Title: What is the function of orb-web spider decorations?

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Date: 28-04-2023

Abstract:

Spiders in the families Araneidae, Uloboridae and Tetragnathidae sometimes include conspicuous constructions in their orb-webs called 'decorations' or 'stabilimenta'. These decorations consist of silk, debris and/or egg sacks and occur in several shapes including linear, cruciate, disc, spiral or tuft forms. The possible function of these web decorations is addressed by various hypotheses. Most studies have assumed a visual function that serves to (1) attract prey, (2) offer predator protection or (3) avoid inadvertent web damage by non-prey. Other hypotheses exploring non-visual functions have received considerable less attention. Despite a body of literature and several reviews no consensus has been reached. In this essay I addressed what the function of web decorations is. Decorations attract predominantly flying prey through UV-reflectance, which leads to increased prey-capture rates in most but not all studies. Well-fed spiders display a higher decoration frequency and decorated webs are smaller than undecorated webs, which suggests that decoration construction may be an alternative forage tactic. Several decoration types offer protection from predators, but some spiders exposed to predator cues decrease decoration frequency and decorations can also attract predators. Decorated webs sustained less damage likely by acting as a warning signal to non-prey, but this topic is under investigated. Finally, silk decoration frequency may be regulated by aciniform silk glands, which may explain the considerable silk decoration frequency. All in all decorations appear to function mainly as a visual signal, whose exact function may be determined by the decoration type and local environmental circumstances.

Introduction

Spiders (Araneae) are renowned for their silk production and utilization. While silk is deployed in a variety of ways including protection, travel and mating (Brunetta & Craig, 2010), its most noticeable use is to catch prey generally through trap-like structures. The traps commonly known as webs alert the spider to the presence of prey, and some webs can intercept and restrain prey through entanglement and special adhesives like glue droplets (Bott et al., 2017). Web-building spiders show a wide variety in the type of webs constructed and can be categorized in several distinct web types. One common type is the orb-web. It consists of a framework with vertical radial threads, sticky spiral capture silk, and a hub where the spider may be located (Figure 1) (Anotaux et al., 2012). The orb-web is usually suspended vertically, horizontally or at an inclination depending on the spider family / species (Herberstein et al., 2000a). Orb-web construction occurs in several spider families, of which the Araneidae family is one of the largest group of spiders (188 genera & 3119 species), surpassed only by sheet weavers (Linyphiidae: 635 genera & 4822 species) and jumping spiders (Salticidae: 672 genera & 6534 species) (World Spider Catalog, 2023).

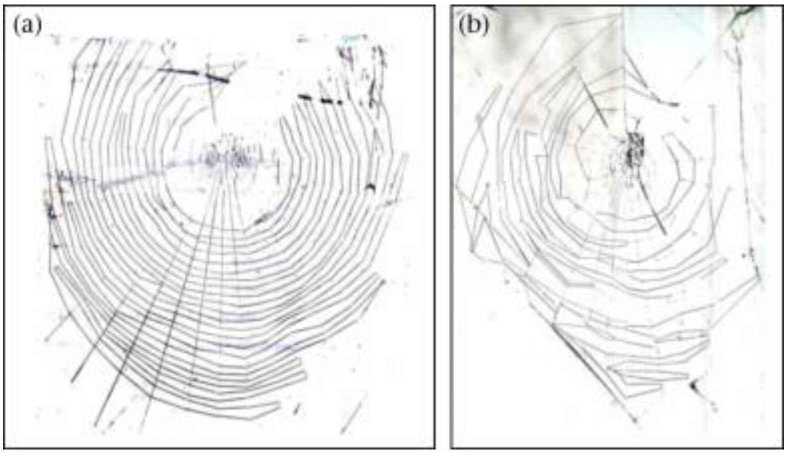

Figure 1: Photographs of webs built by Zygiella-x-notata. (a) The first web built by a spider 21 days old, (b) its last web 7 days before death. Figure from (Anotaux et al., 2012).

Some orb-web spiders across different families (Araneidae, Tetragnathidae and Uloboridae) construct ‘decorations’ or ‘stabilimenta’ upon completion of their web. Decorations generally consist of silk, although debris, prey remains and/or egg sacks can also be used. Decorations vary in form and location on the web, with linear, cruciate, disc, and spiral forms usually located centrally near the hub, whereas tufts are spread throughout the web (Figure 2) (Herberstein et al., 2000a). Linear and cruciate designs can deviate in the completeness of construction with 1 arm for linear or 1, 2 and 3 arms for cruciate forms (Herberstein, 2000; Kim et al., 2012). Incomplete forms are generally not completed later, but retained until the end of the web’s use. The form of web ornamentations varies both ontogenetically and phylogenetically. For example, in some *Argiope* species juveniles add silk discs to the web's centre, whereas adults use linear or cruciate patterns (Herberstein et al., 2000a; Seah & Li, 2002). Moreover, the frequency of decoration varies between species, populations, individuals and even within individuals (Herberstein et al., 2000a). To illustrate, the proportion of decoration construction of *Argiope appensa* populations varied from 16.4% to 56.9% between the neighbouring Mariana Islands, and *A. argentata* varies between 24.5% on Galápagos to 75.4% on Jamaica (Kerr, 1993). Moreover, the proportion remained stable on the Mariana Islands for 100 spider generations (Kerr et al., 2021). Individual spiders can switch between either decorating or not when they construct a new web (Bruce, 2006), and some spiders switch between decoration types, even in a constant environment (Walter & Elgar, 2016).

Figure 2: Various silk type decorations. (A) linear (Starks, 2002), (B) cruciate, (C) Discoid (Kerr et al., 2021), (D) Spiral (Tan et al., 2010), Tufts (https://uwm.edu/field-station/bug-othe-week-spinybacked-orbweaver-a-spider-for-snowbirds/)

Decoration behaviour is influenced by a plethora of factors like developmental stage (Herberstein et al., 2000a), energetic state (Seah & Li, 2002; Watanabe, 1999, but see Tso, 1999), aciniform glands silk reserve (Tso, 2004), moult to adulthood (Walter et al., 2008a), predator cues (Li

& Lee, 2004; Nakata, 2008, 2009), prey interception rate (Herberstein et al., 2000b), prey type history (Craig et al., 2001), light condition (Elgar et al., 1996; Seah & Li, 2002; Herberstein & Fleisch, 2003) and temperature (Herberstein & Fleisch, 2003). This may confound research on the function of web decorations as it may prove difficult to consider all factors and their relative importance, and may hinder comparisons between studies. The variable nature of decoration construction and abundance of factors influencing decoration behaviour suggest that it's function is highly adaptive and conditional on several factors at once. In this essay I address the question: what is the function of (orb-web) spider decorations?

A variety of hypotheses explain the function of web decorations. The more investigated hypotheses state that decorations serve to (1) attract prey to the web, (2) protect spiders from predators or (3) advertise the web's presence to prevent accidental destruction. Other hypotheses that have received considerable less attention propose that decorations function as thermo-, stress- or silk regulation, or as mechanical support (Bruce, 2006). The thirst 3 hypotheses assume a visual signal function of web decorations. As humans are visually oriented and web decorations are conspicuous to us, it may explain why most research has investigated vision based hypotheses and why most evidence supports the first 3 mentioned hypotheses. In accordance this essay will mostly revolve around reviewing and discussing the more prominently featured hypotheses of web decorations as (1) prey attraction, (2) predator protection and (3) web advertisement.

Despite several reviews on the topic no consensus has been reached, perhaps unsurprising given the variety in decoration behaviour and reported contradicting results (Herberstein et al., 2000a; Starks, 2002; Bruce, 2006; Walter & Elgar, 2012). The apparent contradictions may be (partially) due to differences in methodology, but it may also reflect an adaptive nature of silk decorations (Bruce, 2006) as the hypotheses are not mutually exclusive. Studies find support for several hypotheses within the same species (Walter & Elgar, 2012). Decorations may be a conditional strategy serving multiple functions depending on environmental conditions (Seah & Li, 2002; Starks, 2002; Bruce, 2006). For example, a web decoration can attract prey like pollinators (Gálvez, 2009) and also offer protection from predators like mud-dauber wasps (Blackledge & Wenzel, 2001). However, prey attraction may also have a trade-off, as decorations can attract predators such as the jumping spider *portia labiata* (Li & Lim, 2005). The potential decorations to perform multiple functions may therefore be dependent on environmental factors like the type of prey and predators present. Therefore, while this essay will review support for several hypotheses, the aim in not to determine a single most likely hypotheses, but to find a general rule on how to determine what particular function(s) a web decoration may have in a population.

Findings

Prey attraction

While the conspicuousness of web decorations is rather obvious to humans it does not mean that stabilimenta are a visual signal. The aim of a spider web is, after all, to catch prey and should be inconspicuous to prey. If a web could attract prey however, the web need not be inconspicuous or may even profit from an increase in conspicuousness. Spider webs of mygalomorph, primitive and derived cribellate spiders reflect ultra-violet light, which may mimic UV-light patches caused by gaps in vegetation or flowers. This may attract prey through elicitation of a flight response or attract pollinators (Craig & Bernard, 1990). Interestingly, webs from 3 araneids (orb-weavers) did not reflect UV-light, but silken decorations did (Craig & Bernard, 1990). UV-reflectance is confirmed for different silken decoration types including linear and spiral decorations from *Octonoba sybotides* (Watanabe, 1999a), discoid decorations spun by *Argiope versicolor* juveniles (Li et al., 2004) and cruciate forms from *Argiope keyserlingi* (Blamires et al., 2008). Silk decorations form a strong chromatic and achromatic contrast detectible by bees and birds over long and short distances in 4 *Argiope* and one *Zosis* species (Bruce et al., 2005) and in *Cyclosa ginnaga* (Tan et al., 2010). Studies investigating the UV-reflectance of silk decorations have also found that adorned webs exhibit higher prey-capture rates than unadorned ones (Craig & Bernard, 1990; Watanabe, 1999a; Li et al., 2004), or captured more of certain prey types sensitive to UV-light (Blamires et al., 2008). When UV-light was blocked by a filter decorations became less attractive (Watanabe, 1999a; Li et al., 2004; Blamires et al., 2008). It is therefore argued that web decorations are a visual signal that attract prey.

Many studies found an increased prey-capture rate for decorated vs undecorated web (parts), some (older) research by directly relating decoration presence with the prey caught (Table 1). Some issues raised to this straightforward approach have been accounted for in later studies. First of all, well-fed spiders display a higher decoration frequency than lesser fed spiders (Craig et al., 2001; Seah & Li, 2002; Tso, 2004). As one would expect increased foraging effort in response to hunger it appears contradictory to the attraction hypothesis. Furthermore, simply relating decoration presence and increased prey-capture rate does not prove causality. It may be that spiders experiencing high prey-capture rates simply forage more successfully (Blackledge, 1998) or experience higher prey abundance, which results in well-fed spiders that in turn increase decoration frequency. Studies have accounted for this in several ways including assessment of local prey availability (Watanabe, 2001; Tan et al., 2010), directly testing functionality by concealing (Tseng et al., 2011) or removing decorations (Bruce et al., 2001, 2004) and testing attraction to artificial decorations (Tso, 1998a), which have all found increased prey-capture rates for decorations. Although generally not all issues are considered, these studies still provide more robust support for the prey attraction hypothesis.

Table 1: Summary of studies exploring the function of the 3 visual hypotheses.

Species	Study	Type	Test	Prey attraction		Predator protection		Advertisement		
				✓	✗	✓	✗	attraction	✓	✗
Argiope keyserlingi	(Bruce et al., 2001)	cruciate	observation, direct	✓				✓, *mantid*		
Araneus eburnus	(Bruce et al., 2004)	linear	observation, direct	✓						
Argiope argentata	(Craig & Bernard, 1990)	cruciate	direct*(?)	✓						
Argiope savignyi	(Gálvez, 2009)	cruciate	direct	✓						
Micrathena sexspinosa	(Gálvez, 2011)	linear	direct	✓						
Argiope appensa	(Hauber, 1998)	cruciate	observation	✓	X					
Argiope keyserlingi	(Herberstein, 2000b)	cruciate	observation	✓			X			
Argiope bruennichi	(Kim et al., 2012)	linear	indirect	✓						
Argiope versicolor	(Li et al., 2004)	discoid	direct, indirect	✓						
Cyclosa ginnaga	(Tan et al., 2010)	silk & detritus	observation	✓						
Thelacantha brevispina	(Tseng et al., 2011)	tufts	direct	✓						
Argiope trifasciata	(Tso, 1996)	linear	observation	✓						
Argiope trifasciata, A. aurantia	(Tso, 1998a)	linear	direct	✓						
Cyclosa conica	(Tso, 1998b)	linear	observation	✓						
Octonoba sybotides	(Watanabe, 1999a)	linear, spiral	direct, observation	✓						
Argiope trifascia	(Blackledge & Wenzel, 2001)	linear	observation			✓		X		
Allocyclosa bifurca	(Eberhard, 2003)	various	observation, indirect			✓				
Araneus expletus	(Eberhard, 2008)	disc / matt	observation			✓				
Cyclosa fililineata, C. morretes	(Gonzaga & Vasconcellos-Neto, 2005)	linear detritus	direct, artificial		X	✓				
C. fililineata, C. morretes	(Gonzaga & Vasconcellos-Neto, 2012)	silk & detritus, linear	observation			✓				
Argiope aurantia, A. trifasciata	(Horton, 1980)	cruciate	direct			✓			✓	
Argiope appensa	(Kerr, 1993; Kerr et al., 2021)	cruciate	observation			✓			✓	
Argiope versicolor	(Li et al., 2003)	disc, cruciate	indirect			✓				
Argiope argentata	(Lubin, 1974)	cruciate	observation			✓				
Eriophora sagana	(Nakata, 2008)	linear	indirect			✓				
Cyclosa argenteoalba	(Nakata, 2009)	linear	indirect		X	✓				
Argiope argentata	(Schoener & Spiller, 1992)	discoid, cruciate	indirect			✓				
Argiope aurantia	(Blackledge & Wenzel, 1999)	linear	indirect		X				✓	
Various	(Eisner & Nowicki, 1983)	cruciate	direct (artificial)						✓	
Gasteracantha cancriformis	(Jaffé et al., 2006)	tufts	observation						✓	
Argiope keyserlingi	(Walter & Elgar, 2011)	cruciate	indirect						✓	

Gasteracantha cancriformis	(Gawryszewski & Motta, 2008)	tufts	direct	X		X
Argiope versicolor	(Zou et al., 2011)	cruciate	direct		✓, *jumping spider*	

One potential issue is that decorated webs tend to be smaller than undecorated ones (Hauber, 1998; Tso, 1998b; Bruce et al., 2004). Some studies that found similar prey-capture rates for decorated and undecorated webs therefore propose that decorations can form an alternative foraging strategy. A detailed look into types of prey caught more by decorated webs revealed that specific groups of insects such as houseflies, blowflies, stingless bees, honeybees and vespid wasps are attracted to adornments of *A. keyserlingi* (Blamires et al., 2008). Though decorated webs exhibited higher prey-catch rates, both adorned and unadorned webs caught a considerable and similar amount of orthopterans, showing that not all prey caught in decorated webs are necessarily attracted to decorations (Tso, 1996, 1998a). The attractive effect of decorations may therefore only be relevant when such groups are abundant, which may also explain why some studies find no increased prey-capture rate of web decorations (Hauber, 1998; Blackledge & Wenzel, 1999; Gonzaga & Vasconcellos-Neto, 2005; Gawryszewski & Motta, 2008; Nakata, 2009).

Given that the biomass of caught prey can vary considerably, the total number of caught prey or the prey-capture rate may be rather less important than the capture of a few large prey, which may even provide most of the biomass to spiders (Blackledge, 2011). Though the relation between prey size and biomass is not easily calculated due to the variety of body shapes in arthropods (Eberhard, 2013), size variability may still pose an issue for studies utilizing a metric dependent on the total number of prey caught, like most studies discussed so far. However, decorated webs caught more than twice as many insects over 5mm compared to undecorated webs in *Argiope bruennichi*, suggesting that decorations may attract larger prey (Kim et al., 2012). Also, Blackledge (2011) suggested that smaller webs may be better at stopping large prey if spun from thicker and tighter threads. Considering that decorated webs are generally smaller than undecorated webs (Hauber, 1998; Tso, 1998b; Bruce et al., 2004) they may be more suited for catching larger prey. The exact relationship of prey body size, biomass and total number caught and its ramifications on the function of decorations as prey attractant remains to be investigated, but could have important implications.

Predator avoidance and web advertising

Another hypothesis that assumes a visual function states that decorations serve as protection from predators. Debris decorations appear to mostly protect through camouflage by hiding the spider’s outline or body (Eberhard, 2003; Gonzaga & Vasconcellos-Neto, 2005, 2012). Silk decorations may function similarly (Lubin, 1974), or protect by increasing the spider's apparent size (Schoener & Spiller, 1992) or act as a warning signal (Horton, 1980). Silk decorations may also delay predators through distraction or camouflage, providing time for the spider's escape from the web (Blackledge & Wenzel, 2001). Testing for a predator defence function is more difficult compared to prey attraction, which may explain why there are fewer (direct) studies on the topic (Table 1).

One study used artificial decorations and spider models which did not attract prey, but did show a camouflage function (Gonzaga & Vasconcellos-Neto, 2005). Another directly tested the effect of decorations on predation by naïve and experienced blue jays (Horton, 1980). Other studies performed indirect tests or observations that imply anti-predator functionality. Predator avoidance behaviour in *Argiope versicolor* appears specific to age and silk decoration type produced (Li et al., 2003), and both *Eriophora sagana* and *Cyclosa argenteoalba* spiders increase silk decoration area size in their next web in response to a tuning fork, considered a mimic of flying predator cues (Nakata, 2008, 2009). *Philoponella vicina* (Eberhard, 2007) and *Gasteracantha cancriformis* (Jaffé et al., 2006; Eberhard, 2007) adorn webs not used for catching prey with silk tufts, which argues for a function other than prey attraction.

Although decorations may hide the spider from predators, they may also function as a warning signal to avoid inadvertent web damage by non-prey. A predator defence and web advertisement function can in fact be hard to disentangle. Horton (1980) observed that inexperienced birds show no forage preference for spiders on or off their web, but learned to avoid webs later, presumably because the web stuck to their body. Webs containing decorations enhanced this behaviour, which suggests a protective function that both prevents predation and web damage. Other research discovered that artificially decorated webs remained intact longer than undecorated webs (Eisner & Nowicki, 1983) and naturally decorated webs were less likely to sustain damage by birds (Blackledge & Wenzel, 1999). *A. keyserlingi* responded to substantial web damage by increasing decoration size, but did not respond similarly to minor web damage (typically caused by prey) (Walter & Elgar, 2011). *A. appensa* exhibited considerably lower decoration frequency on Guam (16.4 %) compared to other islands (41.9 – 56.9 %) in the Mariana Archipelago (Kerr, 1993) and remains lower to this day (Kerr et al., 2021). Considering that Guam lost nearly all birds due to the invasive snake *Boiga irregularis* but that other isles retain their native fauna, a lower frequency may be related to a lack of animals potentially damaging the web. Kerr et al. (2021) suggests that the lack of bird predators caused an increase in arthropod presence. This may further explain a lower decoration frequency as increased prey presence may trivialize attraction by decorations.

Increased arthropod presence may lower decoration frequency for another reason. Some predators like the jumping spider *P. labiata* (Seah & Li, 2001; Li & Lim, 2005) and mantid *Archimantis latistylus* (Bruce et al., 2001) are attracted to decorations, and *A. argentata* spiders in decorated webs suffered lower survivorship (Craig et al., 2001). *A. versicolor* juveniles reduced decoration frequency and size in response to chemical cues from the jumping spider *P. labiata* (Li & Lee, 2004), but *A. keyserlingi* adults did not alter web or decoration construction in the presence of the mantid *Pseudomantis albofimbriata* (Bruce & Herberstein, 2006). A general increase in arthropod presence may also increase presence of predators attracted to decorations, leading to selection on lower decoration frequency. This reiterates the potential importance of environmental conditions in determining the function of decorations.

Non-visual hypotheses

Other hypotheses ascribing non-visual functions to web decorations are understudied (Bruce, 2006). A mechanical strengthening function was proposed as early as 1895 but lacks support, and considering that decorations are loosely attached to the web and unrelated to wind conditions it seems unlikely (Herberstein et al., 2000a; Bruce, 2006). One study found that *Neogea* spp. individuals regulate body temperature by shuttling to and from the shaded side of disc-shaped decorations, which can therefore provide a thermoregulatory function (Humphreys, 1992). But most decoration types like cruciate and linear designs (Figure 2) are unable to provide shade, and decorations are generally found in dim light (Herberstein et al., 2000a). A thermoregulatory function is therefore likely inapplicable to most decorations and might have evolved as a secondary function.

Silk regulation is another proposed function for silk decorations. *Argiope* spiders immobilize prey by wrapping them in aciniform silk before killing them, and exhibit highly active aciniform glands (Walter et al., 2008b). A high prey-capture rate likely stimulates aciniform gland productivity which may result in aciniform silk build up, possibly prompting the spider to deposit it onto the web. In *Argiope aetheroides* aciniform silk depletion resulted in a reduced decoration frequency, suggesting a threshold in aciniform silk availability linked to decoration construction (Tso, 2004). It should be noted that this study lacks a control group and has low sample size (n = 7). Also, in 3 other *Argiope* species gland stimulation through prey removal after wrapping resulted in increased decoration frequency (Walter et al., 2008b). These findings may both explain why well-fed spiders exhibit increased decoration frequency (Craig et al., 2001; Seah & Li, 2002; Tso, 2004) and the wide variability in decoration frequency between studies. It also offers a proximate explanation of silk decoration regulation that could be combined with visual functions of decorations, though possibly not for spiders producing non-aciniform decorations.

Discussion

The precise function of web decorations remains a controversial topic to date. Decorations can clearly be attractive to specific types of prey and lead to increased prey-capture rates in most but not all studies. Considering that well-fed spiders display a higher decoration frequency and that decorated webs are smaller than undecorated webs, decoration construction may be an alternative forage tactic. The relation between prey-capture rate and biomass should be investigated as prey biomass may be more relevant to a spider than sheer prey numbers. How a decoration can offer protection from a predator likely depends on the decoration – and predator type. Some decorations can attract rather than ward off predators, so the decoration frequency and protectiveness may be dependent on the prevalence of particular predators types. Decorations may also serve as a warning signal to prevent inadvertent damage by non-prey, but there is a lack of studies on this topic. Regulation of aciniform silk offers a promising proximate explanation of silk decorations and should be further investigated. All in all decorations appear to function mainly as a visual signal.

Decoration frequency

The variability in decoration frequency and form can be somewhat challenging to explain. The body of literature about the advantages that decorated webs may provide begs the question why spiders not always decorate their web, especially if it is to act as a signal. Several reasons may explain this. (1) Decorations can attract predators (Bruce et al., 2001; Seah & Li, 2001; Li & Lim, 2005) which may make decorations a strategy only viable in low abundance or absence of certain predators. This poses an issue when only considering one ability of decorations, for example to attract prey given that well-fed spiders display a higher decoration frequency. When considering that decorations may additionally offer protection against predators and prevent inadvertent web destruction even in the same species (Walter & Elgar, 2012), predator attraction becomes somewhat less problematic. (2) Some prey attracted to decorations like stingless bees can learn to avoid decorated webs, though they could not apply this learned behaviour to similarly decorated webs on other sites (Craig, 1994). Daily variation in decorations slowed the association learning, suggesting that variation in decoration frequency and type serves to prevent prey from learning to avoid decorated webs. (3) Finally, variation in silk decoration frequency may result from variation in aciniform gland stimulation related to prey wrapping (Walter et al., 2008b) or presence of a threshold in the glands (Tso, 2004). While this is a promising explanation that offers a proximate explanation, the relation between aciniform gland activation & storage and prey wrapping & consumption requires further study. Reason 1 may be more broadly applicable given that reason 2 also assumes prey attraction and reason 3 only applies to the prey-wrapping genus *Argiope*. But so far the only predators known to be attracted to decorations are jumping spiders and mantids, and only to cruciate silk decorations. Decorations consisting of silk tufts, debris or egg-sacks may not be as attractive to either prey or predator (Table 1). The variation in decoration frequency is therefore not fully explainable and requires further investigation.

Decoration function

Different web decoration types occur in several spider families at once. Araneidae and Uloboridae spiders construct linear, cruciate, discoid, spiral and debris types, and Tetragnathidae spiders construct both linear and debris types (Herberstein, et al., 2000a). Decoration types were phylogenetically uninformative in one study, which could only add presence or absence of decoration types after tree construction based on other spider characterstics (Scharff & Coddington, 1997), which suggests that decoration types represent a convergent state (Herberstein, et al., 2000a). Still, assessment of phylogeny may help establish the evolutionary origin and original function, and provide information on current functions of web decoration. For example, in Asian *Argiope* spiders the linear decoration type likely represents the ancestral state, from which the cruciate form derived presumably because insects prefer bilateral symmetric patterns (Cheng et al., 2010). Flying insects were indeed more attracted to both artificial and natural silk cruciate designs than linear ones (Cheng et al., 2010). Walter & Elgar (2012) propose that silk decorations may have originally evolved as a silk regulatory mechanism or storage for aciniform silk. Subadult *A. keyserlingi* spiders produce 'supersized' silk decorations just prior to their moult into adulthood (Walter et al., 2008a) which may act as a temporary storage of aciniform silk as they generally consume their web before constructing a new one. Silk decorations may therefore have evolved into a visual signal only later on, with specific types fitting particular environments and functions. However, this is likely not the case for non-silk decorations, as they cannot serve as silk regulation or storage. Possibly silk and non-silk decorations have a different evolutionary origin. This may be difficult to investigate for now, as most literature about decorations is based on some well-known genera like *Argiope*.

Web decorations can likely serve multiple functions, but the supporting literature could stand to improve. Most studies relied on observations or indirect tests which can provide useful implications, but considering the plethora of factors influencing decoration behaviour lack the convincing power of direct tests. The lack of any study directly measuring the effects of web decoration on spider fitness further argues for some scrutiny. Although some studies have investigated several hypotheses at once (Table 1), they generally do not find support for more than one. This is somewhat surprising given that multiple functions were found for the same spider species across studies (Walter & Elgar, 2012). Perhaps decorations mainly serve one particular function, but what function that is may vary between populations. Future research should nonetheless assume multiple functions to apply simultaneously. One line of research could be to investigate the populations of a species for which multiple decoration functions were found in different studies, and measure the different environmental properties. This may shed some light on which circumstances result in which decoration functions. Measured properties should include factors know to influence decoration behaviour like prey and predator type presence, light condition (Elgar et al., 1996; Seah & Li, 2002; Herberstein & Fleisch, 2003) and temperature (Herberstein & Fleisch, 2003). Other factors like the energetic state (Seah & Li, 2002; Watanabe, 1999, but see Tso, 1999), prey interception rate (Herberstein et al., 2000b) and prey type history (Craig et al., 2001) may prove difficult to assess or control, but may still be worthwhile. Future research on decoration function should take care to (1) distinguish between silk and non-silk decoration type and asses (2) specific prey types caught, (3) local prey and predator types and abundance and (4) presence of non-prey that may damage the web. This may allow for better comparisons between future studies and possibly show what exact factors determine the function of web decorations.

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