

A natural history of web decorations in the St Andrew's Cross spider (*Argiope keyserlingi*)

Dinesh Rao^{A,C}, Ken Cheng^B and Marie E. Herberstein^{A,B}

^ADepartment of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia.

^BCentre for the Integrative Study of Animal Behaviour, Macquarie University, North Ryde, NSW 2109, Australia.

^CCorresponding author. Email: dinrao@gmail.com

Abstract. A long-running debate in the spider literature concerns the function of the extra silk decorations in some spider webs. These decorations are appended to the web and constitute a highly visible signal, which is inconsistent with the trend towards web invisibility. Despite the sustained attention of researchers, the exact function of these decorations is yet to be understood. While most studies have focussed on testing particular hypotheses, there has been a dearth of natural history data regarding web decorations in field conditions. In this study we present baseline data regarding the influence of seasonality, microhabitat characteristics and ecology on the presence of web decorations in an Australian orb web spider, *Argiope keyserlingi*. In particular, we show that there is preference among spiders to build their webs between bushes and to face the south-east, but this preference does not influence decoration building.

Introduction

Sit-and-wait predators depend on either ambushing prey or building traps to catch prey. Trap-building is quite rare in the animal world and only a few taxa are known to exhibit this behaviour. Some examples of traps are ant-lion sand pits, caddisfly larvae nets, arboreal ant platform traps and spider webs (Eberhard 1990; Eltz 1997; Lowe and Hauer 1999; Dejean *et al.* 2005). Building a physical structure as a method of catching prey has potential disadvantages. First, visually orienting prey could detect the trap and subsequently avoid it. Second, the presence of traps could also serve as a cue to predators. Therefore any trap-building organism has to consider a trade-off between the efficacy of the trap and its visibility. Orb web spiders have evolved a trap that is very hard to detect by their insect prey, though there is some evidence that some insects, especially Lepidoptera are able to see and avoid webs (Craig 1986). The effectiveness of a spider's web in deceiving prey increases with the fineness of the silk and, in some species, spider silk is beyond the range of detectability of their prey (Craig 2003). Therefore, the presence of highly visible silk structures (known as decorations or stabilimenta) in the web in some diurnal spider species is a conundrum. Decorations typically consist of thick zigzag bands of silk and are built out of the same silk that the spider uses to wrap prey (Peters 1993). Decorations are thought to be highly visible mainly because they reflect the UV part of the light spectrum, and it is known that a variety of insects and birds are able to see this reflected light (Bruce *et al.* 2005, but see Zschokke 2002). Therefore, web decorations can be potentially utilised by a wide variety of receivers, including prey (flying insects), predators (wasps, mantids and araneophagic spiders) and low-flying birds (Herberstein *et al.* 2000b). Because of the potentially detrimental increased visibility of the web, it has been thought that web decorations play an important role in the life history of these spiders. However, the exact

function of web decorations has been under debate for well over 100 years (Herberstein *et al.* 2000b).

Of the 22 known genera of orb-web-building spiders in the world, only 78 species are known to decorate their webs with bands of silk (Herberstein *et al.* 2000b). These decorations, seen in the families Araneidae, Tetragnathidae and Uloboridae, have evolved independently nine times and are found only in diurnal species (Scharff and Coddington 1997). Functional explanations for web decorations range from predator avoidance and prey attraction to thermoregulation (for detailed reviews, see Herberstein *et al.* 2000b and Bruce 2006). Furthermore, there is evidence that decorations attract specialist predators such as araneophagic spiders and mantids (Bruce *et al.* 2001; Seah and Li 2001). Proponents of the prey-attraction hypothesis suggest that the reflectance of UV from the decorations mimics those of nectar guides in flowers, and thus cause an increase in the rate of prey capture (Craig and Bernard 1990; Tso 1998; Herberstein *et al.* 2000b; Li *et al.* 2004). The predator-avoidance hypothesis suggests that spiders use decorations for camouflage, or to make the spiders look bigger, as well as reduce web damage (Eberhard 1973; Eisner and Nowicki 1983; Blackledge and Wenzel 1999). Juvenile spiders are known to shuttle back and forth between the two sides of the web, and it has been suggested that they use web decorations as sun shields to keep them from overheating (Humphreys 1992). Despite a series of studies testing these hypotheses, there is no consensus regarding the function or functions of web decorations (Herberstein *et al.* 2000b; Bruce 2006).

One of the reasons why it has been so difficult to track down the exact nature of web decorations is the occurrence of large interspecific and intraspecific variation in web-decorating species (Robinson and Robinson 1974). Even within a single population, there are several different patterns of decorations

(Robinson and Robinson 1970). For example, in webs of *Argiope keyserlingi*, there are up to four bands radiating from the centre towards the edge. Juveniles of this species often build a discoid decoration, and switch to the two-armed vertical form as they grow older (D. Rao, pers. obs.). Variation in decoration building is also poorly understood, as there may be a variety of influencing factors. For example, studies have shown that decoration construction is influenced by low light conditions, a high level of satiation of the spider, and the size or stage of the spider (Herberstein *et al.* 2000a; Seah and Li 2002; Herberstein and Fleisch 2003). This, in turn, suggests that decoration building is dependent on the local ecological context of the spider. Understanding the role of the decoration within the context of the spider's native habitat is a first step in determining the evolutionary significance of web decorations.

This study was therefore aimed at providing ecological data on three main factors, namely (1) biotic/abiotic factors, (2) seasonality and (3) microhabitat characteristics, and their possible influence on the presence and extent of decoration construction in an Australian orb web spider (*Argiope keyserlingi*).

Methods

Argiope keyserlingi Karsch, 1878 (Araneae:Araneidae), also known as the St Andrew's Cross spider, is an orb web spider recorded from the eastern coast of Australia (Platnick 2005) in a wide variety of habitats, ranging from rainforest margins to urban gardens. It is locally abundant and typically found on short long-leaved bushes such as *Lomandra* sp. and *Pandanus* sp. (D. Rao, pers. obs.). There is extreme sexual dimorphism in this species, with females being 3–4 times larger than the males (Elgar *et al.* 2000). Females build webs in the early morning, and are known to rebuild the main web daily, while leaving the frame threads in place. Males build webs only until they become adult and then they wander around searching for females, and subsequently cohabit the female web. This species often builds web decorations in the form of zigzag deposits of silk (hereafter referred to as 'bands', see Fig. 1) stretching outwards from the centre of the web. Both males and females build decorations in the form of bands, while juveniles typically build circular decorations and switch to the band form as they grow older. A maximum of four diagonal bands is normally seen in this species.

A natural population of subadult and adult female *Argiope keyserlingi* was surveyed in the Bicentennial Park in West Pymble, Sydney, Australia from 9 December 2004 to 27 January 2005. Webs were located in a patch of *Lomandra* sp. bushes. We measured the total body length of the spider, web area, height of web above ground (distance from the hub of the web to the ground), nearest vegetation (distance from the dorsal abdomen of the spider to the next vegetation in a straight line), location of the web with respect to the bushes (i.e. between bushes, inside, on the outer edges or on the top of individual bushes). We also determined the compass direction (i.e. east, west, north, south, north-east, north-west, south-east and south-west) that the spider faced on its dorsal side (i.e. away from the web). Decoration patterns and lengths were also recorded. Web area was measured as horizontal and vertical diameter of the web, and the web area was considered as an ellipse for calculations (Herberstein and Tso 2000). In this study we refer to seasonality with respect to the

period of the year when the spiders are active. Since they are rare or absent for most of the year all seasonality results refer to the summer. A subset of spiders were monitored daily for 7 days to determine frequency of decoration construction.

The software packages SPSS ver. 11 and Graphpad Prism ver. 5 were used for data analysis. When necessary, data were transformed for normality or non-parametric tests were used.

Results

Biotic and abiotic factors

The surveyed population exhibited a high degree of variation in decorating behaviour between individual spiders. Subadult spiders were less likely to decorate than adults (Fisher's exact test: $P < 0.0001$). In this species, decorating webs was not an obligate behaviour and the four-band pattern was not the dominant pattern, and spiders were more likely to decorate the lower part of the web (Fig. 2). We investigated the effect of specific biotic and abiotic factors on the length of web decorations using a General Linear Model. The overall model showed a significant effect of these parameters on decoration length ($R^2 = 0.2$, $F_{4,78} = 4.9$, $P = 0.002$). Of the four factors, longer decorations were associated with spiders that were bigger and further away from the surrounding vegetation (Table 1).

A subset of six marked adult female spiders was observed for 7 days. There was no significant difference in the number of days that individual spiders built decorations when compared with the number of days they did not build decorations (Mann–Whitney U -test, $U = 15$, $n = 6$, $P = 0.69$).

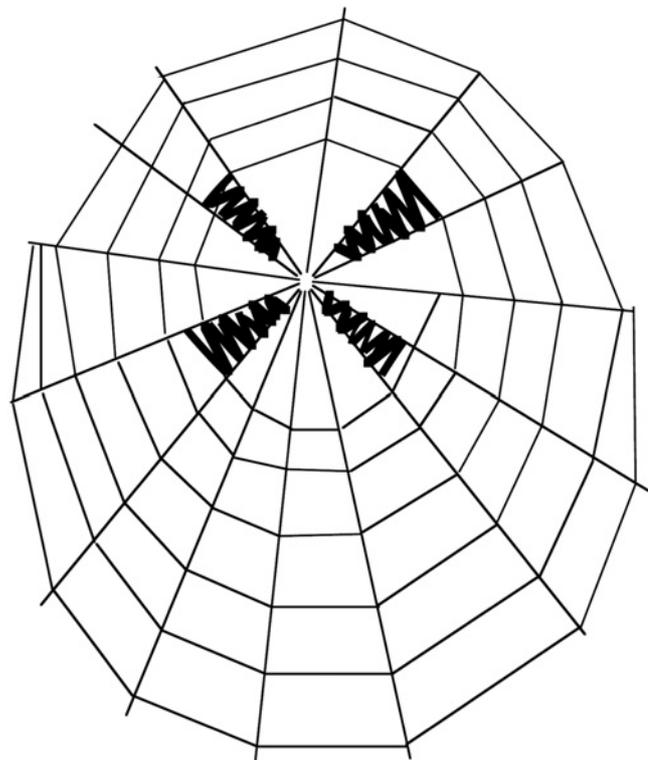


Fig 1. Schematic representation of a typical *Argiope keyserlingi* web showing the four-band pattern of web decorations. Redrawn from Herberstein (2000).

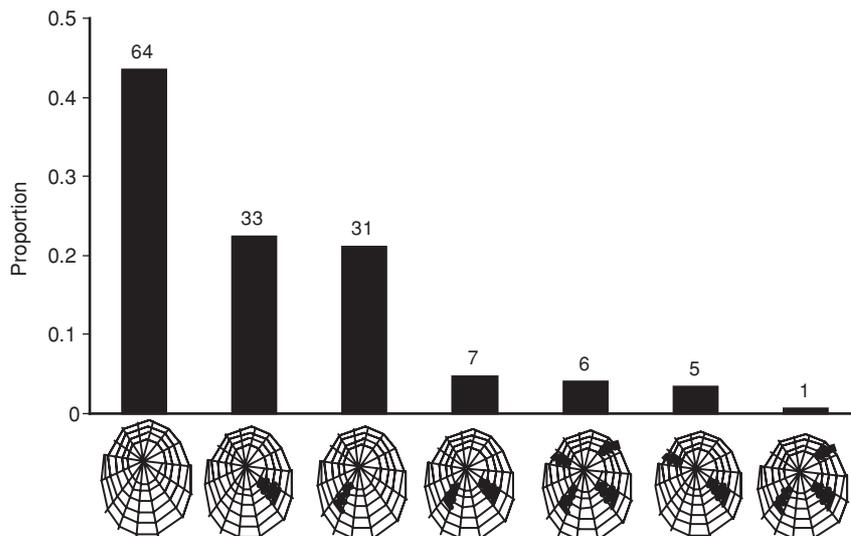


Fig 2. Variation in web-decorating patterns in adult female *Argiope keyserlingi*. Numbers above the bars denote the total number of individuals sampled.

Seasonality

Not unexpectedly, there was a decrease in the number of spiders present in the study site over the period of the study. We grouped the dates into three blocks, namely early in the study period, the middle of the study period and late in the study period. The proportion of spiders that built decorations also decreased over time (Chi-square test for independence: $\chi^2 = 17.26$, d.f. = 6, $P = 0.0084$). This general decline was also seen when we considered the dates separately, and irrespective of the stage of the spider. However, the decline was not significant when fitted with a linear regression (adults: $R^2 = 0.56$, $F = 6.33$, $n = 7$, $P = 0.053$; subadults: $R^2 = 0.19$, $F = 1.23$, $n = 7$, $P = 0.32$) (Fig. 3).

Microhabitat characteristics

Among the spiders in the *Lomandra* patch, there was a significant preference for facing south-east (Chi-square test for goodness of fit for aspect: $\chi^2 = 43.23$, d.f. = 7, $n = 239$, $P < 0.0001$) (Fig. 4). However, there was no significant relation between the directional preference and decoration presence (Chi-square test of independence for aspect with and without decorations:

$\chi^2 = 4.12$, d.f. = 14, $P = 0.995$). Of the possible locations of spiders among the bushes, there was a preference to build webs between two bushes as opposed to within or on a single bush (Chi-square test for goodness of fit for location: $\chi^2 = 116.72$, d.f. = 3, $n = 200$, $P < 0.0001$) (Fig. 5). This preference in location was not related to decoration presence (Chi-square test for independence of aspect with and without decoration: $\chi^2 = 1.099$, d.f. = 3, $P = 0.772$).

Discussion

This study aimed to characterise the ecological conditions that could influence the building of decorations in orb web spiders. To this end, we focussed on three main factors, namely biotic/abiotic factors, seasonality and microhabitat characteristics. We also determined the extent of variation of patterns and frequency of decoration building in *A. keyserlingi*. From this study, it is apparent that *A. keyserlingi* is not an obligate decoration builder. Over the study period, ~60% of individuals sampled built web decorations. This variation extends to the patterns of decorations as well. As in other species of *Argiope*, the

Table 1. The effect of distance to nearest vegetation, size of the spider, web area and web height on the total length of decorations

Larger spiders and spiders that were further away from the vegetation built longer decorations ($R^2 = 0.2$, $F_{4,78} = 4.9$, $P = 0.002$). The values associated with the constant refer to the y intercept, i.e. the point where the regression line crosses the y-axis. The coefficients are the numerical terms associated with the regression equation. Dependent variable: total decoration length (mm)

Variables	Unstandardised coefficients	Standard error	Standardised coefficients	t	P
(Constant)	-3.499	15.806		-0.221	0.825
Total body length (mm)	2.650	0.930	0.311	2.849	0.006
Web area (cm ²)	1.081E-03	0.002	0.068	0.651	0.517
Distance to nearest vegetation (cm)	0.285	0.108	0.269	2.629	0.010
Web height (cm)	-9.915E-02	0.148	-0.070	-0.669	0.506

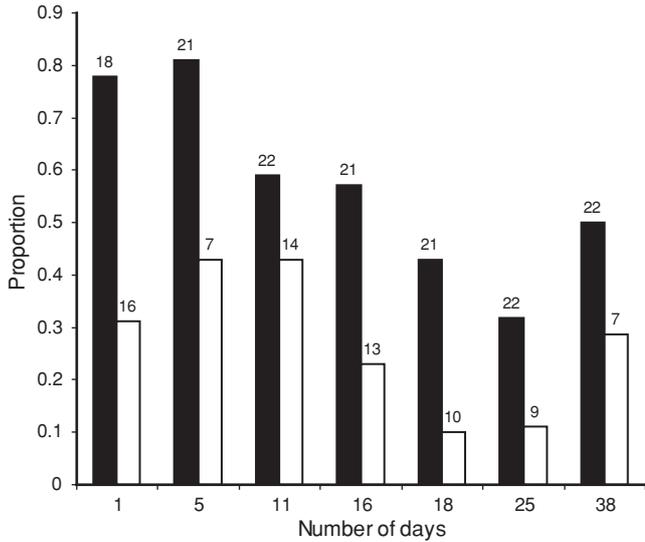


Fig 3. There was a general decline in the proportions of adult (black bars) and subadult (white bars) female spiders that built web decorations over time (9 December 2004 to 27 January 2005). Numbers above bars represent number of individuals sampled.

four-arm decoration was one of the least common patterns, with the exception of *A. florida* (Justice *et al.* 2005) and *A. aemula* (Robinson and Robinson 1974), in which the four-band pattern is dominant. Spiders preferred to build one or two bands on the lower part of the web, which has more capture area than the upper part of the web (Herberstein and Heiling 1999). Variation in decoration frequency was also seen in laboratory experiments (Craig *et al.* 2001) as well as in field studies (Robinson and Robinson 1970). There are two explanations for variation in patterns as well as frequency of decoration building. First, since it is known that araneophagic predators learn to associate the decorations with their prey, variation in decoration frequency and type could lessen the chance of predation (Bruce *et al.* 2001; Seah and Li 2001). Second, potential prey, such as stingless

bees, also quickly learn the location of the web and subsequently avoid the web (Craig 1994). Therefore, by varying the appearance of the web over time, the spider minimises the negative impact of producing such a visible signal.

We studied the influence of the microhabitat on decorating behaviour of *A. keyserlingi*. Since previous studies have demonstrated that spiders tend to decorate more under conditions of low light (Seah and Li 2002; Herberstein and Fleisch 2003), we expected to see more spiders decorating when they were closer to the ground, or when they were deeper in the surrounding vegetation, which is their preferred habitat (Enders 1973). However, in concordance with other studies (e.g. Nentwig and Rogg 1988), we found no relationship between these factors and decoration behaviour. Though microhabitat factors such as location of spider in the *Lomandra* bushes or orientation with respect to compass direction had no influence on the presence of web decorations, our study shows that more spiders preferred to build webs in between bushes and face south-east (on their dorsal side). We suggest that this pattern of orientation is preferred by the spiders in order to take advantage of the morning light, as seen in laboratory conditions where spiders tend to orient towards the light (Herberstein and Fleisch 2003). The sun rises in the south-east in the study area during summer, and the spiders may orient this way either to warm up faster or to place the web perpendicular to the light rays. A similar orientation pattern was seen in *A. trifasciata* (Ramirez *et al.* 2003) and in *A. florida* (Justice *et al.* 2005).

While there is sufficient evidence to show that spiders have the ability to alter their webs and decorations to suit local environmental conditions (Seah and Li 2002; Herberstein and Fleisch 2003), the larger picture of the influence of seasonality has been less studied. We found a decrease in the proportion of adult and subadult spiders that build decorations as the season progressed from summer to autumn. The decrease in proportion was also seen in a separate dataset of spiders observed in 1997 in the same study site (Herberstein 2000, reanalysed by permission of the author), suggesting that this decrease is consistent across years. The change in proportions of spiders that decorate may be related to the differential mortality of decorating versus

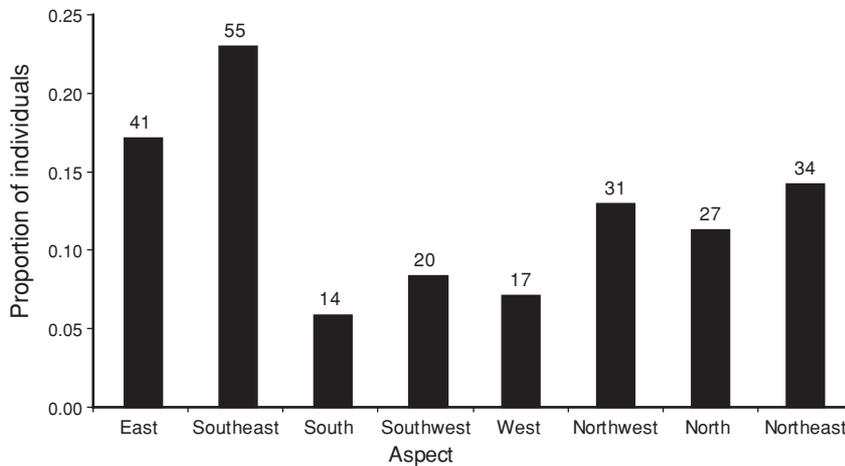


Fig 4. Spiders showed a preference for facing south-east. Numbers above the bars denote the total number of individuals sampled.

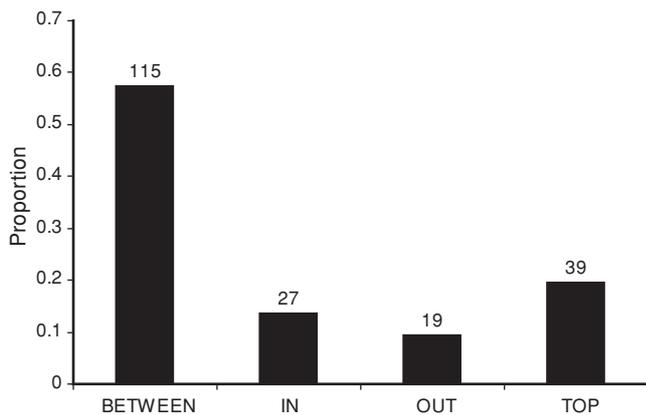


Fig 5. Spiders preferred to build webs between the *Lomandra* bushes rather than inside, on the outer edges or on the top of individual bushes. Numbers above the bars denote the total number of individuals sampled.

non-decorating spiders (Craig *et al.* 2001, but see Herberstein 2000). This change in web-decoration behaviour over time suggests that the spiders are altering their behaviour to suit different needs at different times, and may explain inconsistencies between different studies.

Understanding the function of web decorations is hampered by the possibility that there could be more than one explanation for their utility (Herberstein *et al.* 2000b). It is likely that these different uses may act in conjunction to suit different facets of the spider's life cycle and local ecological conditions (Starks 2002). If these functions vary non-linearly, it may be difficult to untangle the precise specific use of the decorations, since they may be a system that works well as a whole for a multitude of functions, rather than any particular function. In conclusion, we suggest that while designing controlled experiments, a deeper understanding of the natural history of the species and field-based observations are useful in determining the nature of web decorations.

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