

Frame-web-choice experiments with stingless bees support the prey-attraction hypothesis for silk decorations in *Argiope savignyi*

Dumas Gálvez: Animal Ecology Group, University of Groningen, Biological Center, PO Box 9750 AA Haren, the Netherlands. E-mail: galvezd@gmail.com

Abstract. There is controversy about the function of silk stabilimenta, also called silk decorations, on spiders' webs. Most of the proposed hypotheses have been tested using indirect methods. Protection against predators, advertisement for vertebrates to avoid web damage, and increasing prey attraction are the most popular hypotheses. In this study, I tested the prey attraction hypothesis on the silk decorations of the araneid *Argiope savignyi* using a trial tunnel built in the field, in which I exposed stingless bees *Tetragonisca angustula* to decorated and undecorated webs placed on wooden frames. I carried out two experiments: 1) a three-frame choice, consisting of a frame bearing a decorated web, one bearing an undecorated web and a control frame without web and spider; 2) a two-frame choice, in which the bees were exposed to only two frames consisting of "decorated web vs. control," "decorated web vs. undecorated web," and "undecorated web vs. control". In favor of the prey attraction function, I found that decorated webs intercepted more bees than webs deprived of the decoration or controls with no webs. *Argiope savignyi*'s decorations might lure prey to the web by UV-reflectance as it has been suggested for other *Argiope* species.

Keywords: Decorated, foraging, stabilimenta, undecorated

A wide range of orb-weaving spiders builds silk decorations or stabilimenta on their webs (Araneae: Araneidae, Tetragnathidae, Uloboridae; Scharff & Coddington 1997). Five functions have been suggested for these structures: 1) protection against predators, 2) advertisement to vertebrates so as to avoid web damage, 3) prey attraction, 4) stabilization of the web, and 5) a source of shade. Most work has focused on the first three hypotheses (Herberstein et al. 2000; Bruce 2006). However, after more than 100 years of research, no consensus about the functionality of decorations has yet been reached, and a variety of methods have been applied producing contradictory outcomes. In support of functions 1 and 2, decorations on the web of *Argiope aurantia* Lucas 1833 reduced predatory attacks by mud-dauber wasps and web damage by birds; simultaneously, web visibility to prey was increased and prey capture rates declined. Hence, a cost associated with decoration construction was suggested (Blackledge & Wenzel 1999). A different study with *A. aurantia*, on the other hand supported Function 3, that decorated webs attracted more prey although they were compared with undecorated webs of *A. trifasciata* (Forsskål 1775) (Tso 1998a). For *A. appensa* (Walckenaer 1842), no differences in foraging success were found between decorated and undecorated webs. In support of Function 3, Bruce et al. (2001) and Seah & Li (2001) found that decorated webs of *A. keyserlingi* Karsch 1878 and *A. versicolor* (Doleschall 1859) attracted more prey; however, decorations also attracted predators, in opposition to Function 1. Researchers have concluded that there is a trade-off in foraging strategies, since decorated webs are often smaller than undecorated webs (Hauber 1998).

The traditional perception that the spider web is an undetectable trap has changed drastically since the idea that web decorations might attract prey by UV reflectance was suggested (Craig & Bernard 1990). The prey-attraction hypothesis (Function 3) states that the presence of decorations

increases the foraging success of the spiders. Such an outcome has been proposed for various species of the genus *Argiope*: *A. aetherea* Thorell 1881 (Elgar et al. 1996), *A. trifasciata* (Tso 1996), *A. aurantia* (Blackledge & Wenzel 1999), *A. versicolor* (Li et al. 2004; Li 2005), *A. argentata* (Fabricius 1775) (Craig & Bernard 1990; Craig et al. 2001), *A. keyserlingi* Karsch 1878 (Herberstein 2000; Bruce et al. 2001), *A. aemula* (Walckenaer 1842) (Cheng & Tso 2007); as well as for *Octonoba sybotides* (Uloboridae) (Bösenberg & Strand 1906) (Watanabe 1999), *Araneus eburnus* (Keyserling 1886) (Bruce et al. 2004), and some other species (Herberstein et al. 2000; Bruce 2006).

An important aspect to be considered when testing the prey-attraction hypothesis is the interference of web-size: decorated webs, usually smaller than undecorated ones, might attract more prey due to their decoration. Undecorated webs, however, are usually bigger and hence prey-capturing success might be increased due to the larger area. Therefore, the suggested trade-off in foraging strategies and energetic costs remains speculative. For that reason, an appropriate technique to eliminate the influence of web size, when decorated and undecorated webs are compared, has been manual removal of the decorations (Bruce et al. 2001, 2004).

I tested the prey-attraction hypothesis for the poorly studied Neotropical spider *Argiope savignyi* Levi 1968 using a new method that consisted of a trial tunnel combined with decoration removal and prey manipulation. The tunnel is placed in the field, which can mimic natural visual conditions in which spiders and preys are found. Many studies have tested the hypothesis in laboratory conditions (e.g., Y-choice experiments), which might not reproduce natural conditions. As well, the influence of web size can be eliminated while the prey capture history of the spiders, which has an essential effect on the decoration behavior (Craig et al. 2001), can be controlled. If the web decoration functions to attract prey, then I expected that decorated webs would intercept more bees than the undecorated webs and empty control frames.

METHODS

Site.—This study was carried out from 18 July to 4 August 2007 at La Selva Biological Station, Heredia, Costa Rica (10°26'N, 83°59'W), a 1550-ha reserve in the Atlantic lowlands with an annual average rainfall of 4000 mm. See Sanford et al. (1994) for more details about the station.

Animals.—*Argiope savignyi* is an aerial web weaving spider that decorates its web with zigzags of silk laid in a variety of designs that include silk discs (juveniles) or one to four arms of a cross (adults). Some webs lack decorations (Nentwig & Rogg 1988). This species is common at La Selva (Rovner 1989; Timm & Losilla 2007). I confirmed the species identity using the taxonomic key for *Argiope* by Levi (2004). No voucher specimens were collected but some collected from La Selva are available at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Levi 2004).

Experimental Design.—Collected individuals of *A. savignyi* were placed in a large screened cage (7 × 3 × 2 m). This cage contained herbaceous vegetation with insects such as Homoptera, Hymenoptera, Orthoptera, on which the spiders were allowed to forage. In addition, each spider was fed several stingless bees to guarantee that they were satiated, an important factor for inducing the construction of decorations (Craig et al. 2001).

A 300 × 120 × 80 cm tunnel, open at both exits, was constructed (Fig. 1). The different web treatments were set up on wooden frames at one end, and a wooden box (40 × 30 × 20 cm) with a nest of the stingless bee *Tetragonisca angustula* Latreille 1811 was placed in the other end. The frames were put on a 2 × 35 × 120 cm wooden board placed at the exit of the tunnel so that the frames were not in contact with the ground. The exit of the bee nest faced that of the tunnel for the web treatments. Bees could leave the tunnel through the exit containing the frames, which they usually did, or by the other exit. The nest was placed in the tunnel with both exits opened for 48 h before the beginning of the experiment in order to get the bees used to the tunnel and the new nest location. The reason for placing the nest entrance near the tunnel exit was to reduce the stress on the bees, which probably occurs when they are individually manipulated, for instance with CO₂ anesthesia (Bruce 2006). With the intention of comparing the two web treatments, I used spiders of similar sizes, and the control frame never contained a spider. The exit of the tunnel where the frames were placed was in front of herbaceous vegetation, and a dark green mesh placed one m from it.

I performed two experiments with *A. savignyi*: 1) A “Three-frame choice,” consisting of three frames (34.5 × 45.0 cm, or 20 × 20 cm for smaller webs) placed next to each other at the same time and at the same end of the tunnel with different web treatments; one bearing a decorated web, one bearing an undecorated web, and a control without web and spider (Fig. 1) and 2) a two-frame-choice experiment in which the bees were exposed to only two frames placed at the same end of the tunnel and consisting of the following: “decorated web vs. control,” “decorated web vs. undecorated web,” and “undecorated web vs. control.” Small frames (20 × 20 cm) did not cover the entire area of the tunnel’s exit, so I covered the remaining space with cardboard sheets. For the three-frame-choice experiment, I used two spiders per replicate ($n = 8$, 155 bees): one for the decorated web and one for the undecorated web. For the two-frame-choice

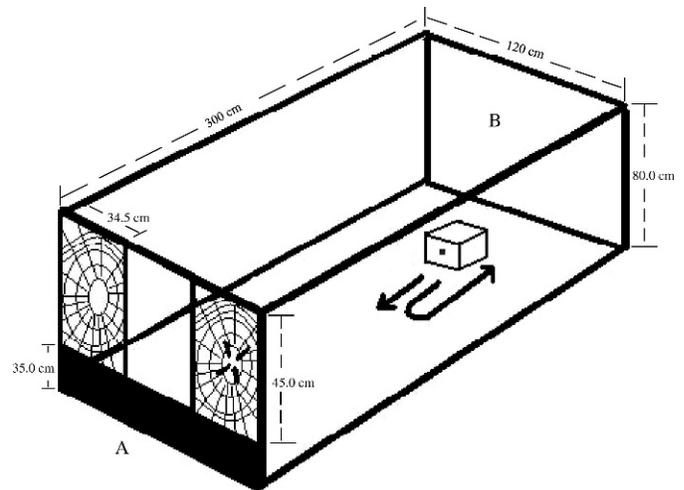


Figure 1.—Trial tunnel in which the stingless bees were exposed to the different web treatments. The walls and roof of the tunnel are removed in order to reveal the inside. Solid arrows show the two possible trajectories of bees to fly out of the tunnel from the nest (N). The exit bearing the web treatments is represented by A and the opposite exit by B.

experiments, I compared “decorated webs versus control” frames for 17 repetitions (175 bees), “undecorated webs versus control” frames for 9 repetitions (86 bees), and “decorated webs versus undecorated webs” for 10 repetitions (100 bees). The three-frame-choice experiment trials lasted approximately 5 to 15 min. Bees were allowed to return to the nest except for those that were collected in order to feed the spiders (or caught and consumed by the spider itself). Only one trial was carried out per day, which greatly reduces the possibility of avoidance learning by stingless bees (Craig 1994b). Craig (1994b) also proposed that even if bees learn to avoid decorated webs (e.g., in one location), they are unable to generalize a similar response to other decorated webs. The two- and three-frame-choice experiments were carried out in random order. The three sets within the two-frame-choice experiments were randomly assigned as well.

All decorations were either cross or linear patterns. Decorations were removed by burning the fine silk lines with heated fine-point forceps while the spider was on the web except on a few occasions when the spider was removed first. The spider was then placed back on the web after the decoration was removed. In some cases, a little damage was done to the web during burning, and in these instances, I used the forceps to produce similar damage to the decorated web.

I counted the numbers of bees either being intercepted (including bees caught by spiders) or flying through each frame, and determined the number of bees intercepted per frame. I switched the positions of the frames each time two bees had exited the tunnel or were intercepted in order to avoid any possible bias due to frame position. The frames were placed at the exit of the tunnel only when no bee was either leaving the nest or flying in the tunnel. In cases in which three or more bees accumulated in the web because the spider did not attack them, I removed the three frames and used forceps to remove the bees in order to avoid the possibility that bees caught there would deter more bees from flying into the web. I did not remove the bees if they were captured by the spider or

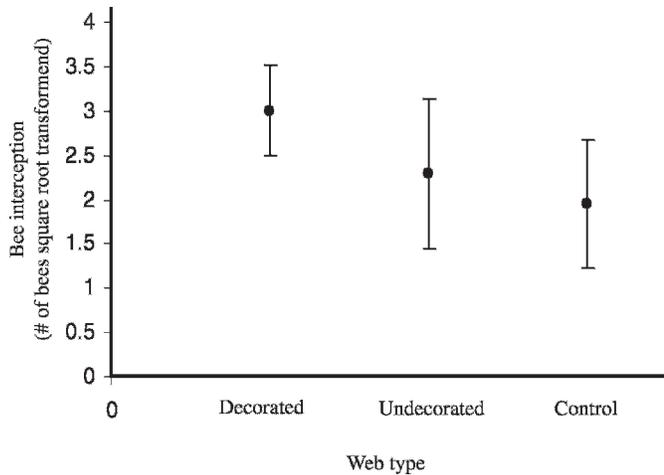


Figure 2.—Number of *Tetragonisca angustula* bees intercepted for the three-frame-choice experiment set for *Argiope argentata*. Mean \pm SD.

wrapped with silk by the spider. After this, I put the frames back at the exit to continue the experiment. I used 10–30 bees per repetition, which required a new set of webs made by spiders not previously used. I did not register numbers of bees wrapped or consumed. Spiders wrapped bees few times, but they usually kept consuming the first bee that was caught. This apparently did not discourage bees from flying into the web. All the trials were carried out at 09:30–12:00 and 13:00–15:00 h, when the light conditions were relatively constant.

The counts from the three- and the two-frame-choice experiments were square root transformed. The transformed data from the three-frame choices was tested for normality and analyzed using a single factor ANOVA. Finally, the transformed data from the two-frame-choice experiments were analyzed with a *t*-test for paired samples. Effects were accepted as statistically significant if $P \leq 0.05$, and all analyses were done using STATISTICA 7.0 (StatSoft 2001).

RESULTS

Bees were intercepted by decorated webs significantly more often than by the undecorated webs or the control frames (48, 30 and 22% of the bees respectively, $F_{2, 21} = 4.65$, $P = 0.02$, Fig. 2). I did not find significant differences between undecorated webs and the control frames (Tukey HSD test, $P = 0.362$). In the “decorated webs versus control” experiment, 64% of the bees chose the frames bearing decorated webs ($t = 2.84$, $df = 16$, $P = 0.006$, Table 1). Decorated webs also intercepted more bees (58%) than undecorated webs (42%), $t = 1.91$, $df = 9$, $P = 0.044$.

Table 1.—Statistical summary and preferences for the two-frame-choice experiments set for *Argiope argentata*. dec: decorated webs; undec: undecorated webs; and control.

Treatment	<i>t</i>	<i>df</i>	<i>P</i>	Total number of bees	% of bees intercepted		
					dec	control	undec
dec vs control	2.84	16	0.006	175	64	36	----
undec vs control	0.22	8	0.42	86	----	49	51
dec vs undec	1.91	9	0.04	100	58	----	42

DISCUSSION

The prey attraction function of silk decorations for *A. savignyi* is supported by both the two- and the three-frame-choice experiments (Fig. 2, Table 1). Decorated webs intercepted significantly more bees than those webs from which the decoration was removed. Webs deprived of decorations showed no significant differences from the control frame that lacked either web or spider. The results from these experiments are also reinforced by the fact that bees did not show an avoidance-learning process which would have decreased the interception of the decorated web (Craig 1994a). The literature covering this hypothesis is controversial; many studies have revealed that decorated webs intercept more prey than undecorated webs (Craig & Bernard 1990; Elgar et al. 1996; Tso 1996, 1998a, 1998b; Watanabe 1999; Herberstein 2000; Bruce et al. 2001; Craig et al. 2001; Li et al. 2004; Li 2005; Bruce & Herberstein 2005; Cheng & Tso 2007) but some studies found no evidence in favor of the hypothesis (Blackledge 1998; Blackledge & Wenzel 1999; Hoese et al. 2006; Jaffé et al. 2006; Bush et al. 2008; Eberhard 2008; Gawryszewski & Motta 2008). This hypothesis has been previously supported for one of the closest relatives of *A. savignyi*, *A. argentata* by Craig (1991) and Craig et al. (2001), but no manipulative experiments (e.g., decoration removal) were performed. Craig et al. (2001) correlated the increase in decoration frequency with the increase in the number of stingless bees. Craig (1991) also calculated an index of predator-prey encounter rates based on the damage found on the web. Such damage is not necessarily caused by prey, however. She also assumed that the prey damage or destroy part of the web, even when they are not captured. I saw several cases in which a bee was intercepted in the web and later escaped without damaging the web.

There is one result from the set “undecorated web versus control” that clearly merits further study. It could be anticipated that the undecorated webs (bearing a spider) would intercept more bees than the control, considering the UV reflective properties of the spider’s dorsal surface that is thought also to play an important role for attracting prey (Craig & Ebert 1994; Cheng & Tso 2007; Bush et al. 2008). This was not observed but partially supported by the three-choice-frame experiments; 30% and 22% bees intercepted undecorated and control frames, respectively. Yet the bright coloration of *Argiope* spiders may have no relation as a prey attraction function, serving more as camouflage for the spiders in *A. bruennichi* (Václav & Prokop 2006) and *A. keyserlingi* (Hoese et al. 2006). The functional significance of body coloration of *Argiope* spiders remains unresolved.

One of the advantages of the method in this study was that stress on prey was reduced, since the experiments were performed in the field. The prey attraction hypothesis can be

directly tested in a number of ways, all of which have their advantages and disadvantages. The field correlation technique involves correlating the presence of web decorations with prey capture rates, but this method has produced contradictory results for different species (Hauber 1998; Tso 1998b; Herberstein 2000; Bruce et al. 2001; Craig et al. 2001; Bruce et al. 2004). A negative aspect of field correlations is that the prey capture history of the spiders is unknown, and satiated individuals can construct more decorations (Blackledge 1998; Tso 1999; Seah & Li 2002). Consequently, decorated webs may just be in sites where prey are abundant.

Another method is the Y-choice experiment, which has been used in laboratory experiments to show that flies are attracted to decorations (Craig & Bernard 1990; Watanabe 1999; Bruce et al. 2001; Li et al. 2004). These studies have been carried out in laboratory conditions using artificial lights. Moreover, decorated and undecorated webs have been contrasted without the presence of the spider on the web, which might reduce the similarity to a natural prey-spider encounter. The third technique is the experimental manipulation of webs by decoration removal to compare decorated and undecorated webs. This allows investigating the effects of these structures on prey capture and predator response without the cause and effect problem as in the field correlation method (see Bruce 2006). Some studies in which decoration removal was used in the field found opposite results for the prey-attraction function. Blackledge & Wenzel (1999) suggested that the decoration in *Argiope aurantia* reduced foraging success, but Tso (1998a) found that the decoration in fact increased it. The possible reason of this difference is that the former study did not control for web size and the latter one used webs of similar size, as I did.

Even though the prey-attraction function is supported by these experiments, other hypotheses, such as advertisement to avoid web damage by vertebrates (Blackledge & Wenzel 1999) and the anti-predator function (Bruce et al. 2001; Schoener & Spiller 1992), are not necessarily discardable. Scharff & Coddington (1997), in their phylogenetic analysis of the family Araneidae, proposed that web decorations evolved nine times independently in the 15 genera in which they are known to occur. Although they reasoned that the widespread convergent evolution of this trait only in diurnal species suggests a search for a common cause, it might be possible to find a wide range of function across the different groups of spiders that evolved this trait. Is a multifunction role possible for *Argiope's* web decorations? For instance, *Argiope trifasciata's* decorations increase foraging success (Tso 1996, 1998a) and also provide protection against predators (Blackledge & Wenzel 2001). For *A. aurantia*, the prey attraction, predator avoidance, and web advertisement functions have found support (Tso 1998a; Blackledge & Wenzel 1999). However, some studies that addressed a multifunction role only found evidence for one function (e.g., Blackledge & Wenzel 1999; Bruce et al. 2001). Bruce & Herberstein (2005) found differences in the decorating behavior of three Australian *Argiope* species that were apparently related to the pattern of decoration that each species built. These dissimilarities suggest that those decoration patterns perform different functions, although with different costs and benefits associated. The other two important visual functions suggested for decorations, the anti-predator and the web advertisement hypotheses

can be tested using a similar approach, employing manual decoration removal in a more natural visual condition similar to this study. In this way, the different web types and their spiders can be exposed to either predator or vertebrates (e.g., birds) in order to quantify their behavioral responses.

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