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Web decoration polymorphism in *Argiope* Audouin, 1826 (Araneidae) spiders: ontogenetic and interspecific variation

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Abstract

Spiders in the genus *Argiope* commonly include curious silk structures, termed web decorations or stabilimenta in their webs. Whilst interesting ontogenetic and interspecific variation in both the form and frequency of web decorations has been documented, to our knowledge this is the first study to compare this variation across a number of decorating species. Here we show that two sympatric species *A. picta* and *A. aetherea* construct different forms of web decorations as adults and that *A. picta* decorates at a higher frequency than *A. aetherea*. Furthermore, this difference in decoration frequency may be related to the different decoration forms (linear or cruciate) across this genus. We also show that native bees responded significantly more quickly to cruciate decorations than to linear decorations. Here we argue that consideration of the different decoration forms and the frequency at which spiders adorn their webs may help illuminate possible context-dependent functions for these curious structures.

Keywords: Anti-predator behaviour, *Argiope*, prey capture, stabilimenta, web decorations

Introduction

Web decorations are conspicuous silk structures included in the webs of many species of diurnal orb-web spiders (Araneidae, Uloboridae, Tetragnathidae). The decorating silk is produced by the aciniform and piriform glands (Peters 1993; Foelix 1996) and arranged in various patterns on the web. Intriguingly, the expression of web decorations is characterized by very high levels of ontogenetic and interspecific variability. The ontogenetic variability has been noted in a number of species, especially in the genus *Argiope*. In this genus juveniles commonly include discoid decorations in their webs, whilst adults include cruciate or linear decorations (Herberstein et al. 2000a). Furthermore, there is significant interspecific variation with at least six forms of decorations found in adult female spiders (Herberstein et al. 2000a). Within just one genus, *Argiope*, adults are known to construct three different decoration forms; linear, cruciate, and discoid (Herberstein et al. 2000a; Bruce et al. 2005). The interspecific variation is not limited to the form of decorations but also the frequency of spiders including decorations in their webs. For

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example, decorating is relatively infrequent in *Argiope argentata* (Fabricius, 1775) in the Galapagos (24.5–41.8%; Lubin 1975) but very common in *A. flavipalpis* (Lucas, 1858) in Ghana (98.7%; Edmunds 1986).

While ontogenetic and interspecific variation of behaviour is intrinsically interesting, these levels of variation in web decorations have significant implications on possible functions attributed to web decorations. Several, non-mutually exclusive functions are currently under discussion, including protection against predators, web advertisement, prey attraction, and mechanical support (Herberstein et al. 2000a). However, it is unclear if the ontogenetic and interspecific variation relates to the function of web decorations. In *Argiope versicolor* (Doleschall, 1859), juveniles with discoid decorations show different anti-predator behaviours to adults with cruciate decorations (Li et al. 2003). One explanation for this is that discoid and cruciate decorations perform different functions in this species. In *Argiope appensa* (Walckenaer, 1842) the low frequency of web decorations on the Island of Guam compared to surrounding islands has been attributed to the island lacking an avian predator (Kerr 1993). However, the relationship between frequency and function has yet to be tested in different species. Sympatric spiders, with different decoration forms and frequencies, are ideal for testing the relationship between these to factors as sympatry removes the ecological factors that may also influence the form and frequency of decorations (e.g. Herberstein and Fleisch 2003).

Argiope aetherea (Walckenaer, 1842) and *Argiope picta* L. Koch, 1871 are common large orb-web spiders found in tropical coastal Queensland, Australia (Levi 1983). These two species are ideal for investigating the variation in decoration frequency and form because adult females construct different decoration types: *A. aetherea* builds a cruciate type; *A. picta* constructs both linear and cruciate decorations. Beyond the type of decorations, very little is known about the decorating behaviour of these two species. One study on *A. aetherea* revealed that this species constructs decorations more frequently in dim light compared to bright light (Elgar et al. 1996). There are no studies of *A. picta* in Australia apart from the description of this species conducted by Levi (1983). Therefore, not only do these species offer an opportunity to study decoration frequency and form, the use of species that are under-represented in the literature as models will increase the overall body of knowledge on web-decorating behaviour and the spiders that engage in this behaviour.

The aim of this study is to quantify the variation in decorating behaviour observed in two sympatric decorating spiders, *Argiope aetherea* and *A. picta*, in their natural environment. Furthermore, we compare the decorating behaviour of both adult and juvenile *A. aetherea* and *A. picta* to that of a common sub-tropical species, *A. keyserlingi* Karsch, 1878. To further investigate the potential reasons for the variation in decorating forms in these two species we experimentally investigated the reaction of a potential prey animal (*Trigona carbonaria* Smith: Hymenoptera) to the different web decoration types. Furthermore, we experimentally manipulated the hunger level of spiders to investigate the influence of hunger on decoration construction. Finally, we conducted a meta-analysis of reported decorating frequency to see if differences in decorating frequency are related to form across *Argiope* species.

Materials and methods

Decoration frequency in wild populations

The aim of the field surveys was to document frequency of decorating behaviour in *A. aetherea*, *A. picta*, and *A. keyserlingi* across all age classes and in both sexes. Field surveys for

A. aetherea and *A. picta* were conducted on three separate occasions, January to February 2002, July to August 2002, and March 2003. We searched extensively for individuals of all age classes, from Hervey Bay (25°12'S, 152°48'E) to Cape Tribulation (16°1'S, 145°31'E) on the coast of Queensland, Australia (Figure 1). When we located an individual we noted the presence or absence of web decorations. If decorations were present we classified them as either discoid, cruciate, or linear (*sensu* Herberstein et al. 2000a). We also measured the body length of the spider to the nearest 0.5 mm. Body length was used as an estimate of size because we could not accurately measure any other parameter in the field. As *A. aetherea* and *A. picta* are sympatric (sometimes within 1 m of each other) and small juveniles look similar, we collected individuals that could not be assigned to one or the other species and housed them in the laboratory in Sydney until they matured and we could identify them. Individuals that did not survive to this point were not included in the analysis. Adult female

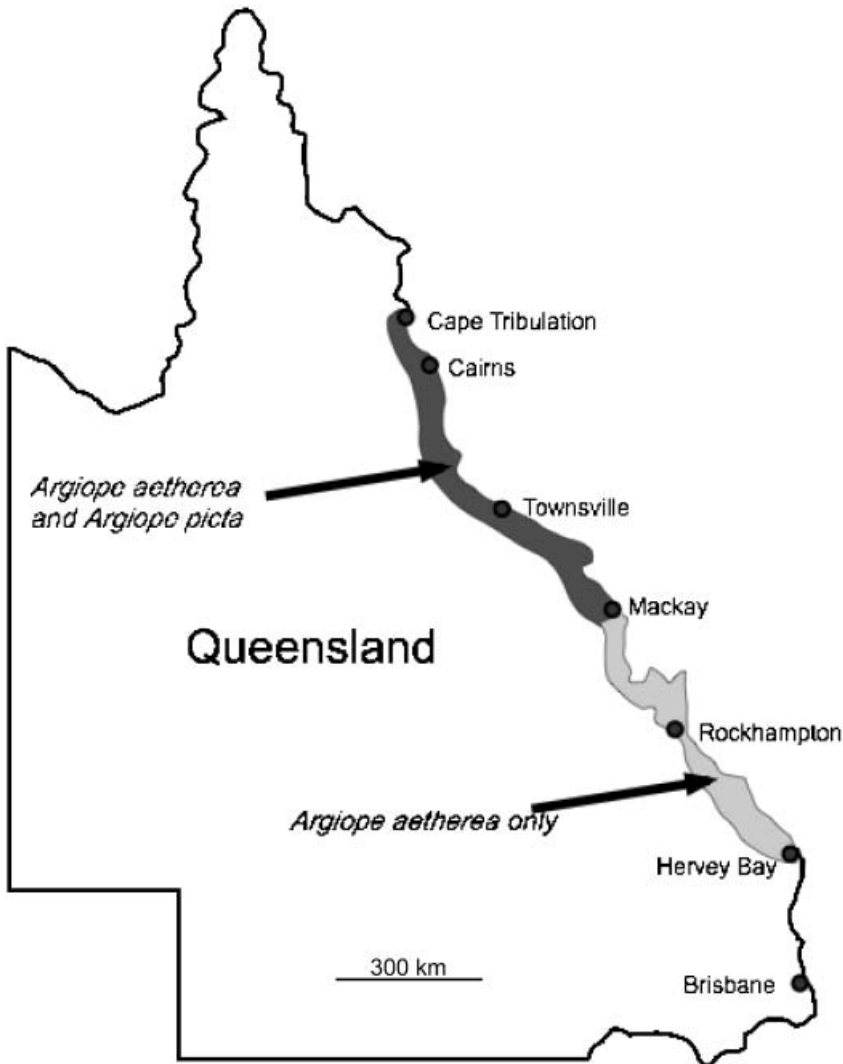


Figure 1. Map of Queensland showing the approximate ranges of *Argiope aetherea* and *A. picta* from this study.

individuals were identified by the presence of a raised epigyne, with two openings, signifying a reproductively mature female. We included both female and male juveniles as males construct webs and decorations in both species. As the males of both species look similar, they were only included in the analysis if they were found in areas where only one species was present and therefore could be unambiguously assigned to that species.

We surveyed juvenile *A. keyserlingi* on three separate occasions in Sydney at Bicentennial Park, West Pymble in December 2003. We noted the features of the decorations and measured spiders as described above. Surveyed individuals were removed from the population after each survey to ensure they were not encountered on subsequent occasions. We obtained data on the frequency of decorating in adult *A. keyserlingi* from Herberstein (2000).

For the purposes of analysis, we assigned juvenile spiders to one of four size classes depending on their body length. These were: (A) below 4.0 mm; (B) 4.0–5.9 mm; (C) 6.0–7.9 mm; and (D) 8.0 mm and above. These size classes corresponded to roughly equal numbers of individuals for each species. We used chi-squared analyses to compare decoration frequency between these size classes for each species, between adults and juveniles of the same species, and between adults or juveniles across species. α was set to 0.05 in all cases.

Does satiation level affect frequency of decorating behaviour in A. aetherea and A. picta?

Juvenile and adult females of *A. aetherea* and *A. picta* were collected from Queensland and transported to the laboratory at Macquarie University, Sydney. We housed them in either upturned plastic cups (11 × 6.5 cm) or Perspex® frames (15 × 15 × 50 cm) where they were fed a diet of *Drosophila melanogaster* Meigen, 1830 (Diptera), *Lucilia cuprina* (Wiedemann, 1830) (Diptera), and *Acheta domestica* (Linnaeus, 1758) (Orthoptera), and were regularly sprayed with water.

Adult female spiders from both species were randomly assigned to either a food-deprived or food-supplemented treatment 1 week prior to the initiation of the treatments. They were weighed and the length of the tibia–patella of the right front leg was measured in order to calculate initial body condition (see below). Each spider was then fed two juvenile crickets (*A. domestica*) and housed in an up-turned plastic cup. After 1 week, food-deprived spiders were each fed one cricket three times over 6 days and food-supplemented spiders were each fed three crickets three times over 6 days. Therefore, food-deprived spiders were fed three crickets each over 6 days and food-supplemented spiders nine crickets each over the same period. We sprayed all spiders with water every 2 days. After the final feed we transferred all spiders to Perspex® frames where they were allowed to construct a web. We measured the first web constructed by each spider, noting the size of the capture area (area covered by the sticky spiral) and distance between capture spirals (see Herberstein and Tso 2000 for calculations). We also noted the presence or absence of web decorations and measured their length. After an individual had constructed a web she was weighed in order to calculate her final body condition (see below).

To account for allometry we calculated the parameter “body condition”, which is known to influence web-building behaviour (Sherman 1994). We performed a linear regression between ln-transformed tibia–patella length (independent variable) and ln-transformed initial or final weight (dependent variable) separately for each species. The residual portion of the variable “body weight” was then taken as an estimate of the body condition of an individual. All data were analysed for normality (Kolmogorov–Smirnov) and equality of

variances (Levene's test). The results for *A. aetherea* and *A. picta* were analysed separately using either Student's *t* tests or the non-parametric Mann–Whitney *U* test. We used chi-squared to compare decoration frequency between treatments. $\alpha=0.05$ for all tests. All data are presented as mean \pm standard error.

Effect of decorating pattern (cruciate versus linear) on prey response

To investigate the influence of decoration orientation on prey response we conducted a paired Y-choice experiment. We used the webs of *A. keyserlingi* as this species was readily available and the reflectance spectrum of web decorations in *A. keyserlingi* is identical to that of *A. aetherea* and *A. picta* (Bruce et al. 2005). Webs with two decorative bands (half a cruciate decoration; one in the upper web half and one in the opposite lower web half) were harvested and offered to native Australian bees (*Trigona carbonaria*) in an opaque Y-maze (Figure 2). Each web was used twice, always paired with an undecorated web. The decorations from each web were arranged in either a cruciate orientation (30° from vertical and identical to *A. aetherea*) or in a linear orientation (0° from vertical and identical to *A. picta*). The order (cruciate or linear first) and exit corresponding to the decorated web (left or right) were determined randomly.

Each trial consisted of the behavioural response of six bees entering the maze consecutively for each decoration pattern (cruciate or linear). Bees were allowed to

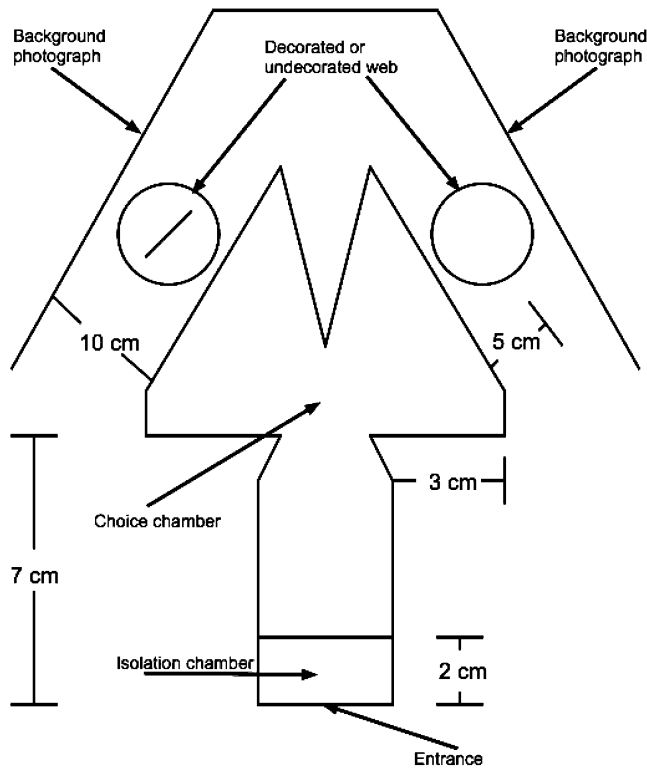


Figure 2. Schematic of the Y-maze used to test the response of prey to cruciate and linear web decorations.

acclimatize to the maze for 1 min in the isolation chamber (Figure 2) and then released into the choice chamber. We conducted each trial with the webs presented against a background photograph of *Lomandra longifolia* Labill., a common plant in which decorating spiders are typically found. The photograph at the background of the right maze exit was the horizontal reverse of that at the left exit. Webs were positioned in front of the equivalent position in each photograph to ensure a consistent background for each web. The Y-mazes were covered with plastic food wrap at each exit to remove the influence of pheromones and air currents on prey choice. This foil does not influence wavelengths of light transmitted. A "choice" of web was recorded when the prey animal contacted the foil at one of the maze exits. Bees were removed from the maze after a "choice" was recorded (only one bee in the maze at any time) and the maze was cleaned with 70% ethanol (to remove olfactory cues) and allowed to completely dry. We conducted a total of 19 trials and thus recorded the choice of 228 bees (19 trials \times 12 bees per trial) was recorded. We used a paired non-parametric Mann–Whitney test and Spearman correlation to analyse our data.

Decoration frequency meta-analysis

In order to determine whether the observed difference between decoration frequency of adult *A. aetherea* (cruciate) and *A. picta* (linear) was related to the difference in decoration form (cruciate or linear) we conducted a meta-analysis of published accounts of decoration frequency. We used the percentage of decorating spiders in a population reported by the authors to calculate a mean frequency of decoration for each form (cruciate or linear). These means were compared using the non-parametric Mann–Whitney test because the number of reported accounts of linear decorations was much lower than that of cruciate decorations.

Results

Decoration frequency in wild populations

We were able to locate a total of 83 adult female *A. aetherea* from Hervey Bay (25°12'S, 152°48'E) to Cape Tribulation (16°1'S, 145°31'E) ranging in length from 8.0 to 18.0 mm. Thirty adult female *A. picta* were located from Mackay (21°1'S, 149°12'E) to Cape Tribulation, ranging in length from 10.5 to 19.6 mm. We located 149 juvenile *A. aetherea* and 45 juvenile *A. picta* across the same ranges as adult spiders. Whilst the range of *A. aetherea* extends further south than that of *A. picta*, 70% of adult *A. aetherea* and 75% of juvenile *A. aetherea* were found in sympatry with *A. picta*. In a separate study, Herberstein (2000) surveyed the webs of 25 *A. keyserlingi* in West Pymble, NSW. To supplement these data we surveyed 80 juvenile *A. keyserlingi* from the same population.

Of the 83 *A. aetherea* adults 24 (28.9%) were on webs with one or more cruciate bands (Figure 3). *Argiope keyserlingi* adults also construct cruciate decorations, 58.7% of surveyed webs contained one or more cruciate bands (Figure 3; Herberstein 2000). By contrast *A. picta* are compulsive decorators with 93.3% of spiders being found on decorated webs (Figure 3).

Furthermore, almost all adults of *A. picta* construct linear decorations (85.7%) with a small minority constructing cruciate decorations (14.3%). The proportion of spiders constructing decorations between these three species was significantly different ($\chi^2_2=35.8$, $P<0.0001$).

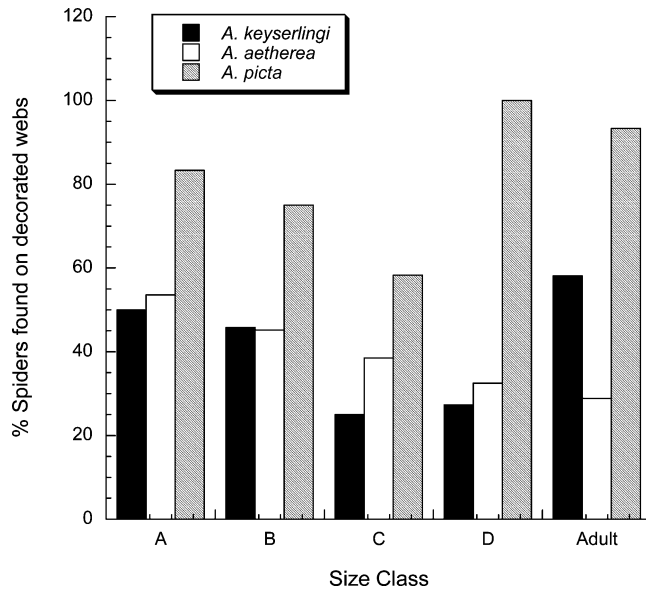


Figure 3. Percentage of spiders from the three species surveyed found on decorated webs sorted by size class: A, below 4.0 mm; B, 4.0–5.9 mm; C, 6.0–7.9 mm; D, 8.0 mm. The frequency of decorations in adult *Argiope keyserlingi* was taken from Herberstein (2000).

In all three species there was an ontogenetic shift in both decoration form and frequency during juvenile development and between juveniles and adults. In *A. aetherea* 40.9% of juveniles were on decorated webs, 77.8% of *A. picta* juveniles were on decorated webs, and in *A. keyserlingi* 36.3% of juveniles were on decorated webs (Figure 3). As with adult spiders, there was an overall difference in the frequency of juvenile *A. picta*, *A. aetherea*, and *A. keyserlingi* adding decorations to their webs ($\chi^2_2=22.91$, $P<0.0001$). In both *A. aetherea* and *A. keyserlingi* juveniles up to 5.9 mm in length included discoid decorations, although this was much more common in *A. keyserlingi* (Figure 4a, b). In *A. picta* discoid decorations were constructed by individuals up to 7.9 mm (Figure 4c). In *A. keyserlingi* and *A. aetherea* there was a general decline in decoration frequency with size (Figure 4a, b), although these frequency differences between size classes were not significant (*A. keyserlingi*: $\chi^2_3=4.86$, $P=0.18$; *A. aetherea*: $\chi^2_3=3.48$, $P=0.32$). *Argiope picta* juveniles also showed a decreased decoration frequency with increasing body size but only until they reach 8.0 mm, after which all juveniles were found with decorations (Figure 4c), again this difference in frequency between sizes was not significant ($\chi^2_3=4.98$, $P=0.17$). Interestingly, the linear decorations characteristic of adults in this species only appear in the largest juveniles (8.0 mm and above) with smaller juveniles constructing cruciate or discoid decorations. Only one species, *A. keyserlingi*, showed a significant difference between juvenile and adult decorating frequency ($\chi^2_1=4.41$, $P=0.04$), adults of this species construct decorations more frequently than juveniles.

Does satiation level affect frequency of decorating behaviour in A. aetherea and A. picta?

There was no significant difference in the initial body condition of food-deprived or food-supplemented spiders in *A. aetherea* (Mann–Whitney $U_{33}=124.0$, $P=0.67$) or *A. picta* (Mann–Whitney $U_{25}=60.0$, $P=0.33$). However, the body condition of food-supplemented

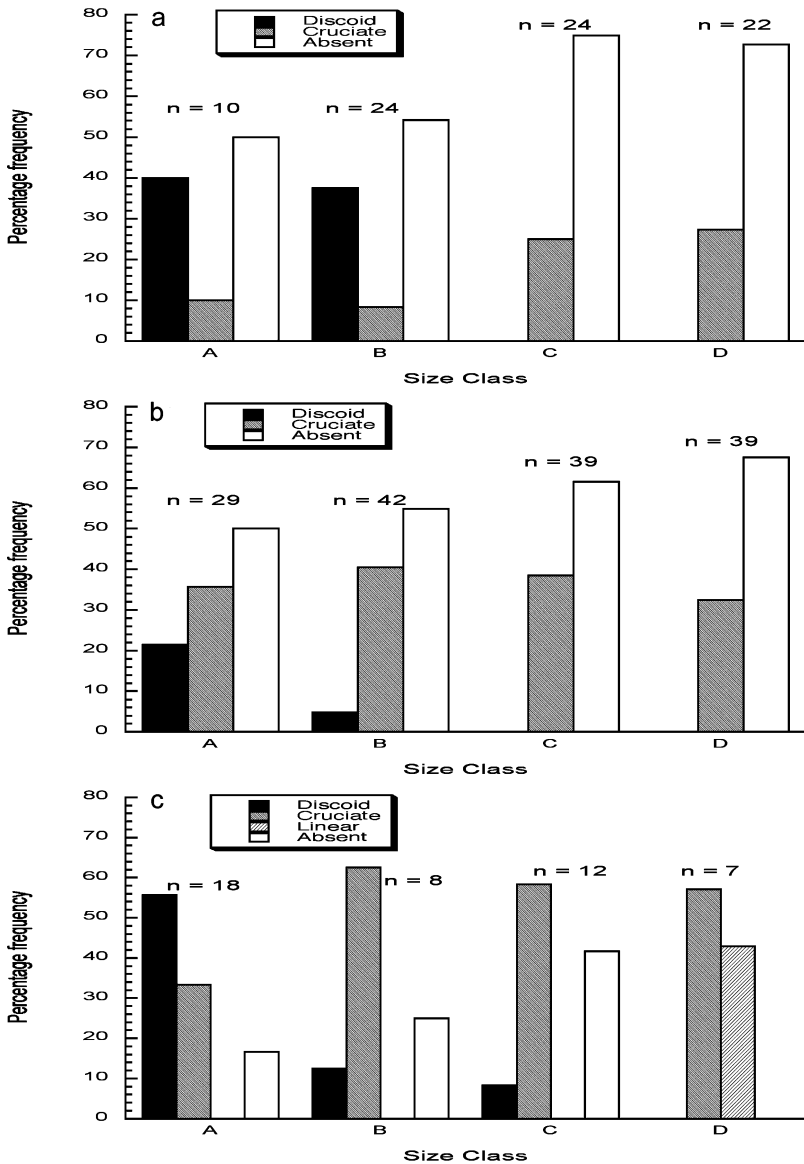


Figure 4. Decoration form by juvenile size class: A, below 4.0 mm; B, 4.0–5.9 mm; C, 6.0–7.9 mm; D, 8.0 mm. (a) *Argiope keyserlingi*; (b) *A. aetherea*; (c) *A. picta*.

spiders was significantly higher for both species after the experiment (*A. aetherea*: Mann-Whitney $U_{32}=18.0$, $P<0.001$; *A. picta*: $U_{25}=13.0$, $P<0.001$).

In both species food-deprived spiders constructed larger webs than food-supplemented spiders, although this difference was not significant in *A. picta* (Table I). There was no significant effect of the feeding treatments on the mesh height for either species (Table I).

In *A. aetherea* food-supplemented spiders constructed significantly longer decorations than food-deprived spiders (Mann-Whitney $U_{33}=88.0$, $P=0.05$; Figure 5). Furthermore, twice as many food-supplemented spiders (56.3%) included decorations compared to

Table I. Summary of web area and mesh height of the webs constructed by spiders in the hungry and satiated treatments (means \pm SE).

Species	Web area (cm ²)			Mesh height (mm)		
	Deprived	Supple- mented	Statistics	Deprived	Supple- mented	Statistics
<i>A. aetherea</i>	828.0 \pm 50.5	455.4 \pm 65.6	$t_{31}=4.53$, $P<0.001$	5.3 \pm 0.3	6.5 \pm 0.8	$U_{33}=117$, $P=0.49$
<i>A. picta</i>	647.0 \pm 110.5	374.8 \pm 89.4	$t_{23}=1.87$, $P=0.07$	6.4 \pm 0.9	5.1 \pm 0.6	$t_{23}=1.23$, $P=0.23$

food-deprived spiders (30.8%; $\chi^2_1=3.7$; $P=0.05$). The feeding treatments had no effect on the length of decorations in *A. picta* ($t_{25}=-0.11$, $P=0.91$; Figure 5) or on the number of spiders including decorations in their webs (food-deprived: 92.6%; food-supplemented: 91.7%; $\chi^2_1=0$, $P=1.0$).

Effect of decorating pattern (cruciate versus linear) on prey response

We found no difference between the frequencies of bees choosing cruciate or linear decorations from the same pair ($Z_{19}=-0.67$, $P=0.50$). Furthermore, there was no correlation between the frequency of bees choosing the decoration in the cruciate orientation and in the linear orientation ($r=-0.24$, $n=19$, $P=0.33$). We also analysed the time taken for bees to approach linear (39.6 \pm 3.9 s) or cruciate decorations (28.4 \pm 3.8 s). Of the bees that approached a decorated web, those approaching a cruciate decoration were significantly faster than those approaching a linear decoration ($t_{32}=2.05$, $P=0.05$).

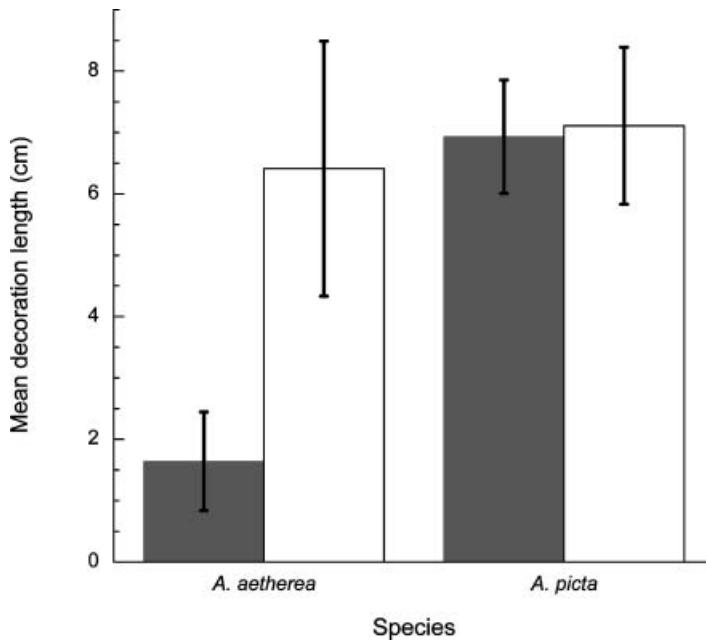


Figure 5. Mean decoration length (\pm SE) in food-deprived (grey bars) and food-supplemented (white bars) spiders.

Decoration frequency meta-analysis

We found decorating frequency data for 12 *Argiope* species from 20 different populations (Table II). As there was considerable variation in the frequency of decorations in different populations of the same species, each population was included separately in the analysis. Of the 20 populations (18 from the literature and two from this study), 17 constructed cruciate decorations and three constructed linear decorations. One species, *A. picta*, has been recorded to construct both cruciate (Robinson et al. 1974) and linear (this study) decorations in different populations. Spiders that construct linear decorations are almost significantly more likely to decorate their webs ($76.3 \pm 5.0\%$) than spiders that build cruciate ($52.9 \pm 5.6\%$) decorations (Mann–Whitney $U_{19}=10.0$, $P=0.10$).

Discussion

Our results revealed that there are pattern-specific frequencies in the web decorations of *Argiope aetherea*, *A. keyserlingi*, and *A. picta*. When spiders build linear patterns (*A. picta*) they decorate their webs far more frequently than when spiders build cruciate decorations (*A. aetherea* and *A. keyserlingi*). This was also apparent in juvenile spiders, with *A. picta* decorating more frequently than either *A. aetherea* or *A. keyserlingi*. Furthermore, pattern-specific frequency is evident across the reported accounts of the decoration frequency in the *Argiope*. Moreover, *A. aetherea* responded to supplemental feeding in a similar way to other species (Blackledge 1998; Tso 1999; Herberstein et al. 2000b; Seah and Li 2002) by

Table II. The frequency of adult spiders including cruciate or linear decorations in their webs.

Species	Location	Type	Frequency (%)	Sample	Reference
<i>A. aemula</i> (Walckenaer, 1842)	New Guinea	Cruciate	91.6	83	Robinson et al. (1974)
<i>A. aetherea</i>	Queensland	Cruciate	28.9	83	This study
<i>A. appensa</i>	Guam, Marianas	Cruciate	16.4	359	Kerr (1993)
<i>A. appensa</i>	Rota, Marianas	Cruciate	56.9	211	Kerr (1993)
<i>A. appensa</i>	Tinian, Marianas	Cruciate	41.9	315	Kerr (1993)
<i>A. appensa</i>	Saipan, Marianas	Cruciate	50.3	310	Kerr (1993)
<i>A. argentata</i>	Panama	Cruciate	34.5	2614	Robinson and Robinson (1970)
<i>A. argentata</i>	Jamaica	Cruciate	75.4	65	Marples (1969)
<i>A. argentata</i>	Daphne Major, Galapagos	Cruciate	24.5	141	Lubin (1975)
<i>A. argentata</i>	Santa Cruz, Galapagos	Cruciate	41.8	134	Lubin (1975)
<i>A. keyserlingi</i>	New South Wales	Cruciate	58.7	25	Herberstein (2000)
<i>A. pulchella</i> Thorell, 1881	Burma	Cruciate	68.3	60	Marson (1947)
<i>A. reinwardti</i> (Doleschall, 1859)	New Guinea	Cruciate	78.5	65	Robinson et al. (1974)
<i>A. trifasciata</i>	Ghana	Cruciate	46.0	752	Edmunds (1986)
<i>A. versicolor</i>	Singapore	Cruciate	40.0	45	Seah and Li (2002)
<i>A. flavipalpis</i>	Ghana	Cruciate	98.7	230	Edmunds (1986)
<i>A. picta</i>	New Guinea	Cruciate	46.8	400	Robinson et al. (1974)
<i>A. picta</i>	Queensland	Linear	85.7	30	This study
<i>A. bruennichi</i> (Scopoli, 1772)	France	Linear	68.7	90	Marples (1935)
<i>A. lobata</i> (Pallas, 1772)	France	Linear	74.6	63	Marples (1969)

increasing decoration investment. However, *A. picta* did not alter its decorating behaviour. We also found evidence that a potential prey animal, *Trigona carbonaria* (Hymenoptera), showed a different response to linear than to cruciate decorations by approaching cruciate decorations significantly faster than linear decorations. Taken together, these lines of evidence suggest that either the different patterns perform a different function and/or there are different costs and benefits to building them. This difference is likely to be related to the angle of decorations (vertical or inclined at 30°) as there is no difference in the spectral properties of different patterns (Bruce et al. 2005). Indeed, both flies (Campbell and Strausfeld 2001) and bees (Lehrer et al. 1995) have the ability to discriminate between vertical lines and those at an angle. It is therefore possible that potential prey insects have the ability to discriminate between linear and cruciate decorations. This may then influence the attractiveness of decorations at different angles, depending on the patterns of other positive or negative cues in the environment.

Whilst we did not explicitly test the function of decorations in this study, it is possible that the ontogenetic differences in decoration form indicate different functions at different life history stages. Indeed, *Argiope versicolor* shows decoration-specific anti-predator behaviours, with juveniles with discoid decorations more likely to shuttle to the other side of the web in the presence of a predator stimulus than those on undecorated webs (Li et al. 2003). Presumably the decoration creates a physical barrier between the spider and the predator. However, there is also evidence that discoid decorations are prey attractants in this species (Li et al. 2004). In adult spiders, there is a growing body of evidence that both cruciate (Herberstein 2000; Bruce et al. 2001) and linear decorations attract prey (Tso 1996, 1998; Bruce et al. 2004), although in some species they may afford the spider protection against predators (Blackledge and Wenzel 2001). Clearly, more comparative experiments are vital to enhance our understanding of the relationship between pattern and function.

The other, non-mutually exclusive, possibility to explain interspecific differences in decoration patterns is that there is a difference in the costs and benefits of the patterns. In some species, such as *A. keyserlingi*, cruciate decorations attract prey and increase foraging success but they also attract predators (Herberstein 2000; Bruce et al. 2001), whilst in *A. trifasciata* (Forskål, 1775) linear decorations have been shown to both attract prey (Tso 1996, 1998) and provide protection against predators (Blackledge and Wenzel 2001). Therefore, cruciate decorations may be more costly in terms of predator attraction, prompting spiders with this pattern to decorate less frequently. Perhaps the payoff for cruciate decorators is that they are more attractive to prey. Whilst we found no overall difference in the number of native bees approaching linear and cruciate decorations, they approached cruciate decorations significantly faster, perhaps indicating that they have an innate preference for this pattern.

Habitat-specific factors therefore may play a role in determining the relative costs and benefits of different decoration patterns. Indeed, the low frequency of cruciate decorations in the webs of *Argiope appensa* on Guam compared to neighbouring islands was attributed to the lack of an avian predator on this island (Kerr 1993). Furthermore, in "*Araneus*" *eburnus* web decorations only influenced foraging success in undisturbed habitats, perhaps due to different prey assemblages (Bruce et al. 2004). It may be that the habitat occupied by the sympatric *Argiope picta* and *A. aetherea* favours the construction of linear decorations in adult spiders due to the presence of particular species of predators and/or prey. Further studies of the predator and prey assemblages of their habitat will assist in illuminating the costs and benefits of the different decoration forms. Interestingly, adult *A. picta* have also

been recorded constructing mostly cruciate decorations (Robinson et al. 1974). Whilst this may simply be a case of mistaken identity, a more intriguing possibility is that this species is able to construct both forms and therefore uses the most profitable strategy in a particular environment. Indeed, in this study we recorded a low number of *A. picta* adults with cruciate decorations.

In this study, we have found intriguing, and to date unexplored ontogenetic and interspecific differences in the frequency of decorating behaviour in the genus *Argiope*. In adult spiders, these differences seem to be related to the pattern of web decorations (linear or cruciate) constructed by the different species. Specifically, consistent differences in linear versus cruciate decorations from convergent lines of evidence suggest that these patterns perform different functions and have different costs and benefits associated with them. This realization may help in resolving the controversy surrounding web decoration functions. Future functional studies should look at linear and cruciate decorations separately and consider the potential costs and benefits of these decoration forms.

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