mean (±SE) stabilimentum parameters for High Prey (HP) and Low Prey (LP) *Argiope trifasciata*. P-values are from Nested ANOVAs comparing the treatments, except for stabilimentum arm frequencies where P-values are the probability that the observed distribution of spiders building stabilimenta arms more or less frequently than the average of both treatments combined could occur by chance (i.e. that this distribution could occur if every spider had a 50% chance of building a stabilimentum arm more often that expected). N is the number of spiders in a treatment and N_w is the total number of webs built in a treatment. n is the number of webs containing the appropriate stabilimentum arm.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>HP (N=15)</th>
<th>LP (N=13)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area of Web (mm²)</td>
<td>40,165±1,206 n=111</td>
<td>39,719±1,164 n=132</td>
<td>&lt;0.37</td>
</tr>
<tr>
<td>Height (mm)</td>
<td>243.6±3.9 n=111</td>
<td>238.5±4.2 n=132</td>
<td>&lt;0.32</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>206.7±3.6 n=111</td>
<td>205.4±3.6 n=132</td>
<td>&lt;0.32</td>
</tr>
<tr>
<td>Free Zone Area (mm²)</td>
<td>8,635±381 n=111</td>
<td>7,362±259 n=132</td>
<td>&lt;0.04</td>
</tr>
<tr>
<td>Height (mm)</td>
<td>112.6±2.7 n=111</td>
<td>102.7±1.7 n=132</td>
<td>&lt;0.02</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>92.8±2.3 n=111</td>
<td>88.3±1.6 n=132</td>
<td>&lt;0.11</td>
</tr>
<tr>
<td>Capture Area (mm²)</td>
<td>31,816±1,159 n=111</td>
<td>32,357±1,108 n=132</td>
<td>&lt;0.45</td>
</tr>
</tbody>
</table>

Table 2.3: Mean (±SE) web parameters for High Prey (HP) and Low Prey (LP) *A. aurantia*. P-values are from t-tests comparing the means of each spider. N is the number of spiders in a treatment and n is the number of webs measured for a parameter.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>HP (N=4)</th>
<th>LP (N=6)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area of Web (mm²)</td>
<td>62,649±3,563 n=63</td>
<td>70,877±3,000 n=88</td>
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</tr>
<tr>
<td>Height (mm)</td>
<td>288.8±9.9 n=65</td>
<td>304.9±8.3 n=88</td>
<td>&lt;0.45</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>257.8±7.3 n=63</td>
<td>285.1±6.3 n=88</td>
<td>&lt;0.45</td>
</tr>
<tr>
<td>Free Zone Area (mm²)</td>
<td>6,811±283 n=62</td>
<td>7,495±248 n=86</td>
<td>&lt;0.25</td>
</tr>
<tr>
<td>Height (mm)</td>
<td>98.9±2.9 n=63</td>
<td>100.7±2.1 n=87</td>
<td>&lt;0.84</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>84.9±2.2 n=62</td>
<td>90.8±2.0 n=86</td>
<td>&lt;0.11</td>
</tr>
<tr>
<td>Capture Area (mm²)</td>
<td>55,564±3,599 n=62</td>
<td>62,507±3,054 n=86</td>
<td>&lt;0.50</td>
</tr>
</tbody>
</table>

Table 2.4: Mean (±SE) web parameters for High Prey (HP) and Low Prey (LP) *A. trifasciata*. P-values are from t-tests comparing the means of each spider. N is the number of spiders in a treatment and n is the number of webs measured for a parameter.
DO STABILIMENTA IN ORB WEBS ATTRACT PREY OR DEFEND SPIDERS?

Conflict between foraging and predator avoidance can have a profound impact on the behavior of organisms (Sih 1980; Stephens & Krebs 1986; Lima & Dill 1990). Animals may forage in lower energy patches that have reduced risks of predation (Lima 1985; Lima et al. 1985; Holomuzki 1986; Gilliam & Fraser 1987) or engage in defensive behaviors that reduce foraging efficiency within patches, such as vigilance or hiding (Sih et al. 1992; Skelly 1995 Rothley et al. 1997; Schmitz et al. 1997). 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 like barrier webs can also serve as defenses against predators (Tolbert 1975; Edmunds & Edmunds 1986; Rayor & Uetz 1990; Higgins 1992; Cloudsley-Thompson 1997). Unlike the transient behavioral trade-offs between foraging and defense made by animals engaging in vigilance or hiding, the making of 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. Stabilimenta 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 (Eberhard 1990; Blackledge 1998a). I 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 & Bernard 1990; Craig 1991, 1994a; Elgar et al. 1996; Tso 1996, 1998a, 1998b; Hauber 1998). Craig and Bernard (1990) and Tso (1996, 1998a) used correlations between high prey capture and presence of stabilimenta in webs to support this hypothesis. But, Blackledge (1998a) 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
1998b). 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 & Coddington 1997) and rest at the centers 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. (Lubin 1975; Kerr 1993). 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.

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

Stabilimenta and Prey Capture.

I collected adult and sub-adult female *A. aurantia* along a drainage culvert in Gainesville, Florida during mid-July and immediately transported them back to Ohio. This allowed me to begin the experiment before native *A. aurantia* were mature. The experiment was conducted in a field adjacent to the Rothenbuhler Honeybee Laboratory at The 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 bee hives were scattered to the north, south and west, most within a 0.5km 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 x 75 x 12 cm) with the large sides being removable plastic sheets. This allowed me to confine spiders to the stations while spiders built webs overnight, yet let spiders 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 I varied orientation haphazardly between stations. Therefore, both webs at a station experienced similar micro habitat variation.

I placed a single female *A. aurantia* in each frame, with an effort being made 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 in 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. I also performed a sham removal 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 & Buskirk 1992; Sherman 1994).

Prey capture was observed over foraging trials lasting three hours each, beginning between 0830-1000 hr. Because the trials ran into the afternoon, stabilimenta were exposed to a wide range of light conditions under which *Argiope* spp. forage (Endler 1993a). I 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, I restricted my analysis to prey larger than 3mm. I 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 1998a) 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, I categorized each station as to whether the majority of paired comparisons at that station had experimental webs catch
more prey than control webs. I 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, I used set-ups at two sites each of 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). Birds were allowed to acclimate to the set-ups containing empty frames before the experiment began. The west campus site was in a small field in a grassy forest clearing (approximately 15m diameter) 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 that 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. I conducted 12 trials at each site using webs without spiders. Then I 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 me to determine whether the spider itself had any influence on bird avoidance of webs.
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 (2.9±0.3 (±SE) vs. 2.0±0.3 (±SE) prey/3 hr 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<0.025; Figure 3.1).

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 3.1). 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 spiders were removed from the webs ($P<0.001$; Table 3.2) and the trials when spiders were present in webs ($P<0.005$; Table 3.2). There was no significant difference in the distribution of damage between the trials with and without spiders ($\chi^2 = 0.0985$, $df = 1$, $P > 0.754$).

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 & Dill 1990; Sih 1992; Scrimgeour & Culp 1994; Skelly 1995; Schmitz et al. 1997). My study suggests that one function of stabilimenta is as behavioral defenses against birds, because webs without stabilimenta are damaged more often by flying birds (Table 3.2). 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 3.1). 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.

My results contradict the hypothesis that stabilimenta attract prey to the webs of spiders (Craig & Bernard 1990; Craig 1994a; Tso 1996, 1998a, 1998b; Hauber 1998), because I found that webs containing stabilimenta caught 34% fewer prey. Previous studies used web damage (Craig & Bernard 1990; Tso 1996; Hauber 1998) or infrequent censuses (Tso 1998a) as indices of prey interception rates and found correlations between the presence of stabilimenta in webs and high prey capture success. However, Blackledge (1998a) demonstrated that this same pattern is caused when spiders that catch more prey increase their frequency of stabilimentum construction. I controlled for this effect through direct manipulation of the presence of stabilimenta. Furthermore, I measured the actual number of prey captured by spiders rather than inferring it from web damage. This gave me a direct measure of the effect of stabilimenta on spider foraging success. Thus, my 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). However, all but two 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. I also conducted my 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 I 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 my 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. (Robinson & Robinson 1970b; Brown 1981; Horton & Wise 1983; Howell & Ellender 1984; McReynolds & Polis 1987), and *Apis* spp. may account for more than 15% of prey captured by *Argiope bruennichi* (Nyffeler & Breene 1991) and *Argiope amoena* (Murakami 1983). However, the large percentage of Diptera captured by spiders in webs without stabilimenta is unusual (Table 3.1). 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 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, my data suggest that at least some of the specialization on non-dipteran taxa by *Argiope* spp. might be attributed to the common inclusion of stabilimenta in their webs.

Stabilimenta and Defense.

My data corroborate the hypothesis that stabilimenta can function as defenses against birds (Lubin 1975; Horton 1980; Eisner & Nowicki 1983; Kerr 1993), because I found that stabilimenta can reduce the frequency of damage to webs from flying birds by 45% (Table 3.2). I 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, I never saw birds actively avoid webs that did not contain stabilimenta. My 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 & Rogg 1988), at least to flying birds, because webs were damaged no less frequently in trials with spiders than in trials without spiders (Table 3.2).

Damage to webs in the field by birds is rare (pers. obs.) and is unlikely to alone 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 (Marples 1969; Edmunds & Edmunds 1986). Horton (1980) demonstrated that the stabilimenta of *A. aurantia* can function as aposematic warnings to predatory blue jays (*Cyanocitta cristata*), signaling that otherwise palatable spiders were in orb webs containing irritating sticky silk. I 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 me.
Conflicts in Stabilimentum Building.

Many spiders vary their behaviors in response to changes in predation risk and foraging success (Rayor & 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. I have supported the hypothesis that stabilimenta can help defend spiders against birds (Horton 1980; Eisner & Nowicki 1983) 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 frequencies 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. I also found that stabilimenta cause a 34% reduction in prey capture by *A. aurantia* and Blackledge (1998a) 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 non-capture webs by several genera of spiders that increase the frequency of stabilimentum building just prior to molting or egg laying (Robinson & Robinson 1970a, 1973; Eberhard 1973; Nentwig & Heimer 1987). Such spiders do not
feed and the costs of including stabilimenta in their non-sticky 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 inter-population 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. My 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.
Figure 3.1: The distribution of differences in prey capture for a total of 55 paired comparisons at eight stations (difference = prey capture at webs without stabilimenta - prey capture at webs containing stabilimenta). Seven of eight stations had webs without stabilimenta catch more prey than webs containing stabilimenta for greater than 50% of the trials at the station (G=5.603, df=1, P<0.025). The mean (±SE) prey capture rate over three hr was 2.9±0.3 for spiders in webs without stabilimenta and 2.0±0.3 for spiders in webs with stabilimenta.
<table>
<thead>
<tr>
<th>Taxa</th>
<th>no stabilimentum</th>
<th>stabilimentum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apidae</td>
<td>62</td>
<td>37</td>
</tr>
<tr>
<td>Muscidae</td>
<td>25</td>
<td>11</td>
</tr>
<tr>
<td>Calliphoridae</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Halictidae</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Pompilidae</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Acrididae</td>
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<td>3</td>
</tr>
<tr>
<td>Formicidae</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Cantharidae</td>
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<td>4</td>
</tr>
<tr>
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<td>2</td>
</tr>
<tr>
<td>Pieridae</td>
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<td>2</td>
</tr>
<tr>
<td>Scarabidae</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
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</tr>
<tr>
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<td>10</td>
</tr>
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<td>unidentified</td>
<td>37</td>
<td>23</td>
</tr>
<tr>
<td>total</td>
<td>163</td>
<td>107</td>
</tr>
</tbody>
</table>

Table 3.1: Families of prey captured by *A. aurantia* in 55 pairs of webs, with and without stabilimenta. Miscellaneous taxa are those families for which fewer than three individuals were captured.
Table 3.2: Number of days on which webs were damaged by birds. Chi-square values were computed from the expectation that webs with stabilimenta would be damaged at the same frequency as webs with no stabilimenta.
CHAPTER 4

SIGNAL CONFLICT IN SPIDER WEBS DRIVEN BY PREDATORS AND PREY

Sensory biases in reception of signals are caused by variation in the sensory physiologies of receivers and can affect the evolution of signal design in a process termed sensory drive (Endler 1978, 1992, 1993b; Guilford 1990; Guilford & Dawkins 1991; Fleishman 1992; Ryan & Rand 1993). Sensory drive has been used to account for the diversification of a variety of visual and vocal signals in vertebrates (Basolo 1990; Endler 1991, 1992; Fleishman 1992; Ryan & Keddy-Hector 1992; Ryan & Rand 1993) and arachnids (Clark & Uetz 1992, 1993; Proctor 1992; McClintock & Uetz 1996). However, most of these studies involved sexual signaling, leaving the role of sensory drive in the evolution of inter-specific signals to be examined. Furthermore, the physiological bases of the sensory biases involved have rarely been well documented. While such study typically demands elaborate experiments to demonstrate sensory biases and determine the ancestral state of signal features, I already have the relevant data to examine the possible role of sensory biases in the form and function of stabilimenta in the webs of spiders. Stabilimenta are conspicuous silk designs that many diurnal orb-weaving spiders include at the center of their webs (Fig. 4.1). Stabilimenta can function
as visual warnings to predators for the presence of noxious sticky silk in orb webs (Table 4.1; Horton 1980; Eisner & Nowicki 1983; Blackledge & Wenzel 1999), but stabilimenta also provide visual signals that prey can use to avoid webs (Table 4.1; Blackledge & Wenzel 1999). This creates a conflict in the selection for visibility of stabilimenta to different receivers. I suggest that the design of stabilimenta reflects this conflict between visibility to the predators and to the prey of spiders, and is such that stabilimenta are obvious signals to predators while remaining relatively cryptic to insect prey.

The Orb Web as a Visual Signal to Predators

The primary function of orb webs is prey capture (Eberhard 1990), but webs can also be valuable defenses (Edmunds & Edmunds 1986; Jackson et al. 1993; Cloudsley-Thompson 1995). The sticky capture silk of webs is capable of entangling predators such as jumping spiders (Salticidae) and wasps (Sphecidae and Pompilidae) (Edmunds & Edmunds 1986; Cloudsley-Thompson 1995), and it is a noxious stimulus avoided by vertebrate predators such as birds (Table 4.1; Horton 1980; Eisner & Nowicki 1983; Blackledge & Wenzel 1999). Yet, there is little advertisement of these noxious and sometimes lethal aspects of webs to the predators of spiders. Instead, orb webs are usually quite cryptic, indicating the great importance of low visibility of webs for effective prey capture (Rypstra 1982; Craig 1986, 1988; Uetz 1990; Craig & Freeman 1991).

Unlike the web itself, a stabilimentum is a highly conspicuous signal to predators. The designs include broad bands of bright white silk that form vertical lines or crosses at the center of the webs of Argiope spp. and several other genera of orb-weaving spiders in
the Orbiculariae (reviewed in Eberhard 1990). While once thought to stabilize webs, there is no evidence to support such a hypothesis, because stabilimenta are the last structures added to webs and they are only loosely attached to the webs (Eberhard 1973; Edmunds 1986). Furthermore, webs with stabilimenta removed function better at catching prey (Table 4.1). However, there is substantial evidence that such linear stabilimenta are defensive signals that may be aposematic, obfuscate the outline of spiders, or startle predators (Hingston 1927; Marson 1947a, 1947b; Marples 1969; Ewer 1972; Eberhard 1973; Lubin 1975; Tolbert 1975; Edmunds 1986; Neet 1990; Schoener & Spiller 1992; Kerr 1993; Blackledge 1998a). In particular, experiments have demonstrated the effectiveness of stabilimenta as highly visible aposematic signals, which can warn birds away from webs (Table 4.1; Horton 1980; Eisner & Nowicki 1983; Blackledge & Wenzel 1999).

Linear stabilimenta consist of broad bands (see Fig. 4.1) of thin silk fibers, which greatly enhances the visibility of stabilimenta compared to that of the individual fibers that constitute them. Stabilimentum silk is a bright white (Eberhard 1973; Craig & Bernard 1990). This maximizes photic stimulation of vertebrate eyes and differentiates the silk from a background of soil and foliage, which both weakly reflect most wavelengths of light (Endler 1993a; Chittka et al. 1994). Unlike the sticky silk of many orb webs, the reflectance spectrum of stabilimentum silk includes a strong ultraviolet (UV) component, similar in magnitude to other reflected wavelengths (Craig & Bernard 1990). The possibility that this may further enhance visibility of stabilimenta to vertebrates needs to be investigated because UV is an important additional wavelength of light in the vision of a wide variety of birds (Goldsmith 1980; Burkhardt 1982, 1996;
Bennett & Cuthill 1994; Maier 1994; Viitala et al. 1995) and many other potential vertebrate predators including lizards (Fleishman et al. 1993; Loew 1994; Ellingson et al. 1995) and rodents (Jacobs et al. 1991; Jacobs 1992). While the capture silks of webs are inconspicuous, the shape and reflectance of stabilimenta seem to maximize the potential for vertebrate predators to differentiate stabilimenta from environmental noise such as soil and foliage, as supported by use of stabilimenta in web avoidance by birds (Table 4.1; Horton 1980; Blackledge & Wenzel 1999).

Stabilimenta are Inconspicuous to Prey

Although a consideration of the entire reflectance spectra of stabilimenta suggests otherwise (see below), the reflectance of UV light by stabilimenta has been used to argue that the designs attract insect prey, particularly foraging bees, to webs (Craig & Bernard 1990; Craig 1991, 1994a; Tso 1996). The prey attraction hypothesis has been supported by correlations between the presence of stabilimenta in webs and high prey capture success in both Argiope argentata and A. trifasciata (Craig & Bernard 1990; Tso 1996). However, Blackledge (1998) found that increased feeding success increased the probability that A. trifasciata would include stabilimenta in webs, causing the same pattern. Thus, correlations between prey capture and stabilimentum presence could result from the influence of high prey capture success increasing the frequency of building stabilimenta, rather than from stabilimenta increasing prey capture. Furthermore, Blackledge and Wenzel (1999; Table 4.1) demonstrated that stabilimenta caused a reduction, not an increase, in the prey capture success of A. aurantia when webs with and without stabilimenta were paired in the field. Thus, the ability of prey to use stabilimenta
as visual signals in web avoidance is likely to have been a serious selective constraint on
the evolution of the design of stabilimenta, just as it has been on the capture silks of orb
webs.

The innate color preferences of insects, their ability to learn colors, and the design
of floral signals all suggest that the visibility of stabilimenta to insects is greatly reduced
by the spectral properties of stabilimentum silk. Hymenoptera, particularly bees, are one
of the most common prey items of Argiope spp. (Robinson & Robinson 1970b; Brown
1981; Murakami 1983; Howell & Ellender 1984; McReynolds & Polis 1987; Nyffeler &
Breene 1991; Bradley 1993; Craig & Ebert 1994) and are also among the most
maneuverable and visual insect fliers. Bees and many other insects possess trichromatic
vision, similar to that of humans but shifted approximately 100nm shorter, with
photopigments sensitive to three broad categories of light; long UV (~350nm), blue
(~440nm), and green (~530nm) (Goldsmith & Bernard 1974; Peitsch et al. 1992; Troje
1993; Chittka 1996). Additional red photoreceptors or red-shifted green photoreceptors
can be found in some insects but do not appear to be the norm, particularly for pollinating
hymenoptera (Bernard & Remington 1991; Peitsch et al. 1992). Color is the primary cue
used in floral discrimination by many pollinating insects even when other cues such as
intensity or pattern differences are available (Giurfa et al. 1995a, 1995b; Giurfa &
Yet, few pollinating insects are attracted to stimuli with achromatic reflectances, like
stabilimenta. Naive honeybees show innate preferences for bee-green and bee-UV-blue
colors (Giurfa et al. 1995b), while bumblebees (Bombus terrestris) have innate
preferences for any spectrally pure color that stimulates only one or two classes of their
photoreceptors (Lunau & Maier 1995; Keasar et al. 1997), and the hover fly (*Eristalis tenax*) is attracted to only human yellow (Lunau 1988). For each of these species, spectrally impure (white+UV) objects that stimulated all three classes of photoreceptors were the least attractive to naive insects, regardless of their intensity (Lunau et al. 1996). Even with previous foraging experience, many insects are still not attracted to white+UV objects (Allan & Stoffolano 1986; Scherer & Kolb 1987; White et al. 1994).

Insects can also be easily trained to distinguish and associate colors, including human white, with foraging rewards (Goldsmith 1961; von Frisch 1967). Again any chromatic stimulus is easily associated with food while an achromatic (white+UV) signal is poorly learned by many hymenoptera, diptera, and lepidoptera (Hertz 1939; von Frisch 1950; Daumer 1963; Troje 1993; White et al. 1994; Giurfa & Vorobyev 1997). Hertz was the first to demonstrate this phenomenon in honey bees (*Apis mellifera*) and her findings are summarized in von Frisch (1950):

"It is always very easy to train them to a true color, but training to a white paper or cardboard is sometimes easy and sometimes quite difficult...She tested various white papers and found that some of them absorbed ultraviolet rays. To these papers the bees could be trained very easily. But other white papers reflected the ultraviolet, just as they did the rays visible to us. This white the bees could not remember, and they could not learn to seek it out with certainty..."
It has already been shown that the color of spider silks can be an important cue in avoidance of webs by insects (Craig 1994b). The unattractiveness of white+UV signals to naive pollinating insects and their difficulty in learning white+UV indicates that such signals are poorly perceived by some of the most common prey of *Argiope*.

Why are achromatic (white+UV) objects treated so differently by insects that are otherwise quite adept at using colors in foraging tasks? Simply put, white+UV objects have poor color contrast with typical backgrounds of soil and foliage when viewed by insects. Both soil and foliage reflect weakly all wavelengths of light perceived by bees and other trichromatic insects, thus appearing achromatic at the center of insect color space (von Frisch 1967; Kevan 1972; Chittka *et al.* 1994; Lunau 1996). They are used as neutral gray standards for comparison to other objects (von Frisch 1967; Kevan 1972; Chittka *et al.* 1994; Kevan *et al.* 1996). Humans differentiate soil and foliage largely on the basis of the strong absorption of red light by the latter, thus perceiving them as having different colors (Chittka *et al.* 1994; Kevan *et al.* 1996). Unlike white-UV objects, the presence of a UV component in white coloration also causes an equal stimulation of the three photoreceptor classes of insects. Thus, white+UV objects will appear achromatic, again near the center of the color space of bees (Chittka *et al.* 1994; Kevan *et al.* 1996). Because honeybees and many other insects do not use brightness cues when discriminating colors (von Frisch 1950; Backhaus *et al.* 1987; Fukushi 1990; Backhaus 1991; Chittka *et al.* 1992; Troje 1993; Giurfa *et al.* 1995a), the difference between the brightness of stabilimenta and soil or foliage also does not help differentiate them through color. Therefore, stabilimenta, soil, and foliage all appear as non-descript grays
at the center of honeybee color space and stabilimenta therefore provide signals of poor color contrast with environmental noise to insect prey.

These findings are also supported by, and may account for, the difficulty that the stingless bee, *Trigona fuscipennis*, has in learning to associate stabilimenta with the webs of *A. argentata* (Craig 1994a). The bees have particular difficulty associating stabilimenta with webs when the stabilimenta vary in shape, suggesting that color is not the only cue that insects can use to avoid webs. If the bees had been able to use color as a signal in avoidance of stabilimenta they should have generalized their avoidance response to all shapes of stabilimenta in the experiment, as they do with chromatic colors when foraging (Backhaus *et al.* 1987; Chittka *et al.* 1992; Giurfa *et al.* 1995a).

Stabilimenta can still be differentiated from the background on the basis of their shape and any non-target object, like leaves, will still be avoided when in the direct flight path of an insect. However, such motion- and form-sensitive responses are color blind in insects and mediated only by green photoreceptors (Wehner 1981; Lehrer *et al.* 1985, 1988; Lehrer 1994). Detection of stabilimenta through green-contrast visual pathways is likely the most important factor accounting for the avoidance of stabilimenta found by Blackledge and Wenzel (1999). Despite this, the white+UV reflectance of stabilimenta causes the designs to be cryptically colored to insects. This eliminates one of the most important visual cues for pollinating insects, making it difficult for insects to associate stabilimenta with dangerous spider webs.

The poor ability of white+UV surfaces to function as obvious signals to pollinating insects is further supported by the scarcity of white+UV reflective flowers. The reflectance spectra of flowers appear to be designed to maximize the potential of the
visual systems of pollinating hymenoptera and diptera to differentiate flowers from the background and to discriminate between species of flowers (Chittka & Menzel 1992; Troje 1993; Chittka et al. 1994; Lunau 1996). While blue, red, and yellow flowers often include UV in their reflectance spectra, human white flowers rarely reflect UV light (Daumer in von Frisch 1967; Kevan 1983; Menzel & Shmida 1993; White et al. 1994). In one survey only 4% of 219 species of plants with white flowers tested included a substantial UV component in their reflectances (Chittka et al. 1994). The scarcity of white+UV flowers is again thought to be due to the poor contrast of such signals with soil and foliage backgrounds (Chittka et al. 1994; Kevan et al. 1996). Craig (1994a) suggested that there could be little selection for insects to associate stabilimenta with webs because insects had to use those same colour cues in discriminating flowers while foraging. However, it is clear that the achromatic spectra of stabilimenta are not similar to the spectra of flowers and that the ability of pollinating insects to learn to associate stabilimenta with spider webs will not be inhibited by counter selection from the necessity of using color cues in floral recognition. Instead, such learning in insects will be inhibited by the poor color contrast of stabilimenta with the background, simply making the designs difficult for insects to detect.

Summary

Stabilimenta represent a compromise in visual signaling between advertising spider webs to predators and keeping webs cryptic to prey. The presence of stabilimenta in webs reduces the prey capture of *A. aurantia* (Table 4.1; Blackledge & Wenzel 1999) and both *A. aurantia* and *A. trifasciata* reduce their investment in stabilimenta when
starved (Blackledge 1998a). Yet, stabilimenta also reduce the frequency of web
destruction and predation by birds (Table 4.1; Horton 1980; Eisner & Nowicki 1983;
Blackledge & Wenzel 1999). Variation in the frequency with which stabilimenta are built
by spiders results, in part, from trade-offs made between protection and foraging
(Blackledge & Wenzel 1999). This conflict in signaling is greatly ameliorated by the
spectral properties of stabilimentum silk. The white+UV reflectance spectrum of
stabilimentum silk appears to be derived from bluer ancestral silks with a strong UV
reflective peak (Craig et al. 1994). While either spectrum would make stabilimenta
contrast against environmental noise (soil and foliage) to vertebrate predators, only the
relatively flattened spectrum of stabilimentum silk also results in a signal that is
achromatic to insects and thus cryptic to the main prey of spiders. These observations
suggest that conflicts in signal visibility and function between predators and prey of
spiders have been important influences in the evolution of stabilimenta. They also
demonstrate the importance that sensory drive can have in the evolution of defensive
signals.
Figure 4.1: Female *Argiope aurantia* in a web containing a stabilimentum. The web itself has been coated with corn starch to enhance its visibility. Scale bar approximates three cm.
Table 4.1: Comparison of a defensive advantage and associated foraging cost of including stabilimenta in the webs of *A. aurantia*. Data are from paired comparisons of webs containing stabilimenta and webs from which stabilimenta have been removed (adapted from Blackledge & Wenzel 1999).

<table>
<thead>
<tr>
<th></th>
<th>% webs damaged by birds</th>
<th>prey capture rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>webs containing stabilimenta</td>
<td>39</td>
<td>2.0±0.3 prey/3 h</td>
</tr>
<tr>
<td>webs without stabilimenta</td>
<td>71</td>
<td>2.9±0.3 prey/3 h</td>
</tr>
<tr>
<td>$\chi^2=17.2$, df=1, P&lt;0.005 (n=41)</td>
<td>G=5.603, df=1, P&lt;0.025 (n=55)</td>
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CHAPTER 5

THE EVOLUTION OF CRYPTIC SPIDER SILK: A BEHAVIORAL TEST

Function of signals in animal communication is determined as much by their effective reception as by the information they contain. Variation in the sensory physiologies of organisms affects the efficiency with which they can perceive and process signals. This leads to sensory biases that can act upon the evolution of signals through selection for signal conspicuous or processing, rather than information content, in a process termed sensory drive (Guilford & Dawkins 1991; Endler 1992; Ryan & Rand 1993). Recently, sensory drive has been identified as a particularly important mechanism of evolution for conspicuous sexual signals (Basolo 1990; Ryan & Rand 1990; Proctor 1992; McClintock & Uetz 1996). And, it is thought to be a major force leading to the evolution of signal diversity (Endler 1992; Basolo & Endler 1998; Ryan 1998).

Little is known about the role of sensory drive in the evolution of other forms of animal communication, particularly between predators and prey (Endler 1991; Fleishman 1992). How insects perceive silk in spider webs provides a system to study the effect of sensory drive in an inter-specific context. Phylogenetic comparison of the color properties of spider silks demonstrates that many evolutionarily derived silks have lower
ultraviolet (UV) reflectance than do primitive silks (Craig & Bernard 1990; Craig et al. 1994; Bond & Opell 1998). Craig et al. (1994) suggested that reduced reflection of UV light by silks enhances prey capture of spiders by reducing the visibility of webs to insects. Because decrease in UV reflectance is associated with an increase in species diversity, it has also been hypothesized to be a key innovation contributing to the radiation of orb-weaving spiders (Bond & Opell 1998).

Yet, many orb webs with otherwise low UV reflectance contain "conspicuous" designs of silk termed stabilimenta (Fig. 5.1). These linear or spiral swaths of silk are added to the centers of orb webs by many diurnal spiders and are unusual in that stabilimenta have bright reflectances across all wavelengths of light visible to insects, including UV (Craig & Bernard 1990; Blackledge TA & Rowe MP, unpublished). The function of stabilimenta is a contentious issue (Edmunds 1986; Craig & Bernard 1990; Eberhard 1990), and the debate centers upon two hypotheses (Blackledge 1998a; Blackledge & Wenzel 1999). Stabilimenta may be "predator defenses", functioning by distorting or camouflaging the outline of spiders (Eberhard 1973; Schoener & Spiller 1992), advertising presence of sticky webs (Horton 1980; Eisner & Nowicki 1983; Kerr 1993; Blackledge & Wenzel 1999), or distracting attackers (Tolbert 1975; Schoener & Spiller 1992). Alternatively, stabilimenta might act as "prey attraction" for insects (Craig & Bernard 1990; Tso 1996, 1998a; Hauber 1998).

The "prey attraction" hypothesis argues that reflection of UV light makes spider silk more conspicuous to insects (Craig & Bernard 1990). In primitive silks, conspicuous silk decreases effectiveness of webs. However, stabilimentum silk, found in webs with silks that otherwise reflect little UV light, provides an attractive signal to pollinating
insects, by mimicking flowers or open sky (Craig & Bernard 1990; Craig et al. 1994). But, Blackledge (1998b) suggested that stabilimentum silk is instead cryptic to many insects because objects with a white+UV reflectance (i.e. bright but flat spectra), like stabilimentum silk, are perceived to be the same color as natural backgrounds of soil and foliage by many insects (Chittka et al. 1994; Kevan et al. 1996). This is in contrast to primitive spider silk which has a UV reflective peak, making it conspicuous to insects. Therefore, a direct comparison of the visibility of primitive silk and stabilimentum spider silk to insects is necessary to fully understand the implications of the evolution of the coloration of spider silks. In this study, I compare the visibility of primitive tarantula silks (Pterinochilus sp.) and derived stabilimentum silks (Argiope aurantia) to honey bees (Apis mellifera). Bees are common prey of Argiope (Blackledge & Wenzel 1999) and share many aspects of their visual system with other insect prey of spiders (Blackledge 1998b).

Methods

I used the ability of bees to learn to forage at targets of spider silk, rewarded with sucrose, as an index of the visibility of those silks. Individual bees were initially trained to forage at two stations, 1m apart. Each station consisted of two 3x4cm artificial plexiglass flowers, 15cm apart. The flowers were placed at approximately the same height as the top of the grass in the field where the experiment took place. Microliter syringes were used to inject 2μl rewards of 1.5M sucrose solution into the tubular bases of the flowers. Bees were trained to make a single choice between the two flowers at a station before that station was covered by a wooden board, forcing bees to fly to the other
station. Thus, in a single bout of foraging, a bee would make approximately 15-35 choices at the two stations before it returned to the hive. Bees were individually marked and were only used during the day on which they were trained. A visit to a flower was scored if a bee completely entered the 3cm high tubular base of the flower.

Once a bee was trained to the artificial flowers, usually within a single foraging bout, it was randomly assigned to a group trained to either primitive silk (n=10) or stabilimentum silk (n=10) targets. Targets were constructed by wrapping silk around two cm diameter wire hoops until an opaque disk was formed. Primitive silk targets were made from silk from captive raised specimens of the tarantula *Pterinochilus* sp., while stabilimentum silk targets were constructed by wrapping approximately 15 stabilimenta, built by mature female *A. aurantia*, around a single target. Then targets were suspended off the front of all flowers. At each station, one target was a blank, consisting of only the wire hoop itself, while the other hoop was a silk target. Bees were again allowed a single choice at a station before it was covered, but were only rewarded when they chose flowers with the silk targets. Thus, the ability of bees to learn to forage at the rewarded flowers was a function of the visibility of the silk targets, against a background of grass, compared to the blank targets. After each choice, the flowers at a station were switched with a random probability of 0.5, to prevent bees from using spatial cues in their learning (Orth & Waddington 1997). Bees were allowed six bouts of foraging over a single day, for a total of 100-200 choices per bee.
Results

I computed the % rewarded choices for each bee using all choices made after the first time a bee encountered both rewarded and unrewarded flowers. Bees trained to primitive tarantula silks made more correct (rewarded) choices than did bees trained to stabilimentum silk (Fig. 5.2; Mann-Whitney U test, U = 79, P < 0.025). Six of ten bees showed significant learning when primitive silks were associated with rewards (binomial test compared against 50% rewarded choices, P < 0.05), while zero of ten bees trained to rewarded stabilimentum silk showed significant learning (binomial test compared against 50% rewarded choices, P < 0.05). The number of bees showing learning, versus those that did not, was significantly different between the two treatments (chi-square test, df = 1, P<0.001). I controlled for the possibility that insects evolved to avoid stabilimentum silk specifically by training additional bees (n=4) in a sign-negative experiment where the blank target was rewarded and the stabilimentum target was unrewarded. Even when stabilimentum silk was associated with the unrewarded stimulus, honey bees failed to discriminate stabilimentum silk from a blank target (Fig. 5.2), and this distribution was significantly different from bees trained to primitive spider silks (Mann-Whitney U test, U=36, P < 0.025). Bees rarely touched the silk or blank targets during the experiment (once or twice maximum), indicating that their choices were made upon primarily visual criteria.

Discussion

My study is the first direct comparison of the visibility of primitive and derived spider silks to insects and supports the general hypothesis of evolution of spider silks
toward low visibility. My behavioral assay demonstrates that stabilimentum silk is less visible than primitive spider silk to bees foraging in a natural environment. Previous studies have indicated the importance of low visibility of webs for prey capture (Rypstra 1982; Craig 1986, 1988; Craig & Freeman 1991) and suggested that the color of spider silks has evolved to decrease visibility of webs to insects (Craig et al. 1994; Bond & Opell 1998). But, they misplace emphasis on patterns of evolution of UV reflectance alone. I found that visibility of spider silk can only be assessed by considering the spectral reflectance of that silk across all wavelengths of light perceived by insects and how that contrasts with the background (Blackledge 1998b). Both primitive and stabilimentum silks reflect large amounts of UV light (Craig & Bernard 1990; Blackledge TA & Rowe MP, unpublished). But, primitive tarantula silks have a UV reflective peak that contrasts with the flat reflectance spectrum of soil and foliage. The spectrum of stabilimentum silk includes strong blue and green reflectance, as well as UV, resulting in a flat spectrum, similar to that of soil and foliage (Blackledge 1998b).

My findings are inconsistent with the hypothesis that stabilimenta attract insect prey. I found that stabilimentum silk is neither attractive to, nor highly visible to bees. Instead, my study supports the finding of Blackledge and Wenzel (1999) that spiders include stabilimenta in webs at the cost of prey capture. My findings are also consistent with the "predator defense" hypothesis. Stabilimenta are still clearly visible to vertebrate predators of spiders such as birds or lizards (Fig. 5.1; Horton 1980; Schoener & Spiller 1992; Blackledge 1998b; Blackledge & Wenzel 1999). Furthermore, the cryptic properties of stabilimentum silk do not preclude their function as physical barriers or camouflage against insect predators of spiders such as sphecid or pompilid wasps. Such
functions may even be enhanced, if the low visibility of stabilimentum silk prevents wasp predators from reliably using stabilimenta as signals to locate spider prey.

The cryptic nature of stabilimentum silk is particularly interesting because it indicates that sensory drive may account for the evolution of spider silk coloration. Insects can use stabilimenta to avoid webs, costing spiders prey (Blackledge & Wenzel 1999). Yet, the cryptic properties of the silk used to make stabilimenta likely reduces this cost to spiders. The color perception of insects, which interprets stabilimenta as cryptic, appears to be based upon a very ancient bauplan, and is perhaps ancestral for arthropoda (Chittka 1996). Stabilimenta, by definition a feature of orb webs, could not have evolved before the appearance of orb-weaving spiders in the early Cretaceous (Selden 1989).

Therefore, the sensory bias in the insect visual system, which causes stabilimentum silk to be cryptic to insects, was in place prior to the evolution of stabilimenta and thus likely acted as a selective agent upon the spectral properties of spider silk.

The evolution of spider silk coloration through sensory drive is unusual in two respects. Previously described examples of sensory drive acting upon signal evolution are largely confined to sexual signals. And, in the context of sexual selection, sensory drive has usually been found to lead to increased conspicuousness rather than crypsis of signals. Thus, my research demonstrates the broader applicability of sensory drive to signals evolving under natural selection. But, it also cautions that such evolution can have novel effects such as selecting for a signal that is cryptic to one class of receivers, such as insect prey, but not to others, such as vertebrates (Endler 1991).

Many new questions arise. What are the adaptive consequences of color for other types of spider silks? The sticky capture silks of a typical orb web reflect little UV light
(Craig et al. 1994), making them blue-green colored and likely moving them back into the color space of insects (Blackledge 1998b). This suggests that decreased UV reflectance of these silks may not be an adaptation to reduce visibility to insects. Instead, sticky silk threads are so thin that they may not subtend a sufficient visual angle for insects to perceive their color (Giurfa et al. 1995; Giurfa & Vorobyev 1997). Perhaps, the color properties of such derived silks are imperceptible to insects and are a nonadaptive by-product of changes in their biochemical or physical properties associated with silk stickiness (Foelix 1996). Also, orb weaving spiders produce at least seven different types of silks produced from a similar number of glands (Foelix 1996). We cannot fully understand interactions between the evolution of silk coloration and insect vision until we better understand the homologies between different silks. For instance, prey wrapping silk is produced from the same gland as stabilimentum silk (Foelix 1996), perhaps that silk is also cryptic, allowing spiders to camouflage captured prey in their webs.
Figure 5.1: Female *Argiope aurantia* in a web containing a stabilimentum. These designs typically are built in the non-sticky centers of webs, where spiders wait when foraging. The silk is a bright white to humans and also reflects large amount of ultraviolet light.
Figure 5.2: Discrimination of primitive and stabilimentum spider silk targets versus blank targets. Bees which chose the rewarded target more often than expected by chance are denoted by * (binomial test versus random, P<0.05). Six of ten bees trained to primitive silk showed significant learning but zero of ten bees trained to stabilimentum silk showed significant learning. These two distributions are significantly different (chi-square test, df = 1, P<0.001). Sign-negative bees (n=4) were trained to rewarded blank targets versus unrewarded stabilimentum silk targets and demonstrated that lack of learning was due to crypsis of the stabilimentum silk, instead of simple avoidance of stabilimentum silk.
Sphecid wasps are common predators of orb-weaving spiders. Because individual wasps capture several spiders to provision each cell in a nest and build multiple cells over their lives (Coville 1987), mud-dauber wasps can act as particularly potent selective forces on the evolution of spider defensive behaviors. Many studies have examined the numbers and species of spiders provisioned in wasp nests, providing insight into which spiders may be most vulnerable to wasps (e.g. Muma & Jeffers 1945 and references in Krombein et al. 1979). These studies indicate that different species of wasps that hunt in the same habitat, such as Chalybion caeruleum and Sceliphron caementarium, often catch different prey. This suggests that sympatric species of sphecids may employ different predatory tactics, perhaps due to niche partitioning. There are few, mostly anecdotal, observations on the hunting tactics of sphecids (Peckham & Peckham 1905; Rau 1928, 1935; Eberhard 1970; Endo 1976; Coville 1987; Rayor 1997). But, there has
been no comparative study of the hunting behaviors of sympatric *C. caeruleum* and *S. caementarium*.

Little is known about the primary and secondary defensive behaviors orb web spiders use against sphecids. Yet, it is the interaction of spider defensive behaviors and the predatory tactics of wasps that determine if individual spiders survive predation attempts (Cloudsley-Thompson 1995; Edmunds & Edmunds 1986; Tolbert 1975). There are two detailed studies of wasp-spider interactions, but these focus on wasps hunting nocturnal or colonial orb weavers (Eberhard 1970; Rayor 1997). What is missing, therefore, are studies of the interactions of wasps with solitary, diurnal spiders, such as *Argiope*.

*Argiope* is among the most intensively studied genera of spiders and is likely to be particularly vulnerable to visually hunting predators because it rests at the center of its web during daylight. *Argiope* is also an important model for testing hypotheses concerning possible defensive functions of structures such as barrier webs (Higgins 1992) or stabilimenta (Blackledge & Wenzel 1999, subm.; Chapter 7). Here I report on my efforts to maintain two species of sphecid wasps (*C. caeruleum* and *S. caementarium*) in field and laboratory enclosures and my observations of their predatory interactions with the orb-weaving spiders *Argiope aurantia* and *A. trifasciata*.

**Methods**

I observed the hunting behaviors of *C. caeruleum* and *S. caementarium* in one indoor enclosure (1998 and 1999) and three outdoor enclosures (1999). All wasps were collected as adults in the field (Dublin, Ohio), except for a single *C. caeruleum* that
emerged from a previously collected nest during the 1998 study. The collection site consisted of old barns surrounded by old fields. The primary prey caught by wasps at this site was immature *A. trifasciata* (pers. obs.). Individual wasps were distinguished by paint on the thorax or abdomen.

The 3.4 x 2.7 x 2.2 m screened indoor enclosure was located in Ohio State University's Insectary, Columbus, Ohio, in a greenhouse room with light and temperature maintained near outdoor levels. Assorted plants, including flowering *Echinacea* (Asteraceae) and *Lantana* (Verbenaceae), were scattered throughout the enclosure to provide resting places for wasps. The plants also simulated the natural background of foliage in which wasps hunt spiders, a potentially important feature of the study because background may influence the conspicuousness of spider silks to insects (Blackledge 1998b; Blackledge & Wenzel 2000). A 20 x 30 cm plastic pan was placed in one corner of the enclosure and contained a layer of earth from the same pond at the field site where wild *S. caementarium* collected mud for their nests. The pan was partially filled with water and then tilted to create a moisture gradient from completely saturated to nearly dry, simulating the bank of the pond. Mud nests of *S. caementarium* were collected at the field site and then glued to wooden boards in the upper corners of the enclosure to encourage building of new nest cells by *S. caementarium*. These nests also provided vacant cells for *C. caeruleum*, which nests only in abandoned *S. caementarium* cells (Rau 1928). In 1998, petri-dishes containing a sucrose and honey mixture were placed on the floor of the cage to provide wasps with a nectar source. In 1999, a plastic hummingbird feeder filled with a 1:1 honey:water solution was used instead. The honey water was changed every two days to prevent fermentation.
The three outdoor enclosures consisted of nylon screening over wood frames (3.8 x 2.3 x 2.0m) and were located in a field at Ohio State University's Rothenbuhler Honeybee Laboratory, Columbus, Ohio. I found it necessary to cover the bottom edge of the screening with a thick layer of bark mulch and stone to prevent wasps from crawling under the enclosures. The natural ground cover consisted of various grasses (Poaceae) and thistle (Asteraceae), with a thick layer of thatch. There were some naturally occurring *A. trifasciata* in the surrounding field. Each enclosure again had a 20 x 30 cm plastic pan containing mud and water, wooden boards with mud *S. caementarium* nests glued to them, and a hummingbird feeder as a nectar source.

Immature *A. aurantia* and *A. trifasciata* were collected from roadside ditches in and around Columbus. Most of the spiders were uniquely marked and weighed immediately after collection. Spiders were allowed to build their webs in 35 x 35 x 10 cm wooden frames as described in Blackledge (1998b) but modified with both plastic sides being removable. I placed individual frames containing spiders within the enclosures and I then recorded my observations on audio and video tape. I also include some observations on *A. trifasciata*, in webs on natural plant supports, which I placed in the same outdoor enclosures and I used for a second study examining the role of stabilimenta as wasp defenses (Blackledge & Wenzel submit.; Chapter 7). I released a variety of araneid, linyphiid, and tetragnathid spiders into the indoor enclosure to provide alternative prey, while the outdoor enclosures naturally contained a variety of agelenids, salticids and thomisids as well as *Cyclosa conica* (Pallas 1772) and *Uloborus glomosus* (Walckenaer 1841). Because I later found few individuals of these species in wasp nests (10 of 142 excavated spiders), I never directly observed a predation event involving
them, and they were so much less common than *Argiope*, I exclude them from further discussion.

**Results**

In the indoor enclosure, I observed 24 attempted predation events during 20 days of observation (between 4 - 28 August 1998 and between 28 July - 17 August 1999). In the outdoor enclosures, I observed 50 predation attempts during observations every day between 21 August and 11 September 1999. *C. caeruleum* did not usually open their nests and begin hunting until 1200-1400 hr and sometimes resealed their nests after only 30 min. *S. caementarium* typically opened nests for the entire day (1100-1600hr). Like other sphecids, both *C. caeruleum* and *S. caementarium* often did not hunt on overcast, rainy days and became active much later than normal on cooler days (see also Powell 1967; Freeman and Johnston 1978). Encounters were sometimes brief – lasting only a few seconds if spiders were caught at the centers of webs, and sometimes much longer, lasting 2-3 min if spiders attempted to escape by dropping and then moving rapidly through the grass. I combined all of the data for each species of wasp (Table 6.1) and, within each species, I had approximately the same number of observations for each individual wasp. I only included observations on predation attempts on spiders that were within the size range captured by wasps during the experiment (Table 6.1).

Both wasp species seemed to locate webs by chance while flying along the top of the vegetation in a seemingly haphazard flight path. However, *S. caementarium* and *C. caeruleum* differed greatly in their hunting tactics once webs were located (Table 6.1). *S. caementarium* bumped into webs while flying, but then flew off without seeming to react
to webs as anything other than physical barriers. But, *S. caementarium* vigorously pursued spiders that dropped from webs, spending as much as 2-3 min crawling around the thatch and grass stems under webs in gradually enlarging circular patterns until either spiders were located or wasps began flying again.

In contrast, *C. caeruleum* often landed in webs or on the substrate supporting webs and then used their middle legs to pluck the silk. When in webs, *C. caeruleum* sometimes contracted their entire body every few seconds for up to two minutes. In 68% of these instances, spiders ran to wasps after wasps had landed in or plucked at webs. Many of these spiders (70%) were caught as they approached wasps or as wasps chased them back to the center of webs, but others immediately dropped out of webs upon contacting wasps.

Captured spiders were stung between the carapace and sternum in the posterior of the cephalothorax. Paralysis appeared to be instantaneous, but spiders were occasionally stung multiple times, stings lasting up to a few seconds. Wasps carried spiders by holding the pedipalps in their mandibles, with the venters of spiders facing toward the venters of wasps. Wasps commonly pressed their mandibles against the chelicerae of spiders for a few seconds after capture, perhaps drinking hemolymph. In 25% of captures, both species of wasps drank hemolymph from the chelicerae or coxae of spiders for periods of up to 1 minute. Four of those spiders were subsequently discarded instead of being provisioned in nests.

I observed 9 instances (not in Table 6.1) where a wasp attacked a spider, grasped the spider in its legs, wrapped its abdomen around the spider as though stinging it, but then released the spider and flew away. In each instance the spider was still alive and ran
away when touched by me. All but two of those spiders weighed within the mean ± 2 standard deviations of *Argiope* captured during the study.

**Discussion**

Eberhard (1970) concluded that contrast between a spider and the background upon which the spider rested was one of the most important cues used by *S. caementarium* to locate *Araneus cornutus*, which were hiding in retreats near webs. In my study, both *C. caeruleum* and *S. caementarium* often alighted upon dark spots of debris or the shadows of insects or spiders on the opposite side of the screen tent, which supports Eberhard's hypothesis that wasps respond to contrast. However, *S. caementarium* attacked very few spiders at the centers of webs, instead seeming to stumble into and out of webs without regard for the possible presence of spiders. *C. caeruleum* and *S. caementarium* often flew within 2 cm of spiders on webs or grasses, without reacting to the spiders, but quickly chased spiders once spiders dropped from or moved within webs. Both of these observations suggest that contrast was not actually used to locate *Argiope* in my study. There are at least two potential explanations for these differences. The light colored bodies of juvenile *Argiope* may reflect significant UV light (Craig & Ebert 1994), and this may provide a poor contrast against natural backgrounds to insects, much as stabilimentum silk can (Blackledge 1998b; Blackledge & Wenzel 2000). Another possibility is that motion may be an important cue in eliciting attacks by *S. caementarium*. This second explanation seems particularly likely because *S. caementarium* pounced on small moving insects or even falling debris, particularly when the wasps were searching for spiders flushed from webs.
S. caementarium aggressively pursued spiders that dropped from webs, catching most prey by chasing spiders on the ground, while C. caeruleum used aggressive mimicry to catch spiders that were still in webs (Table 6.1). C. caeruleum would land in webs and then pluck at the silk in webs, luring spiders to themselves. In almost 70% of encounters where C. caeruleum landed in or plucked webs, spiders approached wasps, and most of those spiders were captured with little chase. I even observed one instance where a spider, which had dropped out of its web into the grass, proceeded to crawl back up its dragline to the web center and then to a C. caeruleum as the wasp plucked the web. This plucking behavior is similar to anecdotal observations in the wild for Chalybion spp. (Schwarz, in Howard 1901; Coville 1976) and Trypoxylon sp. (Rau 1926; pers. obs.). And, it may be a particularly effective method to hunt retreat dwelling spiders by luring spiders onto their webs (Coville 1976). One vespid is also thought to use its antennae to lure spiders to the hubs of webs (MacNulty 1961).

S. caementarium nests contain a wider range of spider prey than the nests of C. caeruleum. S. caementarium provisions nests with both web building and cursorial spiders, while the nest contents of C. caeruleum are largely restricted to orb- and tangle-web building spiders (Muma & Jeffers 1945; Krombein et al. 1979). These differences in nest provisioning likely reflect the different hunting tactics used by these two species of wasps. The use of old Sceliphron nests by Chalybion (Rau 1928) restricts Chalybion to hunting in habitats occupied by Sceliphron. Thus, competition may have been an important selective factor in the evolution of Chalybion and Sceliphron hunting behaviors. The specialization on web building spiders by Chalybion may therefore have evolved through niche partitioning.
*Argiope* used similar defensive behaviors against both species of wasps (Table 6.1). The most common response to attacks was for spiders to drop from webs (50% of encounters) and then either freeze or run toward nearby cover. Spiders often maintained contact with their webs via draglines and returned 2-10 min later. But, spiders sometimes abandoned webs completely, moving up to 1m away, in deep grass. *A. trifasciata* on natural webs built in the grassy outdoor enclosures also sometimes abandoned webs when attacked. Spiders would then build webs in new locations the next day, without having consumed the abandoned webs. These observations suggest that abandoning webs is itself a defensive strategy and field researchers must therefore use caution when assuming that vacant webs always indicate predation. Occasionally spiders ran to the tops or sides of webs (30% of encounters), remaining motionless for up to several minutes before returning to the web centers. Finally, spiders that remained at web hubs often stilted, holding their bodies far out from webs and angling their abdomens away from the plane of the webs. I suggest that these defensive behaviors might be relatively specialized responses to wasp predators (see also Cushing & Opell 1990), because spiders did not engage in other common defensive behaviors such as web flexing or shuttling (Tolbert 1975; Edmunds & Edmunds 1986; Cloudsley-Thompson 1995). Web flexing is often initiated when humans approach webs (pers. obs.) and may function against salticid predators (Tolbert 1975) but was never used against wasps. While my observations supplement descriptive works on the behavioral interactions of wasps and spiders, I hope that the use of enclosures will also facilitate a more experimentally based approach to the study of wasp-spider interactions.
<table>
<thead>
<tr>
<th></th>
<th><em>C. caeruleum</em></th>
<th><em>S. caementarium</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed attacks</td>
<td>48</td>
<td>26</td>
</tr>
<tr>
<td>Location of capture:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>web center</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>capture zone or frame threads</td>
<td>14</td>
<td>6*</td>
</tr>
<tr>
<td>ground below web</td>
<td>4</td>
<td>11**</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td>Wasp landed in web</td>
<td>22</td>
<td>3***</td>
</tr>
<tr>
<td>Wasp plucked web</td>
<td>11</td>
<td>0**</td>
</tr>
<tr>
<td>Spider approached wasp¹</td>
<td>15</td>
<td>1**</td>
</tr>
<tr>
<td>Response of spider:²</td>
<td></td>
<td></td>
</tr>
<tr>
<td>drop from web</td>
<td>21</td>
<td>15</td>
</tr>
<tr>
<td>abandon web</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>move to web periphery</td>
<td>15</td>
<td>6</td>
</tr>
<tr>
<td>Mass of spiders captured:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean ± standard deviation</td>
<td>0.038 ± 0.01mg</td>
<td>0.044 ± 0.02mg</td>
</tr>
<tr>
<td>range</td>
<td>0.02 - 0.07mg</td>
<td>0.02 - 0.08mg</td>
</tr>
</tbody>
</table>

Table 6.1: Predatory tactics of two sphecid wasps, *C. caeruleum* and *S. caementarium*, and the common defensive responses by immature *A. aurantia* and *A. trifasciata*. Observations were made on 3 individuals of *C. caeruleum* and 5 individuals of *S. caementarium*. ¹ Includes approaches by spiders to either wasps landing in webs or plucking webs. ² Defensive behaviors were not mutually exclusive. Asterisks denote significant differences, using binomial probability, between species of wasps in frequency of behaviors (*P < 0.05, **P < 0.01, ***P < 0.005).
Behavioral, morphological, and physiological defenses against predators often have profound impacts on other aspects affecting the fitness of organisms (Edmunds 1974; Lima & Dill 1990; Sih 1994). Investment in defense may be 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 defensive behaviors varies dependent upon predation risk and the physiological status of organisms. This then results in highly labile expression of defensive behaviors (Mangel & Clark 1986; McNamara & Houston 1986; Lima & Bednekoff 1999). Understanding the functional consequences of defensive behaviors is therefore critical to understanding variation in their expression.

Many genera of orb weaving spiders include conspicuous designs of bright white silk at the centers of their webs called stabilimenta (Lubin 1986; Eberhard 1990). Stabilimenta are usually shaped as vertical or diagonal lines of silk when built by older spiders and as spirals or disks when built by very young spiders (Ewer 1972; Nentwig & Heimer 1987). Many researchers argue that these silk designs are defensive structures
because stabilimenta are largely built by diurnal spiders that rest at the hubs of webs and are therefore more vulnerable to visually hunting predators than are retreat dwelling or nocturnal spiders (Eberhard 1973; Scharff & Coddington 1997), although other hypotheses have also been proposed (Nentwig & Rogg 1988; Craig & Bernard 1990; Humphreys 1992). Also, studies of island populations where spiders are exposed to reduced levels of predators have found that stabilimenta are less frequent in webs than in populations on adjacent islands where predators are more common (Lubin 1975; Kerr 1993). Finally, Blackledge and Wenzel (1999), Eisner and Nowicki (1983), and Horton (1980) have shown experimentally that stabilimenta can warn birds about the presence of potentially noxious sticky silk webs, protecting spiders from predation or webs from damage. But, these experiments were performed on adult *Argiope* or other large orb-weaving spiders that build webs in relatively open areas. Instead, most stabilimentum building spiders are smaller and locate webs in locations that are less conspicuous such as deep in grasses, overhanging banks, and tree buttresses (Eberhard 1973, 1990) where webs are relatively protected from flying birds and bird predation. So, there is relatively little direct experimental evidence for how stabilimenta would act as defenses for most spiders.

Stabilimenta are also unusual because of the high variability with which they are included in webs. Most orb webs are rebuilt daily and a few species of spiders include stabilimenta in almost every new web (Tolbert 1975; Blackledge 1998a). Most spiders include stabilimenta in only about 30-70% of webs and vary the shape or size of stabilimenta (Eberhard 1973; Edmunds 1986; Nentwig & Rogg 1988; Kerr 1993). Blackledge (1998a) and Herberstein *et al.* (2000) demonstrated that the foraging success
of spiders is an important determinant of stabilimentum variability and that spiders build larger and more frequent stabilimenta under good foraging conditions. This trade-off between foraging success and stabilimentum building appears to be caused by the ability of insects to use stabilimenta as visual cues to avoid webs, so that only well-fed spiders that can afford the loss of prey build stabilimenta (Blackledge & Wenzel 1999). This predator-prey conflict is also hypothesized to have led to selection for the cryptic color properties that stabilimentum silk has to many insects (Blackledge 1998b; Blackledge & Wenzel 2000). Yet, lack of experimental data on defensive functions of stabilimenta versus non-avian predators has made it difficult to incorporate defensive benefits into a predator-prey conflict model of stabilimentum variation.

I examined the hypothesis that stabilimenta function as defenses against predatory mud-dauber wasps (Hymenoptera: Sphecidae). Many species of mud-dauber wasps prey exclusively upon spiders, capturing spiders and depositing them in mud nests where the spiders serve as food for developing wasp larvae (Bohart & Menke 1976; Krombein et al. 1979). Mud-dauber wasps are common and ubiquitous threats to orb weaving spiders of many sizes (Coville 1987) and therefore have the potential to act as a serious selective agent on stabilimentum variability. I tested the effect of stabilimenta on predation of immature *Argiope trifasciata* (Araneae: Araneidae) by two mud-dauber wasps, *Chalybion caeruleum* and *Sceliphron caementarium* (Hymenoptera: Sphecidae).
Methods

Organisms

I observed the predatory interactions of wasps and spiders in three outdoor field enclosures between 28-Jul and 11-Sept 1999. Adult female sphecid wasps, *C. caeruleum* and *S. caementarium*, were collected from an old farm in Dublin, OH. Both species of wasps are common predators of orb-weaving spiders in mid to late summer and prey upon predominately *A. trifasciata* at the collection site (pers. obs.). Both wasp species hunt and nest in the same areas but differ in the behaviors they use to attack spiders. *S. caementarium* usually catches spiders, after spiders drop out of webs, by pursuing spiders into the vegetation, while *C. caeruleum* chases spiders in webs and often lands in webs, vibrating the webs in a form of aggressive mimicry that can lure spiders to them (Blackledge and Pickett submit.; Chapter 6).

Wasps were individually marked with paint prior to being released in the enclosures (see below). Initially, one enclosure was randomly selected to contain *C. caeruleum*, another *S. caementarium*, while the third contained no wasps, instead serving as a control. On 18-Aug the control enclosure was designated as a second *Sceliphron* enclosure and I added several *S. caementarium* to it. Each enclosure was provisioned with multiple wasps initially. But, several wasps escaped or died before building nests so that, once wasps began hunting, two enclosures contained a single adult female *S. caementarium* each and the third enclosure contained two adult female *C. caeruleum*.

*A. trifasciata* include stabilimenta in about 50% of their webs (Blackledge 1998a; Tso 1999). Therefore, I was 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 on an almost daily basis during the experiment. Each spider was individually marked with colored ink (Pigma Micron pens) on its thorax and abdomen, and weighed to the nearest µg. Prior to the start of the experiment, 10-20 A. trifasciata were released into each enclosure. Spiders were added to enclosures at the end of each day as necessary to maintain a constant density of spiders. Young A. trifasciata build disk shaped stabilimenta and shift gradually to a linear form of stabilimenta as they mature. But, all spiders included in my study were old enough that they built only linear stabilimenta. I also excluded from the analysis all spiders that weighed more than the largest spider captured by wasps during the experiment.

Enclosures

Each enclosure consisted of nylon screen suspended over a wood frame (3.8 x 2.3 x 2.0m), with the bottom edge sealed by a thick layer of bark mulch and pebbles to prevent escape of wasps. The 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 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 20 x 30 x 10cm plastic pan with mud from the pond at the collection site where wild S. caementarium collected mud for nest building. The pans were partially filled with water and then tilted to create gradients from dry to completely saturated. I glued mud S. caementarium nests to wooden boards along the tops of the enclosures because C. caeruleum reuses vacant S. caementarium nests (Rau 1928) and because S. caementarium often built new nest cells attached to old
nests. A hummingbird feeder, containing a 1:1 honey:water solution, was suspended in each cage to provide a nectar source for wasps. Honey water was changed every two days to prevent fermentation.

Free Trials

I censussed each enclosure for *A. trifasciata* every morning between 0700 and 0900hr, before wasps began hunting. I recorded the presence of each spider, web, and if that web contained a stabilimentum. I 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 (see below), I 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 in gaps in the vegetation) while covered webs were suspended entirely below the grass canopy. Although somewhat arbitrary, this distinction should not have biased the experiment because exposure of webs was determined prior to predation for each day. Each evening between 1900 and 2100hr, after hunting ceased, I again assayed enclosures, recording presence or absence of spiders in webs.

I examined the association of stabilimenta and wasp predation in two ways. I measured the known rate of predation of spiders for which I 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. I excavated the nest cells of wasps one to
five days after nest cells were filled with spiders and had been sealed with mud by the wasps. Therefore, a spider was classified as dead either if its capture was observed directly or it had disappeared and its body was found within a wasp nest cell that had been closed on that same day. I then tested the null hypothesis that the proportion of spiders known to have been captured from webs that contained stabilimenta was the same as that predicted from webs that did not contain stabilimenta using a G-test, applying a William's correction (Sokal & Rohlf 1981).

I 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 they remove their webs just prior to dawn (Enders 1976; Horton & Wise 1983; Blackledge & Pickett submit.; Chapter 6). Therefore, I 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 that web site was occupied by a different spider on the next day. 3) The original web builder was never found again within the enclosure. I again used a G-test and William's correction 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. I included this data set because of its larger sample size and because it was analogous to data dealt with by field researchers who normally cannot directly observe predation events.

Both the inferred and known predation data sets include some spiders that built webs on more than a single day (i.e. spiders that were not captured). I consider these observations to be independent of one another because I am examining an effect of web
structure, stabilimenta, on foraging bouts by wasps, rather than variation within the abilities of individual spiders to avoid capture by wasps. Webs are built anew each day and therefore each web is a unique structure.

I also compared the frequency with which spiders built stabilimenta in each enclosure before and during days upon which predation occurred. This allowed me to examine if spiders responded to increased wasp predation pressure by altering their frequency of stabilimentum building. I calculated the mean frequency of stabilimenta on all days prior to the first predation event for each enclosure. I then classified the frequency of stabilimenta in webs on each day that followed a day with at least one wasp predatory event as being higher or lower than the pre-predation mean. I then used a G-test and William's correction to compare the distribution of days above and below the mean pre-predation frequency versus an expected distribution of 50:50, if wasp predation did not affect stabilimentum building.

Individual Observations

I examined directly the effect of stabilimenta on success of individual predation attempts by *C. caeruleum* on *A. trifasciata*. Spiders were allowed to build webs within standardized 35 x 35 x 10cm wood frames overnight (Blackledge & Pickett submit.; Chapter 6). Then one to three frames were placed within the *C. caeruleum* enclosure and observed until each spider was attacked by a wasp and either captured or escaped predation. By using the standardized wood frames, this technique allowed me to control better for any effects of differences in web height, substrates to which webs were attached, or exposure of webs. I used a G-test with William's correction to compare the
proportion of spiders captured that had stabilimenta in webs versus those that did not have stabilimenta in webs. Because I directly observed each predation attempt, I 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**

**Free Trials**

I excluded from the analysis all webs that were classified as being covered by vegetation because wasps usually hunted at or above the upper level of grass, only entering deeper layers when actively pursuing spiders flushed from their webs (Blackledge & Pickett submit.; Chapter 6), and because I found that only 2 of 43 spiders known to be killed were in webs classified as "covered". This distinction removed 18% of webs from the analysis and was important to make because exposed webs were as much as 45% more likely to contain stabilimenta than webs built deep in the grass. Therefore, there was an *a priori* bias toward wasps encountering spiders in webs containing stabilimenta, regardless of any effect of the stabilimentum itself.

In both *S. caementarium* enclosures, spiders were more likely to be captured when in webs that did not contain stabilimenta (*G* = 8.147, *df* = 1, *P* < 0.005 & *G* = 9.768, *df* = 1, *P* < 0.005 for enclosure 1 & 2 respectively; Table 7.1). I was unable to make this comparison for the *C. caeruleum* enclosure because I was able to verify the identity of only 6 spiders excavated from nests. This was because I had difficulty determining when *C. caeruleum* finished filling their nests and the spiders were generally
already partially eaten by wasp larvae or severely desiccated by the time I opened nest cells, making individual identification impossible.

The inferred rate of predation was lower for spiders in webs that contained stabilimenta for both *S. caementarium* enclosures (*G* = 4.713, df = 1, *P* < 0.05 & *G* = 4.930, df = 1, *P* < 0.05) and the *C. caeruleum* enclosure (*G* = 5.0157, df = 1, *P* < 0.05; Table 7.1).

Spiders were more likely to build stabilimenta after days on which wasps actively hunted, compared to the mean frequency prior to any predatory events. Stabilimenta were more frequent than the pre-predation mean on 21 of 26 days following predation events for spiders in the *C. caeruleum* enclosure (*G* = 9.54, df = 1, *P* < 0.005) and on all 15 days following predation for the first *S. caementarium* enclosure (*P* < 0.0001, computed as binomial probability; see Table 7.2). Because predation occurred in the second *S. caementarium* enclosure on only three days, I did not have a sufficient sample size to conduct a G-test, but stabilimenta were still more frequent on all three days following predation.

Individual Observations

Individual *A. trifasciata* in standardized wooden frames were 36% less likely to be captured by *C. caeruleum* when in webs that contained stabilimenta compared to webs without stabilimenta (*G* = 9.798, df = 1, *P* < 0.005; Table 7.3).
Discussion

I found that mud-dauber wasps were 8-35% less likely to capture the orb-weaving spider *A. trifasciata* when spiders were in webs that contained stabilimenta compared to webs without stabilimenta (Table 7.1). Direct observation of predatory bouts by *C. caeruleum* also showed that spiders in webs containing stabilimenta were 36% more likely to escape predation (Table 7.3). Comparison of the behavioral interactions of wasps and spiders during the individual observations (Table 7.4) suggests that stabilimenta provide visual shields or distractions against wasps (see also Eberhard 1973). The most effective defense against wasps is for spiders to drop from webs or retreats when attacked (Eberhard 1970; Rayor 1997; Blackledge & Pickett submit.; Chapter 6; Table 7.4). Wasps were at least 20% more likely to catch spiders that were still in webs if the webs were without stabilimenta (Table 7.4). But, spiders were equally likely to drop out of webs, regardless of presence or absence of stabilimenta (Table 7.4; but see Cushing & Opell 1990). This argues that stabilimenta likely made the defensive dropping behavior of spiders more effective, perhaps by camouflaging the dropping spiders so that they were not seen or by distracting wasps so that spiders had extra time to drop.

The hypothesis that stabilimenta allow spiders to drop more effectively from webs is reinforced by differences between the known and inferred rates of predation in the free spider trials. The inferred rate of predation was based upon the presence of empty webs as an indicator of capture. The inferred and known rates of capture were similar for spiders without stabilimenta but the known rate of capture was much lower than the inferred rate for spiders in webs containing stabilimenta (Table 7.1). This
suggests that many of the empty stabilimentum webs were vacant not because the spiders had been captured, but because spiders successfully escaped predation by abandoning their webs.

Previous studies have found that the color properties of stabilimentum silk are cryptic to many insect prey of spiders, and that this likely reduces the ability of insects to see and avoid webs (Blackledge 1998b; Blackledge & Wenzel 2000). The visual system of sphecid wasps may be very similar to many of the hymenopteran prey of spiders (Peitsch et al. 1992), suggesting the possibility that sphecids also do not perceive the silk in stabilimenta as being colored conspicuously. Thus, while stabilimenta may provide visual signals that help spiders to escape from webs through distraction or camouflage, stabilimenta are unlikely to provide conspicuous cues that wasps can use to locate spiders. This is, of course, consistent with the lower rate of capture of spiders in webs containing stabilimenta.

Although there has been much circumstantial evidence suggesting that stabilimenta are included in webs as defensive structures (Eberhard 1973; Lubin 1975; Edmunds 1986; Schoener & Spiller 1992; Kerr 1993), the only experimental tests of defensive hypotheses have been directed at the role of stabilimenta in preventing predation or web destruction for *Argiope* spp. by birds (Horton 1980; Eisner & Nowicki 1983; Blackledge & Wenzel 1999). Many stabilimentum-building spiders locate webs in sheltered sites such as tree buttresses, crevices and under overhangs. And, young *Argiope* spp. often build their webs relatively deeply in grasses, so that the cited experiments have been justifiably criticized as not providing a functional explanation for stabilimenta that is generally applicable (Edmunds 1986; Craig & Bernard 1990; Eberhard 1990).
However, even spiders that select locations for webs that are out of the flight paths of birds are still subject to predation by a variety of wasp predators. Thus, the protection from wasp attacks associated with stabilimenta in *A. trifasciata* could provide a selective force for the repeated evolution of stabilimenta in a variety of other diurnal orb web spiders (Scharff & Coddington 1997).

Blackledge and Wenzel (1999) proposed that much of the variation in stabilimentum frequency can be explained by a trade-off between the defensive benefits of stabilimenta and the associated cost to prey capture of including stabilimenta in webs. Well-fed spiders are more likely to include stabilimenta in webs because they can afford the loss of prey capture (Blackledge 1998a; Blackledge & Wenzel 1999). And, several studies have suggested that inter-population stabilimentum variation is associated with variable predator densities among island populations of spiders (Lubin 1975; Schoener & Spiller 1992; Kerr 1993). In my study, *A. trifasciata* built stabilimenta more frequently on days after wasps hunted compared to the frequency before any hunting had occurred (Table 7.2). This argues that spiders may assess predation risk and alter the frequency with which they include stabilimenta in webs accordingly. Thus, the ability of spiders to adjust to conflict between the defensive benefits and costs to prey capture of stabilimenta may be much more dynamic than generally thought (Blackledge & Wenzel 1999). Prior to predation, spiders neither changed web sites nor disappeared with any great frequency, but during predation spiders often changed web sites and new spiders were added almost daily to replace captured individuals. Thus, the increased frequency of stabilimenta in webs could also have been due to spiders responding to overall levels of disturbance rather than to spiders assessing presence of actively hunting predators, *per se*.

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In this study, I found that spiders that include stabilimenta in their webs were less likely to be captured by two species of sphecid wasps. These data support the hypothesis that stabilimenta are included in webs as defensive structures. Because spider hunting wasps are an ubiquitous threat to web-building spiders, the association of stabilimenta with reduced capture of spiders could provide a common selective factor for the evolution of stabilimentum-building in multiple taxa. Stabilimenta provide an ideal system to study how individual organisms deal with conflicting pressures from predators and prey because individual webs and stabilimenta represent discreet, quantifiable investments in foraging and defense (Higgins & Buskirk 1992; Sherman 1994; Blackledge 1998a), that remain constant for the duration of webs. Furthermore, decisions to build webs and stabilimenta are based almost exclusively upon the experiences of spiders on days prior to web construction (Higgins & Buskirk 1992). In addition, stabilimentum-building is an unusual example of a defensive behavior with direct impacts upon foraging because not only does there appear to have been selection on the frequency of expression of the behavior but also on its form (Blackledge 1998b; Blackledge & Wenzel 2000), allowing spiders to express this defensive behavior at a reduced cost to foraging. Future research should examine how spiders assess and deal with simultaneous variation in predator and prey densities through variation in the shapes and frequencies of stabilimenta.
<table>
<thead>
<tr>
<th></th>
<th>known</th>
<th>inferred</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>S. caementarium</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>enclosure 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>stabilimentum</td>
<td>0.28 (n=32)</td>
<td>0.41 (n=55)</td>
</tr>
<tr>
<td>no stabilimentum</td>
<td>0.54 (n=11)***</td>
<td>0.58 (n=19)*</td>
</tr>
<tr>
<td>enclosure 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>stabilimentum</td>
<td>0.15 (n=20)</td>
<td>0.29 (n=24)</td>
</tr>
<tr>
<td>no stabilimentum</td>
<td>0.50 (n=12)***</td>
<td>0.54 (n=13)*</td>
</tr>
<tr>
<td><strong>C. caeruleum</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stabilimentum</td>
<td>0.14 (n=135)</td>
<td>0.22 (n=107)*</td>
</tr>
</tbody>
</table>

Table 7.1: Effect of stabilimenta in spider webs on predation by wasps. * Data are not provided because I could only determine the identities of 6 spiders provisioned in nests. * P < 0.05, *** P < 0.005; G-test, df = 1.
Table 7.2: Effect of wasp predation on the frequency of stabilimentum construction by *A. trifasciata*. Probability was calculated as the binomial probability of all 15 days following predation, having a higher frequency of stabilimenta than the mean frequency prior to predation. Although all 3 days had a stabilimentum frequency higher than the pre-predation mean, no statistical comparison was performed because of the small sample size. G-test (df = 1) comparing the # of days following predation with a stabilimentum frequency higher than the pre-predation mean versus the # of days below the pre-predation mean. d = # days following predation.

<table>
<thead>
<tr>
<th>Stabilimentum frequency</th>
<th>prior to predation</th>
<th>during predation</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. caementarium</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>enclosure 1</td>
<td>0.36</td>
<td>0.64 (d=15)</td>
<td>&lt; 0.0001&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td>enclosure 2</td>
<td>0.43</td>
<td>0.86 (d=3)</td>
<td></td>
</tr>
<tr>
<td><em>C. caeruleum</em></td>
<td>0.31</td>
<td>0.47 (d=26)</td>
<td>&lt;0.005&lt;sup&gt;3&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>captured</td>
<td>survived</td>
<td></td>
</tr>
<tr>
<td>--------------------------</td>
<td>----------</td>
<td>----------</td>
<td></td>
</tr>
<tr>
<td>stabilimentum</td>
<td>6</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>no stabilimentum</td>
<td>13</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>

Table 7.3: Effect of stabilimenta on predation of *A. trifasciata* by *C. caeruleum* in individual observations. Spiders in webs that did not contain stabilimenta were significantly more likely to be captured (G-test, $G = 9.798$, df = 1, $P < 0.005$).

<table>
<thead>
<tr>
<th></th>
<th>webs without stabilimenta</th>
<th>webs with stabilimenta</th>
</tr>
</thead>
<tbody>
<tr>
<td>% spiders captured</td>
<td>0.68</td>
<td>0.32</td>
</tr>
<tr>
<td>at web hub</td>
<td>0.18</td>
<td>0.17</td>
</tr>
<tr>
<td>in capture zone or frame of web</td>
<td>0.73</td>
<td>0.50</td>
</tr>
<tr>
<td>on ground</td>
<td>0.00</td>
<td>0.33</td>
</tr>
<tr>
<td>aggressive mimicry used by wasp</td>
<td>0.53</td>
<td>0.42</td>
</tr>
<tr>
<td>spider responds to mimicry</td>
<td>0.42</td>
<td>0.21</td>
</tr>
<tr>
<td><strong>spider defensive behaviors</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>runs to edge of web</td>
<td>0.39</td>
<td>0.35</td>
</tr>
<tr>
<td>drops from web</td>
<td>0.47</td>
<td>0.47</td>
</tr>
<tr>
<td>runs through grass</td>
<td>0.06</td>
<td>0.13</td>
</tr>
</tbody>
</table>

Table 7.4: Predatory interactions between *C. caeruleum* and *A. trifasciata* for webs with (n=19) and without (n=19) stabilimenta. Data are presented as % of total encounters in which behavior was observed, except for location of spider capture which is expressed as % of successful captures.
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