Ann. Zool. Fennici 39: 307–315 ISSN 0003-455X
Helsinki 9 December 2002

The adaptive significance of stabilimenta in orb-webs: a hierarchical approach

Philip T. Starks

University of California at Berkeley, Environmental Science, Policy and Management, Division of Insect Biology, 201 Wellman Hall #3112, Berkeley, CA 94720-3112, USA; Present address: 310 Dana Labs, Department of Biology, Tufts University, Medford, MA 02155, USA (e-mail: philip.starks@tufts.edu)

Received 7 December 2001, accepted 11 March 2002

Starks, P. T. 2002: The adaptive significance of stabilimenta in orb-webs: a hierarchical approach. — *Ann. Zool. Fennici* 39: 307–315.

Conditional strategy theory provides a theoretical and experimental framework from which to predict both population differences in the expression of alternative behavioral phenotypes and the condition above and below which individuals will perform different tactics. Here I briefly review the current functional explanations for stabilimentum production in orb-web spiders and reinterpret previous results within a conditional strategy framework. I argue that using this framework and incorporating a hierarchical approach to the multiple possible selective benefits of the structure is sufficient to explain some of the seemingly contradictory results in the literature.

Introduction

Stabilimenta are conspicuous silk structures that are often attached to the webs of some species of orb-web constructing spiders (Araneae: Araneidae, Tetragnathidae, Uloboridae; Fig. 1). In addition to attracting predators (Bruce *et al.* 2001, Seah & Li 2001) and prey (Craig & Bernard 1990), these structures have long attracted the attention of naturalists (McCook 1889, Simon 1895). The stabilimenta are categorized by their shape, location with the web, and/or number (Table 1). In general, these structures are located at the center of the web and may extend toward its periphery. The specific form that a spider may construct, however, is likely to vary both across the animal's lifetime and in response to its immediate surroundings (Herberstein *et al.* 2000a).

Because these structures are attached to the web — an external and, due to its prey capturing function, essential component of spider fitness — stabilimenta offer a unique opportunity to study the adaptive significance of an extended phenotype (Dawkins 1983). Although non-adaptive explanations for the production of stabilimenta have been proposed (e.g., a response to stress or a result of silk regulation), these explanations are not well supported by empirical data (Herberstein *et al.* 2000a). Conversely, many studies have shown an adaptive benefit of having stabilimenta in the web (*see* Herberstein

Fig. 1. Orb-web spider with stabilimenta. The photograph was taken in Ithaca, NY, USA (42°27´N, 76°29´W) and is provided courtesy of Dr. C.A. Blackie.

et al. 2000a). A single unifying adaptive function for stabilimenta, however, has been difficult to support due to within and across population (and species) variation in its production (Herberstein *et al.* 2000a). I argue that, within the theoretical framework of a conditional strategy, taking a hierarchical approach to the selective benefits of stabilimenta may explain some of the seemingly contradictory results previously published.

Several adaptive functions for stabilimenta have been suggested; these adaptive functions include mechanical augmentation, thermoregulation, web protection, predator avoidance, and foraging enhancement (Table 2; Herberstein *et al.* 2000a). The mechanical augmentation hypothesis, suggesting that stabilimenta strengthen or fine-tune the web, has not been well supported either theoretically or by empirical data (Herberstein *et al.* 2000a; but *see* Wanatabe 2000). Indeed, stabilimenta often appear so loosely attached to the web that any mechanical advantage would likely be slight (but *see* Wanatabe 2000). Discriminating between the remaining hypotheses has been challenging, and a dearth of experimental studies has left these questions open. Recent empirical studies have tried to discriminate between the foraging enhancement and predator avoidance hypotheses (Blackledge 1998a, 1998b, Blackledge & Wenzel 1999, 2000, 2001, Bruce *et al.* 2001, Craig *et al.* 2001). These adaptive hypotheses, however, may not be mutually exclusive. Thus, focusing on "disproving" one to support another may be more likely to inhibit, than to enhance, progress.

Much correlational evidence has been gathered suggesting a relationship between stabilimenta and elevated foraging success (Herberstein *et al.* 2000a, but *see* Blackledge & Wenzel 1999). This relationship has been presented as causal, that is, stabilimentum presence *results in* higher foraging success. Blackledge (1998a) critically tested this assumption by providing different amounts of food to captive spiders and recording stabilimentum production and length. Because well-fed spiders produced more and larger stabilimenta than did "starved" spiders, the author concluded that the causal relationship was in the other direction, that is, stabilimentum presence *results from* higher foraging success. Consequently, further research (Blackledge & Wenzel 1999, 2000, 2001) was conducted to determine the non-foraging related adaptive benefits of stabilimentum production.

Given the importance of causation in the relationship between foraging and stabilimentum production, the data presented in Blackledge (1998a) deserve a closer examination. Arguing against a foraging benefit, the author states, "it is difficult to believe that a structure which attracts prey and is energetically inexpensive would be less common and smaller in the webs of starved spiders" (Blackledge 1998a: p. 26). This may be an overstatement for three reasons. First, it is unclear that a structure accounting for 10% of the total web weight (Blackledge 1998a: p. 25) is energetically inexpensive. Second, only two of the four results presented show a significant difference in stabilimentum production between well-fed and starved spiders, and this significant result is confined to one of the two studied species (in *Argiope aurantia* and not *A. trifasiata*). Finally, and most importantly, the spiders do not appear to have been effectively starved: weight changes during the experimental period were not significantly different between well-fed and starved spiders of either species (Blackledge 1998a). Indeed, starved *A. trifasiata* more than doubled their weight during this period. Still, significant differences between well-fed and less well-fed spiders in the length of stabilimenta remain for all comparisons, which suggests that this relationship should be examined in greater detail.

With current interpretations in conflict, there remain at least four possible adaptive functions for stabilimenta: thermoregulation, web protection, predator avoidance, and foraging enhancement (Table 2). Indeed, conflict in interpretation is expected because there is some support for all of these functions. When one seeks a single explanation of the production of the structure,

Table 1. Schematic representations of webs containing stabilimenta (after Herberstein *et al.* 2000a).

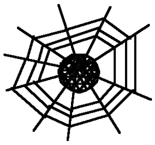
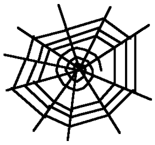
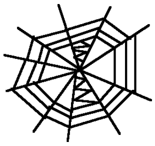
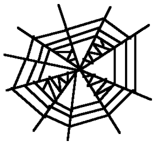
Basic forms	Schematic representation
Discoid: Discoid stabilimenta are found at the hub of webs and are common in juvenile spiders of the genus *Argiope.*	
Spiral: Spiral stabilimenta are found at the hub of webs and are common to spiders within the family Uloboridae.	
Linear: A linear pattern is represented by two zigzag shaped structures which radiate out from the center of the web (e.g., *see* Fig. 1)	
Cruciate: A cruciate pattern is represented by up to four zigzag shaped structures that radiate out from the center of the web and form a cross.	

Table 2. Adaptive explanations for stabilimenta. (*See* text for references and for additional, more in-depth explanations.)

Hypothesis	Explanation
Mechanical augmentation	Stabilimenta may be used to strengthen the web or otherwise increase its relative stability.
Thermoregulation	Stabilimenta may be used to shield the sun and thus prevent overheating.
Web protection	Stabilimenta may signal web presence to larger animals to induce avoidance, thereby decreasing web damage.
Predator avoidance	Stabilimenta may inhibit predators from successful attacks by shielding or altering the appearance of the spider.
Foraging enhancement	Stabilimenta may attract prey items by mimicking flower appearance or open space for movement.

problems arise for four major related reasons. First, stabilimentum production has evolved at least nine times within the Araneidae (Scharff & Coddington 1997) and there is no guarantee that it evolved each time due to the same selection pressure. Second, the current utility of stabilimenta may differ from the original benefit, that is, stabilimenta may have evolved due to selection pressures different from the ones that currently maintain the trait. Third, because current selective pressures may differ greatly across the diversity of environments these animals are found, the current primary adaptive benefit (e.g., foraging success, predator avoidance) is also likely to differ across populations. Finally, the primary benefit of stabilimenta may differ greatly during the life history of the spider. As such, a single explanation that can be extended to all stabilimentum-producing spiders is unlikely.

Conditional strategies

Taking a hierarchical approach to the selective benefits of stabilimenta may provide a suitable framework for understanding within and between species differences in the observed frequencies of stabilimentum production (and related phenomena), as well as changes in web design over the course of a spider's lifetime. A hierarchical approach simply means that all adaptive functions are considered for a single population, and then ranked in order of importance. The ranking is not essential for the model (*see* below), but may be useful in determining a series of experimental tests to examine any given population. The function-specific difference between fitness costs and benefits can then be summed, and the resulting condition-dependent values can be envisaged within the framework of a conditional strategy containing two tactics: stabilimentum presence and stabilimentum absence (Fig. 2).

I have assumed that stabilimentum attachment behavior is a single genetically monomorphic conditional strategy with at least two resultant tactics. In general, there are three descriptors used in models of the selective maintenance of alternative behavioral phenotypes (Gross 1996). One of the three — alternative strategies or genetic polymorphisms — can be immediately ruled out: individuals within populations displaying alternative strategies cannot perform more than one tactic. Since individual spiders sometimes build stabilimenta (one tactic), and other times do not build stabilimenta (another tactic), these animals do not fit the restrictions of alternative strategy models. The remaining two classes of strategies are mixed strategies and conditional strategies. It is possible that presence and absence of stabilimenta are different tactics in a mixed strategy, and that both tactics have the requisite negatively frequency dependent fitness that equalize at a point of average fitnesses (*see* Hauber 1998). However, I use the framework of a conditional strategy due to its overwhelming representation in nature (Gross 1996, Kain 1999) and because stabilimentum production shows context-dependent changes based on ontogeny (e.g., *see* Nentwig & Heimer 1987) and environmental conditions (e.g., *see* Herberstein *et al.* 2000b, Craig *et al.* 2001). Transferring between a conditional strategy and a mixed strategy is easily done if empirical data suggest the need.

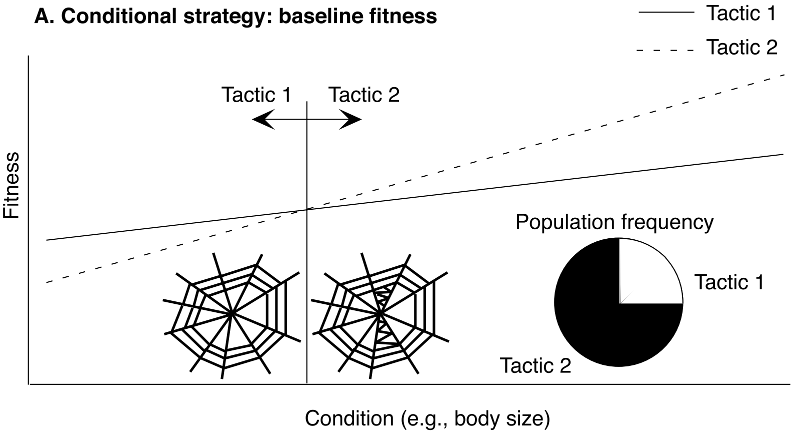
Tactics in a conditional strategy differ in their expected fitness payoffs. These payoffs are also predicted to differ as a function of the condition of the animal. Natural selection should favor animals that maximize their potential fitness payoff, thus we expect that an animal will perform the tactic that maximizes its fitness given its current condition. For the system examined here, these fitness curves will vary with environmental conditions (e.g., the relative predator population size). The assumption that the animal is capable of altering its web and stabilimentum building behavior in response to environmental conditions is well met by these spiders (e.g., *see* Blackledge 1998a, Chmiel *et al.* 2000, Herberstein *et al.* 2000b, Craig *et al.* 2001). This basic conditional strategy framework can be used to make sense of some of the seemingly contradictory results previously published.

Adaptive functions

Web protection

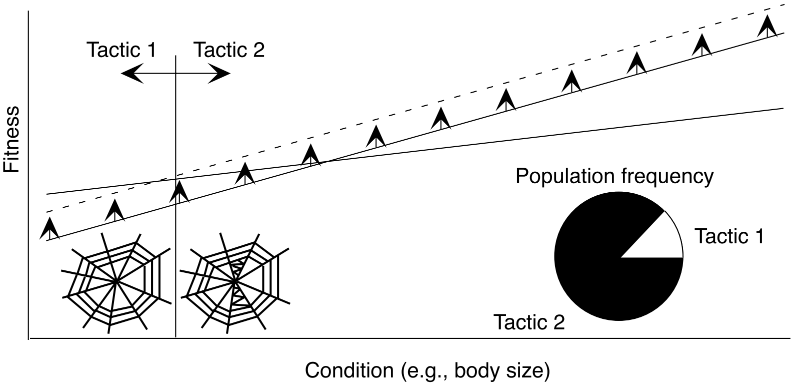
Stabilimenta have been suggested to be honest indicators to animals (predominantly birds) of

Fig. 2. Heuristic diagram of a conditional strategy defined by two tactics: stabilimentum absence (Tactic 1) and stabilimentum presence (Tactic 2). The point of intersection between the tactic-specific fitness curves is the condition where the fitness for both tactics is equivalent. At points above or below this point of intersection, individuals are predicted to perform the tactic with the highest expected fitness payoff. Circles represent the population and differently shaded regions represent the observed proportion of the different tactics. **A** represents the baseline fitnesses in a population and **B** represents the same population after the fitness of Tactic 2 has increased. The fitness of Tactic 2 could increase, for example, if the population of non-predatory web damaging birds increases. (Adapted from Gross 1996, Starks & Reeve 1999).



A. Conditional strategy: baseline fitness

B. Conditional strategy: increased fitness for tactic 2



the presence of noxious sticky webs (Eisner & Nowicki 1983, Kerr 1993, Blackledge & Wenzel 1999). As such, animals tend to avoid the stabilimenta, which protects both the spider and its web. Using the framework of a conditional strategy, we expect the fitness of the stabilimentum present tactic to rise with an increase in the non-predatory bird population (*see* Fig. 2). This increase in tactic fitness will result in a greater proportion of webs containing stabilimenta. Empirical evidence supports this hypothesis: the frequency of webs containing stabilimenta is greater in environments with larger bird populations than in environments with smaller or no bird populations (Kerr 1993). Because stabilimenta may attract predators (Seah & Li 2001, Blackledge & Wenzel 2001, Bruce *et al.* 2001) and because some birds prey on orb-web spiders (e.g., hummingbirds), one would predict that given two environments with equal *non-predatory* bird populations, a larger proportion of webs containing stabilimenta would be observed in the environment with the smaller *predatory* bird population.

Predator avoidance

While stabilimenta may be an honest signal to birds, they may also be used for deception. Disk-shaped stabilimenta may shield a spider from a predator's view (Ewer 1972, Eberhard 1973), while linear stabilimenta may disguise a spider's silhouette (Edmunds 1986) or falsely suggest that the spider is a good deal larger than it is (Schoener & Spiller 1992). Blackledge & Wenzel (2001) present data that suggests that stabilimenta can block or visually impede wasp attacks, and that this impediment may offer a time delay sufficient for escape. Using

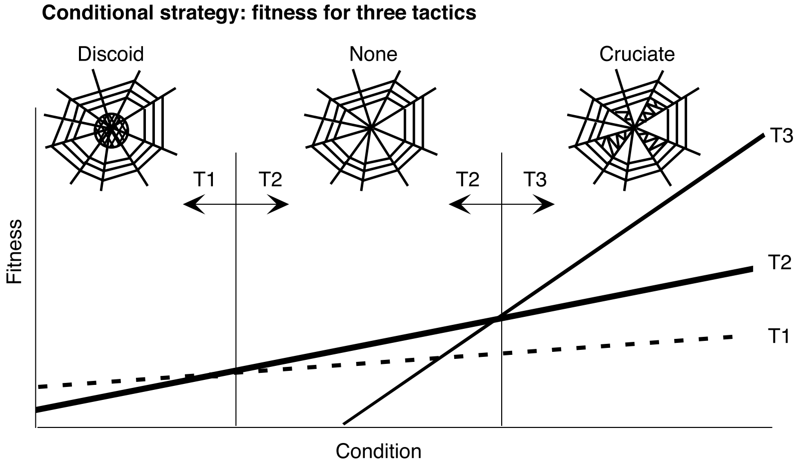


Fig. 3. Heuristic diagram of a conditional strategy defined by three tactics. Tactics represent different stabilimentum patterns. The point of intersection between any two tactic-specific fitness curves is the condition where the fitness for both tactics is equivalent. Individuals are predicted to perform the tactic with the highest expected fitness payoff for their given condition. Constraints have been assumed such that not all tactics are available for individuals of different conditions. For example, not all tactics may be available to juvenile spiders. (Adapted from Gross 1996, Starks & Reeve 1999).

an elegant design incorporating field cages and captive wasps, the researchers recorded and compared the web characteristics of spiders that were and were not preyed upon. A larger proportion of spiders without stabilimenta were preyed upon than those with stabilimenta.

The form of stabilimentum (disk-shaped or linear) used for protection is likely to vary with the predator population. For example, a cruciate pattern (four linear structures; Craig & Bernard 1990) may be more effective at increasing the spider's apparent size and thus is more beneficial in environments with a large proportion of gape-limited predators such as lizards (Schoener & Spiller 1992). Conversely, linear stabilimenta (Horton 1980; Fig. 1) may be optimal for altering the silhouette or visually impeding wasp attacks and thus may be more beneficial in environments with a large proportion of invertebrate predators (Blackledge & Wenzel 2001). Considering different stabilimentum patterns as separate tactics in a conditional strategy provides a framework for examining questions related to predator-dependent population differences in the frequencies of stabilimentum pattern and/or presence (*see* Fig. 3).

Recent research has shown that the predator population is a strong predictor of stabilimentum presence: *A. keyserlingi* decrease stabilimentum production in dense vegetation environments likely to have a high proportion of praying mantids, a predator of orb-web spiders (Bruce *et al.* 2001). Interestingly, Blackledge & Wenzel (2001) report a different trend: *A. trifasciata* increase stabilimentum production in exposed environments. The primary difference between systems may not be the spider species, but rather the predator species. Whereas Bruce and colleagues (2001) examined an ambush predator, Blackledge & Wenzel (2001) examined an airborne predator (the mud-dauber wasp). As such, the relative proportions of predator types may be a strong predictor of the frequency of stabilimentum production.

Foraging enhancement

Another deceptive role for stabilimenta has been suggested: stabilimenta may enhance the primary function of webs — prey capture. The spectral properties of stabilimenta may deceive prey by altering the appearance of the web to make it resemble a flower or a gap in vegetation (Craig & Bernard 1990). As such, a web with a stabilimentum may attract more pollinating insects or simply more insects in transit. In accordance with this hypothesis, a number of research projects have shown that prey interception rates are higher in webs with stabilimenta than in webs without stabilimenta (e.g., Craig & Bernard 1990, Tso 1996, 1998a, 1998b, Herberstein 2000, Bruce *et al.* 2001, Craig *et al.* 2001; but *see* Blackledge & Wenzel 1999).

The question one may ask is, if stabilimenta increase foraging success, why do some spiders produce webs without stabilimenta? Besides two obvious answers — spiders do not hunt continuously and spider predators may use stabilimenta in their search image (Seah & Li 2001, Blackledge & Wenzel 2001, Bruce *et al.* 2001) — there seems to be a cost to predictable stabilimentum production (Herberstein *et al.* 2000a). Some prey learn to avoid stabilimenta (Craig 1994a, 1994b), thus forcing spiders to either relocate webs or alter the pattern of stabilimenta.

Not only may there be a cost to repetitious web patterns, prey may differ in their susceptibility to stabilimentum-adorned webs. Blackledge & Wenzel (1999) show that dipterans are much more frequently captured in webs without stabilimenta than in those with stabilimenta. Using flies in the feeding protocol, Watanabe (1999) showed that *Octonoba sybotides* decreased its production of linear stabilimenta in response to high levels of (dipteran) prey availability. As such, population-specific prey differences in stabilimentum susceptibility will likely influence the frequency of both stabilimentum production and form (*see* Craig *et al.* 2001).

Accordingly, experiments using a single prey species that show differences in stabilimentum production between high and low feeding protocol spiders (e.g., Blackledge 1998a, Watanabe 1999) may provide valuable information specific to a single prey species, but not information generalizable to the overall foraging biology of the animal. Once again viewing behavioral differences as alternative tactics in a conditional strategy, experimental manipulation (e.g. altering prey type and/or diversity) can be used to alter the relative success of producing stabilimenta, of producing specific forms of stabilimenta, and of producing stabilimenta in the same web position. Altering the fitness payoff of each tactic should result in stabilimentum production differences across different experimental systems.

The foraging success of orb-web spiders is going to be a direct reflection of population-specific prey and predator characteristics (Blackledge & Wenzel 2001, Bruce *et al.* 2001, Craig *et al.* 2001). A recent experimental study by Bruce and colleagues (2001) has taken advantage of the conflict between foraging success and predator avoidance. These researchers found that, although stabilimenta increase foraging success, they are not as frequently constructed if the likelihood of predator presence is high. These results are analogous to the hypothesized results in Fig. 2: when the cost of stabilimentum production increases, its observed frequency in the population decreases.

Thermoregulation

Although not all forms of stabilimenta are likely to have any thermoregulatory effects, stabilimenta in a disk-shaped pattern may provide shade and thus prevent overheating (Humphreys 1992). Disk-shaped stabilimenta are more common in juvenile spiders than in adults (Clyne 1969, Ewer 1972, Nentwig & Heimer 1987, Herberstein *et al.* 2000a) and thus may reflect different selection pressures across an animal's life history. Given the size differences between juvenile and adults, and given that smaller individuals are more susceptible to fluctuating temperatures, use of stabilimenta for thermoregulation may be a tactic beneficial to small individuals of a given developmental stage but not to large ones (*see* Fig. 3). Assuming this to be the case, one would expect to see small individuals of a given species construct more disk-shaped stabilimenta in environments where high temperatures occur frequently than in environments where temperatures are more stable. In addition, if disk-shaped patterns of stabilimenta are thermoregulatory structures whose production is dependent on condition, a condition threshold above which animals no longer construct such structures should be identifiable experimentally.

Conclusions

I have discussed each of the four current adaptive explanations of stabilimenta separately and have placed them within the framework of a conditional strategy. I have shown that this framework can be used to make sense of published differences in stabilimentum production, specifically those results based on differing (1) bird populations, (2) predator populations, (3) prey populations, and (4) spider developmental stages. The true benefit of this approach, however, will not be reached until the combined effect of the separate adaptive functions are calculated and compared across populations. A holistic approach to stabilimenta is likely to show great fluctuations in population-specific selection pressures. Uncovering these fluctuations will allow for species-specific examinations of behavioral plasticity as well as fine-tuned experimental manipulations of the given systems.

It may be that the predominant factor leading to stabilimentum production in one population (e.g., web protection) will be of secondary importance in other populations. Conversely, different levels of conflicting selection pressures may lead to similar stabilimenta prevalence across different populations. For example, populations containing high proportions of airborne invertebrate predators and stabilimentum avoiding prey may have the same frequency of stabilimentum production as populations containing low proportions of airborne invertebrate predators and stabilimentum avoiding prey. Without adopting a hierarchical approach to the system, however, such subtle differences will remain unidentified.

I have used the term hierarchy because the specific adaptive benefits and functions of stabilimenta are likely to vary across populations. As such, the primary fitness benefit in one environment (e.g., prey capture) may be of secondary importance (or even detrimental) in other environments. Identifying the environment-specific primary adaptive functions of stabilimenta will enable more fine-tuned experimental analysis of the systems in question. The hierarchical view presented here represents a multicomponent approach that could be enveloped within a multifactorial framework. The added complexity of this approach, however, is unlikely to augment the intuitive explanatory power of the conditional strategy framework.

The goal of this brief report was to promote a potential framework for understanding the variability in stabilimentum production observed in nature. In order to accomplish this goal, I have provided a brief review of some of the possible adaptive functions of stabilimenta. In no way should this review be considered exhaustive: many fine projects have not been discussed (*see* Herberstein *et al*. 2000a for a comprehensive review). I hope that enough has been discussed, however, to provide a foundation for understanding the basic questions and, more importantly, to provide a holistic framework from which to continue to study this fascinating behavior.

Acknowledgements

PTS is supported by a Miller Fellowship from the Miller Institute for Basic Research in Science. I thank Todd Blackledge for helpful conversations leading to the production of this manuscript. An early version of this manuscript benefited from the careful and critical reviews by CA Blackie, WM Getz, ME Hauber, K Rankin & CC Wilmers.

References

Blackledge, T. A. 1998a: Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). — *J. Zool*. 246: 21–27.

Blackledge, T. A. 1998b: Signal conflict in spider webs driven by predators and prey. — *P. Roy. Soc. Lond. B* 265: 1991–1996.

Blackledge, T. A. & Wenzel, J. W. 1999: Do stabilimenta in orb webs attract prey or defend spiders? — *Behav. Ecol*. 10: 372–376.

Blackledge, T. A. & Wenzel, J. W. 2000: The evolution of cryptic spider silk: a behavioral test. — *Behav. Ecol*. 11: 142–145.

Blackledge, T. A. & Wenzel, J. W. 2001: Silk mediated defense by an orb web spider against predatory mud-dauber wasps. — *Behaviour* 138: 155–171.

Bruce, M. J., Herberstein, M. E. & Elgar, M. A. 2001: Signalling conflict between prey and predator attraction. — *J. Evol. Biol*. 14: 786–794.

Chmiel, K., Herberstein, M. E. & Elgar, M. A. 2000: Web damage and feeding experience influence web site tenacity in the orb-web spider *Argiope keyserlingi* Karsch. — *Anim. Behav*. 60: 821–826.

Clyne, D. 1969: *A guide to Australian spiders*. — Thomas Nelson, Ltd., Australia.

Craig, C. L. 1994a: Limits to learning: effects of predator pattern and color on perception and avoidance-learning by prey. — *Anim. Behav.* 47: 1087–1099.

Craig, C. L. 1994b: Predator foraging behavior in response to perception and learning by its prey: interactions between orb-spinning spiders and stingless bees. — *Behav. Ecol. Sociobiol.* 35: 45–52.

Craig, C. L. & Bernard, G. D. 1990: Insect attraction to ultraviolet-reflecting spider webs and web decorations. — *Ecology* 71: 616–623.

Craig, C. L., Wolf, S. G., Davis, J. L. D., Hauber, M. E. & Maas, J. L. 2001: Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. — *Evolution* 55: 986–993.

Dawkins, R. 1983: *The extended phenotype: the gene as the unit of selection*. — Oxford University Press, New York.

Eberhard, W. G. 1973: Stabilimenta on webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. — *J. Zool. Lond.* 171: 367–384.

Edmunds, J. 1986: The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in West Africa, with a discussion of the function of stabilimenta. — In: Eberhard, W.G., Lubin, Y. D. & Robinson, B. C. (eds.), *Proceedings of the 9th International Congress of Arachnology, Panama 1983*: 61–72. Smithsonian Institute Press, Washington.

Eisner, T. & Nowicki, S. 1983: Spider web protection through visual advertisement — role of the stabilimentum. — *Science* 219: 185–187.

Ewer, R. F. 1972: The devices in web of the African spider *Argiope flavipalpis*. — *J. Nat. Hist.* 6: 159–167.

Gross, M. R. 1996: Alternative reproductive strategies and tactics: Diversity within sexes. — *Trends Ecol. Evol.* 11: 263–263.

Hauber, M. E. 1998: Web decorations and alternative foraging tactics of the spider *Argiope appensa*. — *Ethol. Ecol. Evol.* 10: 47–54.

Herberstein, M. E. 2000: Foraging behaviour in orb-web spiders (Araneidae): Do web decorations increase prey capture success in *Argiope keyserlingi* Karsch, 1878? — *Aust. J. Zool.* 48: 217–223.

Herberstein, M. E., Craig, C. L., Coddington, J. A. & Elgar, M. A. 2000a: The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. — *Biol. Rev.* 75: 649–669.

Herberstein, M. E., Craig, C. L. & Elgar, M. A. 2000b: Foraging strategies and feeding regimes: Web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). — *Evol. Ecol. Res.* 2: 69–80.

Horton, C. C. 1980: A defensive function for the stabilimenta of two orb weaving spiders (Araneae: Araneidae). — *Psyche* 87: 13–20.

Humphreys, W. F. 1992: Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae, Argiopinae) and its thermal behaviour. — *Bull. Br. Arachnol. Soc.* 9: 47–52.

Kain, S. M. 1999: Patterns in the evolution of alternative male mate-acquisition behaviors in insects. — In: *The evolution of alternative male mate-acquisition behaviors in the water strider Limnoporus dissortis (Heteroptera: Gerridae)*: 1–109. Ph.D. thesis, Cornell. 270 pp.

Kerr, A. M. 1993: Low frequency of stabilimenta in orb webs of *Argiope appensa* (Araneae: Araneidae) from Guam: An indirect effect of an introduced avian predator? — *Pacific Science* 47: 328–337.

McCook, H. C. 1889: *American spiders and their spinningwork, I*. — Philadelphia: Academy of Natural Sciences of Philadelphia.

Nentwig, W. & Heimer, S. 1987: Ecological aspects of spider webs. — In: Nentwig, W. (ed.), *Ecophysiology of Spiders*: 211–225. Berlin: Springer Verlag.

Schoener, T. W. & Spiller, D. A. 1992: Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support of the predator-defense hypothesis. — *Behav. Ecol. Sociobiol.* 31: 309–318.

Seah, W. K. & Li, D. 2001: Stabilimenta attract unwelcome predators to orb-webs. — *P. Roy. Soc. Lond.* B 268: 1553–1558.

Scharff, N. & Coddington, J. A. 1997: A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). — *Zool. J. Linn. Soc.* 120: 355–434.

Simon, E. 1895: *Historie naturelle des Araignees*. — Roset, Paris.

Starks, P. T. & Reeve, H. K. 1999: Condition-based alternative reproductive tactics in the wool-carder bee, *Anthidium manicatum*. — *Ethol. Ecol. Evol.* 11: 71–75.

Tso, I. M. 1996: Stabilimentum of the garden spider *Argiope trifasciata*: A possible prey attractant. — *Anim. Behav.* 52: 183–191.

Tso, I. M. 1998a: Stabilimentum-decorated webs spun by *Cyclosa conica* (Araneae, Araneidae) trapped more insects than undecorated webs. — *J. Arachnol.* 26: 101–105.

Tso, I. M. 1998b: Isolated spider web stabilimentum attracts insects. — *Behaviour* 135: 311–319.

Watanabe, T. 1999: The influence of energetic state on the form of stabilimentum built by *Octonoba sybotides* (Araneae: Uloboridae). — *Ethology* 105: 719–725.

Watanabe, T. 2000: Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour. — *P. Roy. Soc. Lond. B* 267: 565–569.