

A possible role of decorations in spiderwebs as protection devices that distract predators
Una posible función de los estabilimentos en telas de araña como estructuras defensivas que distraen a los depredadores

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Abstract

Several functions have been proposed for silk decorations (i.e., stabilimenta) in spiderwebs. One hypothesis is that web decorations protect spiders from predators, either by concealing the spiders, physically shielding them, or by deflecting predatory attacks. This study uses data gathered in opportunistic manner when studying the behavior of *Stenolemus giraffa*, an assassin bug that preys almost exclusively on web-building spiders. *Stenolemus giraffa* approach orb spiders on foot, and usually capture the spiders at the hub region of the web. When pursuing spiders, *S. giraffa* routinely tap the web with their antennae, and also tap the spiders prior to attacking them. The observations available from this study suggest that *S. giraffa* got “distracted” momentarily by the decorations in the webs of *Purumitra* sp. (Uloboridae) and *Argiope katherina* (Araneidae). In some instances, the assassin bugs tapped these structures for several seconds or minutes instead of tapping the adjacent spiders. In interactions with *A. katherina*, *S. giraffa* was more successful at capturing the spiders when the webs lacked decorations; however, sample sizes are small (this could not be tested for *Purumitra* sp. because only one web lacked decorations). Finally, some of the spiders detected *S. giraffa* tapping the decorations or that had begun tapping the spiders and that had interrupted this behavior to tap the decorations. The data available suggest that, for *S. giraffa*, the decorations in these webs interfered with the process of locating the spiders. If further experiments corroborate this idea, this information would be in accord with Hingston’s (1927) hypothesis that web decorations can confuse spider predators.

Key words: stabilimenta; web decorations; camouflage; *Stenolemus giraffa*; araneophagy; spiderweb; predator avoidance.

Resumen

Muchas arañas agregan a sus telas estructuras de seda, detritos, u otros, que son conocidas como “estabilimentos” o “decoraciones”. Varias funciones han sido propuestas para estas estructuras. Una de las hipótesis plantea que las decoraciones protegen a las arañas de los depredadores, ya sea porque ocultan a las arañas, o porque funcionan como una barrera física que separa al depredador de la araña, o porque desvían los ataques de los depredadores. En este estudio, se utilizan datos que fueron tomados de manera oportunista mientras se estudiaba el comportamiento del chinche asesino *Stenolemus giraffa*, un insecto que se alimenta casi exclusivamente de arañas que hacen tela. *Stenolemus giraffa* ataca a las arañas en el meollo de la tela, y se acerca hasta estas caminando. *Stenolemus giraffa* usualmente “toquetea” a las arañas con sus antenas (comúnmente sin hacer

contacto con la araña) antes de atacarlas. Las observaciones de este estudio sugieren que *S. giraffa* se distrajo de forma momentánea con las decoraciones en las telas de *Purumitra* sp. (Uloboridae) y *Argiope katherina* (Araneidae). En algunas ocasiones, los chinches toquetearon con sus antenas estas estructuras por algunos segundos o incluso minutos, en vez de toquetear a las arañas que estaban adyacentes a estas. En interacciones con *A. katherina*, *S. giraffa* capturó en mayor proporción a las arañas que se encontraban en telas sin decoraciones; sin embargo, el tamaño de la muestra es pequeño. No se pudo realizar una comparación similar para *Purumitra* sp., ya que todas las telas, excepto una, tenían decoraciones. Algunas de las arañas detectaron a los chinches cuando estos estaban toqueteando las decoraciones, o después de que hubieran toqueteado a las arañas e interrumpieran este comportamiento para toquetear las decoraciones. Dichas observaciones sugieren que las decoraciones en estas telas interfirieron con el proceso de *S. giraffa* de localizar a las arañas. Si esto se corrobora mediante futuros experimentos, esta información apoyaría la idea de Hingston (1927) de que las decoraciones en las telas funcionan para confundir a los depredadores de arañas.

Palabras clave: estabilmientos; decoraciones en telas; camuflaje; *Stenolemus giraffa*; depredadores de arañas; telas de araña; protección de depredadores.

Introduction

Many web-building spiders add visually conspicuous structures to their webs (i.e., bands or tufts of silk, detritus, or egg sacs), which are commonly placed near or at the hub of the web (Hingston, 1927; Eberhard, 1973, 1990; Herberstein, Craig, Coddington, & Elgar, 2000). These structures are commonly referred to as “decorations” or “stabilimenta”, and are present in several genera of spiders, mainly in the orb-web families Araneidae and Uloboridae (Herberstein et al., 2000; Bruce, 2006). Depending on their placement, web decorations can be classified as being discoid or spiral (both centered and confined to the hub region), or as having linear or cruciate patterns that start in the capture area of the web and end near the spider’s legs or body (Hingston, 1927; Herberstein et al., 2000; Walter & Elgar, 2011).

Several, non-exclusive functions have been proposed for decorations in webs (reviewed in Eberhard, 1990; and more recently in Herberstein et al., 2000; Craig, 2003; Bruce, 2006), and the ones receiving most attention are: i) advertising the web to non-prey organisms (e.g., birds) to prevent structural damage from potential collisions, ii) increasing foraging success by attracting prey, and iii) protecting spiders from predators. Protection from predators could be achieved by concealing the spiders, physically shielding the spiders, or by deflecting the predatory attacks (for details on defensive hypotheses, see Robinson & Robinson, 1970). Experimental evidence has provided support for all these hypotheses, with some prevailing in different species or ecological contexts (Eberhard, 1990; Herberstein et al., 2000; Blackledge & Wenzel, 2001; Bruce, 2006).

Although these hypotheses are not restricted to a particular sensory modality (see Robinson & Robinson, 1970, 1973; Eberhard, 1973), historically, functional interpretations of web decorations have focused on the visual domain (e.g., Hingston 1927, Robinson & Robinson, 1970; Blackledge, 1998; Blackledge & Wenzel, 1999; Chou, Wang, Shen, & Tso, 2005; Bruce, Heiling, & Herberstein, 2005; Bruce, 2006; Tseng & Tso, 2009; Tan et al., 2010). Web decorations are highly conspicuous to human observers and this might explain the bias towards visual interpretations of these structures. Further, web decorations often conceal the spider’s body in a visual manner

(Hingston, 1927; Eberhard, 1973; Herberstein et al., 2000; Bruce, 2006), and this leads to the logical interpretation that they may protect spiders from visual predators (Hingston, 1927; Robinson & Robinson, 1970; Bruce, 2006), but the protection could also occur via chemical stimuli (i.e., smell, or taste), or by acting as a mechanical barrier (Robinson & Robinson, 1970). An overlooked hypothesis in relation to the protective function of decorations in webs is that of Hingston (1927), which states that these structures function as “confusing” elements that draw attention away from the spider. This study explores Hingston’s idea from the perspective of *Stenolemus giraffa*, an araneophagic assassin bug. Data were gathered in opportunistic manner when studying the behavior of this predator (described in Soley, Jackson, & Taylor, 2011; Soley & Taylor, 2012, 2013). Although Hingston did not confine his hypothesis to a particular sensory modality, emphasis was placed in the visual domain (Hingston 1927, Robinson & Robinson, 1970, 1973). Because *S. giraffa* appears to rely on chemical cues (perhaps in addition to visual stimuli) to locate and attack spiders (Soley et al., 2011; Soley & Taylor, 2013), and because web decorations have been considered mainly from a visual perspective, it is of special interest to consider the effect that web decorations have on this predator.

Materials and methods

This paper uses observations that were recorded in opportunistic manner while studying the predatory behavior of *Stenolemus giraffa* (Soley & Taylor, 2012, 2013). Observations are from staged interactions between *S. giraffa* and two orb spiders that occasionally incorporate silk decorations into their webs: *Purumitra* sp. (Uloboridae) and *Argiope katherina* (Araneidae). Both spiders are preyed upon by *S. giraffa* under natural conditions (Soley et al., 2011). Observations were done at El Questro Station, Western Australia (15°53.675’ S & 128°07.986’ E) during August 2008, August-October 2009, and July-August 2010. All interactions were staged during the day, but some of these continued during the night. However, most observations of behavior occurred during the day.

Assassin bugs: *Stenolemus giraffa* inhabits rock escarpments in North Western Australia, where it feeds almost exclusively on web-building spiders (Soley et al., 2011). This assassin bug uses a tactic based on stealth to approach spiders on foot and capture the spiders at their resting sites (i.e., the hub in orb webs) (Soley & Taylor, 2012, 2013; Soley, 2016). Once within range of attack, *S. giraffa* strikes in a split second (< 0.3 s), lunging forward to grasp the spider with its raptorial forelegs, and stabbing it with its rostrum (Soley et al., 2011; Soley & Taylor, 2012). Because *S. giraffa* has an elongated pronotum and very long legs, it can often reach the spiders without stepping onto the web (Soley & Taylor, 2012). An advantage of studying the predatory behavior of *S. giraffa* in relation to web decorations is that *S. giraffa* moves very slowly (Soley et al., 2011) and that the movement of their antennae (which can be easily observed) can provide information about the interests of these assassin bugs.

While approaching web-building spiders (a process that may take several hours) *S. giraffa* always orient their antennae intermittently towards the spider and the web, and “wave” their antennae up and down, so that the distal ends smoothly delineate an arc (Soley et al., 2011; Soley & Taylor 2013). Moreover, throughout a pursuit, *S. giraffa* routinely tap the web by moving their antennae toward and away from the silk (i.e., the distal ends are usually brought very close to the silk (< 2

mm), and they sometimes contact it) (Soley et al., 2011). Unless attacked by the spiders, *S. giraffa* always tap the spiders for several seconds or minutes before attacking (Soley et al., 2011; Soley & Taylor 2013). Waving and tapping can easily be discerned from each other (Soley et al., 2011), and tapping refers only to instances in which the assassin bugs direct their antennae towards the silk or the spider. *Stenolemus giraffa* hunt spiders during the day or at night (Soley et al., 2011; Soley & Taylor 2013), and under experimental conditions, *S. giraffa* can adopt predatory behavior in the absence of visual stimuli from spiders (see experimental procedure in Soley, 2016).

The predatory behavior of *S. giraffa* suggests that they use chemosensory and tactile information to locate the spiders (however, the use of visual stimuli in this process cannot be ruled out). For instance, when approaching spiders from adjacent, non-web surfaces, *S. giraffa* intersperses episodes of orienting/waving the antennae towards the spider with episodes of tapping the web. While doing this, *S. giraffa* may lean towards the spider (with its body raised above the web and the antennae extended forward), and if the spider is out of reach, *S. giraffa* will usually move to another location and repeat the same behaviors (Soley & Taylor 2012, 2013). These behaviors allow *S. giraffa* to reach a vantage point from where it can tap the spider and attack it without needing to step onto the web (Soley & Taylor 2012, 2013). Even though the use of visual stimuli in hunts cannot be discarded at present, the fact that *S. giraffa* always orient their antennae towards the spiders, and the fact that they use them to tap the webs and the spiders, suggests that chemosensory and/or tactile information is important for these bugs. The use of chemosensory information from webs was demonstrated experimentally for *Stenolemus bituberus*, another assassin bug that preys on web-building spiders (Wignall & Taylor, 2009).

Spiders: The webs of *A. katherina* have a vertical orientation and commonly present cruciform decorations with a varying number of arms (one to four), or discoid decorations; both of these structures are composed of white silk and are very similar to the decorations described for other species in the genus (Robinson & Robinson, 1970). Occasionally, two arms of an incomplete cruciform decoration are aligned (with the spider resting at the middle); therefore, the arrangement could be considered linear (hereafter, “linear decoration”) (Fig. 1A). Because adult *A. katherina* usually build webs on vegetation, away from where *S. giraffa* are found (pers. obs.), they were not included in the interactions. Both juvenile and adult *Purumitra* sp. build webs of horizontal or close-to-horizontal orientation and usually place linear or circular decorations of white silk at the hub of the web (Fig. 1B), in a very similar manner to *Uloborus diversus* (Eberhard, 1973). Occasionally, some individuals place both types of decorations.

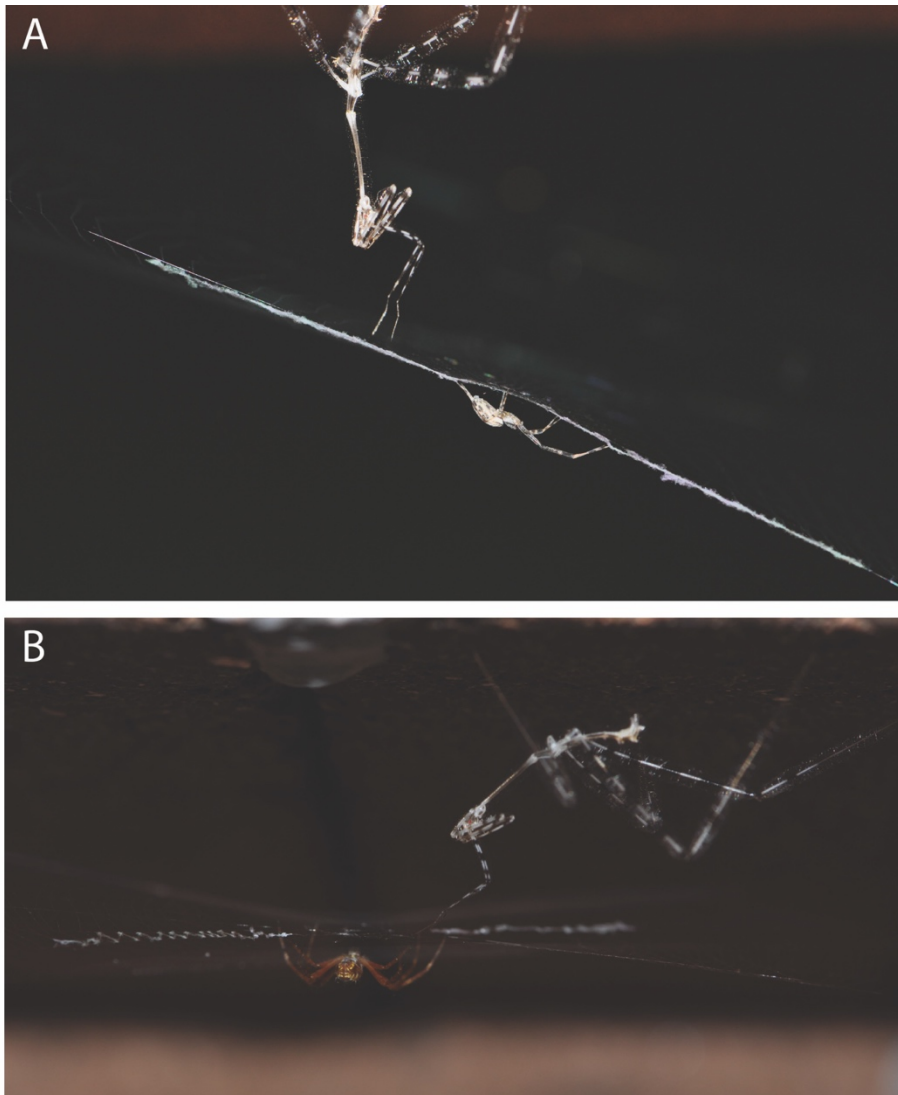


Fig. 1. **A.** *Stenolemus giraffa* tapping the horizontal web of *Purumitra* sp. from the opposite side of the orb. **B.** *Stenolemus giraffa* tapping the vertical web of *Argiope katherina* from the opposite side of the hub; the picture was taken from above. Note the linear decoration present in both webs.

Staged interactions: Interactions between *S. giraffa* and orb spiders were staged in an open shed at El Questro Station. These involved adult or large nymphs (3rd-5th instar) of *S. giraffa*, and juvenile spiders (in the case of *Purumitra* sp., adult spiders were used as well), so that the assassin bug to spider size (body length) ratio varied from 5:1 to 2:1. Assassin bugs and spiders were collected as needed from the surrounding rock escarpments and were paired randomly; each was used only once. Spiders were placed to build webs in brick arenas that simulated the rock environment in which the spiderwebs are normally built (for a detailed description, see Soley & Taylor, 2012).

The spiders were placed in the arenas one to three days before staging the interactions. Only entire webs with a typical structure were used. Because assassin bugs in the lowest of five ranks of body condition (identified by a thin, curled abdomen) are more likely to be active (Soley et al., 2011), only assassin bugs in this body condition were used. Assassin bugs were released into the arena at

approximately 20 cm away from the spiderweb. Spiders and assassin bugs could move freely and in naturalistic manner inside the arena (the texture of the bricks was similar to the rock escarpment and both participants could abandon the arena at any time during the interaction). For further description of staged interactions, see Soley & Taylor (2012, 2013).

The possible outcomes of the interactions were: *S. giraffa* captured the spider, the spider killed *S. giraffa*, the spider abandoned the arena, or *S. giraffa* abandoned the arena (Soley & Taylor, 2013). The results from this study, unless otherwise stated, use data exclusively from interactions in which the assassin bugs managed to reach the hub region of the web and started tapping the spider with their antennae. This is the last step prior to capturing the spider, and *S. giraffa* may spend several seconds or even minutes tapping the spider before attacking (Soley & Taylor, 2013). When sample sizes allowed for statistical testing, a Fisher's exact test was used.

Results

Webs of *Purumitra* sp.: In interactions with *Purumitra* sp., *S. giraffa* captured the spiders in three out of six occasions. In the unsuccessful pursuits, the assassin bugs interspersed episodes of tapping the spider with episodes of tapping the decorations. Each bout of tapping the decorations lasted for at least 7 s, and up to 3 min. In two of these interactions, the assassin bugs were detected by the spiders when tapping the decorations (one decoration was linear and the other was circular); one spider abandoned the web and the other one suspended itself from a safety line below the web (see Soley & Taylor, 2013). In the third unsuccessful pursuit, *S. giraffa* grabbed a thread of the web with its foretarsi when it was detected by the spider; the spider suspended itself from a safety line.

In the pursuits in which *S. giraffa* captured the spider ($n = 3$), one occurred in a web without decorations. In this case, *S. giraffa* captured the spider while hanging from the roof of the arena. This web had a capture area that was smaller than usual, and this probably facilitated access for *S. giraffa*, which was able to reach the spider through the large gap left between the frame of the web and the outer turn of the sticky spiral. The other two webs had linear decorations, but the assassin bugs did not tap them.

Webs of *A. katherina*: After tapping *A. katherina* ($n = 14$), the outcome of the interactions were as follows: *S. giraffa* captured the spider ($n = 8$), the spider killed *S. giraffa* ($n = 2$), the spider abandoned its web after detecting *S. giraffa* ($n = 3$), and *S. giraffa* abandoned the pursuit after the spider pumped vigorously (causing the web to shake back and forth; see Soley & Taylor, 2013) ($n = 1$). All but one of the unsuccessful pursuits ($n = 6$) occurred in webs with decorations (one had a cruciform decoration and five had linear decorations). The assassin bugs always tapped the decorations. All but one of the successful pursuits ($n = 8$) occurred in webs without decorations (one web had a linear decoration, but the assassin bug did not tap it). *Stenolemus giraffa* was more successful at capturing *A. katherina* when the webs lacked decorations (Fisher's exact test, $p = 0.03$).

In three out of the five unsuccessful pursuits that took place in webs with decorations (Table 1), the assassin bugs tapped the decorations in an intermittent manner, but the spider responses were not preceded immediately by tapping of decorations. In the other two unsuccessful pursuits that occurred in webs with decorations, the assassin bugs tapped the decorations (for several seconds

and up to 3.5 min) while standing in close proximity to the spiders (i.e., the spiders were adjacent to the decorations and within range of attack). On one of these occasions, the assassin bug interspersed tapping a leg of the spider with tapping the decoration; three minutes later, the assassin bug grabbed a thread with its foreleg and was attacked and killed by the spider (Table 1). In the other interaction, the assassin bug interspersed bouts of tapping two legs of the spider with bouts of tapping the decoration. Twelve minutes later, the assassin bug was tapping the abdomen and legs of the spider and was attacked and killed by the spider (Table 1).

TABLE 1
Outcome of interactions in which *Stenolemus giraffa* failed to capture *Argiope katherina*

Outcome of interaction	N*	Behavior of the assassin bug and the spider**	Type of decoration in web(s)
<i>Stenolemus giraffa</i> abandoned the pursuit after being detected by the spider.	2	The assassin bug was placing a middle leg on the orb-region of the web and the spider approached and grasped the assassin bug (n = 1); the assassin bug became still, and the spider returned to the hub, leaving behind (stuck to the capture spiral) a swath of silk that was going to be used for wrapping. The assassin bug was tapping the spider (n = 1), and the spider pumped vigorously (causing the web to shake back and forth; see Soley & Taylor, 2013).	Respectively, one web with a linear decoration; one web with a single-armed, cruciform decoration.
<i>Argiope katherina</i> abandoned the arena after detecting <i>S. giraffa</i> .	2	The assassin bug was grabbing a thread of the capture region of the web with its foretarsi (n = 1) (see Soley et al., 2011). The assassin bug was tapping the spider.	Respectively, one web lacking decorations; one web with a complete, cruciform decoration.
<i>A. katherina</i> killed <i>S. giraffa</i> .	2	The assassin bug was tapping the spider (n = 1). The assassin bug was grabbing a thread of the capture region of the web with its foretarsi (n = 1).	Linear decorations in both webs.

*N refers to the sample size.

**Refers to behaviors of *S. giraffa* that were immediately followed by a response from the spider and were decisive in the outcome of the interaction.

Other instances of tapping decorations in webs: The following data are from other interactions (not considered in the previous analysis) in which the assassin bugs did not reach the hub of the web. In two interactions with *A. katherina*, the assassin bugs had their antennae oriented towards the spiders but re-oriented their antennae towards the decorations and tapped these for several seconds (one decoration was discoid in shape, and the other one was linear). This occurred on

several occasions in both webs. Similarly, in two interactions with *Purumitra* sp. in which the assassin bugs had their antennae oriented toward the spiders, the assassin bugs re-oriented their antennae to tap the linear decorations for several seconds or minutes. In one of these instances, an antenna of the assassin bug got momentarily stuck to the web.

Tapping the empty hub of the web: In several instances, the assassin bugs tapped for several seconds or minutes the hub of the web, in the absence of a spider. This was observed on two occasions, some minutes after the spiders (*A. katherina*) had abandoned their webs; the assassin bugs tapped the hub region for four and five minutes, respectively. In one interaction with *A. katherina*, the spider had abandoned the web 27 min before the assassin bug arrived at the hub; the assassin bug tapped the hub for at least two minutes. In two other interactions with *A. katherina*, the spiders had moved one body distance away from the hub, and the assassin bugs tapped the hub for at least 1 min, instead of orienting their antennae towards the spiders. Similarly, another assassin bug tapped the hub of the web of *Purumitra* sp. for several minutes, despite the fact that the spider had already abandoned its web.

Discussion

In the predatory interactions considered here, *Stenolemus giraffa* was more successful at capturing *Argiope katherina* when the webs lacked decorations. A similar analysis could not be performed for webs of *Purumitra* sp. because only one of these webs lacked decorations. Although sample sizes are small, the available data suggest that the decorations in these webs could have hindered the ability of *S. giraffa* to locate the spiders. For both spiders, there were various instances in which *S. giraffa* tapped the decorations for several seconds and even minutes, and in webs of *Purumitra* sp., the assassin bugs were detected twice by the spiders when tapping the decorations. Most importantly, there were various instances (three while pursuing *Purumitra* sp. and two while pursuing *A. katherina*) in which *S. giraffa* interspersed bouts of tapping the spiders with bouts of tapping the adjacent decorations.

In the interactions in which *S. giraffa* interspersed bouts of tapping the spider with bouts of tapping the decorations, the spiders eventually responded in a defensive or aggressive manner. The outcome of these pursuits is of special interest, since the assassin bugs were already tapping the spiders (i.e., they were already in the final stages of the pursuit, after which, they usually attack the spiders; Soley et al., 2011; Soley & Taylor 2013). It is possible that the decorations in these webs acted as close-range distracting features that confused the assassin bugs. A previous study demonstrated that *S. giraffa* were more often detected by the spiders when they were in proximity (<2 assassin bug body lengths; Soley & Taylor, 2013). Hence, it appears that the decorations in these webs worked to the spiders' advantage by delaying the pursuit in a context in which *S. giraffa* was particularly vulnerable to detection.

Although there is strong support for the idea that decorations function to protect web-building spiders from predators (Eberhard, 1973, 2007, 2008; Schoener & Spiller, 1992; Blackledge & Wenzel, 2001; Li, Kok, Seah, & Lim, 2003; Tseng & Tso, 2009; for reviews see Starks, 2002; Bruce, 2006), the exact mechanisms by which this is accomplished remain relatively unexplored. Decorations could work by physically shielding the spider (at least from one side of the orb), changing its apparent shape, blurring its outline, by confusing predators or by diverting their

attacks (see Robinson & Robinson 1970, 1973; Eberhard, 2003; Chou et al., 2005; Bruce, 2006). In the case of *S. giraffa*, it appears that the decorations confused or distracted these predators, which gives support to Hingston's idea that decorations function as "confusing" elements that draw attention away from the spiders (Hingston, 1927).

It is unknown whether *S. giraffa* rely more on chemosensory or visual stimuli when pursuing spiders. It appears that chemotactile cues are important for *S. giraffa* because they always tap the webs of spiders, and tap the spiders prior to attacking (Soley et al., 2011; Soley & Taylor, 2013). Also, *S. giraffa* has been observed pursuing spiders at night (Soley et al., 2011), and during daytime but in the absence of visual stimuli from the spider (Soley, 2016). *Stenolemus giraffa* has been observed tapping (but not attacking) bundles of silk from destroyed spiderwebs, empty egg sacs, and wrapped-up prey (pers. obs.), which suggests that chemotactile information may be of importance to these bugs. *Purumitra* sp. and *A. katherina* spend most of their time resting at the hub of their web (as many orb weavers; Eberhard, 1973; Blackledge & Wenzel, 2001); it is possible that this region of the web has a higher or different constitution of chemotactile cues than the rest of the web. This could explain why *S. giraffa* tapped empty hubs in this study. However, it is also possible that visual stimuli guided this behavior.

Many spider predators or parasitoids are known to use chemical cues to locate spiders or direct their attacks (e.g., van Baarlen, Topping, & Sunderland, 1996; Uma & Weiss, 2010; Wignall & Taylor, 2009). For instance, chemotactile cues are necessary to produce stinging behavior in the spider-hunting wasps *Sceliphron caementarium* and *Agenoideus humilis* (Eberhard, 1970). Thus, it would be worthwhile to explore the function of decorations from a chemosensory and tactile perspectives in addition to the visual domain. Some species of spiders incorporate their shed cuticles into detritus decorations (Eberhard, 1973; Sewlal, 2016), possibly to cause chemotactile confusion, as suggested by Eberhard (2003) for *Allocyclosa bifurca*. The decorations of *Cyclosa* spiders are often composed of prey carcasses or egg sacs; these have been shown to divert the attacks of *Vespa affinis* (Vespidae) (Chou et al., 2005; Tseng & Tso, 2009). It is possible that these wasps are confused by visual stimuli from the decorations as suggested by the authors of these studies. It is also possible that the confusion arises from chemical stimuli, or a combination of visual and chemical information.

In summary, the decorations in the webs of spiders may provide protection against predatory attacks, by providing visual or chemical cues that interfere with the process of locating the spider within the web. The observations from this study give partial support to this idea, which was originally proposed by Hingston (1927). However, direct testing of this hypothesis through experimental manipulation is needed. It would be worthwhile to further investigate if the apparent confusion of *S. giraffa* and other predators (e.g., wasps) arises from visual information (as proposed by Hingston), chemical information, or from a combination of both types of stimuli.

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