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Web decorations and foraging success in *'Araneus' eburnus* (Araneae: Araneidae)

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Visual signals are commonly used by animals to manipulate both their prey and predators. The conspicuous silk structures included in the webs of many orb-web spiders, termed web decorations or stabilimenta, could be an example of this. The function of these curious structures remains controversial with some authors suggesting that they attract insect prey, while others suggesting that they camouflage the spider or deter predators. Here we test the hypothesis that web decorations increase the foraging success of *'Araneus' eburnus* by attracting prey to the web. Using field correlations and field manipulations we show that decorated webs capture more prey per web area than undecorated webs under certain conditions.

Introduction

Animals use a variety of visual signals, which may manipulate the receiver's behaviour in a way that benefits the signaller (Johnstone 1997). Signals may attract prey species, repel non-prey animals, such as predators, or even achieve both functions simultaneously. Many orb-web spiders incorporate highly visible, white zigzag bands or discs of silk into their webs (Herberstein *et al.* 2000a). These web decorations most likely have a visual signalling function (Scharff & Coddington 1997) but their effect on predators and prey has been the subject of ongoing debate with little, if any, consensus (Herberstein *et al.* 2000a). A variety of functions have been suggested (Herberstein *et al.* 2000a) with the three functions best studied being prey attraction (Craig & Bernard 1990, Tso 1996, 1998a, Blackledge 1998b, Watanabe 1999b, Herberstein 2000, Bruce *et al.* 2001), preventing accidental damage by larger, non-prey animals (Eisner & Nowicki 1983, Blackledge & Wenzel 1999) or deterring predators by obscuring the spider or increasing its apparent size (Schoener & Spiller 1992, Blackledge & Pickett 2000, Blackledge & Wenzel 2001).

While these curious silk structures attract the attention of researchers, field and laboratory studies published thus far have generated mostly contradictory data. For example, Blackledge and Wenzel (1999) showed that in *Argiope aurantia* the presence of web decorations reduces web damage by birds as well as predatory attacks by mud-dauber wasps. However, there is a cost associated with utilising web decorations, as they appear to increase web visibility to prey, resulting in lower prey capture rates (Blackledge & Wenzel 1999). By contrast, isolated decorations of the same species (Tso 1998a) and the decorated webs of *A. keyserlingi* (Bruce *et al.* 2001) and *Octonoba sybotides* (Watanabe 1999b) attracted prey to the web. However, prey-attracting decorations also reduce the survivorship of *A. argentata* (Craig *et al.* 2001) possibly by luring spider predators as was found in *A. keyserlingi* (Bruce *et al.* 2001) and *A. versicolor* (Seah & Li 2001).

In addition to the conflicting data, research has been biased towards the genus *Argiope* (*see* Herberstein *et al.* 2000a). Web decorations evolved nine times independently in 15 genera across three families (Araneidae, Uloboridae, and Tetragnathidae; Scharff & Coddington 1997). Therefore, it is likely that the selective pathways may be fundamentally different amongst these three families (Herberstein *et al.* 2000a). However, Eberhard (2003) argued that, amongst other things, the apparent ease with which web decorations have arisen favours the predator defence hypothesis (camouflage) for all groups. For these reasons it is important to gather evidence from a number of different taxa to gain a broader understanding of the function, evolution, and selective pressures that maintain decorating behaviour in orb-web spiders. A review of all of the literature on this topic is beyond the scope of this work, but Table 1 summarises the studies that have attempted to test one of the many functions ascribed to web decorations.

The prey attraction hypothesis can be directly tested in a number of ways all of which have their advantages and disadvantages. The field correlation technique involves correlating the presence of web decorations with prey capture rates. Different results have been obtained in different species by using this technique. For example, Herberstein (2000) found for *A. keyserlingi* that the presence of decorations is positively correlated with foraging success, however Blackledge and Wenzel (1999) found that the presence of web decorations reduced prey capture in *A. aurantia*. This technique has the advantage of being relatively simple to undertake but it has one major downfall. It has been shown experimentally that *A. keyserlingi*, *A. aurantia* and *A. trifasciata* construct more decorations when they are satiated (Blackledge 1998b, Herberstein *et al.* 2000a). Therefore, a correlation between the presence of web decorations and prey capture rates is unable to determine whether decorated webs capture more prey or if spiders build decorated webs at sites where more prey is available. This problem can be overcome by either comparing spiders constructing webs in close proximity (Craig 1991; the assumption being that these spiders will have similar prey capture histories), by comparing decorated and undecorated web halves of the same web (Craig 1991) or by estimating the prey available to the spider by erecting insect traps adjacent to webs (Bruce *et al.* 2001).

Y-choice experiments have been used to show that flies (Diptera) are attracted to web decorations (Craig & Bernard 1990, Watanabe 1999b, Bruce *et al.* 2001). The advantage of this approach is that it can directly test the response of potential receivers (predators or prey) to web decorations in the laboratory and thus the experimental conditions can be controlled. However, the biological significance of these experiments is doubtful because they may not accurately reproduce the conditions under which predators or prey perceive webs in the field and therefore an unnatural set of stimuli may be presented. Furthermore, Y-choice experiments can only consider the reaction to decorations of one prey species at a time so any results, positive or negative, may not be generally applicable to the entire spectrum of prey available to the spider (*see* also Eberhard 2003).

The experimental manipulation of the presence of web decorations in the field provides an opportunity to investigate the effects of these structures on prey capture and predator response without the cause and effect problem present in field correlations. Furthermore, these manipulations may be conducted in the spider's natural habitat to eliminate the potential problem of biological relevance present in laboratory experiments, as conditions in the laboratory may not mimic natural conditions closely enough. Such an approach has been attempted by Bruce *et al.* (2001) who removed web decorations from webs in the field. They selected naturally occurring webs with two bands of decorations and randomly selected a sub-sample of webs from which they removed the bands. The control treatment contained webs with the bands still present. They then compared the prey capture of these manipulated webs with that of the webs contain-

Table 1. Summary of studies that test a function for web decorations. "Direct" experiments involved measuring the response of animals (predators, prey or accidental web damagers) to web decorations. "Indirect" experiments were those used to infer web decoration function or correlate web decorations with prey capture, predator attack, mortality or web damage.

Function	Species	Test	Outcome	Source
Anti-predator	*Argiope trifasciata*	Indirect (laboratory experiment)	Juvenile spiders reduce decoration building in the presence of predator cues (jumping spiders)	(Li & Lee 2004)
	Allocyclosa bifurca	Indirect (laboratory experiment)	Decorations are camouflage devices	(Eberhard 2003)
	Argiope trifasciata	Indirect (laboratory experiment)	Adult and juvenile spiders show decoration specific predator avoidance behaviours	(Li *et al.* 2003)
	A. trifasciata	Direct (field enclosures)	Decorations defend spiders against wasps	(Blackledge & Wenzel 2001)
	A. keyserlingi	Direct (Y-choice)	Decorations attract predators — praying mantids	(Bruce *et al.* 2001)
	A. argentata	Indirect (field correlation)	Frequent decorators have reduced survivorship	(Craig *et al.* 2001)
	A. versicolor	Direct (Y-choice)	Decorations attract predators — jumping spiders	(Seah & Li 2001)
	A. argentata	Indirect (field correlation)	Decorations defend spiders	(Schoener & Spiller 1992)
	Cyclosa insulana	Indirect (field observation)	Linear decorations seem to be defensive structures	(Neet 1990)
	A. aurantia, *A. trifasciata*	Direct (laboratory experiment)	Decorations defend spiders against birds	(Horton 1980)
	A. argentata	Indirect (field observation)	Decorations defend spiders	(Lubin 1975)
	A. punchella	Indirect (field observation)	Decorations are camouflage devices	(Marson 1947)
Foraging	*A. keyserlingi*	Indirect (field correlation)	Spiders build more decorations on hotter days, may be to take advantage of increased insect activity	(Herberstein & Fleisch 2003)
	A. keyserlingi	Direct (Y-choice)	Decorations attract prey — flies	(Bruce *et al.* 2001)
	A. argentata	Indirect (field correlation)	Spiders increase decorating behaviour in the presence of stingless bees	(Craig *et al.* 2001)
	A. keyserlingi	Indirect (field correlation)	Decorated webs catch more prey	(Herberstein 2000)
	A. keyserlingi	Indirect (laboratory experiment)	Hungry spiders invest less in web decorations than satiated spiders, spiders with unpredictable prey encounter rates invest more in web decorations — argue for prey attraction	(Herberstein *et al.* 2000b)
	Octonoba sybiotides	Indirect (laboratory experiment)	Spiral decorations may increase web tension allowing hungry spiders to respond quickly to small prey	(Watanabe 2000)
	A. aurantia, *A. trifasciata*	Indirect (field correlation)	Decorated webs have reduced prey capture	(Blackledge & Wenzel 1999)

continues

Table 1. Continued.

Function	Species	Test	Outcome	Source
	A. trifasciata	Indirect (field correlation)	No effect of feeding on decoration building	(Tso 1999)
	A. trifasciata	Indirect (laboratory experiment)	Well fed spiders increased decoration building	(Tso 1999)
	O. sybiotides	Direct (Y-choice)	*Drosophila* attracted to decorated webs	(Watanabe 1999b)
	O. sybiotides	Indirect (field correlation)	Decorated webs intercept more prey than undecorated webs	(Watanabe 1999b)
	O. sybiotides	Indirect (laboratory experiment)	Hungry spiders tend to form spiral decorations, satiated spiders form linear decorations	(Watanabe 1999a)
	A. aurantia, *A. trifasciata*	Indirect (laboratory experiment)	Hungry spiders invest less in web decorations than satiated spiders — argue against prey attraction	(Blackledge 1998b)
	A. appensa	Indirect (field correlation)	Decorated webs are significantly smaller than undecorated webs but have similar foraging success	(Hauber 1998)
	A. aurantia, *A. trifasciata*	Direct (field experiment)	Artificial webs containing decorations intercepted more flying insects than those without decorations	(Tso 1998a)
	Cyclosa conica	Indirect (field correlation)	Decorated webs intercept more prey than undecorated webs despite being smaller	(Tso 1998b)
	A. trifasciata	Indirect (field correlation)	Decorated webs intercepted more flying insects but not orthopterans	(Tso 1996)
	A. aetherea	Indirect (laboratory experiment)	Spiders in dim light conditions construct more decorations than those in bright light — argue that this is consistent with prey attraction	(Elgar *et al.* 1996)
	A. argentata	Indirect (field correlation)	Decorated webs capture more prey than undecorated webs in web clusters	(Craig 1991)
	A. argentata	Direct (Y-choice)	*Drosophila* attracted to decorated webs	(Craig & Bernard 1990)
	A. argentata	Indirect (field correlation)	Decorated webs with the spider present intercepted more prey than undecorated webs with the spider removed, decorated web halves intercepted more prey than undecorated halves	(Craig & Bernard 1990)
Mechanical	*Cyclosa insulana*	Indirect (field correlation)	Circular decorations probably strengthen the web	(Neet 1990)
	Nephila clavipes	Indirect (field correlation)	Decorations most common in skeleton (non-capture) webs	(Robinson & Robinson 1973)

continues

Table 1. Continued.

Function	Species	Test	Outcome	Source
Stress	*A. argentata*	Indirect (laboratory experiment & field observation)	Spiders varied decorating behaviour in response to factors thought to induce stress, this was not replicated in the field	(Nentwig & Rogg 1988)
Thermo-regulation	*Neogea* sp.	Indirect (field observation)	High temperatures induce spiders to move to the sheltered side of disc decorations, resulting in a reduction in body temperature	(Humphreys 1992)
Web advertisement	*A. aurantia*	Direct (field experiment)	Webs without decorations suffered significantly more damage than those with decorations	(Blackledge & Wenzel 1999)
	A. appensa	Indirect (field observation)	The low frequency of web decorations on Guam (as compared with surrounding islands) may be in response to the recent elimination of native birds	(Kerr 1993)
	A. florida, *A. aurantia*	Direct (field experiment)	Webs with artificial (paper) decorations survived intact more often than undecorated webs	(Eisner & Nowicki 1983)

ing two bands (Table 1). A similar and elegant approach was used by Tso (1998a) who added decorations to artificial webs and compared the prey capture of decorated and undecorated artificial webs. These were erected at the same sites as natural webs. The advantage of this study was that it removed any influence of web size and web location from the results (Table 1). A third study used paper as a substitute for decorations in order to test the web advertisement hypothesis (Eisner & Nowicki 1983), the biological relevance of the results of this study are doubtful as it is unlikely that paper mimics the reflectance spectrum of decoration silk (Table 1).

The removal of web decorations in the field is relatively easy and the measurement of prey capture rates can be performed without too many problems. However, field manipulations testing the response of predators are few as predators are often difficult to identify and predator attacks can be rare. One study (Blackledge & Wenzel 2001) attempted to overcome some of these problems by using field enclosures that contained spiders (*A. trifasciata*) and their predators (mud-dauber wasps). Clearly there is scope to improve on the various methods outlined above in order to study the function of web decorations more thoroughly from the perspective of all potential receivers whether they are prey, predators or other animals that cause web damage.

Here, we present field observations describing the relationship between foraging success and the presence of web decorations in *'Araneus' eburnus* (Keyserling, 1886 *sensu* Davies 1988) a species in which web decorations evolved independently to those of the well-studied decorating genus *Argiope*. Furthermore, this is the first study to describe the web decorating behaviour in this species. We present the results of both a field correlation and a field manipulation investigating the influence of web decorations on prey capture. In order to eliminate the cause and effect problem the field correlation was performed by surveying spiders constructing webs in close proximity over a number of days. Moreover, the experimental removal of web decorations further eliminates this problem by comparing webs with the same number of

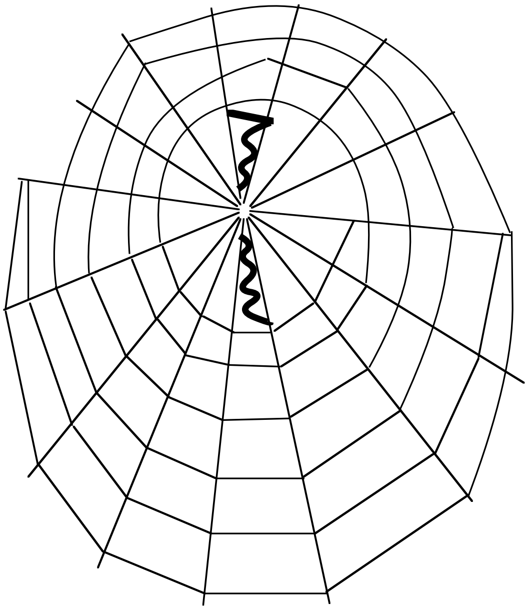

Fig. 1. A schematic representation of the web of *'A.' eburnus* with two bands of linear decorations.

decorative bands and removing these bands in a random sub-sample. These field correlations and manipulations may support one of two mutually exclusive hypotheses: (1) If web decorations attract prey, decorated webs are expected to capture more prey than undecorated webs (*see* Craig & Bernard 1990, Herberstein 2000); (2) decorations may deter non-prey animals at the cost that prey also use decorations to avoid the web (*see* Blackledge & Wenzel 1999), in which case we predict that decorated webs should capture less prey than undecorated webs.

Material and methods

Study animal and study sites

We conducted prey capture surveys on adult female *'Araneus' eburnus*, a small orb-web spider common in the Sydney region. This species has been placed in the genus *Araneus*, like many other small Australian orb-web spiders, even though several morphological characteristics distinguish it from that genus (Davies 1988). We have deposited a voucher specimen with the Australian Museum.

'A.' eburnus is a diurnal forager, constructing a vertical oriented orb-web containing between zero and two decorative bands in a linear configuration (Fig. 1). We carried out web surveys in September and October 2001 on the grounds of Macquarie University, North Ryde, NSW, Australia. The vegetation at this site ranged from mature Eucalypt forest, isolated trees and shrubs to formal gardens. We performed field manipulations over nine days in September and October 2003 in the North Ryde area in Sydney NSW using two different vegetation types. Mature forest consisting of Eucalypt trees with undergrowth of *Lomandra longifolia*, ferns and grasses and a disturbed site consisting of mostly weeds (*Lantana camara*, blackberries) and grasses, with a small area of natural bush land.

Prey capture surveys

Spiders were located between 07:00 and 07:30 each morning. In addition, we searched for new spiders throughout the morning as some individuals began construction later in the day. Upon location we measured the vertical and horizontal diameters of the web in order to calculate web area (*see* Herberstein & Tso 2000) and the web height (distance between the ground and the hub of the web). Moreover, we counted the number of decorative bands and measured their lengths. Monitoring of prey capture events commenced at 07:30 for those spiders that had already completed web construction or at the half hour survey after web completion. Completed webs were surveyed every 30 minutes until 18:00 or until the web was abandoned or destroyed. At each survey we recorded the body length (to the nearest millimetre) and distance from the hub of each new prey item captured to prevent double counting. In order to maintain natural prey capture conditions, prey was not removed from the web. Similarly, spiders were not marked individually but we flagged the web site. We collected spiders at the end of each day to measure carapace width and body length. To minimise pseudoreplication, each day we searched for new individuals that were located at least 50 m from our previous site. A minimum of four individuals were observed each day and individuals were commonly located within ten to twenty metres of each other.

Field manipulation

Spiders constructing webs containing one or two decorative bands were located between 06:30 and 07:30. Upon location, the parameters mentioned in the previous section, were measured. In addition we counted the number of sticky spirals above and below the hub to calculate an estimate of the average distance between sticky threads (mesh height). Spiders were then randomly assigned to either a removal (undecorated) treatment or a control (decorated) treatment. Spiders in the removal treatment had their decorations cut from the web, whilst those in the control treatment had their webs cut to match the damage of the webs in the removal treatment, but they retained their decorations. To minimise disturbance, the spiders were not marked but the web sites were flagged. Prey capture events were surveyed every 30 minutes for 8 hours or until the webs were involuntarily destroyed. Spiders foraging for less than three hours were excluded from the analysis. Each prey capture event was recorded and the length (to the nearest millimetre) and distance from the hub was measured to avoid double counting. Prey items were not removed from the webs in order to maintain natural prey capture conditions. At the end of the foraging period spiders were taken to the laboratory where the carapace width and weights were measured. These spiders were kept in the laboratory for the duration of the experiment to prevent pseudoreplication. A minimum of two individuals was observed each day (one per treatment).

Calculation of body condition

We used data on spider size (carapace width) and spider weight to calculate body condition, which is known to influence web-building behaviour in spiders (*see* Sherman 1994, Herberstein *et al.* 1998, Herberstein & Heiling 1999). To account for allometry, a linear regression between carapace width, (ln-transformed) as the independent variable, and body weight (ln-transformed), as the dependent variable, was calculated for the prey capture surveys ($R^2 = 0.22$, $F_{1,22} = 6.03$, $p = 0.02$) and the decoration manipulation ($R^2 = 0.13$, $F_{1,34} = 5.04$, $p = 0.03$). In this regression analysis, the original variable 'body weight' was split into two portions. These were the predicted portion as a result of allometric and a residual portion, which can be viewed as an estimate of the individual body condition in *'A.' eburnus*.

Data analysis

Prey capture surveys

All data were tested for normal distribution (Kolmogorov-Smirnov) and equality of variances (Levene's test). For the purposes of analysis we allocated the spiders to two groups, those constructing decorated webs and those constructing undecorated webs. We compared web size, web height and body condition between decorating and non-decorating spiders using Student's *t*-tests or Mann-Whitney *U*-tests. Further, we correlated (Pearson) prey capture rates with web size separately for decorated and undecorated webs.

Decoration manipulation

Again all data were tested for normal distribution and equality of variances. We compared body condition and carapace width between removal and control spiders using Student's *t*-tests or Mann-Whitney *U*-tests. Further, we calculated prey capture rate by dividing the number of prey items by the number of hours spent foraging for each spider. This was then divided by web area to provide a measure of the amount of prey captured per amount of capture area. The data from the mature forest sites were analysed separately from the data from the disturbed site. We compared carapace width, body condition, web area, web height, mesh size and prey capture between the mature forest and the disturbed site using *t*-tests. We compared prey capture success between decorated and undecorated webs using ANCOVA with mesh height and web height as covariates as these variables are known to influence prey capture in orb-web spiders (Chacón & Eberhard 1980, Herberstein & Heiling 1998).

Results

Prey capture surveys

A total of 47 spiders were sampled over a period of five days. Twenty-two individuals included decorations in their webs and 25 constructed webs without decorations. Of the spiders constructing decorations, 10 constructed only one linear band (above the hub in all but one case) and 12 constructed two bands (one above and one below the hub). The duration of continuous foraging ranged from two to ten hours with 92% of spiders completing web construction by 09:30. However, individuals also commenced web construction later during the day, until 15:00.

There were no differences in spider size, body condition and web height between spiders on decorated webs and those on undecorated webs (Table 2). However, decorated webs captured significantly more prey per unit area of web than undecorated webs (Table 2). Furthermore, decorated webs were significantly smaller (30%) than undecorated webs (Table 2). Prey capture rates were related to web area in undecorated webs ($r = 0.44$, $n = 25$, $p = 0.03$) but not in decorated webs ($r = –0.08$, $n = 22$, p = n.s.; Fig. 2).

Decoration manipulation

A total of 45 spiders were sampled over nine days, 31 at the mature forest site (15 decorated and 16 undecorated) and 14 at the disturbed site (seven decorated and seven undecorated). The sites were sufficiently different to warrant separate analyses (Table 3): specifically webs at the disturbed site were significantly larger and significantly lower than in the mature forest. There were no differences between spider size, body condition, mesh height or prey capture between the sites (Table 3).

There were no differences between body condition and carapace width of spiders in either treatment at either site (Table 4). However, in the mature forest the decorated treatment captured significantly more prey than the undecorated treatment per unit area of web. This was not the

Table 2. Spider size, body condition, web height, web size and prey capture of decorated and undecorated webs in *'Araneus' eburnus* (mean ± S.E.) from the prey capture survey.

	Decorated webs	Undecorated webs	Statistics (Student's *t*-test; Mann-Whitney *U*-test)
Carapace width (mm)	1.74 ± 0.13	1.86 ± 0.05	$t_{22} = –0.79$, p = n.s.
Body condition	0.09 ± 0.12	–0.11 ± 0.10	$t_{22} = 1.27$, p = n.s.
Web area (cm^2)	171.5 ± 13.6	254.2 ± 20.6	$t_{45} = –3.26$, $p < 0.01$
Web height (m)	1.01 ± 0.10	0.99 ± 0.07	$U_{45} = 264$, p = n.s.
Prey capture rate (items h$^{–1}$ m$^{–2}$)	25.3 ± 4.0	15.7 ± 2.7	$U_{45} = 182$, $p = 0.047$

Table 3. Comparisons between spider size, body condition, web area, mesh height, web height and prey capture between the mature forest and disturbed forest sites in the decoration manipulation experiment (mean ± S.E.).

	Mature forest	Disturbed forest	Statistics Student's *t*-test
Carapace width (mm)	2.07 ± 0.06	2.07 ± 0.07	$t_{34} = 0.004$, p = n.s.
Body condition	0.16 ± 0.20	–0.31 ± 0.29	$t_{34} = 1.35$, p = n.s.
Web area (cm^2)	229.9 ± 12.1	275.3 ± 13.25	$t_{43} = –2.26$, $p = 0.03$
Mesh height (mm)	2.9 ± 0.1	3.0 ± 0.1	$t_{43} = –0.56$, p = n.s.
Web height (m)	0.98 ± 0.06	0.73 ± 0.05	$t_{43} = 2.64$, $p = 0.01$
Prey capture rate (items h$^{–1}$ m$^{–2}$)	17.22 ± 3.13	16.61 ± 3.64	$t_{43} = 0.11$, p = n.s.

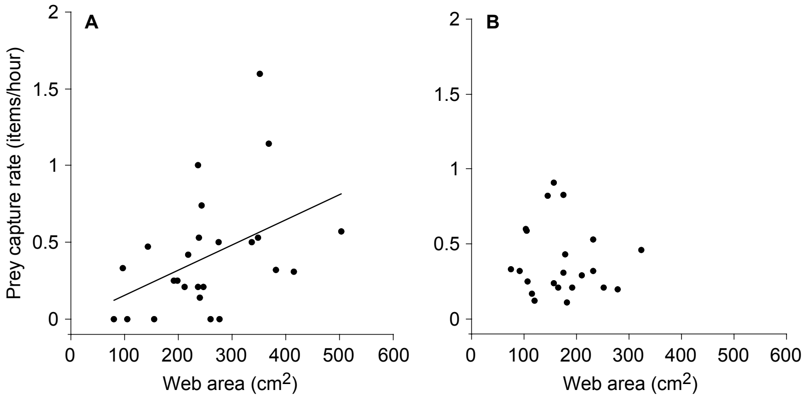

Fig. 2. The relationship between web area and prey capture in undecorated (**A**) and decorated (**B**) webs: only in undecorated webs did prey capture increase with web size ($r = 0.44$, $n = 25$, $p = 0.03$).

case at the disturbed site where prey capture rates in decorated and undecorated webs were similar (Fig. 3).

Discussion

The results of our prey capture surveys suggest that decorated webs of *'Araneus' eburnus* capture more prey per unit area of web than undecorated webs. This result is consistent with the prey attraction hypothesis. These results were further supported by our decoration manipulation experiment, where webs with decorations artificially removed captured significantly less prey than decorated webs in mature forest. However, this was not the case in the disturbed forest, where the presence of web decorations did not influence foraging success. Furthermore, the webs at the disturbed site were significantly closer to the ground and significantly larger than those in the mature forest.

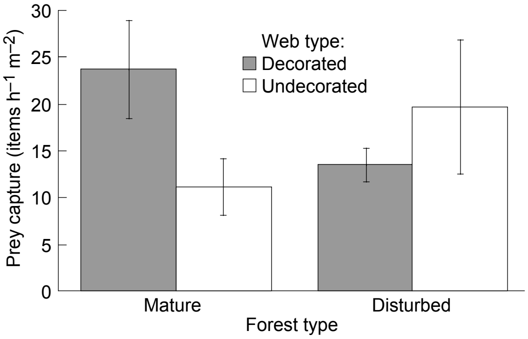

Fig. 3. Prey capture per unit web area for the two treatments at the mature and disturbed sites. At the mature forest the decorated treatment captured significantly more prey per unit area of web than the undecorated treatment (treatment $F_{3,31} = 4.65$, $p = 0.04$: mesh height $F_{1,31} = 0.37$, p = n.s.: web height $F_{1,31} = 0.47$, p = n.s.). However, at the disturbed site prey capture rates between decorated and undecorated webs were similar (treatment $F_{3,13} = 0.55$, p = n.s. (power = 0.1): mesh height $F_{1,13} = 0.16$, p = n.s.: web height $F_{1,13} = 0.10$, p = n.s.).

Table 4. Spider size and body condition comparisons between the decorated and undecorated treatments at mature and disturbed forest sites in the decoration manipulation experiment (mean ± S.E).

	Carapace width (mm)	Body condition
Mature forest		
Decorated webs	2.21 ± 0.08	0.23 ± 0.23
Undecorated webs	2.03 ± 0.09	0.09 ± 0.31
Statistics	$t_{22} = 0.77$, p = n.s.	$t_{22} = 0.36$, p = n.s.
Disturbed forest		
Decorated webs	2.07 ± 0.11	–0.31 ± 0.32
Undecorated webs	2.08 ± 0.09	–0.31 ± 0.59
Statistics	$U_{12} = 16.0$, p = n.s	$t_{10} < 0.01$, p = n.s.

The methods used in our study, especially the experimental removal of web decorations to create artificial undecorated webs, removed a potential bias as it controls for the influence of satiation on the tendency of spiders to build decorations (Blackledge 1998b, Herberstein *et al.* 2000b). By selecting spiders with the same number of decorative bands and randomly assigning them to either a decorated or undecorated treatment we have avoided the possibility that previous foraging success might bias our results. Furthermore, in our field surveys there was no difference between the body condition of spiders on decorated and undecorated webs suggesting that spiders on decorated and undecorated webs had similar recent foraging histories. Therefore, the locations at which we found spiders on decorated webs were unlikely to be more profitable than those locations where we surveyed spiders on undecorated webs.

The differing results from the mature and disturbed forest sites suggest that web decorations may have a population specific effect depending on factors such as predator and prey assemblages, background contrast and ambient light. Indeed it was suggested by Starks (2002) that web decorations are a conditional strategy and that the fitness payoff of web decorations is likely to be influenced by factors such as the density of various types of prey and/or predators. Despite the controversy surrounding the function of web decorations and the conflicting results of previous studies the idea that the function of web decorations is population specific has received little attention. Perhaps the only such study was that of Kerr (1993) who concluded that the low frequency of web decorations in *Argiope appensa* on Guam (as opposed to surrounding islands) was the result of an introduced predator that reduced bird numbers. Indeed, we know that other factors such as temperature, ambient light (Herberstein & Fleisch 2003) the presence of prey (Craig *et al.* 2001) and the density of the surrounding vegetation (Bruce *et al.* 2001) can influence the frequency of web decorations. The presence and density of introduced prey may also have an influence on the effect of decorations on foraging success. For example, the introduced honey bee (*Apis melifera*) is attracted to the colouration of the predatory crab spider, *Thomisus spectabilis* (Heiling *et al.* 2003), whereas the native bee, *Austroplebia australis*, is not (Heiling & Herberstein 2004).

If decorations attract prey, one may expect that these spiders always adorn their webs with decorations. Nevertheless, our field observations show that only around 47% of webs were decorated and spiders that included decorations constructed smaller webs than those that did not include decorations. The fact that not all spiders adorn their webs with decorations suggest that there is a trade-off between their effects on predators and prey (Bruce *et al.* 2001) and this result is also consistent with the idea of conditional strategies as proposed by Starks (2002). However, due to the small area of the disturbed site (we were only able to locate 14 decorating spiders) our power to detect a difference in prey capture rates between the decorated and undecorated treatments was low (0.1).

These spiders may also be pursuing a mixed strategy with two different foraging tactics, both providing comparable capture rates. Spiders may build smaller webs but maintain high prey capture success by incorporating attractive decorations. Alternatively, they may forgo decorations but must increase web size to guarantee adequate prey capture. Previous studies on the distantly related *Argiope appensa* (Hauber 1998) revealed identical patterns: smaller decorated webs captured similar amounts of prey to larger undecorated webs. Hauber (1998) argued that variation in decorating behaviour represents two alternative foraging strategies, each yielding similar relative benefits. If this spider is employing alternative tactics, the costs associated with these two tactics are likely to be different. Decorated webs may be less costly, as they are smaller presumably containing less sticky silk and taking less time to construct. Building decorations only takes seconds, and the silk type used for decorations is less limited than the viscous silk used for the capture spiral (e.g. Denny 1976).

Alternatively, spiders that build smaller webs may be more satiated and likely to redirect energy from foraging into alternative activities, such as egg production and defense (Blackledge 1998a, Herberstein *et al.* 2000b). However, we found no relationship between body condition, i.e. pervious foraging success, and the absence and presence of web decorations. Moreover, in our prey capture survey, foraging success was similar in decorating and non-decorating spiders, giving no indication that decorating spiders are reducing their foraging effort. As we did not directly test for any interaction between web size and prey capture, further studies need to be undertaken to test the alternative foraging strategy hypothesis.

The precise mechanism of how decorations may attract prey is unknown, but decorations reflect light in the UV range and thus may mimic the floral guides used by flowering plants to attract pollinating insects (Craig & Bernard 1990). Similarly, they may exploit an escape response to UV-bright patches exhibited by flying insects (Craig & Bernard 1990, Goldsmith 1990). Furthermore, the linear bands in the webs of *'A.' eburnus* may also deter undesirable non-prey animals such as predators or larger animals that may damage the web (*see* Herberstein *et al.* 2000a for a review). This may be achieved by obscuring the outline of the spider or by making the spider appear larger (Schoener & Spiller 1992, Blackledge & Wenzel 1999). We did not measure mortality in our field studies and never observed a predatory attack. Therefore, we cannot evaluate this idea for *'A.' eburnus*. Nevertheless, an anti-predatory function may not be mutually exclusive of other functions such as prey attraction, although, to date, there is little evidence for this. In the sympatric *Argiope keyserlingi*, the cruciate web decorations attracted prey to the web, but also predators, resulting in a signalling conflict (Bruce *et al.* 2001). Conversely, in the northern hemisphere *Argiope aurantia*, the linear decorations reduced web damage but also prey capture success (Blackledge & Wenzel 1999).

Our results suggest that the effects of web decorations on prey and predator populations are species specific and perhaps population specific and do not allow generalisations. However, Eberhard (2003) argued that despite conflicting results, web decorations evolved solely to camouflage spiders. It may be that the original function of web decorations was to camouflage spiders (but *see* Starks 2002), but our results suggest that in *'A.' eburnus* as in other species (Craig & Bernard 1990, Tso 1996, 1998a, Watanabe 1999b, Herberstein 2000, Bruce *et al.* 2001) the current function in some populations is to attract prey.

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