WEB ORIENTATION, STABILIMENTUM STRUCTURE AND PREDATORY BEHAVIOR OF *ARGIOPE FLORIDA* CHAMBERLIN & IVIE 1944 (ARANEAE, ARANEIDAE, ARGIOPINAE)

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ABSTRACT.   This study was undertaken to describe the web orientation, stabilimentum structure and predatory behavior of *Argiope florida* Chamberlin & Ivie 1944 (Araneae, Araneidae, Argiopinae), a virtually unstudied orb-web spider of the southeastern United States. Adult female *Argiope florida* were sampled from five sandy ridge areas of Florida. Compass orientation of the spider's dorsum, incline of the web from vertical and hub height were measured. The presence of male *A. florida*, barrier webs, kleptoparasitic species of *Argyrodes* Simon 1864 (Araneae, Theridiidae), wrapped prey and large areas of web damage were noted. Predatory behavior was elicited by touching a radius with a 100 Hz tuning fork. The number of stabilimentum arms was measured, along with their arrangement, length and number of silk bands. On average, webs faced 100° E of N, were inclined 19° from vertical and were 1 m from the ground at the hub. Responses to the tuning fork, which closely resembled the responses to actual prey, were more vigorous when *Argyrodes* spp. were present on the web, but were not different when wrapped prey were present on the web. Most webs had stabilimenta and most stabilimenta had four arms in a cruciate pattern. The upper arms tended to be smaller and spaced further apart than the lower arms. Spider size was related to the angle between the lower arms of the stabilimentum, but not to other measures of the stabilimentum.

Keywords: Orb web, prey capture, Florida scrub, tuning fork, *Argyrodes* kleptoparasites

The behavior of orb-web spiders has long been a topic of interest. Much of the research has focused on the building of the web and the variables that affect its final structure, especially its size, asymmetry, number of radii and distance between loops of the sticky spiral (e.g., Craig 1987; Sandoval 1994; Sherman 1994; McReynolds 2000; Venner et al. 2000). Other behavioral research has been dedicated to web site selection (e.g., Enders 1973, 1976), compass orientation (e.g., Carrel 1978; Tolbert 1979; Biere & Uetz 1981; Caine & Heiber 1987), sexual behavior (e.g., Elgar et al. 2000), thermoregulatory posturing (e.g., Humphreys 1991; Higgins & Ezcurra 1996),

predatory behavior (e.g., Robinson & Robinson 1974; Klärner & Barth 1982; Masters & Moffat 1983; Masters 1984) and the effects of kleptoparasitic *Argyrodes* spp. Simon, 1864 (Araneae, Theridiidae; e.g., Larcher & Wise 1985; Elgar 1989; Cangialosi 1990).

Many orb-web spiders add bits of debris, egg cases, or conspicuous tufts or bands of silk to the frame, radii and/or hub of their webs. This web-decorating behavior is seen in a number of Araneidae, spanning 15 genera and occurring in both ecribellate and cribellate spiders (Scharff & Coddington 1997). A phylogenetic analysis of this family by Scharff & Coddington (1997) suggests that web-decorating behavior has evolved nine separate times in Araneidae. The extent to which web-decorating behavior has established itself in the Araneidae suggests that this behavior serves

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an important function(s) in spiders that build orb webs.

Spiders in the genus *Argiope* Audouin 1826 often decorate their nearly invisible orb webs with conspicuous zigzags of silk called stabilimenta. However, the ecological function of stabilimentum building is still unresolved (see Herberstein et al. 2000a). Because of its reflectivity in both the visible and ultraviolet (UV) regions of the spectrum (Craig & Bernard 1990, Watanabe 1999, Zschokke 2002), many authors have suggested that the stabilimentum is used as a visual signal. However, it is much debated whether the primary recipients of this signal are predators, prey or megafauna. Arguments that the primary recipients are predators suggest the stabilimentum thwarts predators by displacing attacks or changing the apparent size or shape of the spider (Hingston 1927; Ewer 1972; Eberhard 1973; Horton 1980; Edmunds 1986; Schoener & Spiller 1992). Arguments that the primary recipients are prey center around the UV reflectivity of the stabilimentum, which may attract insects by simulating flowers or patches of daylight in vegetation (Craig & Bernard 1990; Craig 1991; Tso 1996; Hauber 1998; Tso 1998a, 1998b; Watanabe 1999; Herberstein 2000; but see Blackledge & Wenzel 1999, 2000). Finally, the stabilimentum may signal the presence of the orb to megafauna that may otherwise walk or fly through it; this is mutually beneficial because the spider keeps its web intact and the megafauna do not have to groom the sticky spiral (Eisner & Nowicki 1983; Eberhard 1990; Kerr 1993; Blackledge & Wenzel 1999). In any case, the effectiveness of a visual signal is in part a function of the light that strikes it, which in any season would be affected by the web's compass direction and angle from vertical. However, this basic natural history information is often missing, even for some of the best-studied species. Indeed, many species are virtually unstudied beyond their description and classification.

One of the relatively unknown species is *Argiope florida* Chamberlin & Ivie 1944. In the most recent description and classification of this species, Levi (1968) summarizes the little that is known of its natural history: adults range from central North Carolina south to the panhandle and peninsula of Florida, mature from July to November and build a cruciate stabilimentum. In Florida, the species lives in sand scrub and pine flatwoods. The only other study mentioning the species is that of Eisner & Nowicki (1983), who noted that removing the stabilimentum did not seem to affect prey capture or evasive behaviors. The purpose of the present study was to further characterize the web and stabilimentum of *A. florida*, to gather baseline data on predatory behavior via responses to a tuning fork and examine any interesting relationships that were revealed.

METHODS

Numerous areas of the Florida panhandle, peninsula and keys were visited during 2000–2002 and locations where *A. florida* were found are summarized in Table 1. A search for adult female *Argiope* was carried out by walking through the habitat during the daytime and scanning the vegetation from the ground to a height of about 2.5 m. *Argiope florida* hang head down at the hub on the underside of their slightly tilted webs all day, like its congenerics (Comstock 1948). Upon locating an individual, the date, time, location, temperature and weather were noted.

Next, two measures of the web were taken from a distance of about 1–3 m, with careful effort to avoid disturbing the spider. The compass direction its dorsum faced was recorded to the nearest 5°. The angle of the plane of the web was measured with a clinometer and recorded to the nearest 1° from vertical. Sometimes the web was significantly flexed at the hub, so that the incline of the web above the hub was quite different from that below the hub. In these situations, the incline of a line connecting the tips of the spider's 4th legs to the tips of its 1st legs was used.

Several measures were then taken from a distance of less than 1 m, again being careful to avoid disturbing the spider. First, it was noted whether any large sections of the web were missing or damaged. Then, both sides of the web were inspected for the presence of barrier webs, which are cobweb-like tangles of non-sticky silk placed adjacent to the orb. Next, the orb and barrier webs were carefully searched for male *A. florida* and the kleptoparasitic *Argyrodes* spp. (the frame threads and nearby vegetation were not searched for males or *Argyrodes* spp.). Lastly, the presence of wrapped prey was noted.

Table 1.—Dates and locations where *A. florida* were found. SP = State Park, NF = National Forest, SF = State Forest, CO = County.

n	Ridge	Locality and/or Land-mark, County	Latitude/Longitude	Dates Found
9	Atlantic Coastal	Jonathan Dickinson SP, Hobe Sound, Martin CO	27°01′01″N 80°06′37″W	31 Aug 2001 17 Oct 2001 05 Oct 2002
1	Bell	Bell, Gilchrist CO	29°47′25″N 82°51′13″W	15 Oct 2001
38	Lake Wales	Archbold Biological Station, Highlands CO	27°10′55″N 81°21′08″W	15–17 Sep 2001 19 Oct 2001 15 Aug 2002 13 Sep 2002
3	Lake Wales	Hickory Lake Scrub, Polk CO	27°41′47″N 81°32′23″W	03 Sep 2001
4	Lake Wales	Sun 'N Lake, Lake Placid, Highlands CO	27°14′55″N 81°18′02″W	02 Aug 2002
6	Mount Dora	Alexander Springs, Ocala NF, Lake CO	29°07′24″N 81°34′40″W	02 Sep 2001
1	Mount Dora	Healing Waters, Ocala NF, Lake CO	29°10′14″N 81°38′14″W	02 Sep 2001
1	Unnamed	Camel Lake, Appalachicola SF, Liberty CO	30°06′30″N 84°58′51″W	14 Oct 2001
1	Unnamed	Pine Log SF, Panama City, Bay CO	30°24′18″N 85°52′06″W	14 Oct 2001

A predatory response was then elicited by touching the web with a 100 Hz tuning fork. In controlled experiments, 100 Hz vibrations increased at the hub of empty *Larinioides sclopetarius* (Clerck 1757) orbs when flies (*Calliphora erythrocephala*), mosquitoes (*Culex* spp.) and bees (*Apis mellifora*) began buzzing while trying to free themselves (Masters 1984). Tuning forks produce pure tones at an initial amplitude of 100–110 dB (reference 0.0002 dynes/cm^2), which rapidly decay (Frings & Frings 1966). Amplitude is thus difficult to control with tuning forks, but natural prey produce a very wide range of amplitudes (Barrows 1915; Landolfa & Barth 1996). Pilot work and previous research (Boys 1880; Wells 1936; Frings & Frings 1966) revealed that striking the tuning fork near the spider can produce a number of behavioral responses without even touching the web, probably due to the significant near-field air vibrations of a tuning fork. For this research, the tuning fork was struck at least 1 m from the spider and not passed near the spider before touching the web. Five seconds after striking the fork, a single tine of the fork was gently pressed onto a radius at a 45° angle. This angle should produce a high amplitude (about 2 mm) combi-

nation of transverse and longitudinal vibrations, which are believed to be important for prey detection, localization and recognition (Masters & Markl 1981; Klärner & Barth 1982; Masters 1984). The stimulated radius was to the right or left of the hub, approximately halfway from the hub to the edge of the orb (typically 15–25 cm from the hub). The radius was pushed in about 1.5 cm with the tine for about 3 s and then allowed to return to its original position. The fork was left in place about 10–15 s.

Pilot testing revealed that tuning fork stimulation of other areas of the web was less satisfactory. Stimulation above the hub was difficult because this area of web was often small, and the response may be inhibited by having to rotate 180° and climb upward (cf. Masters & Moffat 1983). Stimulation below the hub did not allow for an assessment of rotation of the body toward the stimulus, an important element of the response (Boys 1880), and could potentially confuse an attack with an escape-drop. Stimulation of the frame threads often produces a vigorous response (Boys 1880; pers. obs.), but prey items are not typically caught there.

Predatory responses were easily scored

from no response at all (=0.0) to exhibiting the full range of behaviors that a real prey item would elicit (=5.0). The following are listed from least to most vigorous response, and were scored as numbered: 1) moving a leg, typically to place a tarsus on or near the radius being stimulated, 2) rotating the body so that the axis of the cephalothorax and abdomen is aligned with the point of stimulation, 3) plucking or tugging on radii, 4) approaching the fork and making physical contact with it, usually with the 1st and 2nd tarsi (if the approach were interrupted by stopping or returning to the hub, 0.5 points were deducted from the score) and 5) wrapping the tip of one or both tines with silk. Thus, a spider that quickly rotated, approached and wrapped the fork with silk scored 5.0. A spider that paused during the approach but ultimately wrapped the fork with silk scored 4.5. A spider that rotated but never approached scored 2.0. Spiders that bit the fork consistently did so after wrapping, but this behavior was not factored into their predatory response score because the 10–15 s that the tuning fork was in the web may not have been sufficient time for a full predatory response if an individual spent several seconds wrapping a large area of the fork. An avoidance response such as dropping off the web or moving away from the fork was rare.

The remaining measures were taken last because they required close proximity to the spider and often caused the spider to leave the hub. The height of the hub above ground was measured with an extension rule. The number and pattern of stabilimentum arms was noted, after which three measures were taken on each arm: 1) its length, measured with dial calipers, 2) the number of bands of silk crossing from one radius to another (hereafter "bands") and 3) the angle it formed with the next arm, measured with a transparent goniometer. Next, dial calipers were used to obtain an index of size from leg #2. Specifically, the chord of the distance from the proximal end of the metatarsus to the distal tip of the tarsus was measured. Although there may be some flexion at the tarsometatarsal joint, this chord was very close on average to the sum of Levi's (1968) averages for the tarsal and metatarsal lengths.

After these data were collected in the field, the azimuth of the sun at the dawn of the day was obtained to the nearest 0.1° from the U. S. Naval Observatory's Astronomical Applications Department (http://aa.usno.navy.mil/). Statistics involving angles were calculated using the methods described by Mardia (1972), Batschelet (1981) and Zar (1996). Sample sizes vary because some measures were added after some data collection had taken place, and not all measures could be taken successfully on all spiders. Voucher specimens of *A. florida* and *Argyrodes* spp. are deposited in the arthropod collection at the Archbold Biological Station in Lake Placid, Florida.

RESULTS

Argiope florida were only found between August and October in the sand scrub and sandhill habitats of the Florida ridges. Specifically, *A. florida* were found on the Atlantic Coastal Ridge ($n = 9$), the Bell Ridge ($n = 1$), the Lake Wales Ridge ($n = 45$), the Mount Dora Ridge ($n = 7$) and in unnamed ridge areas in the panhandle ($n = 2$) (see Table 1). *Argiope florida* and *A. aurantia* Lucas 1833 were frequently sympatric on the ridges, even though *A. aurantia* is often found in wetter habitats such as lake margins and swamps. There was no obvious horizontal or other niche separation between *A. florida* and *A. aurantia*; in fact, their webs were often close together, and occasionally in clusters with both species present. *Argiope florida* were not found south of Martin County, and thus their distribution did not overlap that of the *Argiope argentata* (Fabricius 1775) commonly found in southern peninsular Florida and the keys. All *Argiope* spp. in Florida are easily recognizable by shape and color patterns; also, *A. florida* and *A. argentata* construct cruciate stabilimenta, whereas *A. aurantia* construct linear stabilimenta.

During data collection, temperature ranged from 21–38°C and was typically about 30–35°C. Spiders were frequently observed with their abdomens flexed away from the orb or off to the side, presumably to minimize exposure to the sun. Webs were never observed to be vertical, but instead were inclined by a mean $\bar{\phi} = 18.7°$, $s = 8.9°$ ($n = 63$). Twenty percent ($n = 13$ of 64 webs examined) had large sections of the web missing or damaged. Some of these were excluded from further measures and later analyses as appropriate. Twenty-five percent had barrier webs ($n = 12$

of 48 examined); barrier webs were occasionally on both sides of the orb, but usually only on the same side as the spider. No male *A. florida* were found on $n = 48$ webs searched. *Argyrodes* spp. were present on 8 (42%) of $n = 19$ webs searched (range 1–4 individuals per web). Individual *Argyrodes* were not identified to species. Fourteen of 49 webs searched (29%) had wrapped prey present either in the sticky spiral, at the hub, or at the spider's mouth. The height of the hub above the ground was measured on $n = 48$ webs and varied from 0.43 m to 1.61 m ($\bar{x} = 1.06$, $s = 0.28$). Although genitalia were not inspected, all were likely adults or at least subadults based on size: the chord of the tarsus + metatarsus on leg II averaged 10.9 mm ($n = 61$, $s = 1.1$, Min = 7.0, Max = 13.3).

The sampled *A. florida* showed a significant tendency to orient the plane of their webs parallel to the N-S axis so that their dorsa faced E or W. Using the direction the dorsum faced (*mod* 180°), the mean ± s compass direction was $\bar{\phi} = 99.6° ± 52.6°$ E of N (95% CI = 83.6°–115.6°). With $n = 64$, the Rayleigh test for directional preference was significant (mean vector length $r = 0.58$, $P < 0.001$). On the days of data collection, the sun's azimuth at dawn ranged from 69.6°–101.1° E of N. However, the orientation of the web did not correlate with the dawn azimuth ($r = 0.24$, $n = 64$, $P > 0.40$).

The 100Hz tuning fork was applied to $n = 61$ webs. Thirty-seven spiders approached the fork and wrapped it in silk (score = 4.5 for $n = 17$ that paused on the way and 5.0 for $n = 20$ that did not). Ten spiders approached but did not wrap the fork (score 3.5 for $n = 7$ and 4.0 for $n = 3$). Five spiders moved a leg but nothing more (score = 1.0). Nine spiders did not respond at all (score = 0.0). Overall, the mean ± s response to $n = 61$ stimulations was 3.57 ± 1.84. Mean predatory responses were not different when wrapped prey were present ($\bar{x} = 3.27$, $s = 1.99$, $n = 13$) *vs.* absent ($\bar{x} = 3.92$, $s = 1.62$, $n = 33$; equal variances $t = 1.16$, $df = 44$, two-tailed $P = 0.25$). However, predatory responses were stronger and less variable when *Argyrodes* were present ($\bar{x} = 4.86$, $s = 0.24$, $n = 7$) *vs.* absent ($\bar{x} = 3.40$, $s = 2.16$, $n = 10$); the variance difference was significant ($F = 78.21$, $df = 9, 6$, $P < 0.0001$) and the mean difference was nearly significant (unequal variances $t = 2.11$, $df = 9$, two-tailed $P = 0.06$).

Most webs had a four-arm, cruciate stabilimentum, but other patterns were observed (Fig. 1). Descriptive statistics on the stabilimentum measures are given in Table 2. Paired difference tests were used to compare lower arms and upper arms on the same web. Lower arms were closer together than upper arms (Hotelling's $F = 3.66$, $df = 2, 25$, $P = 0.040$). Lower arms were longer ($t = 8.00$, $df = 46$, two-tailed $P \ll 0.0001$), but there was no difference between lower and upper arms in their length asymmetry ($t = 0.37$, $df = 30$, two-tailed $P = 0.716$). Lower arms had more bands ($t = 10.07$, $df = 46$, $P \ll 0.0001$), but there was no difference between lower and upper arms in the number of bands per cm arm length ($t = 0.40$, $df = 46$, two-tailed $P = 0.691$). Given that length would be added to an arm by adding more bands, the amount of variation in length explained by bands was surprisingly low: for $n = 46$ upper arms, $r^2 = 0.49$ and for $n = 56$ lower arms, $r^2 = 0.63$ (for these calculations, one arm was chosen at random from stabilimenta with more than one upper or lower arm). This suggests that other factors play a significant role in the spacing between bands.

The size index was not related to the total number of bands ($r = +0.07$, $n = 55$, $P = 0.61$), the total length of the arms of the stabilimentum ($r = +0.12$, $n = 55$, $P = 0.38$), the bands/cm in the stabilimentum arms ($r = -0.19$, $n = 55$, $P = 0.16$), or the angle between the two lower arms of the stabilimentum ($r = +0.12$, $n = 32$, $P = 0.51$). The size index was related, however, to the angle between the two upper arms of the stabilimentum ($r = +0.41$, $n = 25$, $P = 0.04$).

DISCUSSION

Areas where *Argiope* spp. were found correspond fairly well with the distribution maps of Levi (1968) with two exceptions. First, Levi (1968) found *A. florida* on the Atlantic Coastal Ridge south of Martin County, whereas they were not found in these areas in the present study. This may be due to a reduction in sand scrub habitat in these areas (Myers 1990). Second, based on collecting reports with habitat information, Levi (1968) states that *A. aurantia* in Florida are found "rarely in sand scrub", whereas they were easily

No Stabilimentum: ⭕ **3.5%**

One Lower Arm: **12.3%**

Two Arms: **3.5%**   **10.5%**

Three Arms: **1.8%**   **7.0%**

Four Arms **57.9%**   **1.8%**
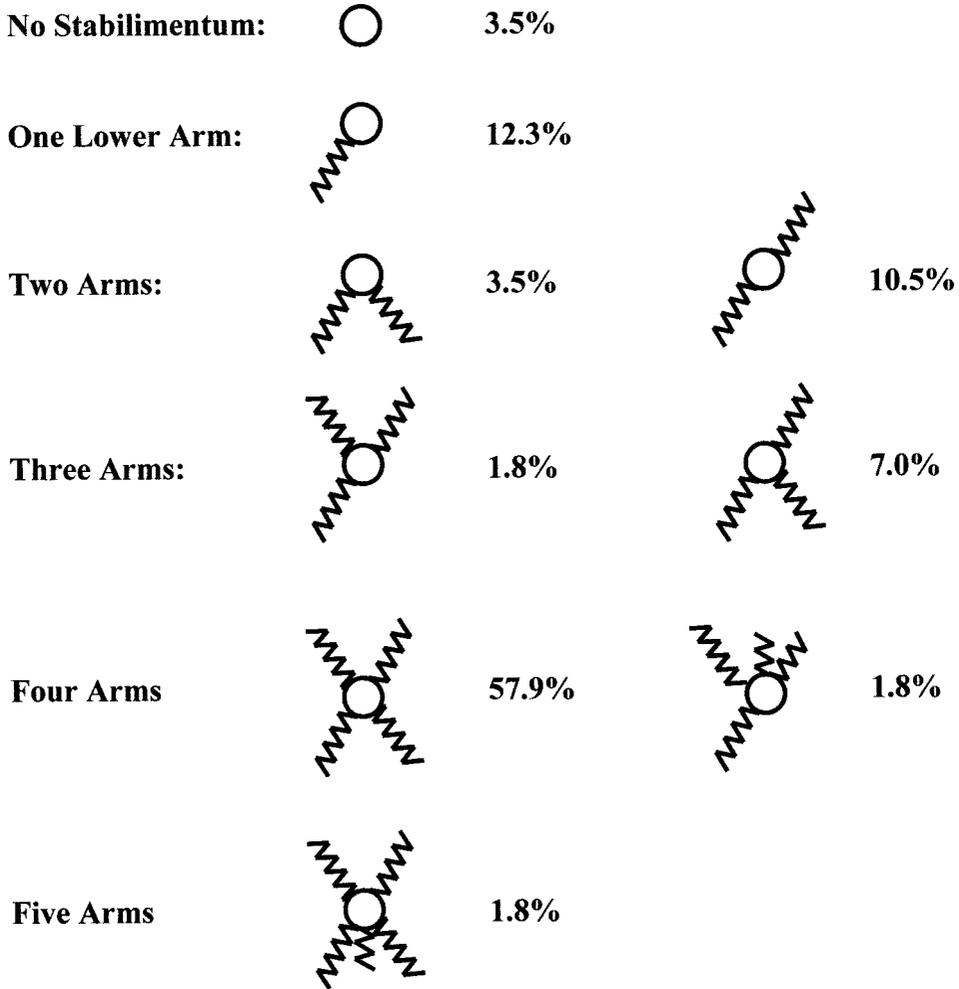
Five Arms **1.8%**

Figure 1.—Observed patterns of stabilimentum structure and their frequencies. Percentages are based on $n = 57$ webs.

found and quite numerous in sand scrub in the present study. Of course, the collecting reports and present authors may be defining ''sand scrub'' quite differently.

In open habitat with highly reflective sand, at subtropical latitudes, and at the hottest times of the year, *A. florida* hang at the hub of fairly exposed webs with their dorsa facing due east/west on average. It may be worthwhile to examine the behavioral and physiological responses to the heat load that could result from this combination of temperature, exposure and orientation. Orb-web spiders with webs in open areas can regulate insolation (and thus heat load) by retreating to shade

at high temperatures, posturing their bodies to adjust exposed surface area (i.e., Pointing 1965; Suter 1981), orienting their webs in a particular compass direction (i.e., Carrel 1978; Biere & Uetz 1981; Caine & Heiber 1987), building reflective silk shields over the hub (Humphreys 1992), and/or reflecting light with hairs on the cephalothorax and abdomen (Robinson & Robinson 1978). *Argiope florida* orbs are parallel to the N-S axis, which on nearly vertical webs would seem to maximize exposure to the sun. *Argiope* do not use retreats (Levi 1968; Tolbert 1979), and their stabilimenta do not cross the hub and thus do not provide a sun shield. Thermoregulation in *A.*

Table 2.—Descriptive statistics on stabilimentum characteristics. Sample sizes refer to number of spiders. If a web had two upper arms, their measures were averaged and the averages were used in the analyses. If a spider had built only one upper arm or only one lower arm, the length of this arm was used but this spider could not contribute to the analyses of asymmetry and angle. Analyses of the angle between upper and lower arms required an upper arm and a lower arm on the same side of the hub.

Variable	n	Mean	s	Min	Max
Angle Between the Upper Arms	27	68.8°	10.3°	46°	87°
Angle Between the Lower Arms	34	60.2°	13.9°	24°	95°
Length of the Upper Arms (cm)	47	1.18	0.73	0.41	4.32
Length of the Lower Arms (cm)	56	2.04	1.09	0.54	6.29
Asymmetry in the Length of the Upper Arms (cm)	34	0.47	0.54	0.01	2.71
Asymmetry in the Length of the Lower Arms (cm)	40	0.52	0.47	0.04	1.84
Bands in the Upper Arms	47	4.78	2.23	1	12
Bands in the Lower Arms	56	8.96	4.25	2	18
Bands/cm in the Upper Arms	47	4.77	2.27	0.98	11.43
Bands/cm in the Lower Arms	56	4.72	1.47	1.45	8.38
Angle Between the Upper and Lower Arms	32	112.2°	8.9°	90°	139°
Asymmetry in the Angle Between the Upper and Lower Arms	27	10.0°	7.1°	0°	27°

florida, therefore, would seem to come from behavioral posturing and silvery reflective hairs covering the dorsal cephalothorax and partially covering the dorsal abdomen (cf. Tolbert 1979).

While heat load may be a cost of the placement of their webs, benefits may come from an increase in prey capture and/or a decrease in the frequency of web loss. A large proportion (29%) of webs were found with wrapped prey already in the spiral, at the hub, or at the spider's mouth. Also, a large number of prey impacts probably accounts for the large proportion of webs found with sections damaged or missing. As discussed above, the stabilimentum may increase benefits by attracting prey and/or preventing megafauna from destroying the web. Both of these functions require reflection of light from the stabilimentum; habitat selection, compass direction of the web, and incline of the web from vertical will influence the maximum amount and timing of insolation. Thus, the E-W direction and the 19° incline may be a combination that optimizes reflection of light from the stabilimentum for prey capture and web protection in this habitat.

Barrier webs may not generally be worth their costs for *A. florida*. After comparing three populations of *A. argentata* in the Galapagos, Lubin (1975) suggested that barrier webs help to mechanically strengthen the web because they were more frequent in areas of

high wind. The percentage of webs with a barrier web in a low-wind area (28%) closely matched that of the *A. florida* in the present study (25%); both were much lower than the high-wind areas (68%). It is possible that *A. florida* webs do not need the mechanical stability of a barrier web. Also, if the stabilimentum is serving to deter larger animals from walking or flying through the web, the early warning provided by a barrier web may be superfluous enough to not justify the cost of the additional silk. The barrier web also provides a habitat for kleptoparasitic *Argyrodes* spp. By living in the barrier web, *Argyrodes* spp. likely can detect, through vibrations, when a prey item has been captured and wrapped; further, by not living on the orb, the threat of being depredated by the host is reduced (Vollrath 1979). On the other hand, barrier webs may benefit the host by deterring or warning of hymenopteran predators or parasites (Tolbert 1975).

The tuning fork stimulation elicited naturalistic predatory responses. Specifically, the sequence of observed responses closely follow the sequences described by (1) Frings & Frings (1966) for 20–160 Hz stimulation with a modified audio-oscillator in the webs of *A. aurantia*, (2) Robinson & Olizarri (1971) for heavy prey with sustained vibrations in the web of *A. argentata*, (3) Harwood (1974) for large, active, non-lepidopteran prey in the web of *A. aurantia*, (4) Robinson & Robinson

(1974) for orthopterans in the webs of *Argiope picta* L. Koch 1871, *Argiope aemula* (Walckenaer 1842) and *Argiope reinwardti* (Doleschall 1859), and (5) Olive (1980) for slowly escaping, large acridid orthopterans in the webs of *A. trifasciata*. Thus, naturalistic responses can be obtained in the field without having to transport electronic equipment or live prey. Live prey items placed on webs are also likely to be more variable in stimulation than a tuning fork.

The response to the tuning fork was usually vigorous. Almost 80% of the tested spiders approached and touched the fork, and over 60% wrapped it in silk. This sequence of predatory behavior was unaffected by recent prey capture; the response to the tuning fork was not different when wrapped prey were already present in the web. This is consistent with the arguments set out in Wise (1993) that spiders may be food-limited in general; each additional prey item can further increase survival and fecundity. It may be that spiders with kleptoparasitic *Argyrodes* spp. in their webs had higher and more consistent predatory response scores because some proportion of their captured prey is stolen, reducing their total consumption (cf. Rypstra 1981).

Argiope florida stabilimenta were remarkable in four ways. First, 13 other species of *Argiope* are known to add cruciate stabilimenta to their webs, but these often comprise only a couple of arms, with full crosses usually being relatively rare (Hingston 1927; Yaginuma 1960; Levi 1968; Marples 1969; Robinson & Robinson 1970, 1974; Lubin 1975; Robinson & Lubin 1979; Robinson & Robinson 1980; Edmunds 1986; Nentwig & Heimer 1987; Nentwig & Rogg 1988; Kerr 1993; Elgar et al. 1996; Hauber 1998; Herberstein et al. 2000b). In comparison, *A. florida* has a relatively high proportion of webs with a complete cross (almost 60%). Second, Hingston (1927) remarked that the four arms in the cruciate stabilimentum of *Argiope pulchella* Thorell, 1881 were ''evenly separated. . . at equidistant points''. This is a very different arrangement from *A. florida* stabilimenta, in which the upper and lower pairs of arms are each separated by about 65°. No other studies have quantified the angular arrangement of the arms in *Argiope* cruciate stabilimenta. Third, there were a substantial number of differences between the upper and lower arms of *A. flor-*

ida stabilimenta. While this may be related to the function of the stabilimentum, it may also be reflective of the asymmetry in the orb itself: the area above the hub is almost always smaller than the area below the hub. It would be interesting to know how closely stabilimentum asymmetry is related to the structural asymmetries of the orb itself. It may be relevant that size was related to the angle between the upper arms but not to the angle between the lower arms, because size is known to contribute to asymmetries in orb webs (Herberstein & Heiling 1999). Fourth, the number of bands is sufficiently independent of the length of the stabilimentum arm to continue separate consideration. Arms of the same length can show considerable differences in the number, thickness, spacing, silk density, and even pattern of the bands (personal observations). For example, Hingston (1927) counted an average of 6.3 bands/cm on the linear stabilimenta of *Argiope sector* (Forskål, 1775), over 30% more dense than the bands of *A. florida* in the present study.

Further research into the distribution, natural history and behavior of *A. florida* could make valuable contributions to conservation and behavioral biology. A phenology of the presence of males and reproductive behavior of the species is needed. Also, the few patches of sand scrub remaining in Palm Beach, Broward and Dade Counties should be checked for the presence of *A. florida*. Behavioral research on *A. florida* could facilitate and extend comparative work with its more extensively studied congeners. If the stabilimentum is a visual signal, there may well be costs or benefits for spiders that deviate from the mean on web orientation from vertical and compass direction of the plane of the orb. If variability in these characters can account for variability in prey capture success and/or web destruction, this would speak to general theories of stabilimentum function. Investigations into the influence of *Argyrodes* kleptoparasitism on *Argiope* behavior should be pursued. A cost-benefit analysis of barrier web construction that considers *Argyrodes* kleptoparasitism and hymenopteran attacks could be used to address the finding that 25% of *A. florida* built barrier webs. Also, changes in the extent of kleptoparasitism should be related to changes in predatory behavior; the exact nature of this relationship, including *Argyrodes* depredation

by *Argiope*, should be quantified. Lastly, variation in the number of arms in the stabilimentum, the spacing or arrangement of arms and band density within arms could all be related to several proposed functions of the stabilimentum and should be considered in future studies of stabilimentum structure and function.

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