Does decoration building influence antipredator responses in an orb-web spider (*Argiope keyserlingi*) in its natural habitat?

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Abstract. Antipredator strategies adopted by animals need to compensate for temporal changes. Many orb-web spiders add silk decorations to their webs, which principally attract prey but may attract some predators. To identify their influence on antipredator behaviour in adult female St Andrew's cross spiders (*Argiope keyserlingi*) we measured: spider body condition, web characteristics (area, spiral length and decoration building), environmental variables (air temperature, humidity, wind speed, relative prey abundance) and antipredator responses (remaining at the hub, dropping, shifting to the web periphery, or pumping the web) at three distinct periods (July–August, September–October and January–February) in the field. We developed path models from multiple regression analyses to distinguish between factors having direct and indirect effects. We found that even though both antipredator responses and decoration building change over time, antipredator responses and decoration investment are independent. Body condition and wind speed are directly positively associated with pumping frequency, and decoration building is negatively associated with the frequency of remaining at the hub because the likelihood that an object approaching the web is a predator increases if decorations are added. Wind speed is positively associated with antipredator behaviour and decoration building, due to an increased rate of feeding affecting body condition.

Introduction

Diverse antipredator strategies have evolved in animals (Ydenberg and Dill 1986), but it is poorly understood how animals switch strategies when circumstances, such as predation threat or physiological requirements, change (Ydenberg and Dill 1986; Lima and Bednekoff 1999; Lind and Cresswell 2005). The lack of understanding may have arisen because field and laboratory studies alone are unreliable at identifying causal mechanisms (Shipley 2000). Field studies give investigators the functionality to test an organism's responses to natural stimuli but the ability to manipulate the plethora of variables that may be interacting in the system is limited (Underwood 1997). Laboratory studies provide the functionality to manipulate variables, thus are often preferred, but they often do not adequately reflect natural situations (Underwood 1997; Sinervo and Svensson 1998). Additionally, many variables that affect life-history strategies in nature are strongly inter-correlated (Scheiner *et al*. 2002). It is, thus, often impossible to ascribe functional relationships between manipulated variables and an observed behaviour. Path analysis has been used to gain a greater understanding of factors directly affecting animal life-history responses (Shipley 2000; Scheiner *et al*. 2002). We used this approach to determine the influences of a multitude of physiological and environmental factors on the antipredator behaviour of an orb-web spider.

Orb-web spiders of the genus *Argiope* occupy the hub of their webs throughout the day, exposing themselves continuously to predators. If attacked, common responses are to either remain at the hub, drop off the web (dropping), retreat from the threatening stimulus by shifting to the periphery of the web (shifting),

or rapidly pump the web (pumping) (Schoener and Spiller 1992; Cloudsley-Thompson 1995; Li *et al*. 2003). The strategy adopted may depend on the perceived threat weighed against the performance costs of each strategy (Cloudsley-Thompson 1995). Although its precise function remains obscure, pumping involves repeated rapid leg flexion which seems to effectively obscure the spider's location on the web to visually oriented predators (Schoener and Spiller 1992; Li *et al*. 2003). It is usually only conducted in short bursts (<30 s) and is followed immediately by inactivity (Li *et al*. 2003) and, thus, appears energetically expensive to perform. Remaining at the hub is the most energy-conserving strategy and is adopted at times when perceived threat is low (Herberstein and Heiling 2001), or as a cryptic response to non-visually oriented predaters (Cloudsley-Thompson 1995). When dropping from the web, the spider must loosen its grip on the web (Li *et al*. 2003), which may be costly if the web is high off the ground or when the wind is strong, as the spider may be dragged a considerable distance away from the web, or the dragline thread may be ineffective at regulating the fall velocity if it is over-stretched (Brandwood 1985; Herberstein and Heiling 2001). Shifting to the web periphery is generally an inexpensive strategy and adopted at times of moderate or low threat (Schoener and Spiller 1992; Li *et al*. 2003).

Argiope spp. add conspicuous UV-reflecting decorations (also called stabilimenta) to their webs (Herberstein *et al*. 2000*a*, 2000*b*; Seah and Li 2002). Protection against predators by concealing, enhancing the apparent size of, and obscuring the location of, the spider, and advertising the presence of the web to avian predators, have been proposed as possible functions for

decorations (Schoener and Spiller 1992; Herberstein *et al.* 2000*a*). The cruciform-shaped decorations of the St Andrew's cross spider (*Argiope keyserlingi*) reflect light in the UV and attract prey to the web (Herberstein *et al.* 2000*a*, 2000*b*; Bruce *et al.* 2001, 2005). Rather than deterring predators, the decorations of *A. keyserlingi* may permit birds and other visually oriented predators (e.g. mantids, jumping spiders) to locate them in the hub (Bruce *et al.* 2001, 2005; Seah and Li 2001), which may explain why *A. keyserlingi* places its web predominantly in closed, complex habitats such as among sedges (Blamires *et al.* 2007) and why individual *A. keyserlingi* regularly switch between adding no decorations and decorations with either one, two, three or four (fully cruciform) arms to their web (Herberstein 2000; Bruce *et al.* 2001). Since the manufacture of decoration silk is positively related to food (insects) consumption (Herberstein *et al.* 2000*b*; Tso 2004) and insect abundances show strong temporal variations, due to the strong influences of temperature, humidity, wind and photoperiod over activity (Price 1997), orb-web spiders may vary their decoration-building patterns over time. As a consequence, they could experience temporal variations in both foraging success and predation threat. Antipredator behaviours in *Argiope* spp. and decoration building often covary and, accordingly, building decorations has been ascribed as a supplementary antipredator strategy (Schoener and Spiller 1992; Li *et al.* 2003). It has, however, never been elucidated in the field whether antipredator behaviours are directly associated with decoration building.

Here, we conducted a field study to determine whether the antipredator strategies adopted by *A. keyserlingi* shift temporally, and whether decorations or other factors are the underlying causes of the shifts. We measured a multitude of factors in the field: the number and length of decoration arms and the spiral distances of *A. keyserlingi* webs, and spider body length, width and mass, prey abundance, ambient temperature, humid-

ity and wind speed over three climatically distinct periods: July–August (winter), September–October (spring), and January–February (summer). We used multiple regression-derived path analyses to distinguish between factors having direct and indirect relationships with antipredator responses. If antipredator responses and decorations are directly associated their relationship across each period will be independent of the temporal changes in environmental factors, spider body condition or prey availability.

Materials and methods

Predator simulation

Mantids and birds are the main predators of *A. keyserlingi* in Sydney (Bruce *et al.* 2001, 2005; Blamires *et al.* 2007). We therefore simulated a mantid or bird attack by distally prodding with forceps (Jackson *et al.* 1990, 1993) any adult female *A. keyserlingi* (≥12 mm body length) observed occupying the hub of her web, within the University of Sydney, Camperdown Campus. Attacks were carried out as rapidly as possible to minimise the variation in attack time. Attacks were conducted during random walks every third day between 1200 and 1400 hours, over three 4-week periods (July–August, September–October and January–February). Only spiders within sedge habitats (the preferred habitat of *A. keyserlingi* at our site: Blamires *et al.* 2007), were attacked. In all, 183 (40 in July–August, 96 in September–October, 47 in January–February) spiders were observed. The reactions of the spiders were recorded as either: (1) remaining at the hub, (2) dropping, (3) shifting (fleeing the hub to a lower corner of the web or nearby vegetation) or (4) pumping. We captured as many spiders as possible (176 of 183) and measured their body length (head and cephalothorax) and width (cephalothorax) using calipers, and their mass using an electronic balance. Because body length, width and mass are highly correlated and related to satiation or reproductive con-
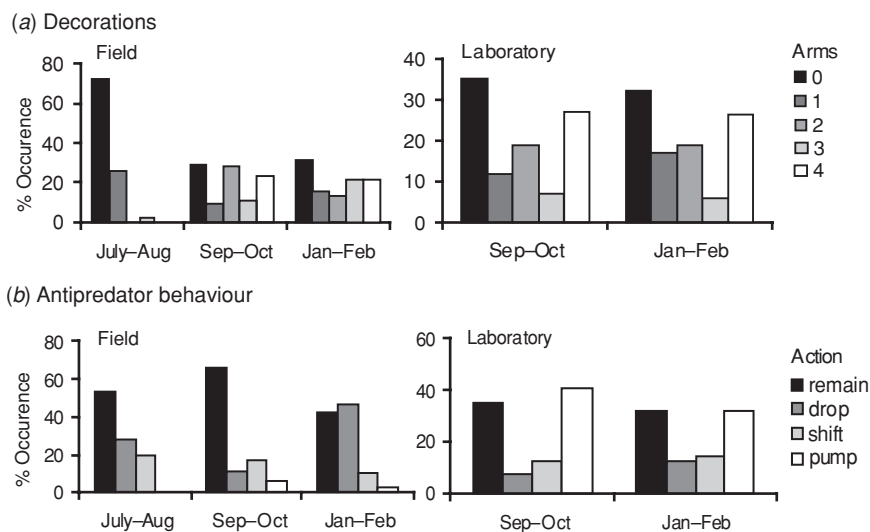

Fig. 1. Percentage occurrence (*a*) of *Argiope keyserlingi* webs containing decorations with 0 (no decorations), 1, 2, 3 and 4 (fully cruciform) arms, and (*b*) antipredator responses: remaining at the hub (remain), dropping from the web (drop), shifting from the hub (shift) and pumping the web (pump), measured in each period, in both the laboratory (*n* = 27 in both periods) and field (July–August: *n* = 40; September–October: *n* = 96; January–February: *n* = 47).

dition, a relative body index was derived from first principal component scores of these variables (Andrade 1998). Each captured spider was marked with a numbered bee tag (Southwood and Henderson 2000) to avoid her inclusion in future observations, and returned to the point of capture.

Web measurements

We recorded the presence or absence of the cruciform-shaped decorations and counted the number of decoration arms (1, 2, 3 or 4, with absence recorded as 0) of each spider we attacked. We measured the lengths of each decoration arm using calipers. Individual arm length did not vary with the number of arms (means ± s.e.: 1 arm = 2.84 ± 0.18 mm, 2 arms = 2.87 ± 0.26 mm, 3 arms = 3.07 ± 0.48 mm, 4 arms = 3.08 ± 1.24 mm; Kruskal–Wallis $\chi^2 = 2.02$, $P = 0.17$), so just the number of arms was used as an index of decoration building. We measured hub and web height and width and counted the number of spiral threads intercepting a preselected radial thread so that the capture area of the web and the length of the sticky spiral (spiral length) could be calculated (Heiling *et al*. 1998; Blackledge and Gillespie 2002).

Environmental factors and availability of prey

To determine whether environmental factors affect changes in the antipredator responses of *A. keyserlingi*, air temperature, relative humidity and wind speed were recorded before and after each sampling episode, using a hand-held electronic thermometer and anemometer (Evolution-N 9001; Cormack, Stevenhage UK) held ~0.5 m above the ground to approximate the height of the hub in *A. keyserlingi* webs within sedge habitats (Blamires *et al*. 2007). As we had previously shown (Blamires *et al*. 2007) that prey availability estimated using 300 × 210 mm plastic sheets lightly covered with resin (Tanglefoot®; Tanglefoot Co., Grand Rapids, USA) correlates with architectural features of the web in *A. keyserlingi*, we placed six Tanglefoot® traps in each of the four locations (*n* = 24 traps) to estimate availability of prey in each of the three periods. Sites chosen were those where *A. keyserlingi* occured in high densities. The traps were placed so that the centre of the sheets were ~0.5 m from the ground, the approximate height of the hub of actual webs. The sheets were attached from above and below to string that was tied to wooden stakes (2 m apart) using Bulldog clips.

Table 1. Log-linear model determining the influence of season and/or the number of arms in web decorations on antipredator response

1 = season (three factors: July–August, September–October and January–February), 2 = decoration arms (five factors: 0, 1, 2 ,3, 4 arms), 3 = behaviour (four factors: frequencies of remaining at the hub, shifting, dropping, and pumping), G^2 = log-likelihood statistic = 2 × (log-likelihood of reduced model – log-likelihood of full model: Quinn and Keough 2002), P = significance level. Akaike Information Criterion (AIC) scores show that the model of best fit (signified by the asterisk) is a two-way interaction between season and behaviour and season and number of decoration arms (season influences both decorations and behaviour independently)

Model	d.f.	G^2	P	AIC
1: $1 \times 2 + 2 \times 3$	2	10.03	0.01	8.29
2: $1 \times 3 + 1 \times 2$	3	1.47	0.68	1.21*
3: $1 \times 3 + 1 \times 2 + 2 \times 3$	5	11.50	0.04	9.51

We ensured that the base of the sheets did not touch the ground, so ground-dwelling invertebrates or vertebrates could not interact with the sheets. The sheets were set up at 0800 hours and taken down at 1600 hours on each day that observations were conducted. All insects and spiders caught in the traps were removed using forceps, soaked in turpentine to remove the resin (Southwood and Henderson 2000), and counted.

Laboratory observations

To control for the effects of exposure to predators on antipredator responses, we conducted a series of laboratory observations at the same time as the September–October and January–February field observations. We caught 27 juvenile spiders of similar body length (mean ± range = 7.4 ± 0.4 mm) in July and reared them in 300 × 300 × 50 mm Perspex frames, feeding them either protein-enriched fruit flies (*Drosophila melangaster*) or house flies (*Musca domestica*) daily to maximise their growth and survivorship (Zschokke and Herberstein 2005). Each spider was transferred to a 500 × 500 × 150 mm Perspex frame after three months, whereupon they were fed three house flies and left for one week to build a web and we counted the number of decoration arms (0, 1, 2, 3 or 4) to estimate the investment in decorations. Each spider was prodded in a similar manner to spiders in the field and their antipredator response was noted. All webs were immediately disassembled and two houseflies were placed in the enclosures. Spiders were
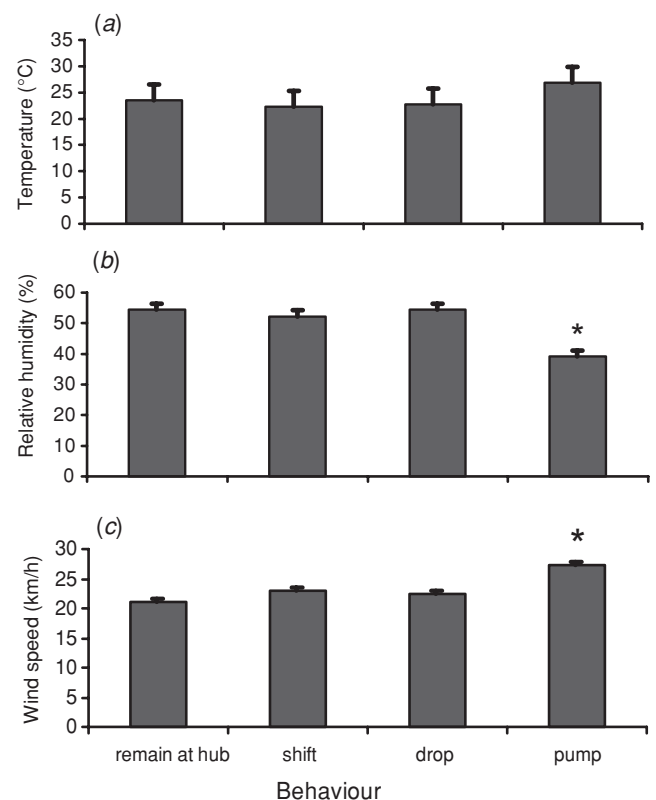

Fig. 2. Mean (±s.e.) temperature (*a*), relative humidity (*b*) and wind speed (*c*) at which remaining at the hub, dropping off the web, shifting from the hub and pumping were used by *Argiope keyserlingi*. An asterisk denotes a significant difference between that variable and the other three (*P* < 0.05).

given one week to build another web whereupon the number of decorations and the antipredator behaviour of all spiders were re-examined. The process was repeated two more times. The above experiment was repeated with 26 spiders (mean ± range = 7.2 ± 0.3 mm body length) collected in October to mature in January for comparison with the field data collected in January–February. All spiders were housed in a room with the window open to receive natural sunlight throughout the day, so the light–dark cycles, and temperature and humidity fluctuations were similar to those experienced by spiders in the field. Sedge (*Lomandra* spp.) was pasted to the back of the Perspex frames to mimic the background experienced by spiders in the field (Bruce *et al.* 2005; Blamires *et al.* 2007).

Analyses

We used contingency tables with χ^2 maximum-likelihood tests to establish whether or not antipredator responses and decoration investment varied between periods. We used a log-linear, marginal rate of substitution model (Quinn and Keough 2002) to determine the relative influences of period on decoration investment (number of arms) and antipredator behaviour. The model that best fitted the data (i.e. whether (1) antipredator behaviour, (2) decorations, (3) both, or (4) neither were influenced by period) were identified using the Akaike Information Criterion (AIC), a statistical model of best fit based on entropy (Quinn and Keough 2002). All observations made in one day were used as replicates of period. We tested the influence of temperature, relative humidity and wind speed on each antipredator response using a Wilk's λ multiple-ANOVA test.

For the laboratory experiments we used χ^2 goodness-of-fit tests to compare antipredator responses and the number of decoration arms added to webs between individual responses between periods, and laboratory and field responses in the same period. We combined the field and laboratory data across periods and used separate multiple regression analyses to determine the relationships between period (as a dummy variable: Underwood 1997), any influential (according to MANOVA)
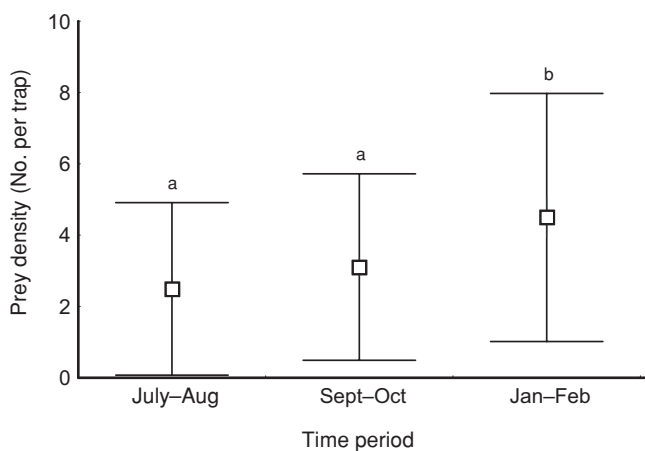
environmental variables, spiral thread length, capture area of the web, relative body condition and availability of prey, on (1) antipredator response frequencies, and (2) decoration building. Standardised partial regression coefficients were used to calculate path coefficients between variables (Legendre and Legendre 1998). By multiplying the path coefficients along pathways linking each variable, we generated two direct-effects path models, where: (1) period is an exogenous variable independent of environmental variables, and (2) period is excluded and environmental variables are included as exogenous variables. The best-fit path diagram was determined from the most appropriate model using χ^2 goodness-of-fit procedures (Legendre and Legendre 1998) with the direction of the path coefficient indicating the direction of the influence (i.e. a positive path coefficient indicates a positive influence).

Results

Temporal shifts in antipredator responses and decoration building

The antipredator behaviours ($\chi^2_3 = 206.85$, $P < 0.01$), and the frequency of building decorations with 0, 1, 2, 3 and 4 arms ($\chi^2_4 = 600.08$, $P < 0.01$), of *A. keyserlingi* in the field differed in each period (Fig. 1). The model best describing the influences on antipredator behaviour was a two-way interaction between (1) period and the number of decoration arms and (2) period and antipredator behaviour, i.e. period independently influenced both decorations and antipredator behaviour (Table 1).

Environmental influences on antipredator behaviour

The antipredator responses ($\chi^2_3 = 4.99$, $P = 0.17$) and decoration-building patterns ($\chi^2_4 = 4.40$, $P = 0.36$) of *A. keyserlingi* did not vary between September–October and January–February in the laboratory. The antipredator responses of spiders in the laboratory differed from those in the field in both September–October ($\chi^2_3 = 207.37$, $P < 0.0001$) and January–February ($\chi^2_3 = 367.02$, $P < 0.0001$), with a markedly higher frequency of pumping, but a lower frequency of remaining at the web and shifting in the laboratory (Fig. 1). Decoration building was similar in the field and laboratory in September–October ($\chi^2_4 = 1.16$, $P = 0.884$) but differed in January–February ($\chi^2_3 = 30.85$, $P < 0.0001$) (Fig. 1). Comparing the body condition of spiders in the field and laboratory in September–October and January–February, we found a difference between periods ($F_{2,24} = 8.87$, $P < 0.001$), but not between laboratory and field spiders ($F_{2,24} = 0.62$, $P = 0.18$). Of the environmental variables measured in the field, relative humidity was lower ($F_{3,174} = 2.26$, $P = 0.04$) (Fig. 2) and wind speeds higher ($F_{3,174} = 2.67$, $P = 0.01$) (Fig. 2) when pumping was done than any other behaviour. Availability of prey differed between periods (one-way ANOVA: $F_{2,175} = 8.82$, $P < 0.001$) (Fig. 3). Antipredator behaviour, decoration arms, body condition, exposure to predators (as either present (the field observations) or absent (the laboratory observations)), relative humidity, wind speed and availability of prey were, accordingly, included in multiple regression analyses, which found: (1) body condition to be significantly positively related to pumping frequency, (2) wind speed and relative body condition to be significantly positively related to the number of decoration arms, and

Fig. 3. Mean (±s.e.) prey density (calculated as the mean number of insects caught per trap, across each of the 24 traps) in July–August ($n = 80$), September–October ($n = 192$) and January–February ($n = 94$), showing that the availability of prey in January–February was higher than in July–August and September–October (b>a) (Tukey's HSD *post hoc* test: all $P < 0.05$).

Table 2. **Results of multiple regression analyses between the frequency of pumping and the number of decoration arms (*n* = 24 days of observations) and the various measured variables**

Variables	Pumping			Decoration arms		
	β	*t*	*P*	β	*t*	*P*
Relative humidity	0.12	1.40	0.16	−0.37	−4.20	<0.0001
Wind speed	−0.07	−0.82	0.41	0.35	3.43	<0.001
Relative body condition	0.51	5.65	<0.0001	0.25	2.61	0.01
Spiral length	0.01	0.09	0.93	0.01	−0.08	0.94
Capture area	−0.10	−1.35	0.18	0.05	0.43	0.67
Availability of prey	−0.07	−0.87	0.39	0.16	0.16	0.87

(3) relative humidity to be negatively related to the number of decoration arms (R^2 = 0.24, P < 0.001) (Table 2). The best-fit path model was one with period included independently of environmental variables (χ^2 goodness-of-fit: Model 1 = 1.31; Model 2 = 9.92), which predicted direct relationships between: (1) period, relative humidity, body condition and pumping frequency, (2) period, wind speed and pumping frequency and (3) period, wind speed, number of decoration arms and frequency of remaining at the hub. All relationships were positive relationships apart from the relationship between decoration investment and remaining at the hub (Fig. 4).

Discussion

In the field *A. keyserlingi* changes both decoration investment and antipredator responses over time. However, in the laboratory, where there are no predators and the spiders are well fed, antipredator behaviours do not differ over time. Our findings suggest that, unlike other studies (Schoener and Spiller 1992; Jackson *et al*. 1993; Li *et al*. 2003), decoration building does not explain the shifts in antipredator strategies observed in the field. The discrepancy between our field-based study and other, predominantly laboratory-based, studies highlights the need for caution when interpreting either type of study (Lind and Cresswell 2005).

We found that remaining at the hub is the only response directly related to decoration building in the field (i.e. spiders on webs without decorations are more likely to remain at the hub). Many objects interact with orb webs other than predators, e.g. prey, other animals, vegetation and debris (Eberhard 1990), with most objects that strike a spider when sitting at the hub unlikely to be predators (Nentwig and Heimer 1987). Orb-web spiders remain at the hub if a stimulus has not been perceived as a threat (Cloudsley-Thompson 1995). Spiders may prefer to remain at the hub most of the time because it is energetically costly to move when the approaching object is not likely to be life threatening (Brandwood 1985; Herberstein and Heiling 2001). However, if adding decorations attracts predators (Bruce *et al*. 2001, 2005), the likelihood that an approaching object is a predator increases when decorations are added. Our findings suggest that adding decorations makes *A. keyserlingi* associate a given stimulus more often as a threat and they compensate by dropping or pumping, rather than remaining at the hub, explaining why they remain at the hub least in January–February, the period when we most commonly found webs with 3 or 4 decoration arms. We found body condition to change with period and

to be positively associated with decoration investment and the frequency of pumping. Thus, any association between antipredator behaviour and decoration investment is likely to be mediated through changes in body condition over time.

Pumping is an energetically costly, yet effective, antipredator strategy that we found to be used most readily by the well fed, predator-naive, laboratory-reared, spiders. *A. keyserlingi* pumps sparingly at all times in the field and did not do so at all in July–August, probably because the recently emerged adults were energetically deprived and continuous foraging was a high priority. Although air temperature and availability of prey fluctuates between periods they have no detectable influence on antipredator strategies. This is because we included body con-
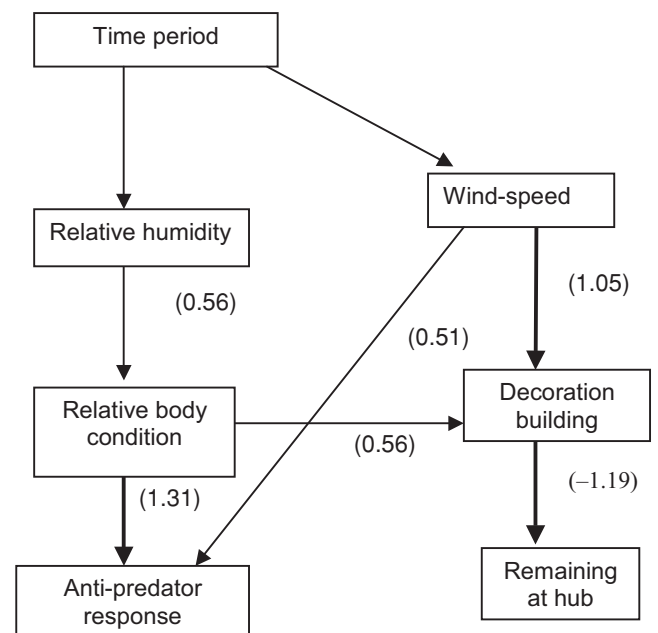

Fig. 4. Direct-effects path diagram showing influences of climatic variables, web (decorations) and spider size, on antipredator responses of *A. keyserlingi*. It shows direct relationships between relative humidity and body condition, body condition and both pumping frequency and decoration building, wind speed and both decoration building and pumping frequency, and decoration building and the frequency of remaining at the hub. Path coefficients are shown in parentheses, and their values are indicated by the depth of the arrows; positive values indicate a positive relationship, while negative values indicate a negative relationship.

dition in the analyses, the effects of which were directly attributable to changes in antipredator response. Pumping and decoration building both increase as wind speed increases. Other orb-web spiders build more decorations when winds are strong (Bruce 2006). The functional significance of this association is, however, ambiguous. Mechanical support, although never directly tested, has been largely dismissed on the basis of the properties of the silk (Herberstein *et al*. 2000*a*). Increased exposure to food is an unlikely explanation as we did not find the availability of prey to have any effect on decoration building. There may be an increased risk of interaction between webs and erratically flying birds in strong winds. Perhaps the increase in decoration building in strong winds is to advertise the presence of the web. The increase in pumping in strong winds may be related to more objects striking the web. Alternatively, birds at close range may propel wind across the web, and the spiders may, accordingly, interpret an increase in wind strength as indicative of the presence of a bird and engage in pumping.

Spiders used in the laboratory experiments were of a similar size when caught and were all reared on the same diet so there should have been little difference in body condition between those used for laboratory experiments in September–October and those used in January–February, explaining why there was no differences in antipredator strategies between periods in the laboratory spiders. It, thus, appears that period has an influence over the antipredator strategies of *A. keyserlingi* in the field because body condition varies between periods. Gravid spiders devote a considerable portion of their energy budget to developing eggs (Benton and Uetz 1986; Andrade 1998), thus they tend to shift to more energetically conservative life-history strategies, e.g. there may be a reduction in movement and/or growth, when gravid (Benton and Uetz 1986). We found the antipredator strategies differed between laboratory and field spiders in both September–October and January–February. Switching, by gravid females in the field, to more energetically conservative strategies may, thus, be partially responsible for the disparity in the responses.

Path analysis revealed some unexpected relationships between environmental fluctuations and temporal shifts in antipredator behaviour in *A. keyserlingi*. We predicted that the antipredator behaviour of *A. keyserlingi* would shift with decoration-building patterns. We found, however, that body condition and wind speed directly influence the antipredator strategies adopted. Body condition and wind speed are factors that may have gone previously undetected as influences on the antipredator behaviour of orb-web spiders because they were unmeasured or masked by other, indirectly acting, influences, such as availability of prey or decoration building. Although we measured as many variables as was logistically possible in the field and laboratory, the antipredator behaviour of *A. keyserlingi* may be influenced by other factors. Body temperature and energetic, nutrient or ion balance, for example, may influence body condition (Riechert and Harp 1987; Uetz *et al*. 2002) and, thus, may additionally indirectly affect antipredator behaviour.

Acknowledgements

References

Andrade, M. C. B. (1998). Female hunger can explain variations in cannibalistic behavior despite male sacrifice in redback spiders. *Behavioral Ecology* **9**, 33–42. doi:10.1093/beheco/9.1.33

Benton, M. J., and Uetz, G. W. (1986). Variation in life-history characteristics over a clinal gradient in three populations of communal orb-weaving spiders. *Oecologia* **68**, 395–399. doi:10.1007/BF01036745

Blackledge, T. A., and Gillespie, R. G. (2002). Estimation of capture areas of spider orb webs in relation to asymmetry. *Journal of Arachnology* **30**, 70–77. doi:10.1636/0161-8202(2002)030[0070:EOCAOS]2.0.CO;2

Blamires, S. J., Thompson, M. B., and Hochuli, D. F. (2007). Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? *Austral Ecology* **32**, in press.

Brandwood, A. (1985). Mechanical properties and factors of safety of spider drag-lines. *Journal of Experimental Biology* **116**, 141–151.

Bruce, M. J. (2006). Silk decorations: controversy and consensus. *Journal of Zoology* **269**, 89–97. doi:10.1111/j.1469-7998.2006.00047.x

Bruce, M. J., Herberstein, M. E., and Elgar, M. A. (2001). Signal conflict between prey and predator attraction. *Journal of Evolutionary Biology* **14**, 786–794. doi:10.1046/j.1420-9101.2001.00326.x

Bruce, M. J., Heiling, A. M., and Herberstein, M. E. (2005). Spider signals: are web decorations visible to birds and bees? *Biology Letters* **1**, 299–303. doi:10.1098/rsbl.2005.0307

Cloudsley-Thompson, J. L. (1995). A review of the antipredator devices in spiders. *Bulletin of the British Arachnological Society* **10**, 81–96.

Eberhard, W. G. (1990). Function and phylogeny of spider webs. *Annual Review of Ecology and Systematics* **21**, 341–372. doi:10.1146/annurev.es.21.110190.002013

Heiling, A. M., Herberstein, M. E., and Spitzer, G. (1998). Calculation of capture thread length in orb webs: evaluation of new formulae. *Behaviour* **91**, 135–138.

Herberstein, M. E. (2000). Foraging behaviour in orb-web spiders (Aranidae): do web decorations increase prey capture success in *Argiope keyserlingi* Karsch 1878? *Australian Journal of Zoology* **48**, 217–223. doi:10.1071/ZO00007

Herberstein, M. E., and Heiling, A. M. (2001). Positioning at the hub: does it matter on which side of the web orb-web spiders sit? *Journal of Zoology* **255**, 157–163. doi:10.1017/S0952836901001224

Herberstein, M. E., Craig, C. L., Coddington, J. A., and Elgar, M. A. (2000*a*). The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biological Reviews* **75**, 649–669.

Herberstein, M. E., Craig, C. L., and Elgar, M. A. (2000*b*). Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evolutionary Ecology Research* **2**, 69–80.

Jackson, R. R., Bassington, R. J., and Rowe, R. J. (1990). Antipredator defenses of *Pholcus phalangioides* (Araneae, Pholcidae), a web building and web invading spider. *Journal of Zoology* **220**, 543–552.

Jackson, R. R., Rowe, R. J., and Wilcox, R. S. (1993). Antipredator defenses of *Argiope appensa* (Araneae, Araneidae), a tropical orb-weaving spider. *Journal of Zoology* **229**, 121–132.

Legendre, P., and Legendre, L. (1998). 'Numerical Ecology.' (Elsevier: Amsterdam.)

Li, D., Kok, L. M., Seah, S. W., and Lim, M. L. M. (2003). Age-dependent stabilimentum-associated predator avoidance behaviours in orb-weaving spiders. *Behaviour* **140**, 1135–1152. doi:10.1163/156853903322589678

Lima, S. L., and Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* **153**, 649–659. doi:10.1086/303202

Lind, J., and Cresswell, W. (2005). Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* **16**, 945–956. doi:10.1093/beheco/ari075

Nentwig, W., and Heimer, S. (1987). Ecological aspects of spider webs. In 'Ecophysiology of Spiders'. (Ed. W. Nentwig.) pp. 211–215. (Springer-Verlag: Berlin.)

Price, P. W. (1997). 'Insect Ecology.' (Wiley: NY.)

Quinn, G. P., and Keough, M. J. (2002). 'Experimental Design and Analysis for Biologists.' (Cambridge University Press: Cambridge.)

Riechert, S. E., and Harp, J. M. (1987). Nutritional ecology of spiders. In 'Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates'. (Eds F. Slansky Jr and J. R. Rodriguez.) pp. 645–672. (John Wiley and Son: New York.)

Scheiner, S. M., Donohue, K., Dorn, L. A., Mazer, S. J., and Wolfe, L. M. (2002). Reducing environmental bias when measuring natural selection. *Evolution* **56**, 2156–2167. doi:10.1554/0014-3820(2002)056[2156:REBWMN]2.0.CO;2

Schoener, T. W., and Spiller, D. A. (1992). Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support for the predator-defense hypothesis. *Behavioral Ecology and Sociobiology* **31**, 309–318. doi:10.1007/BF00177771

Seah, W. K., and Li, D. (2001). Stabilimenta attract unwelcome predators to orb webs. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **268**, 1553–1558. doi:10.1098/rspb.2001.1709

Seah, W. K., and Li, D. (2002). Stabilimentum variations in *Argiope versicolor* (Araneae: Araneidae) from Singapore. *Journal of Zoology* **258**, 531–540. doi:10.1017/S0952836902001693

Shipley, B. (2000). 'Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference.' (Cambridge University Press: Cambridge.)

Sinervo, B., and Svensson, E. (1998). Mechanistic and selective causes of life history trade-offs and plasticity. *Oikos* **83**, 432–442. doi:10.2307/3546671

Southwood, T. R. E., and Henderson, P. A. (2000). 'Ecological Methods.' 3rd edn. (Blackwell Scientific: Oxford.)

Tso, I.-M. (2004). The effect of food and silk reserve manipulation on decoration-building of *Argiope aetheroides*. *Behaviour* **141**, 603–616. doi:10.1163/1568539041166690

Uetz, G. W., Papke, R., and Kilinc, B. (2002). Influence of feeding regime on body size, body condition and a male secondary sexual character in *Schizocosa ocreata* wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signaling trait. *Journal of Arachnology* **30**, 461–469. doi:10.1636/0161-8202(2002)030[0461:IOFROB]2.0.CO;2

Underwood, A. J. (1997). 'Experiments in Ecology: Their Logical Design and Interpretation using Analysis of Variance.' (Cambridge University Press: Cambridge.)

Ydenberg, R. C., and Dill, L. M. (1986). The economics of fleeing from predators. In 'Advances in the Study of Animal Behaviour. Volume 16'. (Eds J. S. Rosenblatt, C. Beer, M. C. Busneland and P. B. J. Slater.) pp. 229–249. (Academic Press: Orlando, FL.)

Zschokke, S., and Herberstein, M. E. (2005). Laboratory methods for maintaining and studying web-building spiders. *Journal of Arachnology* **33**, 205–213. doi:10.1636/CT04-72.1