

STABILIMENTUM-DECORATED WEBS SPUN BY *CYCLOSA CONICA* (ARANEAE, ARANEIDAE) TRAPPED MORE INSECTS THAN UNDECORATED WEBS

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ABSTRACT. In this field study, I tested the insect-attraction hypothesis as one of the functions of stabilimenta spun by *Cyclosa conica* (Pallas 1772) by examining: (1) if stabilimentum-decorated webs trapped more insects, (2) if a larger web diameter was responsible for the higher insect-trapping rate in decorated webs and, (3) if the differential distribution of insects in spiders' habitats was responsible for the higher insect interception rates of decorated webs. The number of wrapped prey, web diameters and presence of stabilimenta was recorded daily from 13 web locations. The stabilimentum-decorated webs of *C. conica* trapped significantly more insects (150% more) than undecorated webs, but they had significantly smaller mean web diameter (19% smaller). Among web locations, there was no significant difference in their insect interception rates, whether the data were collected from decorated or undecorated webs. These results suggest that the higher insect-trapping efficiency of decorated webs spun by *C. conica* resulted from the presence of stabilimenta, instead of from larger web diameters or differential distribution of insects.

Stabilimenta are silky structures on the webs of some diurnal orb-weaving spiders. At least 17 genera of ecribellate and cribellate orb-weavers build various forms of stabilimenta (Eberhard 1990). In most of the genera, stabilimenta are made up entirely of bands of silk that either encircle the hub (e.g., *Lubinella morobensis* Opell 1984 and *Philoponella* sp., see Lubin 1986) or are located at various positions around the hub (e.g., all *Argiope* species, see Levi 1983). Some spiders also incorporate egg sacs, prey remains and/or detritus into the silk bands (e.g., *Cyclosa octotuberculata* Karsch 1879, see Yaginuma 1986), which make the spiders difficult to detect among those objects.

The function of silk stabilimenta have long been a focus of study for arachnologists. For those genera that incorporate other objects into the silk bands, the function of stabilimenta has generally been hypothesized as camouflage (Eberhard 1973). As to the silk stabilimenta, ever since Simon introduced this term in 1895 suggesting a web-stabilizing function (Robinson & Robinson 1970), many functional hypotheses have been proposed and tested (Nentwig & Heimer 1987; Nentwig &

Rogg 1988; Eberhard 1990). Most of the functional studies on silk stabilimenta have focused on *Argiope* species, which spin linear silk bands arranged either vertically (e.g., *A. aurantia* (Lucas 1833) and *A. trifasciata* (Forsk. 1775)) or diagonally (e.g., *A. argentata* (Fabricius 1775)) around the hub (Levi 1983). Investigators have proposed and tested many hypotheses about stabilimenta's possible functions, such as web advertisement, predator defense, web tension adjustment and product under stress (see review in Nentwig & Rogg 1988; Eberhard 1990; Schoener & Spiller 1992 and Kerr 1993).

Recently, insect-attraction has been demonstrated to be one of the functions of *Argiope* spiders' silk stabilimenta. Diagonally arranged silk stabilimenta of *Argiope argentata* were found to reflect ultraviolet-light, and the stabilimentum-decorated webs of those spiders intercepted more insects than undecorated webs (Craig & Bernard 1990; Craig 1991). The webs of *Argiope trifasciata* decorated with vertically-arranged stabilimenta were also found to trap more insects than undecorated webs (Tso 1996). These findings lead me to hypothesize that insect-attraction may also be one of the functions of the silk stabilimenta built by other orb-weaving spiders, such as *Cyclosa* species. The functions of the linear

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stabilimenta build by *Cyclosa* species have not been investigated. Although Rovner (1976) studied how the position of silk stabilimenta and gravity affect wrapped prey placement on the web of *Cyclosa turbinata* (Walckenaer 1841), he did not provide answers regarding the possible functions of the silk stabilimenta of those spiders. To determine the insect attraction ability of *Cyclosa* stabilimenta, I conducted a field study examining whether or not the presence of silk stabilimenta increases the insect-interception of webs spun by *Cyclosa conica* (Pallas 1772).

METHODS

Cyclosa conica (see Levi 1977) builds webs between dry tree branches in the dim forest understory. Only adult female spiders were used in this study since mature males *C. conica* do not build as full a web as did females (Kaston 1948). Sometimes spiders added a stabilimentum made of white silk band on their webs, making the webs relatively easy to be located by researchers. *Cyclosa conica* have been reported to load the stabilimentum with prey pellets, plant detritus or, in subsequent webs, egg sacs (Comstock 1913; Marples & Marples 1937). However, the *C. conica* population at this study site seldom retained the old stabilimenta. Instead, for all the spiders, stabilimentum-decorated webs were built interspersed with undecorated webs. *Cyclosa conica* might have recycled their orb each day because the web diameters as well as number and location of wrapped prey recorded from the same web site varied from day to day. *Cyclosa conica* have also been reported to incorporate wrapped prey into stabilimenta (Marples 1969; Levi 1977); but those in my study frequently left the wrapped prey where the insects were intercepted on the web. The recorded position and number of wrapped prey on webs indicated that spiders seldom retain wrapped prey and stabilimenta. Among the 24 decorated webs recorded, only four of them contained wrapped prey in the stabilimenta.

Tests.—This study was conducted in June and July, 1992, at the University of Michigan Biological Station near Pellston, Michigan. I tested insect-attraction as one of the functions of stabilimenta spun by *C. conica* by comparing the daily insect interception rates (DIIRs) between stabilimentum-decorated and undecorated webs.

However, in addition to stabilimenta, the size and the location of a web may also affect its DIIR. Previous studies suggested that larger webs may potentially trap more insects than smaller webs (Brown 1981; Craig 1989; Higgins & Buskirk 1992). Because of the heterogeneous distribution of insects, the location of a web may also greatly affect its insect trapping ability (Craig 1989). Therefore, I tested the insect-attraction hypothesis by comparing (1) the DIIRs between stabilimentum-decorated and undecorated webs, (2) the difference in web diameter between decorated and undecorated webs, and (3) DIIRs of the same type of web (decorated or undecorated) collected from different web locations. The insect-attraction hypothesis can be supported if (1) the decorated webs intercepted more insects, (2) the decorated webs were no larger webs than undecorated webs, and (3) the average insect trapping rates of the same type of webs did not differ between various web locations.

Census methods.—Web locations of *C. conica* were marked by fastening green tape on the tree trunk a meter below the web. Webs from all locations ($n = 13$) were monitored each day between 0800–1800 h. The number of days those web locations remained occupied ranged from 5–13 days. Web diameter (cm) and presence of stabilimenta were recorded once at 0800 h. The number of wrapped prey per web per 10 hours of observation (between 0800–1800) was used as an estimate of DIIR, and the webs were monitored three times a day. I also mapped the position of wrapped prey on webs to check if the spiders reused the old web, thus recounting of the previously wrapped prey was avoided. In most cases there was no wrapped prey on webs at the time of web diameter measurement. A total of 93 DIIRs was collected, among them 24 were from decorated webs (from seven locations; webs from six other locations were all undecorated) and 69 were from undecorated webs (from all 13 locations).

Statistical analysis.—To examine the effect of stabilimenta, I used a Mann-Whitney *U*-test to compare the DIIRs collected from decorated and undecorated webs. I also used a Mann-Whitney *U*-test to compare the web diameters between two types of webs. Kruskal-Wallis one way ANOVAs were used to

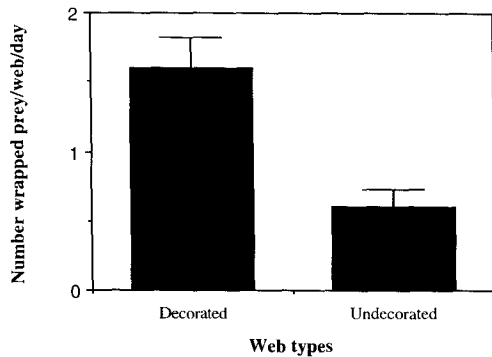


Figure 1.—Means (\pm SE) of daily insect interception rates (number of wrapped prey per web per 10 hours of observation) of the stabilimentum-decorated and undecorated webs spun by *Cyclosa conica* (Pallas).

determine if differences existed between (1) DIIRs of decorated webs collected from seven locations and (2) DIIRs of undecorated webs collected from 13 locations. In both ANOVA analyses, web locations were used as categories to sort DIIRs collected. By performing two Kruskal-Wallis ANOVAs on DIIRs collected from two types of webs, the effect of web location on insect interception can be separated from the effect of the stabilimenta, since only one category was used in each ANOVA analysis.

RESULTS

Decorated webs spun by *Cyclosa conica* intercepted significantly more prey than undecorated webs (Mann-Whitney U statistic = 389.0, $P = 0.000$, Fig. 1). Although decorated webs contained almost 150% more wrapped prey than undecorated webs, their web diameters were significantly smaller by 18.9% (Mann-Whitney U statistic = 1156.0, $P = 0.004$, Fig. 2). Although the web location was known to affect its trapping efficiency, decorated as well as undecorated webs at different locations trapped similar numbers of insects. There was no difference in DIIRs of decorated webs collected from seven web locations (Kruskal-Wallis statistic = 9.363, $df = 6$, $P = 0.154$), nor was there difference in DIIRs of undecorated webs collected from 13 web locations (Kruskal-Wallis statistic = 7.727, $df = 12$, $P = 0.806$). These results suggested that the difference in the number of wrapped prey between decorated and undecorated webs re-

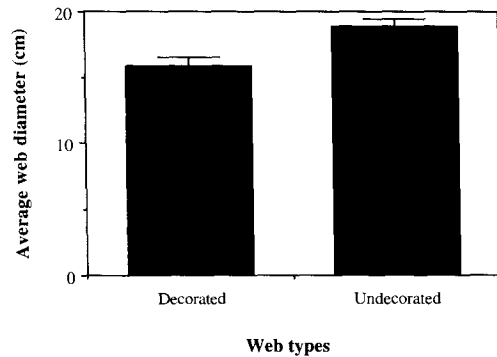


Figure 2.—Means (\pm SE) of web diameters (cm) of the stabilimentum-decorated and undecorated webs spun by *Cyclosa conica* (Pallas).

sulted from the presence of stabilimenta, rather than from the difference in web diameters or the differential distribution of insects among web locations.

DISCUSSION

The hypothesis that presence of stabilimenta increased insect interception of webs spun by *Cyclosa conica* was supported by the results. Decorated webs intercepted almost 150% more insects than did undecorated webs. The higher DIIR of decorated webs seemed to result from presence of stabilimenta, instead of from size variation between two types of webs or from differential insect distribution between web locations. Moreover, the average web diameter of decorated webs was significantly smaller than that of undecorated webs, and prey interception did not differ between different web locations. Compared to similar studies on other stabilimentum-building taxa such as *Argiope argenteata* (31.3%, Craig & Bernard 1990) and *Argiope trifasciata* (72% more flying insects, Tso 1996), this gain in insect interception is exceedingly high.

The higher trapping efficiency and the smaller diameter of decorated webs spun by *Cyclosa conica* provides an important insight to the foraging ecology of this orb-weaving spider. The size of an orb web, in addition to other web characteristics, is known to affect its insect trapping efficiency. Studies on several orb-weaving spiders demonstrated that larger webs tended to trap more prey (Brown 1981; Craig 1989; Higgins & Buskirk 1992). Recent studies further demonstrated that some orb-weaving spiders may manipulate their orb

size when prey intake varies. Sherman (1994) reported that *Larinioides cornutus* (Clerck 1757), while maintaining same mesh size, decreased web diameters after food-satiation and increased web diameter when experiencing a long period of hunger. Higgins & Buskirk (1992) demonstrated that *Nephila clavipes* (Linnaeus 1767) built larger webs in habitats of lower prey abundance. Although some of the studies did not consider the potential effect of other web characteristics, they did indicate that orb size must be considered when evaluating the prey interception of orb-webs. However, in this study the average web diameter of decorated webs was almost 20% smaller than that of undecorated webs, but the average prey interception rate was 150% more. This result suggested that in the future study of foraging ecology using orb-weaving spiders, in addition to the commonly known web characteristics such as orb size, mesh size and web location, silk stabilimenta (if exhibited by the taxa studied) should also be included in the analysis.

The effectiveness of stabilimenta built by *Cyclosa conica* in attracting prey greatly exceeds that of *Argiope* spiders investigated so far, which may result from the different types of habitats occupied by the spiders. *Cyclosa conica* typically build their webs in the differentially shaded forest understory in which the light intensity is dim (Marples & Marples 1937; Levi 1977). In contrast, *Argiope* spiders tend to choose an open field—a very bright light environment—as web sites (Levi 1968). The insects available to *C. conica* are mostly small dipterans and hymenopterans (collected from sticky traps, Tso unpubl. data), characterized by high flight maneuverability and the capability of detecting and avoiding spider webs (Craig 1986). However, those insects respond quite differently to spider webs hanging in different light environments. Webs in the dim forest understory are less visible to those insects, making the webs more difficult to avoid than those in the bright open field (Craig 1988). The dim light environment, plus the extremely fine silk characteristic of *C. conica* (Comstock 1913; Marples & Marples 1937), may make the webs difficult to detect by those insects (Craig 1986). Although the decorated webs of both *Argiope* and *Cyclosa* spiders can attract insects to orient toward them, the lower web visibility of the latter

may allow approaching insects less time to avoid the web, therefore leading to higher insect interception.

The results from this study suggest that the presence of stabilimenta can potentially increase the foraging efficiency of *Cyclosa conica*. However, one important question still remains unanswered. That is, given the gain in prey intake generated by stabilimenta, why do *C. conica* and *Argiope* spiders not always build stabilimenta on their webs? The study by Craig (1994) on *Argiope argentata* provided an evolutionary solution to the riddle of inconsistency in stabilimentum-building. Craig (1994) demonstrated that the highly unpredictable pattern and building frequency of stabilimenta could prevent hymenopteran insects from learning from past experience to associate stabilimenta with danger. Craig (1994) suggested that a consistent building of stabilimenta (in both shape and frequency) was disadvantageous to *Argiope* spiders because some insects could learn from past experience to associate stabilimenta with danger and would actively avoid decorated webs in future encounters. Craig (1994) thus provides a possible evolutionary explanation (an ultimate factor) for the inconsistency in stabilimentum-building. However, although Eberhard (1973) and Lubin (1986) provided evidence that light intensity may affect stabilimentum-building of nocturnal uloborids, how stabilimentum-building is proximately controlled in diurnal orb weavers is not clear. Edmunds (1986) and Nentwig & Rogg (1988) examined the effect of microclimatic conditions, habitat type, web characteristics, presence of males, illumination, prey abundance, ecdysone and even heredity on stabilimentum-building of various *Argiope* spiders. But none of the factors examined could significantly affect the building of silk stabilimenta. Although this study demonstrates that silk stabilimenta may increase spiders' foraging, the lack of knowledge regarding ecological factors controlling the building of stabilimenta (which result in the role stabilimenta play in the ecology of spiders unclear) greatly reduces the validity of prey-attraction hypothesis. Therefore, the identification of proximate factors controlling stabilimentum-building is essential to fully realize how silk stabilimenta is involved in the ecology of more than 17 genera of orb-weaving spiders.

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LITERATURE CITED

- Brown, K.M. 1981. Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia*, 50: 380–385.
- Chacon, P. & Eberhard, W.G. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with consideration of how orb webs trap prey. *Bull. British Arachnol. Soc.*, 5:29–38.
- Comstock, J.H. 1913. *The Spider Book*. Doubleday, Page & Company, Garden city, New York.
- Craig, C.L. 1986. Orb-web visibility: the influence of insect flight behavior and visual physiology on the evolution of web designs within the Araneidae. *Anim. Behav.*, 34:54–86.
- Craig, C.L. 1988. Insect perception of spider orb webs in three light habitats. *Funct. Ecol.*, 2:277–282.
- Craig, C.L. 1989. Alternative foraging modes of orb web weaving spiders. *Biotropica*, 21:257–264.
- Craig, C.L. & G.D. Bernard. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology*, 71:616–623.
- Craig, C.L. 1991. Physical constraints on group foraging and social evolution: observations on web-spinning spiders. *Funct. Ecol.*, 5:649–654.
- Craig, C.L. 1994. Predator foraging behavior in response to perception and learning by its prey: interactions between orb-spinning spiders and stingless bees. *Behav. Ecol. Sociobiol.*, 35:45–42.
- Eberhard, W.G. 1973. Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. *J. Zool., London*, 171:367–384.
- Eberhard, W.G. 1986. Effects of orb-web geometry on prey interception and retention. Pp. 70–100, *In Spiders, Webs, Behavior and Evolution*. (W. Shear, ed.). Stanford Univ. Press.
- Eberhard, W.G. 1990. Function and phylogeny of spider webs. *Ann. Rev. Ecol. Syst.*, 21:341–372.
- Edmunds, J. 1986. The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in west Africa, with a discussion of the function of stabilimenta. Pp. 61–72, *In Proc. of the Ninth Intern. Congr. Arachnol.*, Panama, 1983, Smithsonian Instit. Press. Washington, D.C.
- Higgins, L.E. & R.E. Buskirk. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behavior. *Anim. Behav.*, 44:485–499.
- Kerr, A.M. 1993. Low frequency of stabilimenta in orb webs of *Argiope appensa* (Araneae: Araneidae) from Guam: an indirect effect of introduced avian predator? *Pacific Sci.*, 47:328–337.
- Kaston, B.J. 1948. Spiders of Connecticut. *Connecticut Geol. Nat. Hist. Surv., Bulletin No. 70*.
- Levi, H.W. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). *Bull. Mus. Comp. Zool.*, 136:319–352.
- Levi, H.W. 1977. The American orb-weaver genera, *Cyclosa*, *Metazygia* and *Eustala* north of Mexico (Araneae, Araneidae). *Bull. Mus. Comp. Zool.*, 148:247–338.
- Levi, H.W. 1983. The spider genera, *Argiope*, *Gea*, and *Neogea* from the west region (Araneae: Araneidae, Argiopinae). *Bull. Mus. Comp. Zool.*, 150:247–38.
- Lubin, Y.D. 1986. Web building and prey capture in Uloboridae. Pp. 132–171, *In Spiders, Webs, Behavior and Evolution*. (W. Shear, ed.). Stanford Univ. Press.
- Marples, J. & B.J. Marples. 1937. Notes on the spiders *Hytioties paradoxus* and *Cyclosa conica*. *Proc. Zool. Soc. London*, CVII (A):213–221.
- Marples, B.J. 1969. Observations on decorated webs. *Bull. British Arachnol. Soc.*, 1:13–18.
- Nentwig, W. & S. Heimer. 1987. Ecological aspects of spider webs. Pp. 216–221, *In Ecophysiology of Spiders*. (W. Nentwig, ed.), Springer-Verlag, Berlin.
- Nentwig, W. & H. Rogg. 1988. The cross stabilimentum of *Argiope argentata* (Araneae: Araneidae) – nonfunctional or a nonspecific stress reaction. *Zool. Anz.*, 221:248–266.
- Robinson, M.H. & B. Robinson. 1970. The stabilimentum of the orb web spider *Argiope argentata*: an improbable defense against predators. *Canadian Entomol.*, 102:641–655.
- Rovner, J.S. 1976. Detritus stabilimenta on the webs of *Cyclosa turbinata* (Araneae, Araneidae). *J. Arachnol.*, 4:215–16.
- Schoener, T.W. & D.A. Spiller. 1992. Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support for the predator-defense hypothesis. *Behav. Ecol. Sociobiol.*, 31:309–318.
- Sherman, P.M. 1994. The orb-web: an energetic and behavioral estimator of a spider's dynamic foraging and reproductive strategies. *Anim. Behav.*, 48:19–34.
- Tso, I.M. 1996. Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. *Anim. Behav.*, 52:183–191.
- Yaginuma, T. 1986. *Spiders of Japan in color*. Osaka, Hikusha Publishing Co., Ltd.

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