

ARTÍCULO:

Are web stabilimenta attractive to praying mantids?

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Abstract:

Certain species of orb-weavers add extra silk structures, termed a stabilimentum or web decoration, to their webs. In the genus *Argiope* stabilimenta are silken structures of densely woven zig-zag ribbons. The adaptive value of these stabilimenta is still unclear and controversially discussed. In the course of time, many functional hypotheses have been proposed for silk stabilimenta. Because of their high visibility they are claimed to act as a visual signal for insects. So most recent hypotheses consider them as prey attractants although also predators (e.g. mantids) have been shown to be attracted by these structures. Bruce et al. (2001) reported that the praying mantid *Archimantis latistylus* was attracted to decorated webs of *Argiope keyserlingi* in a Y-maze choice test. In *Argiope*-species spiders construct different basic shapes of stabilimenta which can be cruciate, linear or discoid. The predator attraction hypothesis was supported by testing cruciate forms of *A. keyserlingi*. To test these predictions also for linearly shaped stabilimenta, the web decorations of the palearctic wasp spider *A. bruennichi* were tested in a laboratory experiment, adopting the Y-maze setup of Bruce et al. (2001) to make it comparable. Also a taxonomically similar predator was used for the test, *Mantis religiosa* (Mantodea: Mantidae). *M. religiosa* showed no preference for webs with stabilimenta, but only a very small number of individuals reached one of the both maze exits at all, rendering universally valid conclusions difficult. Generally, *Mantis* showed a scarce locomotor activity in the Y-maze apparatus and no signs of any predatory response, which indicates that the experimental design might be problematic for studying behavioural elements of praying mantids.

Keywords: *Argiope*, stabilimenta, web decorations, praying mantid, Y-maze, choice test.

¿Son los stabilimenta atractivos para los mántidos?

Resumen:

Algunas especies de arañas constructoras de telas orbiculares añaden a sus telas ciertas estructuras de seda denominadas stabilimentum o decoraciones de la tela. En el género *Argiope*, los stabilimenta son estructuras de seda formadas por cintas en zig-zag densamente entreteljadas. El valor adaptativo de estas estructuras no está claro y es objeto de discusión. A lo largo del tiempo se han propuesto varias hipótesis sobre la función de los stabilimenta. Debido a su gran visibilidad se ha afirmado que actúan como señales visuales para los insectos. Por ello, la mayor parte de las hipótesis más recientes, las consideran como atrayentes de presas aunque también se ha demostrado que los depredadores (por ej. mántidos) pueden ser atraídos por estas estructuras. En una prueba de elección en un laberinto en Y, Bruce et al. (2001) encontraron que el mántido *Archimantis latistylus* era atraído por las telas decoradas de *Argiope keyserlingi*. En las especies de *Argiope*, las arañas construyen diferentes tipos básicos de stabilimenta, que pueden ser cruzados, lineales o discoidales. Se encontró apoyo para la hipótesis de la atracción probando formas cruzadas de *A. keyserlingi*. Con el fin de comprobar estas predicciones para los stabilimenta de forma lineal, probamos las decoraciones de las telas de la araña avispa paleártica *A. bruennichi* en un experimento de laboratorio. Para hacerlo comparable se adoptó el procedimiento del laberinto en Y de Bruce et al (2001). Para la prueba también utilizamos un depredador taxonómicamente similar: *Mantis religiosa* (Mantodea: Mantidae). *M. religiosa* no mostró ninguna preferencia por telas con stabilimenta, tan solo solo un pequeño número de animales alcanzó alguna de las salidas del laberinto, lo que dificulta obtener conclusiones universales. En general, *Mantis* mostró una escasa actividad locomotora en el laberinto en Y y ningún signo de respuesta depredadora, lo que indica que el diseño experimental podría resultar problemático para estudiar elementos del comportamiento en mántidos.

Palabras clave: *Argiope*, stabilimenta, decoraciones de la tela, *Mantis religiosa*, laberinto en Y, test de elección.

Introduction

Several araneid, uloborid and nephilid spiders add specific silk decorations so-called stabilimenta (Simon, 1895) to their webs (Hingston, 1927; Robinson & Robinson, 1973; Scharff & Coddington, 1997; Blackledge, 1998a). Stabilimenta can differ in shape from taxon to taxon (Eberhard, 2003; Bruce & Herberstein, 2005). In the genus *Argiope* (Araneidae) they consist of densely woven zig-zag ribbons (Wiehle, 1927; Robinson & Robinson, 1973) built of numerous flimsy strands of aciniform silk (Peters, 1993). These structures can vary largely in shape and size among *Argiope*-species, populations within species, but also among individuals within the same population (Herberstein et al., 2000; Starks, 2002; Herberstein & Bruce, 2005; Bruce, 2006). Stabilimentum building may be temporarily reduced or even ceased as observed in both field and laboratory studies (Robinson & Robinson, 1974; Lubin, 1975; Nentwig & Heimer, 1987; Seah & Li, 2002; Prokop & Grygláková, 2005). Several, partly species-specific, stabilimentum types have been classified: e.g. linear, cruciate or irregular arranged silk bands between adjacent radii, discoid lines, or combined forms of hub-covering silk sheets and silken bands (Wiehle, 1927; Nentwig & Heimer, 1987; Herberstein & Bruce, 2005; Bruce, 2006).

The genus *Argiope* has become a model group in terms of testing hypotheses for possible functions of stabilimentum building behaviour (e.g. Edmunds, 1986; Craig, 1991; Kerr, 1993; Tso, 1996, 1998, 1999, 2004; Blackledge, 1998a, b; Blackledge & Wenzel, 1999, 2001; Herberstein, 2000; Craig et al., 2001; Seah & Li, 2001; Bruce et al., 2001, 2005; Li & Lee, 2004; Bruce & Herberstein, 2005). Yet, in spite of the rapidly growing literature on the stabilimentum phenomenon, the possible adaptive functions of these “web-decorations” remain unclear (see Herberstein et al., 2000; Bruce, 2006; see also Robinson & Robinson, 1970). Initially thought to be strengthening or stabilising web structures (hence called “stabilimenta” by Simon, 1895), a fair number of hypotheses have been proposed over the course of time to explain the ambiguous decoration phenomenon (reviews in Herberstein et al., 2000; Bruce, 2006). Some argue that stabilimenta act as camouflage devices to hide the exposed spider and its outline from visually hunting predators (Hingston, 1927; Ewer, 1972; Eberhard, 1973; Lubin, 1975; Tolbert, 1975). Others suggest that the web decoration enhances the visibility to prevent damage by potential web destroyers like birds (Horton, 1980; Eisner & Nowicki, 1983; Kerr, 1993). Furthermore, it has been argued that stabilimenta might form a moulting platform (Robinson & Robinson, 1973; Nentwig & Heimer, 1987), that they are a response to unspecific stress of the spider (Nentwig & Rogg, 1988) or simply signs of a non-functional evolutionary relict behaviour (Nentwig, 1986). Further hypotheses claim that the decoration should instead attract other animals such as prey insects to increase foraging success (Craig & Bernard, 1990; Tso, 1996, 1998; Hauber, 1998; Bruce et al.,

2001; Li, 2005). This hypothesis is controversially discussed because there is evidence for the existence of a signal conflict. Bruce et al. (2001) state the conflict of attracting prey and predators alike.

Several personal observations and anecdotal statements report mantids preying upon spiders. This is in line with the intraguild predation model (see Holt & Polis, 1997), according to which spiders cannot be excluded from mantids prey spectrum and vice versa. Since mantids prey recognition depends largely on prey movements (Reitze & Nentwig, 1991), “[...] the most important interaction between mantids and other members of the broader generalist predator guild [...] may be with cursorial spiders [vagrant web-spinners, crab spiders, wolf spiders]” (Hurd, 1999; see also Hurd & Eisenberg, 1990; Moran & Hurd, 1994).

However, Bruce et al. (2001) observed three predatory strikes of *Archimantis latistylus* (Mantidae) to the cruciate stabilimentum building orb-web spider *Argiope keyserlingi* in the field. Inspired from these anecdotal events, they tested if silky web decorations could have functioned as visual cues which attract praying mantids. In a Y-maze choice test the authors found that, when the mantid was confronted with decorated vs. non-decorated orb webs of *A. keyserlingi*, they preferred the decorated web. Consequently, Bruce et al. (2001) suggested that *Argiope* has to manage a trade-off between the enhancement of foraging success and the risk of being preyed by mantids. Yet, only little has been published about vision-guided predation upon web-building spiders (Foelix, 1996; Wise, 1993). So Bruce et al. (2001) emphatically demanded comparative data for their result.

Here I test the supposed attractive function of stabilimenta in a comparable European intraguild system, using the common European mantid, *Mantis religiosa* Linnaeus (1758) (Mantodea, Mantidae) and the wasp spider *Argiope bruennichi* (Scopoli, 1772), a common araneid spider with linear stabilimenta. For that purpose I adopted the experimental setup of Bruce et al. (2001) to ensure methodological comparability.

Material and methods

STUDY ANIMALS AND REARING

M. religiosa is an up to 70 mm large southern European praying mantid (Reitze & Nentwig, 1991). This species has a light green, yellow or brownish colouration, probably adapted to its grassy habitats (Kral & Devetak, 1999).

Individuals were raised in the lab after hatching from egg sacs which were originally sampled in Istria (Croatia). First juvenile stages were fed with *Drosophila melanogaster* ad libitum and later with stick insects (Phasmidae). Additionally, all individuals were sprayed with water in a two daily rhythm. Two months old juvenile mantids (5th-6th instar, body length 37.1 ± 4.9 mm) were starved for two days (27 ± 3 °C, 55 ± 10 % RH) before each trial (following Matsura & Inoue, 1999). In Europe the distribution of the palearctic wasp spider *A. bruennichi* was originally restricted to the Mediterra-

nean region (Wiehle, 1931). Its area expanded across central Europe during the last century (Sacher & Bliss, 1990; Jonsson & Wilander, 1999). *A. bruennichi* prefers open grassland habitats (Nyffeler & Benz, 1989; Prokop & Grygláková, 2005) and so can encounter *Mantis religiosa* in the Mediterranean region.

Juvenile spiders (6th and 7th instar) from a laboratory reared population were raised up in groups in a terrarium. Ten spiders were transferred to wooden frames (35 x 35 x 5 cm) for orb web construction to ensure that at least two webs, one with and one without stabilimentum, would be available for each test. Only stabilimentum shapes with the typical linear decoration pattern consisting of two silken zig-zag ribbons, one above and one beneath the hub, were used for the tests.

THE Y-MAZE APPARATUS

I used a Y-maze apparatus following that of Bruce et al. (2001) for the choice tests (Fig. 1). All walls of the maze were lined with non-reflective black foil. The top of the maze was covered with perspex panes. Two fluorescent tubes (20 W) with natural light spectrum above the apparatus illuminated the interior of the Y-maze as well as the webs in front of the two exits. The two test webs (one with and one without stabilimentum) with the spiders at the hub were placed eight cm from the end of each of the two maze-arms. The opisthosoma of the spiders, directly located on the web hub, were placed at

the same height as was the centre of the 'exit-hole'. A black cardboard was placed behind the webs to ensure a maximum contrast for the recognition of stabilimenta by *Mantis*. Using a fan (20 W) that was placed at a distance of 25 cm from the open entrance of the maze, I stimulated each mantid to move by allowing an air current (fan stage one) to pass through the maze.

THE TEST SCHEME

I conducted 25 trials in all. In each trial both web types were randomly assigned to either the left or the right exit of the maze. The orb webs were used more than once but the mantids were exchanged for every trial to eliminate any effect of individual learning that might affect the testing. Naïve juvenile *M. religiosa* were placed individually into the Y-maze recovery chamber. After two minutes of recovering I opened the slide separating this part from the main chamber. The trials started as soon as a mantid was released, and finished after an individual had reached an exit, or at a maximum time of 60 minutes. After each trial the maze was washed out with ethanol (70%) to eliminate potential olfactory cues which might interfere with subsequent tests.

I recorded the elapsed time the mantids needed to get from the starting point to a maze exit. I further observed the behaviour of the animals to identify possible elements of prey recognition or prey capture behaviour.

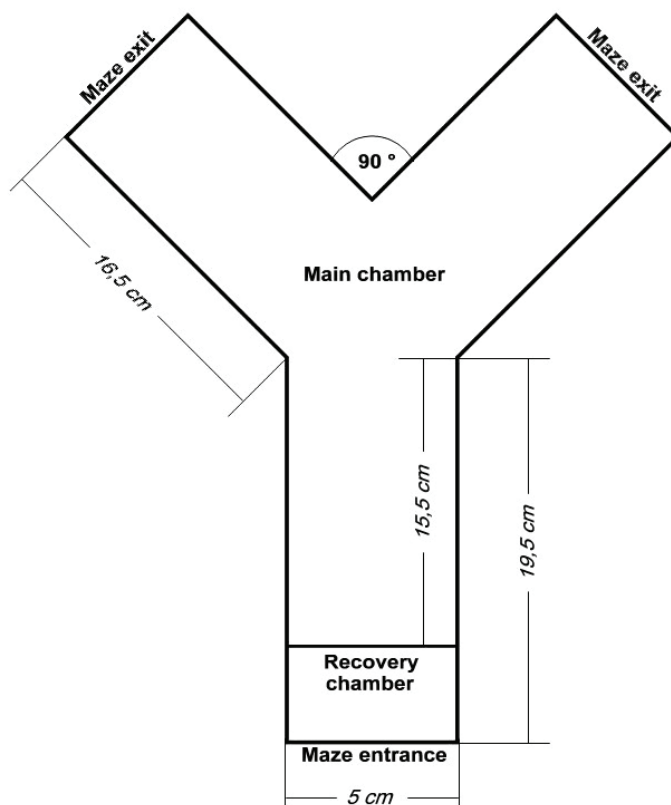


Figure 1. Schematic diagram of the Y-maze apparatus for the choice experiments (reconstruction, following Bruce et al. 2001).

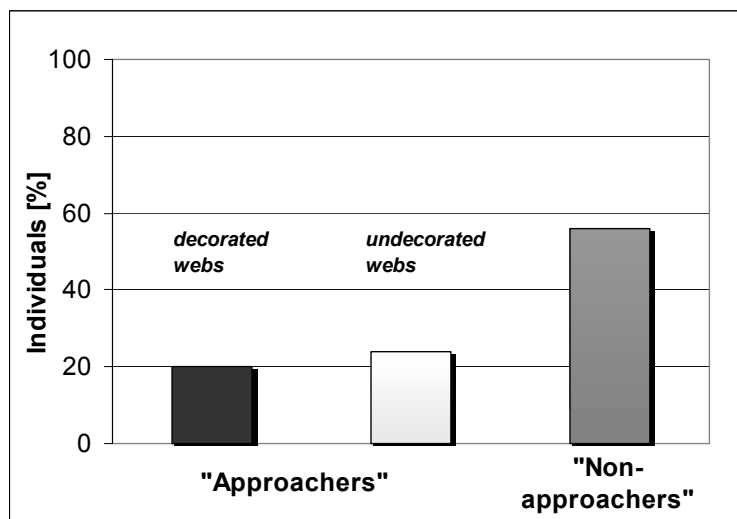


Figure 2. Response of *M. religiosa* individuals (N = 25) to decorated (N = 5) vs. undecorated (N = 6) *A. bruennichi* webs (Y-maze choice test). Approachers: individuals approaching decorated or undecorated webs.

Results

Inside the Y-maze apparatus the individual locomotor behaviour differed widely. All 25 trials were included in the calculation. Nine mantids showed no locomotor activity at all and did not leave the recovery chamber within the observation period of 60 min. The remaining 16 animals (64 %, N = 25) started to move towards the bifurcation of the main chamber. Eleven of them walked on approaching an exit, and will be hereafter referred as "approachers". "Non-approachers" (N = 14) comprised non-locomotory (N = 9) mantids and mantids that stopped in the main chamber (N = 5) (Fig. 2).

Within the "approachers"-group no preference for stabilimenta was recordable. Five mantids chose the exit with decorated web and six the exit with undecorated webs (Fig. 2). The difference is not statistically significant from an equal distribution (Chi-square = 0.763, $p > 0.05$). On average stabilimentum-choosing mantids needed 30.63 ± 3.66 min to reach the exit and mantids which approached the maze exit without stabilimentum 24.81 ± 3.84 min, respectively. Concerning this time lapse there was no statistically significant difference between both groups (t-test, $p = 0.31$).

In all cases no behavioural elements could be observed that indicated either a predatory response or even an attack sequence.

Discussion

In this study I tested a possible attracting function of web stabilimenta of *Argiope bruennichi* to a potential predator, *Mantis religiosa*, using a Y-maze choice test. Bruce et al. (2001) examined this hypothesis using a similar test in *Argiope keyserlingi* and *Archimantis latistylus* system. They found *Archimantis* choosing significantly more often the maze exit with stabilimentum containing webs indicating an attractant function of web-decorations for putative predators. However, my results are not consistent with the results of Bruce et al. (2001). More than half (56 %) of all tested mantids did not show any evaluable movement inside the Y-maze

during the observation period. Remaining 11, exit-reaching individuals eventually showed no preference for webs with a stabilimentum. This may result from species-specific differences between the two tested systems. Apart from that, the small sample size could also conceal differences in mantid's preference in my experiment. But even the large number of non-locomotory individuals implies possible methodological insufficiencies to detect different responses by the predator.

The latter is possibly responsible for not having observed any behavioural sequence of prey recognition, which is actually typical for praying mantids when foraging (Prete, 1999). This may be due to two reasons. One is the distance from the bifurcation to the webs behind one of the exits of the Y-box. The most important prerequisite for prey recognition is spotting a target. This visual stimulus has to be at a minimum distance for detection by praying mantis. Depending on the species (regarding foreleg-length, see Maldonado et al., 1967) and nutritional status this distance has been proved to be only few centimetres (Charnov, 1976). Since the webs were approximately 24 cm apart from the point of decision making (bifurcation) in the maze, the attracting cue might be beyond the visual recognition field of *M. religiosa* (Fig. 1). A second reason arises from the hunting strategy of mantids as such. Praying mantids usually are considered as ambush predators which mainly react on movements of potential prey (Reitze & Nentwig, 1991). Regarding this characteristic of mantids, the problem can be solved by starvation prior to the test. Under unfavourable conditions like starvation or low prey densities mantids can change from their normally performed ambush strategy into an active seeking behaviour (Inoue & Matura, 1983). This might explain the generally stronger pronounced locomotor behaviour of *Archimantis* individuals in the study of Bruce et al. (2001). They used laboratory raised mantids, but no information about the dietary status prior to test was given. In my experiment mantids were starved for two days (following Matura & Inoue, 1999) before starting trials in the Y-

maze in order to elicit moving and seeking behaviour. However, this could not trigger movements sufficiently. Unfortunately, Bruce et al. (2001) did not present an “approachers”-“non-approachers”-ratio, probably because tested individuals were repeatedly placed in the maze after 24 h when remaining motionless within the observation period.

Finally, in case that an individual reached an exit of the maze, no attack sequence (see Corrette, 1990; Reitze & Nentwig, 1991) was recordable. In regard to an ambush foraging strategy of mantids, orb web spiders, like *Argiope*, are vulnerable to be preyed only when moving. So spiders would be at higher risk when relocating web site (Lubin et al., 1993), rebuilding their webs or while courtship and mating (Herberstein & Fleisch, 2003). Neither of these behaviours occurred during the experiment. Consequently, it is not surprising that *Mantis* did not show any typical prey capture sequence when reaching the maze-exit. The motionless impression of the spider and its web should be uninteresting.

Bruce et al. (2001) suggested that the tested mantids did not react on movements but on a visual cue represented by the reflectance (including UV-spectrum) of the stabilimentum of *A. keyserlingi*. Although the authors cannot explain the stimulating effect in detail, it is thoroughly possible. Mantids are known to be “opportunistic predators that will eat a wide range of prey, including very large arthropods and even small vertebrates” (Prete et al., 1999). But also non-predatory ingestive behaviours are reported (Prete et al., 1992), including ingestion of plant parts, like fruits, as well as water droplets. UV-reflectance, for instance by stabilimentum silk, therefore, may be falsely interpret as water drops. If true, spiders, which attached stabilimenta to their webs, were indeed at a higher risk to be preyed by mantids. In my study *Mantis* individuals did not experience any water shortage, hence they were unlikely to forage for water sources. This could explain the sparsely expressed mantid locomotor behaviour compared with the findings of Bruce et al. (2001). These explanations remain yet speculative due to the lack of information about the individual stage in their study.

Conclusions

A potential signal conflict between prey and predator attraction by web decorations is controversially discussed (Bruce et al., 2001 vs. Eberhard, 2003). It is postulated that such a conflict may have favoured the evolution of the highly variable stabilimentum building behaviour in the genus *Argiope*. Different stabilimentum patterns (Blackledge, 1998b; Craig et al., 2001; Starks, 2002; Herberstein & Bruce, 2005) might aggravate the conditioning towards a particular shape in both prey and predator.

In contrast to the study of Bruce et al. (2001), my results do not support the predator attracting hypothesis. But the small sample size possibly does not allow for universally valid conclusions in this case. However, the large number of non-locomotory mantids and the lack of predatory behaviour indicate that the apparatus used is too oversimplified to test the predator attraction hypothesis appropriately and can not account for both the complexity of prey recognition behaviour in mantids (Prete, 1999) and the supposed high plasticity among (intraguild) prey-predator system at the genus level.

So the results of Bruce et al. (2001) on *Archimantis latistylus* may be interpreted alternatively as “an escape rather than a predatory response” (Eberhard, 2003). However, I argue that if stabilimenta have an attracting effect to potential predators, like mantids, it is not yet satisfyingly demonstrated. More sophisticated experiments, considering species-specific characteristics with improved experimental designs and a larger sample size, are needed to test whether stabilimenta may act as visual cues for mantids and other predatory animals.

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