Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): Do they compromise foraging success for predator avoidance?

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Abstract　　Orb web spiders face a dilemma: forage in open habitats and risk predation or forage in closed habitats to minimize risk but at reduced foraging profitability. We tested whether *Argiope keyserlingi* opts for safer habitats at the expense of foraging success by (i) determining habitat selection indices in open and closed habitats; (ii) marking and releasing individual juvenile, subadult and adults over two 4-week periods to determine if life-history stage influences habitat selection; and (iii) determining the biotic and abiotic environmental parameters that relate to *A. keyserlingi* abundance. We found that *A. keyserlingi* selected closed habitats. Sedge and anthropogenic structures were selected and trees were avoided. Juveniles were never found in open habitats, most likely because of high postdispersal mortality. Subadults and adults may shift from closed to open habitats while juveniles never shifted habitat. Foliage density, plant height, potential prey abundance, and mantid and bird abundance were correlated with *A. keyserlingi* abundance, with only bird abundance explaining habitat selection. We measured web capture area, spiral distance (distance between spiral threads) and the number of decoration arms (0, 1, 2, 3 or 4) in the field and did laboratory experiments to test the influence of (i) space and vegetation; (ii) prey abundance; and (iii) web damage, on web architecture. *Argiope keyserlingi* webs exhibited geometric plasticity by having larger prey capture areas and spiral distances in open habitats. Decoration design did not differ between habitats however. Variation in space availability, air temperature, prey abundance and web damage explained the variations in web architecture. Potential prey size and diversity differed between habitats but prey abundance did not. As large prey may be important for spider survivorship, foraging success appears to be compromised by occupying closed habitats.

Key words: *Argiope keyserlingi*, behavioural flexibility, foraging profitability, habitat selection, web architectural plasticity.

INTRODUCTION

Foraging strategies should maximize nutrient and/or energy intake while minimizing costs (Stephens & Krebs 1986; Simpson *et al.* 2004). Accordingly, animals in optimal habitats should encounter as much quality or highly catchable food as they can handle (Gillespie & Caraco 1987; Abrams 1991). Animals, however, often forage in suboptimal habitats if other fitness parameters, such as survival (Lima & Dill 1990), are higher in the alternative habitat. Vigilant animals maintain flexibility in their selection of habitats (Sih *et al.* 2000), responding to changing environmental conditions (continuous habitat shifts) or physiological requisites associated with a particular life history stage (discrete habitat shifts) (de Roos *et al.* 2002).

Because of spatial and temporal variations in insect abundance (Nylin & Gottard 1998) the fitness prospects and life-history strategies of orb web-building spiders (Araneae) depend heavily on food availability (Olive 1980; Riechert & Luczak 1982; Riechert & Harp 1987). Foraging success in orb web-building spiders is positively correlated to the surface area of their webs (Wise & Barata 1983; Opell 1990). Accordingly, orb web spiders should build their webs as large as physically possible. Selecting open habitats, where the vegetation is rigid in structure but of low complexity, allows the construction of large, stable webs (Eberhard 1990; Kohler & Vollrath 1995). These habitats are, however, considered risk prone (Werner *et al.* 1983; Ferguson *et al.* 1988). For example, predation by birds is a substantial risk encountered by spiders in open habitats (Gunnarsson 1983, 1996).

Orb web spiders occupy a range of habitats and, accordingly, there is great diversity in both web architecture and behaviour among genera. For example, members of the genus *Eriophora* build large (often

exceeding 4 m in diameter; Nentwig 1985) two-dimensional orb webs in open habitats but only occupy the hub while feeding (Herberstein & Elgar 1994). On the other hand, members of the genus *Nephila* and *Tetragnatha*, which permanently occupy the hub, also build large webs in open habitats but construct either barrier webs or aggregate their webs to minimize predation (Gillespie 1987; Higgins & Buskirk 1992; Hodge & Uetz 1992). Spiders of the genus *Argiope* adopt a different strategy, preferring to build smaller (rarely exceeding 0.5 m diameter) webs among low, dense (closed) vegetation (Main 1984; Herberstein 2000). Attempts have been made to assimilate orb spider habitat selection with a preferred web geometric structure (Enders 1977; Hatley & MacMahon 1980), however, many species can build webs with a varied array of geometric designs across habitats or when environmental conditions change (Sandoval 1994; Schneider & Vollrath 1998; McNett & Rypstra 2000; Venner *et al*. 2000). Such plasticity in web structure, which we call architectural plasticity to include non-geometric features, provides an orb web spider with the functionality to forage while adapting to changing conditions or avoiding risks (Sandoval 1994; Craig *et al*. 1996; Li & Lee 2004).

The St Andrew's Cross spider, *Argiope keyserlingi*, is common around Sydney (New South Wales, Australia). A distinctive feature of its web is the cruciform silk decorations (also called stabilimenta), with 0, 1, 2, 3 or 4 associated arms emanating outward from the hub. Experimental evidence suggests that the decorations function to attract prey (Herberstein 2000; Herberstein *et al*. 2000a,b; Bruce *et al*. 2001, 2005). We sampled *A. keyserlingi* webs, predators and prey, vegetative structure, and several environmental variables within the grounds of the University of Sydney to investigate factors associated with *A. keyserlingi* distribution, habitat selection and web architectural plasticity. The grounds have a considerable human presence, and many arboreal predatory birds, such as Australian ravens (*Corvis coronoides*) and magpies (*Gymnorhina tibicen*), are present. As both humans and birds affect arthropod distribution and behaviour (Bock *et al*. 1992; Groner & Ayal 2001; Fernandez-Juricic 2002) and predators within closed habitats, such as mantids and other spiders (Moore 1977; Bruce *et al*. 2001), are less abundant and less likely to cause inadvertent web damage, we expected *A. keyserlingi* to infrequently occupy open habitats.

We determined whether foraging success was compromised in closed habitats by determining the size, abundance and ordinal composition of prey from open and closed habitats. We expected that if the prey size, abundance or diversity were compromised within closed habitats, *A. keyserlingi* would shift their habitat preference to open habitats as adults, as (owing to their greater body size) predation threat may be reduced at this stage. Alternatively, adults may develop specific habitat, food or reproductive requirements that involve the use of open habitats (Moore 1977; Uhl *et al*. 2004; Venner & Casas 2005) and/or taking more risks (Gillespie & Caraco 1987).

METHODS

Study site

We selected four sites within the grounds of the University of Sydney, Camperdown-Darlington campus, approximately 5 km from Sydney, Australia. A rectangular area of 100 m^2 was measured at each site and the corners were marked with wooden stakes. We identified habitats as open or closed according to the dominant plants present at 0.5–1.5 m, the typical height range of *A. keyserlingi* webs (Bradley 1993). Closed habitats consisted of densely foliated plants such as sedges, grasses and dense bushes. Open habitats consisted of woody trees, sparsely foliated bushes, flowers (>0.5 m apart), anthropogenic structures (e.g. posts, buildings, bins) and clear space. We measured the sections of closed habitat within each site to determine the proportion of total area they encompassed. We also counted and determined the mean number of individual sedges, grasses and dense bushes present in the closed habitats at each site and the mean number of trees, sparse bushes, annual flowering plants and anthropogenic structures in open habitats.

Habitat selection indices

We thoroughly searched each site twice weekly between August 2004 and February 2005, recording every *A. keyserlingi* encountered, and the habitat and vegetation type (tree, sedge, grass, thick bush, sparse bush, flower or tree) in which it was encountered. When a web was made between two vegetation types both types were recorded. At the end of the sampling period we performed a chi-squared log-likelihood test to determine if habitats were used in the same proportion as availability. We calculated Neu standardized selection indices (β_i) and Bonferroni adjusted 95% confidence intervals (Manly *et al*. 2002) for open and closed habitats (all sites combined in the analysis). Any indices lying outside the confidence intervals denoted either selection (below the lower limit) or avoidance (greater than the upper limit) (Manly *et al*. 2002). A chi-squared log-likelihood test was used to determine if vegetation types within habitats were used in proportion to availability and standardized selection indices and 95% confidence intervals were calculated

Ontogenetic shifts in habitat selection

We marked and measured (with calipers to the nearest 1 mm) every *A. keyserlingi* encountered at the two sites over two separate 4-week periods (in November 2004 and February 2005). We classified all individuals less than 8 mm in body (cephalothorax and opithsoma) length as juveniles, those 8–12 mm in body length as subadults and those more than 12 mm in body length as adults (Brunet 1998). Adults and subadults were marked by pasting a numbered bee tag to their thorax (Southwood & Henderson 2000) while juveniles were marked with a paint mark on the cephalothorax. Individuals were photographed for identification by size and colouration if the mark disappears because of moulting or rain. Each spider was returned to the location and habitat that it was captured in and monitored during twice weekly visits until no longer seen in the area (0–4 weeks). Each time an individual was identified, we noted the vegetation type and habitat it occupied. We used a contingency table (chi-squared goodness-of-fit; Quinn & Keogh 2002) to determine if the frequencies in which juveniles, subadults and adults switched vegetation types or habitats differed. Individuals that were never re-sighted after release were not included in analyses.

Factors affecting habitat selection

We measured biotic and abiotic factors considered likely to influence *A. keyserlingi* web placement over two 4-week periods (October 2004 and January 2005). Canopy cover, foliage density and plant height were used as indicators of vegetative structure. We took photographs at four randomly chosen locations within each habitat at each site ($n = 128$ in each period) using a digital camera with a 360° fish-eye lens attached facing skyward, approximately 0.8 m from the ground (the mean height that adult *A. keyserlingi* sit at the hub of their web; Bradley 1993). Canopy cover was calculated from the images using the program GAP (Academia Sinica, Taipei, Taiwan). We determined foliage density by randomly marking six 0.5×0.5 m areas with wooden stakes within each habitat at each site ($n = 48$ in each period) and running a 0.5 m tape measure horizontally through the marked area and counting how much foliage intersected the tape. We measured the heights of a random sample of 10 plants in each habitat at each site ($n = 80$) in each period. We took all measurements and calculated mean values once in each period.

Temperature and relative humidity were recorded within each habitat approximately 0.8 m from the ground, in the shade to avoid the influence of radiation, by an electronic thermometer (Evolution-N 9001; Cormack, Stevenhage, UK) prior to sampling each area. It was not possible to measure wind so we counted the number of debris items, such as leaves, sticks, petals and paper, entangled in each web as an indication of recent exposure to wind. Dust and pollen were not included as they were not possible to quantify. We observed and counted the number of predatory birds (ravens and magpies), humans, mantids and spiders of other genera (identified by observing the spiders or the spider webs; Brunet 1998) in each habitat, and we measured *A. keyserlingi* body and leg length (to the nearest millimetre), and nearest neighbour (hub to hub, in metres) distances during each set of observations.

Prey were sampled using 300×210 mm transparent plastic sheet traps, coated with transparent resin (Tanglefoot, Tanglefoot Co., Grand Rapids, USA), approximately the capture area of the largest webs measured. Four traps were set up per habitat per site ($n = 32$). Traps were set twice per week (at 0800) over each of the 4-week sampling periods (total traps sampled = 256 per period). Bulldog clips attached traps to string tied between branches in open habitats, while string was tied to wooden stakes to hold up traps in closed habitats. Because the traps set in the open habitats were attached to branches, their orientation was haphazard. To account for this, the orientation of the traps in the sedge (closed habitats) was arranged to mimic those in trees (open habitat). Traps were dismantled at 1700 (because *A. keyserlingi* is diurnal it was not necessary to sample nocturnal insects as they are unlikely prey) and insects were removed and soaked in turpentine overnight to dissolve the resin (Southwood & Henderson 2000). All trapped insects were observed under a dissecting microscope and counted, their body length was measured to the nearest millimetre and, where possible, they were identified to order using the key in Lawrence (1994). Tanglefoot traps, because of their transparency, high retention and ease of manipulation give reliable indices of insect abundance within a spider's habitat (see Spiller & Schoener 1990; Bradley 1993; McNett & Rypstra 2000), but they do not differentiate between prey and non-prey. It could, subsequently, be incorrectly assumed that an area with high insect abundance is profitable even if many of the insects present are undesirable as prey. We accounted for this potential discrepancy by counting, measuring and identifying, to order, all prey entangled in *A. keyserlingi* webs (assuming all prey retained on the web are likely to be consumed) during the same sampling periods. We used chi-squared likelihood-ratio tests (corrected for unequal *n*; Fienberg 1981) to determine if

A. keyserlingi consumed the same proportion of prey types in each habitat as those represented in Tanglefoot traps.

We used generalized linear modelling (GLM), with Poisson error term and log-link function (McCullagh & Nedler 1989) with significance identified by a Wald statistic (Quinn & Keogh 2002) to identify factors significantly related to *A. keyserlingi* abundance. A latent score (first principal component scores, calculated from normalized ordinal abundance data at each trap and web site; Te Braak 1995) of prey diversity for both traps and webs was included in the GLM. Factors found to influence *A. keyserlingi* number or size significantly were subject to a multifactorial permutation analysis of variance (Wilk's λ) to determine if their parameters differed between open and closed habitats.

We used multidimensional scaling ordination procedures, derived from Bray–Curtis dissimilarity measures on square-root transformed data using the program PRIMER (PRIMER-E, Plymouth, UK), to determine if insect ordinal composition differed between open and closed habitats in both Tanglefoot traps and webs. An analysis of similarity (ANOSIM) with 999 permutations and a similarity of percentages (SIMPER) analysis (Quinn & Keogh 2002) were used to identify the orders driving any differences in ordinal composition.

Web architectural plasticity

We measured web length, width (to nearest millimetre) and height (to nearest 0.1 m from ground to hub) and the number of spiral threads of all subadult and adult female webs. As males rarely build webs and juveniles do not use open habitats and build webs of intrinsically different architecture (Main 1984; Herberstein 2000; Seah & Li 2002), only females were used for analyses of web architecture. We calculated web area (circular area within the outermost spiral) to the nearest square metre and spiral distance (mean distance between spiral threads; Krink & Vollrath 2000) to the nearest millimetre using existing formulae taking into account web asymmetry (Blackledge & Gillespie 2002; Li & Lee 2004). Spiral distances along a selected radial thread from the free zone outward were measured on 18 randomly selected webs from both open and closed habitats, and the correlation coefficient between thread number and spiral distance was calculated. This confirmed that the distance between each spiral did not systematically increase ($r = -0.078$; $P = 0.34$; $n = 18$). The presence/absence, number of arms (1, 2, 3 or 4) and total arm length (measured with calipers) of the cruciform decorations were recorded.

We determined the effect of habitat type on web area and height by one-way analyses of covariance (ANCOVA), with spider body length the covariate. We used Parallelism tests (Huitema 1980) to ensure slopes were parallel. Variances were inspected to ensure homogeneity (Bartlett's test) we log-transformed the data when variances were not homogeneous. Tukey's HSD *post hoc* comparisons were used to determine which means differed significantly. As web area and spiral distance were positively correlated (Spearman's rank correlation, $\rho = 0.71$; $P < 0.01$) and spiral distances were non-normally distributed (Kolmogorov–Smirnov test, $P < 0.01$) even after transformation, we used a non-parametric median test (Conover 1971) to compare spiral distances between habitats. We assessed whether the frequencies of web decorations with 0 (no decorations), 1, 2, 3 or 4 (fully cruciform) arms differed between habitats by contingency table analysis. We used a GLM (with Poisson error term, log-link function and Wald statistic) to identify the factors associated with any changes between habitats in web area, spiral distance, and decoration arm length (sum of all arms) per unit web area (to account for increasing decoration length in larger webs; Herberstein *et al.* 2000b). Web architectural parameters measured over the two 4-week periods over which the various environmental parameters were measured (October 2004 and January 2005) were used for GLM.

Laboratory experiments

To test if architectural plasticity in *A. keyserlingi* webs in different habitats was a response to space availability and/or the presence of certain vegetation, we placed 12 spiders of similar mass (0.302 ± 0.002 g) into either large (0.5×0.5 m $\times 0.12$ m) or small (0.3×0.3 m $\times 0.06$ m) enclosures in the laboratory under a 12–12 h dark-light cycle and constant temperature ($25 \pm 1°C$) environment. Half ($n = 6$) of the enclosures of each size had sedge (*Lomandra* spp.) pasted to their back and sides. Once a web was established each spider was fed three houseflies (*Musca domestica*) (mass = 0.007 ± 0.0001 g, mean $\pm$ 1 SE.). Flies were placed in the web to ensure the spiders consumed them and to eliminate the possibility that feeding rate influenced web architecture. After 3 days the webs were dismantled. The webs that were subsequently built (within the next 4 days) were sprayed with water to render them visible and web architecture measured as previously described. The procedure was repeated four times. The experiment ran for 4 weeks to coincide with field measurements (October 2004), with different spiders used each time ($n = 24$ for each treatment).

In a similar experiment, in January 2005, we tested if *A. keyserlingi* web architectural plasticity between habitats was a response to prey availability. We placed

Table 1. Population proportion (π_i; proportion of area represented by each habitat across the four sites), used sample count ($O_i = \mu_i/\Sigma\mu_i$), selection indices ($\hat{W}_i = O_i/\pi_i$), standardized (proportional) selection indices (β_i; proportion of the sum of selection indices $= \hat{W}_i/\Sigma\hat{W}_i$) and 95% confidence intervals for open and closed habitat and the seven vegetation type classified in this study (Σ = column total)

	Population proportion (π_i)	Used sample count (O_i)	Selection index ($\hat{W}_i$)	Standardized selection index (β_i)	95% confidence interval
Habitat					
Open	0.75	0.14	0.003	0.051[†]	0.105–0.173
Closed	0.25	0.86	0.035	0.949[‡]	0.827–0.895
Σ	1.00	1.00	0.037	–	–
Vegetation type					
Sedge	0.34	0.78	0.023	0.220[‡]	0.074–0.151
Grass	0.04	0.02	0.004	0.040	0.014–0.040
Dense bushes	0.06	0.06	0.009	0.099	0.030–0.094
Trees	0.37	0.05	0.001	0.013[‡]	0.003–0.007
Sparse bushes	0.13	0.02	0.001	0.013	0.004–0.020
Flowers	0.03	0.01	0.001	0.007	0.002–0.007
Anthro-pogenic structures	0.02	0.06	0.063	0.617[‡]	0.043–0.092
Σ	1.00	1.00	0.104	–	–

Standardized selection indices lying within the confidence intervals signify neither selection nor avoidance for the habitat/vegetation type. [†]Denotes avoidance; [‡]Denotes selection.

18 spiders in large enclosures with six each exposed to one of three different treatments for 1 week each: (i) no flies; (ii) three flies placed within each enclosure prior to web construction; or (iii) flies available *ad libitum*; approximately 20 flies placed within the enclosure prior to web construction. The experiment was repeated four times ($n = 24$ for each treatment). In another experiment, in October 2005, we tested if *A. keyserlingi* change web architecture in response to web damage. Eighteen spiders were placed in large enclosures, allowed to build webs and fed three houseflies, as described for the first experiment. After the first web was completely removed the spiders were allowed to build a second web. After feeding each spider another three flies, the second web was either left untouched ($n = 6$), subject to 50% damage ($n = 6$), or completely destroyed ($n = 6$). We compared the change in web architectural structure, between tertiary and secondary web, for each treatment; undamaged webs representing the control treatment. The process was repeated four times with different spiders ($n = 24$ for each treatment); the experiment took approximately 40 days to complete.

We assessed the influence of space availability, vegetation type, prey availability and web damage on web area (log-transformed data) using ANCOVA (body length the covariate). We used a two-way ANCOVA to determine the influence of space availability and vegetation type and a one-way ANCOVA to determine the influence of both prey availability and web damage. Spiral distances measured in all experiments were non-normally distributed (Kolmogorov–Smirnov, all $P < 0.01$), so the effect of each of the treatments was determined by a median test. The frequency of webs

with 0, 1, 2, 3 or 4 decoration arms were compared using a contingency table.

RESULTS

Habitat selection

Both habitats ($\chi^2 = 662.79$; $P < 0.0001$) and vegetation types ($\chi^2 = 109.87$; $P < 0.0001$) were used non-randomly relative to their availability. Open habitats were avoided while closed habitats were selected (Table 1). Within the open habitats, trees and anthropogenic structures were selected, while within the closed habitats sedges were selected (Table 1). Larger spiders were found on sedge, trees, sparse bushes, flowers and anthropogenic structures (all, apart from sedge, vegetation types found in open habitats) than on grass and thick bush (i.e. in closed habitats) (one-way ANOVA: $F = 109.87$; d.f. = 1271; $P < 0.001$; Fig. 1). All marked juvenile (88%, 38 of 43, were found in sedge) and subadult (93%, 26 of 28, were found in sedge) spiders were found in closed habitats. Twenty-three of the 32 (72%) of the adult spiders were found in closed habitats (78%, 18 of 23, were found in sedge). More adults (8 of 23) shifted from closed to open habitat than subadults, which had more individuals (4 of 28) shift from closed to open habitats than juveniles (0 of 43; $\chi^2 = 162.08$; d.f. = 2; $P < 0.0001$) (Table 2). No individuals moved from closed to open habitats. More adults (15 of 23) shifted vegetation structure than subadults, which had more individuals (7 of 28) shift vegetation structure than juveniles (0 of 43;
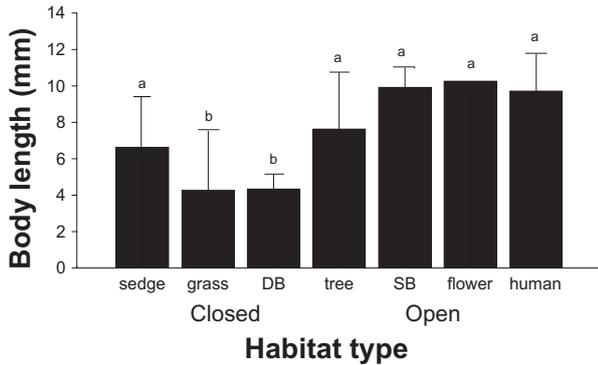
Fig. 1. Mean (±SE) body length (mm) of spiders on sedge, grass, dense bushes (DB), trees, sparse bushes (SB), flowers and anthropogenic structures (human) (all a > b). These vegetation types were further divided into the habitat types in which they were principally found: edge, grass and dense bushes being the vegetation types found typically within the closed habitats, and trees, sparse bushes, flowers and anthropogenic structures being the vegetation types found typically within the in open habitat type.

$\chi^2 = 387.66$; d.f. = 2; $P < 0.0001$) (Table 2). Of the nine adults marked in open habitats, two changed vegetation structure (one moved from an anthropogenic structure to a tree, the other moved from a tree to an anthropogenic structure) (Table 2).

Factors influencing selection

Less insects from each of the major insect orders identified (Hymenoptera, Diptera, Hemiptera, Coleoptera and Orthoptera) were recovered from webs than traps ($\chi^2 = 267.12$; d.f. = 7; $P < 0.0001$; Fig. 2 (using only closed habitats as too few observations were made for webs in open habitats)). Consequently two measures, potential (derived from measures of insects removed from traps) and actual (derived from measures of insects found in webs) of prey size and abundance were used for the GLM. Factors positively related to *A. keyserlingi* abundance were foliage density and potential prey abundance. Plant height, and mantid and bird abundance were negatively related to *A. keyserlingi* abundance (tolerance: $r^2 = 0.794$) (Table 3). Relative humidity, actual prey (size, abundance and diversity), potential prey size and diversity, canopy cover, spider body and leg length, abundance of other spiders, debris and nearest neighbour distance had no relationship with *A. keyserlingi* abundance. Foliage density (closed > open), mantid abundance (closed > open) and bird abundance (open > closed) significantly differed between open and closed habitats (Table 4). The ordinal composition of potential prey differed significantly (ANOSIM: global $R = 0.30$; $P = 0.001$; Fig. 3) between habitats, driven by

Hymenoptera (SIMPER: 32.0% contribution) and Diptera (26.8% contribution) being found in lower abundance in closed compared with open habitats. The ordinal composition of actual prey was not significantly different between open and closed habitats (global $R = 0.96$; $P = 0.08$); dipterans and hymenopterans were found in lower abundance in webs compared with traps in closed habitats (Fig. 2). Potential prey (mean ± SE: open = 1.92 ± 0.37 mm, closed = 1.25 ± 0.24 mm) were larger in the open habitats ($F = 351.67$; d.f. = 1241; $P < 0.0001$), the size of actual prey, however, did not differ between habitats (open = 1.48 ± 0.25 mm, closed = 1.34 ± 0.47 mm; $F = 1.47$; d.f. = 1121; $P = 0.53$).

Web architectural plasticity

Argiope keyserlingi built webs significantly closer to the ground within closed habitats ($n = 221$), than open habitats ($n = 52$) (mean ± SE: closed = 0.46 ± 0.18 m, open = 1.14 ± 0.64 m; one-way ANCOVA: $F = 200.49$, d.f. = 1315; $P < 0.0001$). Webs in closed habitats had significantly smaller capture areas ($0.12 ± 0.02$ m^2 compared with $0.30 ± 0.14$ m^2; $F = 12.85$, d.f. = 1,272; $P < 0.001$) than those in open habitats. Webs in open habitats had larger spiral distances than those in close habitats (mean ± SE: open habitats = 2.25 ± 0.18 mm; closed habitats = 0.76 ± 0.02 mm; median test: $T = 1.0$, d.f. = 266; $P < 0.0001$). There was no difference in the frequency of webs with 0, 1, 2, 3 or 4 decoration arms between habitats ($\chi^2 = 2.95$, d.f. = 4; $P = 0.42$).

Web capture area had a positive relationship with web height and air temperature and had a negative relationship with foliage density, with 95.2% of the variation in the data explained by the model (tolerance: $r^2 = 0.952$). Spiral distance had a positive relationship with web height and potential prey abundance, with 87.6% of the variation in the data explained by the model. Length of decorations had a positive relationship with web height and potential prey abundance, although the model explained only 32.5% of the variation in the data (Table 5). Relative humidity, actual prey (size and abundance), potential prey size, canopy cover, plant height, spider length, the abundance of birds, mantids, or other spiders, debris, and nearest neighbour distance had no relationship with any web architectural parameters.

Laboratory experiments

The capture area of webs differed significantly according to enclosure size (two-way ANCOVA: $F = 68.08$; d.f. = 1,94; $P < 0.0001$) and presence of sedge ($F = 17.78$; d.f. = 1,94; $P = 0.001$), although there was no

Table 2. Number of juvenile, subadult and adult spiders marked in both the open and closed habitats and the number of each size class that either moved habitat or to a different vegetation type within the habitat (percentages are given in parentheses)

	Juveniles	Subadults	Adults	χ^2	P
Closed habitats					
Marked	43 (100)	28 (100)	23 (71.9)		
Moved to open habitat	0	4 (14.3)	8 (34.8)	162.08	<0.0001
Changed vegetation	0	7 (25)	15 (65.2)	387.66	<0.0001
Open habitats					
Marked	0	0	9 (28.1)	–	–
Moved to closed habitat	0	0	0	–	–
Changed vegetation	0	0	2 (22.2)	–	–
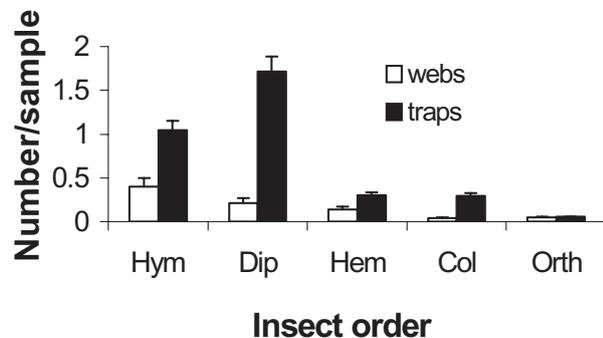
Fig. 2. Mean ($\pm$SE) number of hymenopterans (Hym), dipterans (Dip), hemipterans (Hem), coleopterans (Col) and orthopterans (Orth) caught per web ($n = 103$) or Tanglefoot trap ($n = 64$) in closed habitats (too few data were collected for webs in open habitats for meaningful comparisons).

interaction effect ($F = 1.63$; d.f. = 1,94; $P = 0.20$). Webs in large enclosures had significantly larger capture areas than webs in small enclosures and webs without sedge in the background had significantly larger capture areas than webs with sedge in the background (Tukey's HSD: $P < 0.0001$; Fig. 4). Enclosure size and the presence of sedge also affected spiral distances ($T = 0.30$, d.f. = 49; $P < 0.0001$). Large enclosures with sedge (mean $\pm$ SE = 1.96 $\pm$ 0.13 mm) had significantly larger spiral distances than all other treatments. Small enclosures with sedge (0.81 $\pm$ 0.31 mm) had larger spiral distances than all 'without sedge' treatments. Large (0.37 $\pm$ 0.08 mm) and small enclosures (0.46 $\pm$ 0.07 mm) without sedge did not differ (Table 6). The frequencies of webs with 0, 1, 2, 3 or 4 decoration arms did not differ between treatments ($\chi^2 = 4.81$, d.f. = 8; $P = 0.41$; Fig. 4). However, if the presence of sedge is ignored, there was a significant difference ($\chi^2 = 12.01$, d.f. = 8; $P = 0.001$) with *A. keyserlingi* adding all four arms to their decorations more often when in small enclosures than when in large enclosures (Fig. 5).

There was no influence on web area ($F = 0.48$; d.f. = 1,69; $P = 0.49$), spiral distances (Table 6) or the number of decoration arms added to webs ($\chi^2 = 2.08$, d.f. = 4; $P = 0.68$) according to whether spiders were fed no flies, three flies, or fed *ad libitum*. Damage influenced the capture area of tertiary webs ($F = 12.052$; d.f. = 1,69; $P = 0.005$), with web capture areas significantly reduced when the secondary webs were completely damaged, but not when secondary webs were partially damaged or not damaged (Tukey's HSD: $P < 0.001$; Fig. 6). Partial damage never resulted in the termination of the original web. Of the 24 webs completely destroyed, 20 were rebuilt. Spiral distances (Table 6) and the number of decoration arms ($\chi^2 = 13.48$, d.f. = 4; $P = 0.26$) were unaffected by the degree of web damage.

DISCUSSION

Why did *A. keyserlingi* choose to inhabit sedge habitats instead of open areas? Our models revealed strong associations with foliage density, potential prey abundance, plant height and predator densities. Plant height and potential prey abundance did not differ between habitats so did not explain *A. keyserlingi* preferences. There was a negative influence of mantid presence on spider abundance, but this relationship did not explain spider preferences for sedge, as mantids were only found within sedge and in low numbers. Among the factors examined, only the presence of birds, a common predator of spiders that place their webs within or between trees (Gunnarsson 1983; De Souza & Martins 2004), can adequately explain why *A. keyserlingi* avoided trees and selected closed habitats. The reason why, within the closed habitat, *A. keyserlingi* preferred sedges to dense bushes and grasses is unclear. Higher prey abundance or sturdier supports are often associated with vegetation preferences in orb web spiders (Janetos 1982; Rypstra 1986; McNett & Rypstra 2000), but there was no evidence of any of these factors differing substantially between sedge and dense bushes and grasses. Decoration frequencies did not differ between open and closed habitats, so *A. keyserlingi* did not appear to utilize sedge for contrasting decorations against. Small insectivorous

Table 3. Results of a generalized linear model (where β_i is the estimated (using a goodness-of-fit procedure) coefficient, of variable X_i, in the linear model ($g(x) = \beta_0 + \beta_1 X_1 \ldots \beta_i X_i$) and ASE = asymptotic standard error about the mean), and Wald's tests (the most reliable significance test for GLMs of large sample size; Quinn & Keogh 2002), for environmental parameters found significantly related to *Argiope keyserlingi* abundance

	β_i	ASE	Wald statistic	P
Potential prey abundance	0.001	0.260	25.014	<0.0001
Foliage density	0.04	0.111	7.930	0.030
Plant height	−0.07	0.128	−10.864	<0.0001
Mantid abundance	−0.130	0.570	−8.703	0.001
Bird abundance	−0.06	0.85	−6.563	0.030

Relative humidity, size, abundance and diversity of actual prey, size and diversity of potential prey, canopy cover, spider body and leg length, abundance of other spiders, debris, and nearest neighbour distance had no relationship with *A. keyserlingi* abundance, so the results pertaining to these parameters are not presented. GLM, generalized linear modelling.

Table 4. Results (mean ± SE) of a multivariate analysis of variance to determine if potential prey abundance, foliage density, plant height, and mantid and bird abundance differed between open and closed habitats

	Open habitats	Closed habitats	F (d.f. = 1,22)	P
Potential prey abundance (insects per trap per day)	1.35 ± 1.19	1.49 ± 0.43	1.07	0.11
Foliage density (% cover)	37.50 ± 5.28	90.03 ± 8.58	34.26	<0.0001*
Plant height (m)	1.34 ± 0.001	1.48 ± 0.00	0.38	0.78
Mantid abundance (number per sample)	0.00 ± 0.00	0.25 ± 0.00	13.50	<0.001*
Bird abundance (number per sample)	2.53 ± 0.43	0.27 ± 0.79	3.76	0.004*

*Denotes significance.

birds that prey on juvenile spiders, such as sparrows, may inhabit bushes and grasses within closed habitat (Groner & Ayal 2001) and avoidance of these predators may explain why *A. keyserlingi* selected sedge habitats and only shifted to other vegetative structures as subadults or adults. Particular prey types that are more abundant in sedge, such as orthopterans (Olive 1980; McReynolds 2000), and microclimatic factors, such as ambient light and solar radiation (Biere & Uetz 1981; Ward & Lubin 1993; Herberstein & Fleisch 2003), may also explain the preference for sedge by *A. keyserlingi*.

We found that only subadult and adult *A. keyserlingi* occupied open habitats. No juveniles were ever found within open habitats, which may be because (i) hatchlings never disperse into open habitats; (ii) hatchlings disperse into open habitats but subsequently move by secondary dispersal (Decae 1987); or (iii) hatchlings dispersing into open habitats suffer close to 100% mortality. Ballooning (the means by which *A. keyserlingi* disperses; Bradley 1993) results in random dispersal patterns (Decae 1987), therefore *A. keyserlingi* hatchlings are more likely, owing to the greater availability of open habitats, to disperse into open habitats than closed habitats. Accordingly, it is highly unlikely that the distribution of juveniles is a result of exclusive dispersal into closed habitats. Secondary dispersal is most likely to occur in ballooning
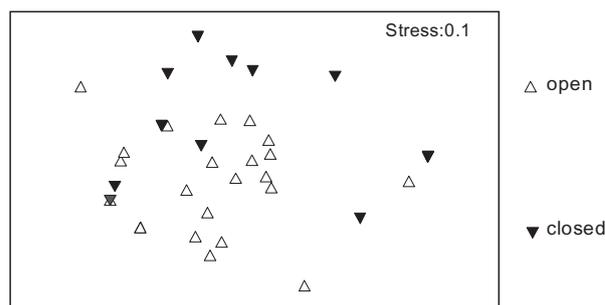

Fig. 3. Multi-dimensional scaling ordination showing differences in potential prey diversity (insects, identified to Order, caught in Tanglefoot traps) between closed and open habitat ($n = 64$ for each habitat; all sites were combined as no site-specific effects were identified).

spiders when relocation to a more favourable location is likely (Riechert & Harp 1987). Secondary dispersal by *A. keyserlingi*, accordingly, is unlikely at our sites. Early instar spiders may suffer high mortality from predation if they disperse into a predator dense habitat (Wagner & Wise 1996). Hatchling spiders have an array of predators and high predation is common but not normally close to 100% (Moore 1977; Greenstone 1983; Wagner & Wise 1996). Hatchlings may starve if they disperse into habitats where the vegetative architecture is unfavourable for web construction or webs

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Table 5. Results of a generalized linear model (where β_i is the estimated (using a goodness-of-fit procedure) coefficient, of variable X_i in the linear model and ASE = asymptotic standard error about the mean) and Wald's tests, for environmental parameters found significant related to the web architectural parameters web area, spiral distance, decoration length

	Web area				Spiral distance				Decoration length			
	β_i	ASE	Wald statistic	P	β_i	ASE	Wald statistic	P	β_i	ASE	Wald statistic	P
Potential prey abundance	–	–	–	–	<0.01	0.01	30.69	<0.01	0.01	0.13	55.59	<0.01
Foliage density	0.01	0.37	–36.06	<0.01	–	–	–	–	–	–	–	–
Air temperature	0.02	0.14	6.09	0.03	–	–	–	–	–	–	–	–
Web height	0.02	0.48	5.07	0.04	0.01	0.04	6.46	0.01	0.11	0.92	6.10	0.03

Relative humidity, actual prey (size, abundance and diversity), potential prey (size, abundance and diversity), potential prey size and diversity, canopy cover, plant height, spider length, the abundance of birds, mantids, or other spiders, debris, and nearest neighbour distance had no relationship with web architecture, so the results pertaining to these parameters are not presented.
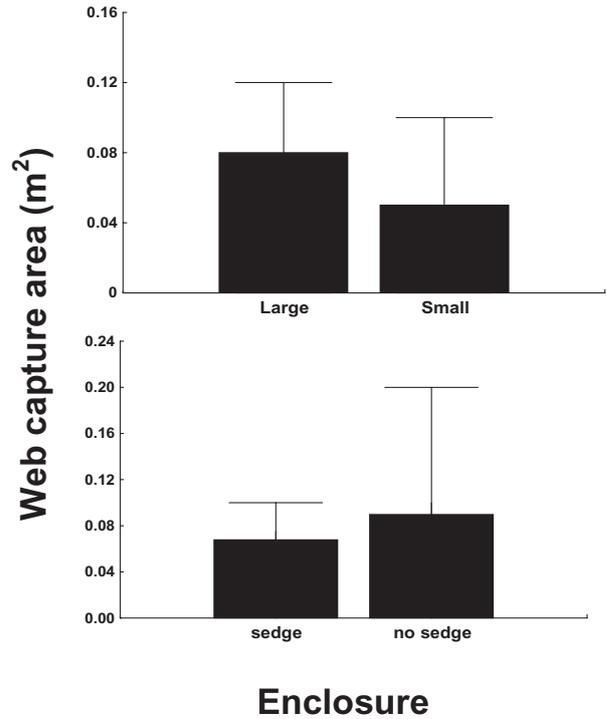
Fig. 4. Comparison of the mean (±SE) web capture areas for webs built in large *versus* small enclosures and enclosures containing sedge *versus* enclosures containing no sedge in the background.

are constructed but exposed to larger, thus difficult to handle and highly damaging, to the web, prey (Wise 1983). A combination of predation by birds, lizards, insects and other spiders, and starvation upon dispersal are most likely responsible for the absence of juveniles in open habitats.

Why did *A. keyserlingi* move into open habitats as subadults and adults? Other requirements (e.g. energetic or nutrient demand, reproductive requirements) may be forcing *A. keyserlingi* to switch to risk-prone foraging (Gillespie & Caraco 1987). Foraging models (e.g. μ/g maximization; Ludwig & Rowe 1990) predict that animals occupy habitats that balance growth with predation risk and, accordingly, if predation risk or growth requirement changes, habitat preferences should also change. Given that the principal predators in open habitats were large ravens and magpies; birds which are capable of consuming prey at least as large as adult *A. keyserlingi* (Kaplan 2004), it seems unlikely that subadults and adults experience marked differences in predation pressure. Large prey are required for sustained growth when in reproductive condition (Uhl *et al.* 2004; Venner & Casas 2005), and may explain why some subadult and adult *A. keyserlingi* switched from closed to open habitats.

Table 6. Results of median tests used to determine the factors affecting the spiral distances of *Argiope keyerilingi* webs constructed in the laboratory

| Experiment	Test parameters	Median spiral distance (mm)	Valid n	T-score	Z	P
Area and presence of sedge	Large Enclosure/sedge *vs* Large enclosure/no sedge	2.05 *vs* 0.36	24	1.0	3.98	<0.0001★
	Large Enclosure/sedge *vs* Small enclosure/sedge	2.05 *vs* 0.82	24	19.0	2.60	0.009★
	Large Enclosure/sedge *vs* Small enclosure/no sedge	2.05 *vs* 0.46	24	8.0	3.62	0.0002★
	Small Enclosure/sedge *vs* Large enclosure/no sedge	0.82 *vs* 0.36	24	11.0	3.51	0.0004★
	Small Enclosure/sedge *vs* Small enclosure/no sedge	0.82 *vs* 0.46	24	12.0	3.47	0.0005★
	Large Enclosure/no sedge *vs* Small enclosure/no sedge	0.36 *vs* 0.46	24	82.0	0.15	0.88
Prey availability	No flies *vs* 3 flies	0.51 *vs* 0.63	12	16.0	1.80	0.07
	No flies *vs* flies *ad libitum*	0.51 *vs* 0.52	12	23.0	0.21	0.21
	3 flies *vs* flies *ad libitum*	0.63 *vs* 0.52	12	27.0	0.53	0.59
Web damage	No damage *vs* 50% damage	0.60 *vs* 0.60	12	34.0	0.39	0.70
	No damage *vs* complete damage	0.68 *vs* 0.68	12	31.0	0.18	0.86
	50% damage *vs* complete damage	0.60 *vs* 0.68	12	76.0	0.41	0.68

★Denotes significance.
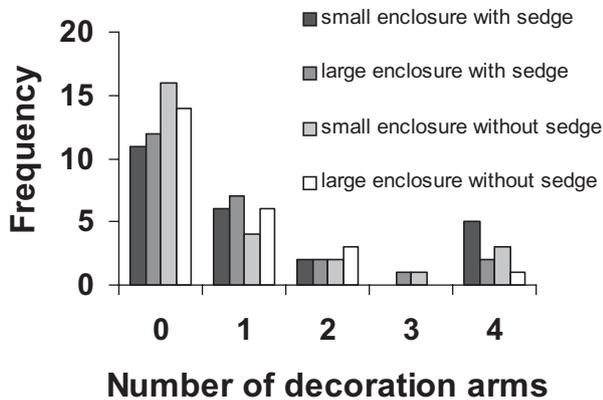
Fig. 5. Number of observations (frequency) of web decorations with 0 (no decorations), 1, 2, 3, and 4 (fully cruciform) arms in small (with and without sedge present) and large (with and without sedge present) enclosures in the laboratory.

Fig. 6. Comparison of the mean (±SE) web capture areas of secondary (2nd; before damage) and tertiary (3rd; after damage) webs (Full = instances where webs were fully destroyed, Half = instances where half of the web was destroyed, and None = instances where the web was not destroyed) showing that fully destroying the secondary webs resulted in significantly smaller tertiary webs being built.

Argiope keyserlingi exhibited web architectural plasticity, so they are capable of exploiting different habitats under different conditions (Ward & Lubin 1993; Sandoval 1994). They built webs with larger capture area and spiral distances in open compared with closed habitats with much (87–95%) of this variation is explained by fluctuations in potential prey abundance, foliage density, air temperature and web height. Our laboratory experiments supported our field observations; when space is limited (e.g. in thick foliage or in small enclosures), *A. keyserlingi* built smaller webs with reduced spiral distances, which in turn may reduce prey capture success (Krink & Vollrath 2000).
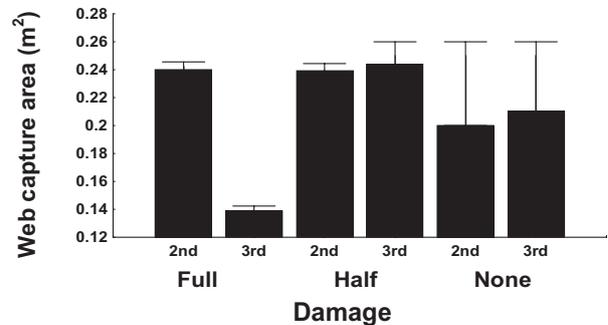
Complete web destruction, such as that caused by human (intentional or inadvertent) disturbance, induces changes in web architecture and reduces foraging success, so *A. keyserlingi* may be occupying closed, inaccessible, habitats to avoid human disturbance.

Decoration designs did not differ between open and closed habitats, indicating that the type (number of arms and length) of decorations added were independent of the geometric arrangement of the web. Potential prey density and web height were related to decoration length, however, variation in the environmental parameters that were measured explain little

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(~33%) of the variation in decorations. Satiated spiders add more decorations more often to their webs (Tso 2004), which explains the positive relationship between availability of potential prey and length of decorations. Perhaps webs placed higher in the vegetation were exposed to more prey, leading to increased investment in decorations. Our models may have accounted for little variation in decoration design because factors such as light intensity (Bruce *et al*. 2001; Herberstein & Fleisch 2003) exert a greater influence than any of the factors we measured. Decorations constitute important components of the foraging regime of *A. keyserlingi* (Herberstein 2000; Bruce *et al*. 2001, 2005) so there may be strong selection pressure towards conservation in decoration designs. In the laboratory we found that if we excluded the influence of sedge *A. keyserlingi* built webs with completely cruciform decorations more often in small enclosures than large enclosures. In the field *A. keyserlingi* may be building less completely cruciform decorations within closed habitats because they attract mantid or spider predators (Bruce *et al*. 2001; Li & Lee 2004), or because there is less light penetrating the vegetation (Bruce *et al*. 2001).

The types and sizes of prey captured in webs were different from those captured in Tanglefoot traps, signifying that insects caught in traps were not representative of the prey consumed. Frequent rejection of certain prey (fewer flies and bees and wasps and smaller insects were found in webs) or poor retention of large insects, because they either fly through, bounce off, or do not adhere to webs, may be responsible for the disparity (Higgins & Buskirk 1992; Sandoval 1994). As both *A. keyserlingi* abundance and orb geometry were unrelated to the availability of actual prey it appears that *A. keyserlingi* does not make foraging decisions based on previous foraging experiences as do some other orb spiders (Vollrath & Houston 1986; Nakata & Ushimaru 1999). The abundance of potential prey did not differ between habitats, but smaller prey were encountered in closed habitats. As the capture of large prey (relative to the size of the spider) may impact on survivorship (Venner & Casas 2005), *A. keyserlingi* appears to be compromising foraging profitability by occupying closed habitats. Trade-offs in nature are, however, rarely as straightforward as the models depict (Ludwig & Rowe 1990; Manly *et al*. 2002; Simpson *et al*. 2004) and other factors impacting on the fitness prospects of *A. keyserlingi* (e.g. nutrient uptake, egg survivorship, physiological requirements) should be assessed before implicating a trade-off.

ACKNOWLEDGEMENTS

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