Journal of Zoology. Print ISSN 0952-8369

Silk decorations: controversy and consensus

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Keywords
stabilimenta; visual signals; foraging behaviour; anti-predator behaviour; Araneae.

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Received 7 April 2005; accepted 8 September 2005

doi:10.1111/j.1469-7998.2006.00047.x

Abstract

Although the occurrence of silk decorations has been noted in scientific literature for over 100 years, there is still little consensus as to their function. This is despite the proliferation of studies examining the five major hypotheses: (1) protection against predators, (2) increasing foraging success, (3) prevention of damage to the web, (4) providing shade and (5) mechanical support for the web. The first three of these hypotheses have received the most attention, and thus generated the most evidence (for and against) suggesting that web decorations are a type of visual signal. However, the effect of this signal on prey and predator receivers is unclear as the evidence is contradictory. Thus, the function of silk decorations may be context specific, depending on factors such as predators, prey, background colour and ambient light. A better understanding of how predators and prey see and process visual information from silk decorations, coupled with experiments examining the mechanisms behind the various hypotheses, are crucial in illuminating their function and resolving the controversy.

Introduction

Web decorations or stabilimenta are included in webs by a diverse range of orb-web spider species (Araneae: Araneidae, Tetragnathidae, Uloboridae). These structures have attracted the attention of scientists for over 100 years. Since their first description by McCook (1889), the function of these curious structures has remained the subject of considerable controversy. Although materials other than silk such as vegetation, egg sacs and prey leftovers can decorate webs, this review will concentrate on decorations consisting only of silk (silk decorations). Silk decorations are constructed of the same silk as that used by orb-web spiders to wrap prey. This silk originates from the aciniform and piriform glands (Peters, 1993; Foelix, 1996).

Silk decorations have evolved at least nine times in three families (Araneidae, Uloboridae and Tetragnathidae) and have been described in 22 genera (Scharff & Coddington, 1997). The form and shape of silk decorations can be categorized into cruciate, linear, discoid, spiral, tufts and an indistinct silk mat (Fig. 1). Furthermore, there is a considerable degree of ontogenetic and phylogenetic variation in decorating behaviour. In *Argiope* sp., juveniles and adults of the same species construct different types (usually discoid in juveniles and cruciate or linear in adults; e.g. Seah & Li, 2002). Furthermore, different species and populations of the same species decorate at different frequencies and individuals can alter their decorating behaviour on a daily basis. This variation has only added to the controversy surrounding decoration function as researchers have attempted to identify the factors contributing to this variation.

In 2000 Herberstein *et al.* (2000*a*) published their seminal review on evidence for (and against) the various functional hypotheses for silk decorations. Since their review this field of study has expanded greatly. A number of new research articles have been published testing the traditional hypotheses. Moreover, new research into factors influencing the construction of silk decorations and the spectral nature of silk decoration reflectance has been published. Encouragingly, many studies have attempted to use field and laboratory experiments to test various hypotheses (Table 1). This represents a shift away from the observational and correlative studies of the past. Furthermore, researchers have moved away from the traditional model genus *Argiope* into other decorating groups such as *Allocyclosa* (Eberhard, 2003), '*Araneus*' (Bruce *et al.*, 2004) and *Octonoba* (Watanabe, 2000).

The aim of this review is twofold. First, I will summarize recent progress in this field, since the review of Herberstein *et al.* (2000*a*). Second, I aim to assess how some of the higher impact studies reviewed by Herberstein *et al.* (2000*a*) have influenced the recent work and in some cases have been superseded by them. I will also pay attention to new areas of study within this field and see how they fit into the overall body of knowledge. I will deal with each of the main hypotheses that have received recent attention in turn as well as with studies focusing on the factors influencing decoration construction, visual nature of the signal and physiological consequences for the spider.

Function of silk decorations

Anti-predator

Silk decorations may act as anti-predator devices in a number of ways. They may make the spider appear larger,

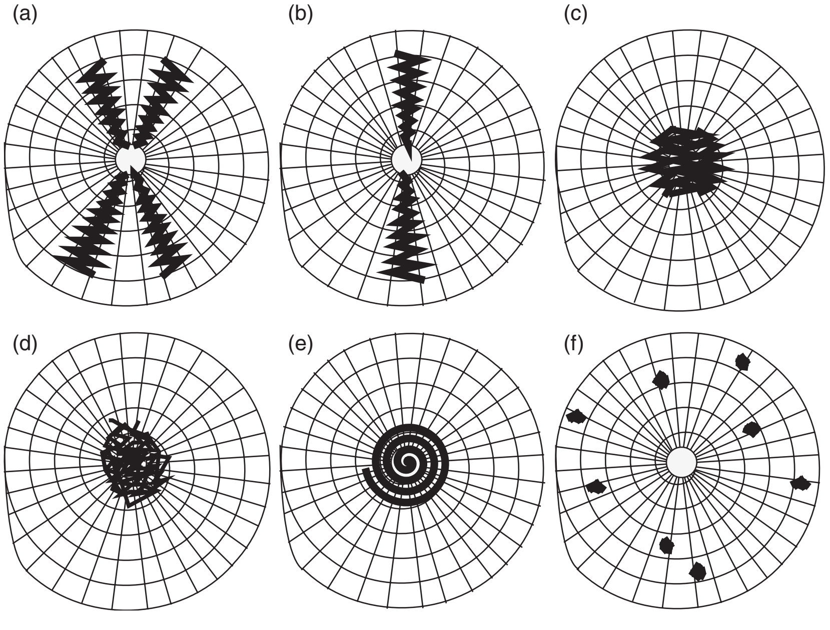

Figure 1 Silk decoration forms: (a) cruciate, for example *Argiope versicolor*, (b) linear, for example '*Araneus*' *eburnus*, (c) discoid, for example juvenile *Arg. versicolor*, (d) irregular mat, for example *Zosis geniculatus*, (e) spiral, for example *Octonoba sybiotides* and (f) tuft, for example *Gasteracantha minax*.

act as a warning signal or camouflage the location of the spider (Ewer, 1972; Eberhard, 1973). Despite being one of the most enduring hypotheses, the anti-predator function received very little direct experimentation. However, some recent evidence for an anti-predator function has emerged. Decorating spiders *Argiope trifasciata* in artificial enclosures were less likely to be taken by predatory wasps than their non-decorating counterparts (Blackledge & Wenzel, 2001). Spiders have also been shown to exhibit decoration-specific anti-predator behaviours. Juveniles of *Argiope versicolor* on webs with discoid decorations were more likely to shuttle to the other side of the web, perhaps to use the decoration as a physical barrier (Li *et al*., 2003). Adult spiders on cruciate decorated webs are more likely to pump the web and this movement may deter gape-limited predators or obscure the outline of the spider (Li *et al*., 2003). Further evidence for an anti-predator function comes from *Allocyclosa bifurcata*. This spider places egg sacs and silk in a line, with the spider at the approximate mid-point. To the human observer, the egg sacs obscure the position of the spider at the hub. The experimental removal of egg sacs induced spiders to construct silk decorations, lending indirect support to the camouflage hypothesis (Eberhard, 2003). This study is of particular note as it directly tackled one of the anti-predator mechanisms and also examined a genus other than the well-studied *Argiope*.

Some of the other recent evidence suggests that decorations actually attract some species of predators. In *Argiope keyserlingi*, the predatory praying mantid *Archimantis latystylus* was attracted to both occupied and unoccupied decorated webs (Bruce *et al*., 2001) in Y-choice tests. A similar result has been reported for *Arg*. *versicolor*, whose jumping spider predators were attracted to silk decorations (Seah & Li, 2001). However, both of these studies were conducted in the laboratory, which may not mimic the natural conditions. Perhaps more compelling evidence for predator attraction to decorations comes from the work of Craig *et al*. (2001), who found that in the field more frequent decorators suffer reduced survivorship. Furthermore, juvenile *Arg*. *versicolor* reduce the frequency of augmenting their webs in the presence of chemical cues from their jumping spider predators (Li & Lee, 2004). The anti-predator function is far from being universally accepted and more direct evidence is required. The lack of direct evidence is understandable given the difficulty in identifying and performing experiments with key spider predators. Furthermore, few authors have directly tackled the mechanism by which decorations could deter predators.

It is also unclear how different decoration patterns may influence their potential anti-predator function. For example, it has been proposed that in medium-sized *Argiope argentata* cruciate decorations extend the apparent length of spider legs, thus protecting spiders against gape limited predators (Schoener & Spiller, 1992). However, this idea has not been experimentally tested. It would be easy to manipulate the size of this leg extension by placing small spiders on large decorations and then recording the responses of predators. Furthermore, disc decorations may form a physical barrier between the spider and a predator or even hide the spider from predators (Li *et al*., 2003). Assessing the ability of predators to attack spiders shielded by a disc compared with those not shielded could quite easily test this idea.

Prey attraction

The prey attraction hypothesis has been around for almost as long as the anti-predator hypothesis. It has received more attention in the literature possibly because it is far easier to conduct prey capture surveys than observe predation events and it is also easier to identify important prey species than

Table 1 Summary of studies on silk decoration function, the nature of silk decoration silk reflectivity and factors influencing their construction and variability

Subject of study	Species	Type of test	Source
Functions			
Anti-predator	*Allocyclosa bifruca*	Indirect (laboratory experiment)	Eberhard (2003)
	Argiope versicolor	Indirect (laboratory experiment)	Li *et al.* (2003)
	Argiope trifasciata	Direct (field enclosures)	Blackledge & Wenzel (2001)
	Argiope keyserlingi	Direct (Y-choice)	Bruce, Herberstein & Elgar (2001)
	Argiope argentata	Indirect (field correlation)	Craig *et al.* (2001)
	Arg. versicolor	Direct (Y-choice)	Seah & Li (2001)
	Arg. argentata	Indirect (field correlation)	Schoener & Spiller (1992)
	Cyclosa insulana	Indirect (field correlation)	Neet (1990)
	Various	None	Edmunds & Edmunds (1986)
	Argiope flavipalpis	None	Edmunds (1986)
	Argiope aurantia, Arg. trifasciata	Direct (laboratory experiment)	Horton (1980)
	Argiope aemula, Arg. argentata	None	Robinson & Robinson (1978)
	Arg. aurantia, Arg. trifasciata	None	Tolbert (1975)
	Uloborus diversus	None	Eberhard (1973)
	Arg. flavipalpis	None	Ewer (1972)
	C. insulana	None	Marson (1947*a*)
	Argiope punchella	Indirect (field observation)	Marson (1947*b*)
Foraging	*Argiope bruennichi*	Indirect (field correlation)	Prokop & Grygláková (2005)
	Arg. versicolor	Direct (Y-choice) and indirect (field correlation)	Li *et al.* (2004)
	'Araneus' eburnus	Direct (field experiment) and indirect (field correlation)	Bruce, Heiling & Herberstein (2004)
	Arg. keyserlingi	Direct (field experiment and Y-choice)	Bruce *et al.* (2001)
	Arg. keyserlingi	Indirect (field correlation)	Herberstein (2000)
	Octonoba sybiotides	Indirect (laboratory experiment)	Watanabe (2000)
	Arg. aurantia, Arg. trifasciata	Indirect (field correlation)	Blackledge & Wenzel (1999)
	O. sybiotides	Direct (Y-choice) and indirect (field correlation)	Watanabe (1999*a,b*)
	Argiope appensa	Indirect (field correlation)	Hauber (1998)
	Arg. aurantia, Arg. trifasciata	Direct (field experiment)	Tso (1998*a*)
	Cyclosa conica	Indirect (field correlation)	Tso (1998*b*)
	Arg. trifasciata	Indirect (field correlation)	Tso (1996)
	Arg. argentata	Indirect (field correlation)	Craig (1991)
	Uloborus glomosus	Direct (Y-choice)	Craig & Bernard (1990)
	Arg. argentata	Indirect (field correlation)	Craig & Bernard (1990)
Web protection	*Arg. aurantia*	Direct (field experiment)	Blackledge & Wenzel (1999)
	Arg. appensa	Indirect (field observation)	Kerr (1993)
	Argiope florida, Arg. aurantia	Direct (field experiment)	Eisner & Nowicki (1983)
Mechanical	*C. insulana*	Indirect (field correlation)	Neet (1990)
	Arg. aemula, Arg. argentata	None	Robinson & Robinson (1978)
	Arg. aemula, Arg. argentata, Argiope picta, Argiope reinwardti	None	Robinson & Robinson (1974)
	Arg. argentata	None	Robinson & Robinson (1970)
	Various	None	Comstock (1912)
	Various *Argiope* spp.	None	Simon (1895)
	Various	None	McCook (1889)
Silk regulation	*Arg. bruennichi, Argiope lobata, Uloborus plumipes, Uloborous walckenaerius*	None	Peters (1993)
Reflex	*Arg. bruennichi*	None	Rabaud (1932)
Stress	*Arg. argentata*	Indirect (laboratory experiment and field observation)	Nentwig & Rogg (1988)
Thermoregulation	*Neogea* sp.	Indirect (field observation)	Humphreys (1992)

Table 1 Continued

Subject of study	Species	Type of test	Source
Construction and variation			
Hunger	*Argiope atheroides*	Direct (laboratory experiment)	Tso (2004)
	Arg. versicolor	Direct (laboratory experiment)	Seah & Li (2002)
	Arg. keyserlingi	Direct (laboratory experiment)	Herberstein, Craig & Elgar (2000*b*)
	Arg. trifasciata	Direct (laboratory experiment)	Tso (1999)
	O. sybiotides	Direct (laboratory experiment)	Watanabe (1999*b*)
	Arg. aurantia, Arg. trifasciata	Direct (laboratory experiment)	Blackledge (1998*b*)
Ambient light	*Arg. versicolor*	Direct (laboratory experiment)	Seah & Li (2002)
	Argiope aetherea	Direct (laboratory experiment)	Elgar, Allan & Evans (1996)
Various abiotic factors	*Arg. keyserlingi*	Indirect (correlations)	Herberstein & Fleisch (2003)
Presence of prey	*Arg. argentata*	Indirect (field correlation)	Craig *et al.* (2001)
Predator cues	*Arg. versicolor*	Direct (laboratory experiment)	Li & Lee (2004)
Heritability	*Arg. argentata*	Pedigree analysis	Craig *et al.* (2001)
Silk decoration reflectance	*Arg. aetherea, Arg. keyserlingi, Argiope mascordi, Arg. picta, Zosis geniculatus*	Calculation of visibility of silk to birds and bees against a common background	Bruce, Heiling & Herberstein (2005)
	Arg. versicolor	Spectrophotometry	Li *et al.* (2004)
	Various	Photography in UV+ and UV− light	Zschokke (2002)
	O. sybiotides	Spectrophotometry	Watanabe (1999*a*)
	Arg. argentata, Uloborus glamosus	Microspectrophotometry	Craig & Bernard (1990)
Phylogeny of decorations	Various	Morphological phylogeny of orb-web spiders	Scharff & Coddington (1997)

After Herberstein *et al.* (2000*a*) and Bruce *et al.* (2004)

predators for further experimentation. However, the prey attraction hypothesis is no less controversial than the anti-predator hypothesis. Surprisingly, it was not until 1990 that this idea received any serious experimental attention. In their groundbreaking study Craig & Bernard (1990) showed that in Y-choice experiments *Drosophila* were attracted to the silk decorations of *Uloborus glomosus*. Furthermore, they showed that decorated web halves intercepted more prey than undecorated halves. They also showed that web decoration silk was highly reflective in the ultraviolet (UV) spectrum of daylight. From this they proposed two potential mechanisms to explain their results. First, decorations resemble UV gaps in vegetation, eliciting escape behaviour in flying insects. Second, they may imitate the UV-reflective floral guides used by plants to attract pollinators. The work of Craig & Bernard (1990) has formed the basis for subsequent experimental studies on the influence of decorations on foraging success.

The prey attraction hypothesis has been tested in a number of ways. Y-choice experiments have demonstrated that a species of fly *Chrysomya varipes* was attracted to silk decorations of *Arg. keyserlingi* (Bruce *et al.*, 2001). However, most recent evidence for prey attraction comes from field correlations and experiments and from indirect correlates of decoration frequency. Furthermore, no study has attempted to test directly the mechanisms of prey attraction proposed by Craig & Bernard (1990).

Since the review of Herberstein *et al.* (2000*a*) there have been two field studies examining the influence of silk decorations on foraging success. In *Arg. keyserlingi* prey capture rate was correlated with web area in undecorated webs but not in decorated webs (Bruce *et al.*, 2001). The authors suggested that this is consistent with the prey capture hypothesis. A similar study on the distantly related *'Araneus' eburnus* found that decorated webs were smaller than undecorated webs, but captured similar numbers of prey animals (Bruce *et al.*, 2004). This suggests that spiders use alternative foraging strategies, small, decorated webs and large, undecorated webs (see also Hauber, 1998). In a manipulative experiment, webs with their decorations experimentally removed suffered a reduced rate of prey interception in an undisturbed habitat compared with decorated webs. Further evidence for the prey attraction hypothesis was found in *Arg. versicolor* juveniles. In Y-choice experiments, webs with discoid decorations attracted more *Drosophila* than those without, but only in the presence of UV light (Li *et al.*, 2004). This study is of particular interest because *Argiope* juveniles adorn their webs with different decoration patterns (discoid) than adults and sub-adults of the same species (linear or cruciate). Therefore, it is possible that the function of decorations differs with the age of the spider according to the pattern of silk decorations.

Although the Y-maze choice technique has been popular and often produced clear results, it may be too artificial. For example, background colour is often chosen for maximum contrast (black), but this may not be ecologically relevant. Clearly, such studies need to consider the contrast of silk decorations against common backgrounds and how this would be perceived by the visual systems of prey species (Chittka, 1996). Indeed, the prey attraction hypothesis relies on silk decorations forming a colour contrast with the background. Experiments should be more ecologically relevant, using natural backgrounds to look at prey approaches to decorated webs. Such an approach has been successfully used to examine the influence of the body colour of crab spiders on their pollinator prey against different flower backgrounds (Heiling, Herberstein & Chittka, 2003; Heiling & Herberstein, 2004; Théry *et al*., 2005).

Perhaps a more ecologically relevant approach to assessing prey attraction is to experimentally remove silk decorations in the field and compare natural prey capture to control decorated webs (Bruce *et al*., 2001, 2004). Such an approach has advantages over simply correlating prey capture with the presence of silk decorations as it removes the influence of web size (decorated webs are often smaller; Hauber, 1998; Bruce *et al*., 2004). It also removes the influence of prey capture history, as satiated spiders construct more decorations (Blackledge, 1998*b*; Tso, 1999; Herberstein *et al*., 2000*b*; Seah & Li, 2002) and therefore webs with decorations may simply be in sites with more prey available. Furthermore, as the spiders are free to choose their web locations prey will perceive silk decorations against the natural background. The one major problem with this approach is that it is unable to distinguish between the spectral properties and some other property of silk decorations, such as web tension (Watanabe, 2000), being the agent for prey attraction (or repulsion).

Web protection

The web protection (or advertisement) hypothesis states that the presence of decorations advertises the spider's web to animals such as birds, and therefore damage to the web is avoided. The advantage to the bird is avoiding being covered in unpleasant silk. This idea has unfortunately received very little experimental attention perhaps because of the difficulty in observing the sources of web decoration. Indeed there are a number of sources of web damage that would not result from birds such as falling vegetation, prey, predators, wind and rain. Furthermore, this idea has not been tested since the review of Herberstein *et al*. (2000*a*), and therefore the only studies to test these ideas remain those that used web damage (Eisner & Nowicki, 1983; Blackledge & Wenzel, 1999) to test this indirectly. Both studies found a reduction in web damage in decorated webs.

Non-visual functions

Non-visual functions such as mechanical support (Robinson & Robinson, 1970), thermoregulation (Humphreys, 1992), silk regulation (Peters, 1993) and stress (Nentwig & Rogg, 1988) have received very little attention compared with the visual hypotheses. Indeed, only four of the 33 studies that attempted to test a function looked at a non-visual hypothesis (Bruce *et al*., 2004). Furthermore, there have been only two studies since that of Herberstein *et al*. (2000*a*) to test a non-visual function. Watanabe (2000) found an increase in web tension caused by the presence of spiral decorations of *Octonoba sybotides*. This allowed hungry spiders to respond more quickly to small prey. In *Arg*. *versicolor*, decorations may provide support to the web during the violent flexing of the web during the anti-predatory pumping behaviour of the spider, making this strategy more effective than dropping off the web (Li *et al*., 2003). It is still unclear if the primary function of decorations in some species is a non-visual one or if the evidence for these structures indicates a secondary use of decorations evolved for another (visual) purpose.

Factors influencing web decoration construction and variation

One of the most interesting aspects of silk decorations is the variability in the frequency with which spiders add them to their webs. Individuals in some genera such as *Argiope* renew their webs almost daily, and thus commonly alter the size and pattern of decorations every day. Furthermore, it is usual to find spiders of the same species investing to a different extent in decorations on any given day. This has led to considerable interest in the factors influencing this variation. However, as studies on variation often do not address the functional hypothesis directly the results remain open to interpretation. For the purposes of this review, these factors can be divided into two broad categories: biotic and abiotic.

Biotic factors

It is well established that satiated spiders are more likely to include decorations than hungry spiders (Blackledge, 1998*b*; Tso, 1999; Herberstein *et al*., 2000*b*; Seah & Li, 2002). This has been argued as strong indirect evidence against the prey attraction hypothesis (Blackledge, 1998*b*) as, according to optimal foraging theory, satiated animals should reduce their foraging investment. However, a similar result has been used to argue for prey attraction (Herberstein *et al*., 2000*b*). These conflicting interpretations for similar data highlight the difficulty in using indirect measures to assess decoration function. Furthermore, this pattern has been very difficult to reconcile with field and laboratory experiments on the same species. For example, decorations increase foraging success in *Arg*. *keyserlingi* (Herberstein, 2000; Bruce *et al*., 2001) but satiated spiders are more inclined to construct them (Herberstein *et al*., 2000*b*). Tso (2004) has perhaps resolved this controversy. He found that food-deprived *Argiope atheroides* still had enough aciniform silk to wrap prey but reduced the size of decorations. He argued that there is a threshold in silk reserves, below which silk decorations are less likely to be constructed.

It is not only the consumption of prey that influences decoration construction; prey abundance may also influence spider behaviour. For example, in the presence of their main prey, stingless bees, spiders *Arg*. *argentata* increased their decoration frequency, which lends support to the prey attraction hypothesis (Craig *et al*., 2001). The presence of predator cues has also been shown to influence decorating behaviour. In *Arg*. *versicolor*, spiders reduce their decoration frequency in the presence of chemical cues from predatory jumping spiders (Li & Lee, 2004). This seems to argue against an anti-predator function in this species for one predator. Furthermore, *Arg*. *keyserlingi* is less likely to decorate webs in more dense vegetation (Bruce *et al*., 2001), possibly because predatory praying mantids have greater access to webs surrounded by vegetation. It may be that spiders are able to use different cues, such as the density of vegetation, to assess the likelihood of a predatory attack and therefore alter their decorating behaviour accordingly.

The genetic basis of the variation in decorating behaviour has received little attention. However, in *Arg*. *argentata* the frequency of spiders adorning their webs with decorations was inherited from both parents (Craig *et al*., 2001). Interestingly, decoration frequency was still correlated with local environmental conditions, and this in turn may influence speciation in isolated populations by conferring an advantage on individuals who decorate more or less frequently according to local conditions (Craig *et al*., 2001). However, this argument remains to be tested experimentally.

Abiotic factors

The first study to test directly the influence of an abiotic factor on silk decorations was conducted by Elgar *et al.* (1996), who found that *Argiope aetherea* housed in dim light were more likely to include decorations than those in bright light. They argued that this result was consistent with a prey attraction function. A similar result was found in experiments conducted on *Arg*. *versicolor* (Seah & Li, 2002). Herberstein & Fleisch (2003) conducted a more comprehensive survey of the abiotic influences on decoration behaviour in *Arg*. *keyserlingi*. They looked at the influence of light and temperature in controlled laboratory experiments, finding that spiders kept at warmer temperatures construct more decorations. They also confirmed that spiders kept in dim light conditions construct more decorations. Furthermore, they correlated decoration frequency observed in the field with a variety of abiotic variables, such as temperature, humidity, mean sea level pressure and cloud cover. Only temperature was correlated with decorations, with spiders having a higher frequency of decorations on hotter days. They argue that this may be to exploit increased insect activity.

Web decoration reflectivity

Decoration silk reflects in the UV region of the light spectrum and it has a different reflectance to other silks (Craig & Bernard, 1990; Watanabe, 1999*a*; Zschokke, 2002; Li *et al*., 2004). However, until recently it has remained unclear as to how the colour of decoration silk appears to and influences other animals. Craig & Bernard (1990) argued that the UV reflectivity of decorations would attract prey and Blackledge & Wenzel (2000) argued that decorations would be cryptic to insects, but there has been no attempt to examine these points of view objectively.

Objective studies assessing the visibility of decorations to both predators and prey would advance our knowledge of the function of web decorations. For a visual signal to be detected it must fall within the range of sensitivity of a receiver and it must form a contrast with the background. This contrast can be chromatic (used for short-distance and small-target discrimination; Chittka, 1996; Giurfa *et al*., 1997) or achromatic (used for long-distance and large-target discrimination; Chittka, 1996; Giurfa *et al*., 1997). On the contrary, to camouflage the spider decoration silk must not form a detectable contrast with either the background and/or the spider's body. The efficacy of silk decorations as visual signals is therefore likely to be influenced by the colour of the silk, the colour of the background and body, ambient light and visual systems of potential prey and predators. Clearly, a starting point is to measure the spectral reflectance of decorations, spiders and backgrounds and relate these to prey and predator visual systems. Such visual system data are currently available for birds (e.g. Hart *et al*., 2000; Hart, 2001, 2004) and honey bees (Chittka, 1996). From these data the relative excitation of the different colour receptors for various decoration/background combinations can be calculated. This will allow an objective assessment of contrast between decorations or the spider's body and background (Bruce *et al*., 2005). Furthermore, as animals use different receptors for short- and long-distance discrimination (Chittka, 1996), it is possible that decorations camouflage over long distances but not short distances (or vice versa). Knowledge of the reflectance properties and their relationship to prey and predator visual systems could consequently be used to design experiments such as analysing the approach paths of predators from different distances and against different backgrounds.

Recent evidence suggests that the silk decorations of a number of species are visible to potential prey (honey bees) and predators (blue tits) over short distances and long distances against a natural green foliage background (Bruce *et al*., 2005). Furthermore, the spectral reflectance of web decorations is similar within the genus *Argiope* (Araneidae) and between the *Argiope* and *Zosis geniculatus* (Uloboridae), despite the separate evolutionary origins of decorations in these two groups (Scharff & Coddington, 1997; Herberstein *et al*., 2000*a*). Although these data do not offer support to any of the visual hypotheses, they do show that decorations are visible and thus support a visual function.

Conclusions

It is clear that despite the recent progress in the study of silk decorations, there is still little consensus surrounding their function. It seems increasingly likely that they are some kind of visual signal, but this may only be because the non-visual hypotheses have been neglected and remain to be tested by direct experiments. One area where progress has been made is in the factors influencing decoration function, although more experiments are required to link these results to the function of decorations. There is a clear need for more comparative experiments to assess multiple functions in multiple species with a consistent methodology. Such an approach would reduce the possibility that differences in methodology account for some of the conflicting results. It may well be that the function of these structures does differ between species and even populations (see also Starks, 2002). These may be related to the specific predator and prey assemblages in an area and to abiotic factors such as temperature or ambient light. Indeed many authors (e.g. Craig *et al.*, 2001; Seah & Li, 2002; Starks, 2002) have argued that silk decorations are a conditional strategy, performing multiple functions to suit particular environmental conditions. Furthermore, more work could be done to highlight potential trade-offs faced by spiders when including decorations, such as those between predator and prey attraction (Blackledge, 1998*a*; Bruce *et al.*, 2001; Seah & Li, 2001). This may also help to illuminate any context-specific decoration function and show that the various functions are not mutually exclusive.

As more information becomes available about the visual systems of different classes of prey and predators, greater opportunities for examining the visibility of web decorations against different backgrounds and for different prey and predators will emerge (e.g. Bruce *et al.*, 2005). Furthermore, information on the spectral reflectance of decoration silk and its visibility to prey and predators should enable the design of better experiments testing the responses of prey and predators to decorations. This can be achieved by mimicking ambient light conditions and background colours more accurately in the laboratory. Furthermore, as there seems to be little variation in the spectral reflectance of decorations across species and even families (Bruce *et al.*, 2005), it may be that the different patterns (e.g. cruciate, linear or discoid) constructed by different species (and even within a species) could account for some of the contradictory results. There is also a role for new technology in illuminating aspects such as predator and prey responses to decorations under different conditions by using video analysis similar to that used to investigate flight dynamics in bees. Clearly, there are many opportunities to expand on the already considerable knowledge in this field. These opportunities exist for scientists in different disciplines whether they are interested in the ontogenetic shifts in decorating behaviour and the relationship to life history, the potential of silk decorations to function as deceptive signals, or even the ability of different potential receivers to discriminate decorations from different backgrounds under different light conditions.

Acknowledgements

I am grateful to Mariella Herberstein and two anonymous referees who provided helpful comments and discussion on this manuscript. The Australian Research Council (DP0449673), Macquarie University and an Australian Postgraduate Award provided financial support for this work.

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