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# Plasticity in extended phenotypes: orb web architectural responses to variations in prey parameters

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## SUMMARY

**A spider orb web is an extended phenotype; it modifies and interacts with the environment, influencing spider physiology. Orb webs are plastic, responding to variations in prey parameters. Studies attempting to understand how nutrients influence spider orb-web plasticity have been hampered by the inability to decouple prey nutrients from other, highly correlated, prey factors and the intrinsic link between prey protein and prey energy concentration. I analyzed the nutrient concentrations of cockroaches, and adult and juvenile crickets to devise experiments that controlled prey protein concentration while varying prey size, ingested mass, energy concentration and feeding frequency of the orb web spider *Argiope keyserlingi*. I found that *A. keyserlingi* alters overall architecture according to feeding frequency. Decoration length was inversely related to ingested prey mass and/or energy density in one experiment but directly related to ingested prey mass in another. These contradictory results suggest that factors not examined in this study have a confounding influence on decoration plasticity. As decorations attract prey as well as predators decreasing decoration investment may, in some instances, be attributable to benefits no longer outweighing the risks. Web area was altered according to feeding frequency, and mesh size altered according to feeding frequency and prey length. The number of radii in orb webs was unaffected by prey parameters. A finite amount of silk can be invested in the orb web, so spiders trade-off smaller mesh size with larger web capture area, explaining why feeding frequency influenced both web area and mesh size. Mesh size is additionally responsive to prey size *via* sensory cues, with spiders constructing webs suitable for catching the most common or most profitable prey.**

Key words: niche construction, nutrients, orb web spider, prey features, trade-offs, web architecture.

## INTRODUCTION

Animals may alter phenotypic form or function in response to changing environmental conditions, a phenomenon called phenotypic plasticity (Whitman and Agrawal, 2009; Auld et al., 2010). Plastic phenotypes are depicted by reaction norms or analyses of variation such as ANOVA and related procedures (Garland and Kelly, 2006; Whitman and Agrawal, 2009). Phenotypes extended beyond the organism, so-called extended phenotypes, are changeable within and among individuals, populations or clades (Dawkins, 1982). Extended phenotypes are complex because multiple factors influence phenotypic expression (Schaedelin and Taborsky, 2009). Additionally, extended phenotypes not only adapt to the demands of the environment, they interact with it, modify it and gain feedback from it, thereby creating phenotype–environment interactions that flow through generations (Lehmann, 2008). Owing to the interactions of multiple traits (Blanckenhorn, 1998), the complexity of the biological feedback mechanisms (Lehmann, 2008), and the interactive complexities of the various costs and limitations of plasticity (Auld et al., 2010), analyses of extended phenotypes are complex (Schaedelin and Taborsky, 2009). For analytical clarity, therefore, it is vital that studies investigating extended phenotypic plasticity minimize the multitudinous environmental effects and control the potentially interactive factors.

The orb web is a conspicuous depiction of the physiological status and foraging stratagem of a spider (Heiling and Herberstein, 2000) and thus can be considered an extension of the spider phenotype (Craig, 2003). Orb-web architectural design is evolutionarily unstable, having been significantly modified over time in adaptation to selective challenges (Blackledge et al., 2009). Orb-web architecture has additionally evolved considerable plasticity (Heiling and Herberstein, 2000; Craig, 2003). Orb-web-building spiders, as a result, are exceptionally good model organisms for studying plasticity in extended phenotypes. Nevertheless, experimental determination of the environmental influences on orb-web plasticity is extremely complex. Firstly, specific architectural parameters respond differently to stimuli. For example, the capture area, web shape, symmetry, number of capture threads, mesh size (the distance between capture threads), the number of radial threads, the size and shape of decorations and silk properties may respond differently to various biotic and abiotic stimuli (Schneider and Vollrath, 1998; Heiling and Herberstein, 2000; Tso et al., 2005; Tso et al., 2007; Mayntz et al., 2009). Secondly, the nature of the stimuli inducing plasticity is multitudinous with prey type, prey abundance, prey nutrients, temperature, water availability, habitat complexity, predation pressure and web vibrations implicit in inducing plastic responses in orb spider webs (Vollrath et al., 1997; Herberstein et al., 2000a; Tso et al., 2005; Tso et al., 2007; Blamires et al., 2009; Nakata, 2009).

There is currently much interest in prey-induced plastic responses of orb webs. The type and abundance of prey in the environment has long been recognized as a significant driver of orb-web architectural plasticity (Heiling and Herberstein, 2000) but recent studies have revealed that specific prey can elicit plastic responses in orb-web-building spiders. For example, the giant wood spider,

*Nephila pilipes*, builds a larger web with a wider mesh size and thicker frame threads when feeding on crickets compared with flies (Tso et al., 2007). Further, Mayntz et al. (Mayntz et al., 2009) demonstrated that juvenile *Zygiella x-notata* build webs with more radii when feeding on protein-enriched flies than when feeding on protein-depleted flies, and Blamires et al. (Blamires et al., 2009) found that *Argiope keyserlingi* invests in more decorations when feeding on high protein prey than when feeding on low protein prey, independent of spider size. Prey, or more specifically prey protein concentration, therefore, appears to be a driver of orb-web-building plasticity. These patterns may, nonetheless, be correlative and it remains unclear precisely what role protein concentration plays on the foraging stratagem of orb web spiders or the mechanisms by which it mediates plastic responses. As silk is proteinaceous (Craig, 2003), consuming more total protein, by consuming more food, or more protein-concentrated food, may make available the constituent amino acids of spider silk thus enhancing synthesis; with more silk availability meaning sovereignty to alter the geometry of the web. However, there is considerable genetic control over the construction of silks independent of nutritional input (Winkler and Kaplan, 2000; Craig, 2003). Additionally, the amino acid sequences of silks appear to have been shaped by the nutritional costs of production (Craig, 2003), explaining why spider silk has numerous small side chain non-essential amino acids (Winkler and Kaplan, 2000). Moreover, lipid and protein concentrations in spider prey are usually inversely correlated (Mayntz et al., 2005; Blamires et al., 2009; Wilder and Rypstra, 2010; Blamires, 2010). As lipids are more energy dense than protein, prey energy concentration may also be inversely correlated with prey protein concentration. Lipids provide the energy to metabolically drive silk synthesis and web building activities (Craig, 2003), so the energy concentration of prey may be more influential at inducing spider orb-web architectural plasticity than prey protein concentration. Nonetheless, because amino acids can be metabolized to produce ATP, protein is a potential source of energy for spiders. Hence, few studies have successfully decoupled the relative influences of energy and protein concentrations in spider prey, and our understanding of how prey influences spider orb-web architectural plasticity remains equivocal.

Non-nutritional influences acting on orb-web architecture hinder our understanding of nutritional mechanisms driving web architecture. The size and/or mass of an entangled insect may elicit vibrations in the radial silks of a specific frequency that provide information to the spider about the prey (Landolfa and Barth, 1996) that, consequently, affects web architecture (Nakata, 2009), creating a phenotype–environment positive feedback cycle. As spiders build webs aimed to capture the largest and/or most nutritionally profitable prey available in their habitat (Venner and Casas, 2005), the vibratory cues of the largest prey may be used to design webs aimed at catching those prey. However, due to the correlated nature of most prey attributes no study, to date, has manipulated the mass and size of different prey to investigate the nutritional and non-nutritional consequences on spider orb-web architectural plasticity without undue manipulation of nutritional factors.

The central silk linear or cruciform (X-shaped) decorations, also often referred to as stabilimenta (Herberstein et al., 2000b), in orb webs of spiders of the genus *Argiope* have been much studied with contradictory findings regarding their function; some authors finding that they deter predators (e.g. Blackledge, 1998; Blackledge and Wenzel, 1999), while others finding that they attract prey (e.g. Craig and Bernard, 1990; Cheng and Tso, 2007). One reason for these contradictory findings is that different-shaped decorations differ in their visual attractiveness to predators and prey, and thus may serve different functions (Cheng et al., 2010). The cruciform decorations appear more likely to attract prey, while the linear decorations appear more likely to deter predators. The use and forms of decorations in the field is nonetheless unpredictable in many *Argiope* spp. (Herberstein et al., 2000b; Bruce et al., 2001). An increased understanding of web decoration plasticity may thus enhance our understanding of their function.

In the present study I performed laboratory experiments with the objective of altering the energy, but not protein, concentration in the prey of the orb web spider *Argiope keyserlingi* Karsch. To accomplish this I measured the energy and protein concentrations of three prey types: cockroaches, adult crickets and juvenile crickets. These prey differed in length, mass and energy concentration but not protein concentration (Table 1). To isolate prey length, mass and energy, I performed three experiments. In the first (cockroaches *vs* adult crickets), prey length and protein were similar but masses and energy concentrations differed. In the second (cockroaches *vs* adult crickets at different feeding frequencies), the difference in prey mass of the first experiment was counteracted but feeding frequency differed from that experiment. In the third experiment (adult crickets *vs* juvenile crickets), the nutrient concentrations in prey were similar but prey masses and lengths differed. Thus, at the completion of these experiments it was possible to determine the relative influences of prey energy concentration, feeding frequency (from the first two experiments) and prey length (from the third experiment) on orb-web architectural plasticity. I measured the number of radii, the web area, mesh size and length of decorations in *A. keyserlingi* orb webs, as these are plastic architectural features (Blamires et al., 2009; Mayntz et al., 2009). All functional studies of the cruciform decorations in *A. keyserlingi* suggest a prey attraction

Table 1. Mean ± s.e.m. length (*N*=30, 30 and 50 for cockroaches, adult crickets and juvenile crickets, respectively), dry mass consumed (mean mass of remaining carcasses subtracted from the mean mass of each item fed to spiders) (*N*=35, 42 and 14 for cockroaches, adult crickets and juvenile crickets, respectively), energy density and percentage protein (*N*=33, 30 and 31 cockroach, adult cricket and juvenile cricket pellets, respectively) of the prey types used in each of the experiments

| | | | | *F*-scores | |
|---|---|---|---|---|---|
| | Cockroaches | Adult crickets | Juvenile crickets | Cockroaches *vs* adult crickets (experiments 1 and 2) | Adult *vs* juvenile crickets (experiment 3) |
| Length (mm) | 11.64±3.39 | 10.05±3.20 | 2.85±1.14 | 0.39 | 26.81** |
| Ingested dry mass (g) | 0.70±0.10 | 0.36±0.29 | 0.25±0.23 | 11.10* | 10.47* |
| Energy density (kJ $g^{-1}$) | 24.35±1.87 | 21.63±3.49 | 21.62±3.85 | 7.06* | 0.39 |
| Protein content (%) | 57.38±3.48 | 58.75±4.70 | 58.98±3.91 | 0.570 | 2.43 |

Showing the results of one-way analyses of variance (*F*-scores, d.f.=1,22), *$P$<0.01, **$P$<0.001.

function (Herberstein, 2000; Herberstein et al., 2000a; Herberstein et al., 2000b; Bruce et al., 2001; Bruce et al., 2005; Blamires et al., 2008) so this function was assumed here. Any orb-web architectural parameter that responded to diet here that did not respond in the studies of Mayntz et al. (Mayntz et al., 2009) or Blamires et al. (Blamires et al., 2009) were considered attributable to factors other than prey protein concentration or overall protein intake. Those parameters responding to my feeding regimes and those of Mayntz et al. (Mayntz et al., 2009) and Blamires et al. (Blamires et al., 2009), e.g. number of radii and decoration length, were considered to be responsive to influences correlative with protein.

## MATERIALS AND METHODS

### Prey nutrient determination

I housed, in the laboratory, approximately 200 adult crickets (*Acheta domestica* Linnaeus), 200 juvenile (second instar) crickets and 200 wood cockroaches (*Panesthia australis* Brunner von Wattenwyl) each in 240 mm × 180 mm × 60 mm plastic aerated enclosures. All of the crickets and cockroaches were fed a similar diet of carrot slices and a protein supplement (Gutload®, Pisces, Brisbane, Australia) daily. After 14 days of feeding 30 adult crickets, 50 juvenile crickets and 30 cockroaches were killed by exposure to $CO_2$, measured to the nearest mm using calipers and weighed to the nearest mg, and dried at 60°C for 24 h. The cuticle and legs of all prey were removed, as they are indigestible to spiders, before they were re-weighed, ground into <1 mm particles using a mortar and pestle, and compressed into 10–25 mg pellets ($N$=33, 30 and 31 for cockroaches, adult crickets and juvenile crickets, respectively). Pellet energy density (energy concentration in kJ $g^{-1}$) and percentage nitrogen were determined using bomb calorimetry (Gentry Micro-Calorimeter, Aiken, SC, USA) and Kjeldahl direct distillation (Kjeltec 2300, Trecator, Hoganas, Sweden), respectively. Percentage protein was then determined from percentage nitrogen using the standard conversion factor [=6.25 × % nitrogen (Horowitz, 2002)]. The indigestible remains (mostly cuticle and legs) of crickets and cockroaches that had been fed to spiders (see 'Experimental regimes') were removed from the webs and weighed to determine the mean mass consumed for each prey type. There were too few cricket and cockroach remains to include them in nutritional analyses. As only the digestible components of prey were used to measure nutrient concentrations, I assumed the nutrients that were extracted from prey were in quantities similar to those measured. The nutritional information derived by these procedures was used to design the ensuing experiments.

### Spider habituation

All of the *A. keyserlingi* used were penultimate instar females that were captured at the University of Sydney, Camperdown–Darlington campus. Spiders were initially placed in 300 mm × 300 mm × 50 mm Perspex® enclosures, large enough to build a web of adequate size for feeding, where they were fed 3–6 *Drosophila melanogaster* Meigen twice weekly for two weeks. Prior to the commencement of each experiment the spiders were removed from the temporary enclosures and weighed on an electronic balance (CP224, Sartorius, Gottingen, Germany), before being transferred to larger (500 mm × 300 mm × 50 mm) enclosures. Spiders were given one week to build a full orb web and those that failed were replaced. Once an orb web was built I began the feeding experiments. Once a week the orb webs were destroyed and silk was collected. Upon completion of each experiment (four weeks) I removed the spider from the web and re-measured it to ensure that it had sustained its mass (±0.05 g) throughout the experiment. Any spiders that had lost more than 10% of their initial body mass in the course of an experiment ($N$=1 in all experiments) were not included in analyses.

### Experimental regimes

In my first experiment, I fed 30 *A. keyserlingi* either one cricket or one cockroach ($N$=15 for each diet) every other day for four weeks. Adult crickets and cockroaches had different dry masses and energy densities (Table 1) so I could not be sure that any observed changes in web architecture were due to differences in ingested prey mass or energy density. I therefore performed a second experiment where I fed 36 habituated *A. keyserlingi* a diet of either: (1) one adult cricket every other day, (2) one cockroach every other day, or (3) one cockroach every fourth day over four weeks ($N$=12 for each). The last diet provided ingested prey mass (g $feeding^{-1}$) similar to those of the cricket diet. To account for any web architectural changes induced by changed frequencies of vibratory information received from struggling prey, I placed cockroaches onto the webs of spiders of both of the cockroach feeding treatments every other day, but for spiders being fed cockroaches every fourth day I removed the cockroaches prior to being attacked on every other feeding occasion. Thus, spiders feeding on cockroaches every fourth day alternated between exposure to cockroaches without being fed and being fed cockroaches every other day, while the other two treatment groups received either cockroaches every other day or crickets every other day. The results of these two experiments were used collectively to determine the influence of prey energy density and feeding frequency on orb-web architectural plasticity. To determine web architectural responses to prey of different lengths I performed a third experiment where I fed another 30 *A. keyserlingi* either juvenile crickets or adult crickets, i.e. prey of similar energy and protein concentration but of different lengths. As the differences in ingested dry mass (g $feeding^{-1}$) (Table 1) were accounted for in the previous experiment, I did not control this parameter in this experiment. All prey remains were removed from the webs before providing each subsequent prey.

### Web architecture measurements

I sprayed each web with water to render it visible and the distances between the outer margin of the hub and web periphery were measured in four directions: (i) right, (ii) left, (iii) upward and (iv) downward. The number of radii threads and the number of spiral threads intercepting radii between the hub and the web periphery in each of the four aforementioned directions were counted in order to estimate web area and mesh size. I measured the total length of cruciform decorations using calipers (combining the lengths of each of four arms of the X, recording 0 when no decorations were added).

### Statistical analyses

I ascertained if prey length, dry mass consumed, energy density or protein concentration varied between (i) cockroaches and adult crickets, and (ii) adult and juvenile crickets by one-factor analyses of variance (ANOVA; Table 1). To account for the multiple interacting features in an orb spider web I used one-factor multiple analyses of covariance (Wilk's λ), using spider body mass as the covariate and Kramer–Tukey $q$-tests to determine whether overall *A. keyserlingi* web architecture differed between feeding treatments. To identify plasticity in web specific parameters according to feeding treatments I used a series of individual one-factor ANOVAs. I used Kolmogorov–Smirnov tests to ensure the data were normally distributed, Levene's tests to ensure the variances were homogeneous, and parallelism tests to ensure all slopes were

homogeneous. I performed either log or probit transformations on any data that failed the tests.

## RESULTS

The overall architecture of *A. keyserlingi* orb webs was not significantly altered by feeding on cockroaches or crickets (MANCOVA, Wilk's $\lambda_{8,22}$=0.696; $P$=0.17) as most architectural parameters were unaffected by diet (Fig. 1A,B,D); the exception being spiders fed crickets built, on average, longer decorations (Fig. 1C). However, when the feeding regime was altered so that the spiders were fed an equivalent biomass of crickets and cockroaches thereby altering the frequency of cockroach feeding, overall orb-web architecture differed between feeding regimes (MANCOVA, Wilk's $\lambda_{16,80}$=0.164; $P$<0.001). This was attributable to the spiders fed cockroaches every four days building: (1) webs with larger capture areas than spiders fed either cockroaches every two days or crickets every two days (Fig. 2A), (2) webs with greater mesh sizes than spiders fed cockroaches every two days or crickets every two days (Fig. 2B), and (3) webs with fewer decorations than those of spiders fed cockroaches every two days but equivalent to those of spiders fed crickets every two days (Fig. 2C). Only the number of radii in webs did not significantly differ under this feeding regime (Fig. 2D). In the experiment where spiders were fed either adult crickets or juvenile crickets (Fig. 3) I found that, while overall web architectures were unaffected (MANCOVA, Wilk's $\lambda_{8,22}$=0.670; $P$=0.14), spiders feeding on juvenile crickets built webs with significantly greater mesh sizes than those feeding on adult crickets (Fig. 3B).

## DISCUSSION

Prey size and/or availability have generally been considered the proximal cues inducing web architectural plasticity in orb web spiders (Venner and Casas, 2005; Blackledge and Zevenberg, 2006). Nevertheless, strict control over particular prey parameters

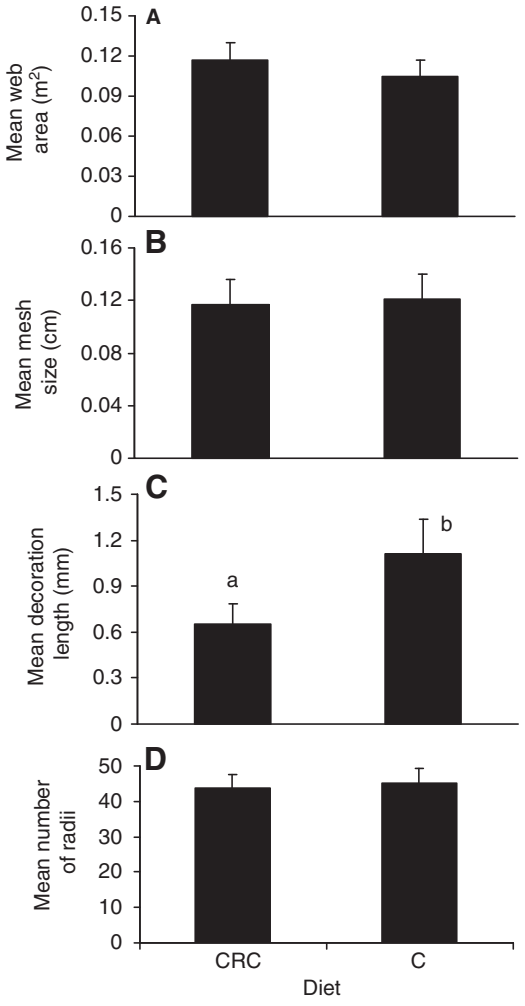


Fig. 1. The architectural parameters: web area (A), mesh size (B), decoration length (C) and number of radii (D) of *Argiope keyserlingi* webs in response to being fed either cockroaches (CR) or crickets (C). Overall web architecture did not differ according to feeding regime (Wilk's $\lambda_{8,22}$=0.696; $P$=0.17). Results of Kramer–Tukey $q$-tests are shown with parameters significantly differing (at $P \leq 0.05$) identified (b>a). Parameters: L, CR=C; DMI, CR>C; ED, CR>C; FF, CR=C. L, prey length; DMI, ingested dry mass; ED, energy density (kJ g$^{-1}$); FF, feeding frequency.

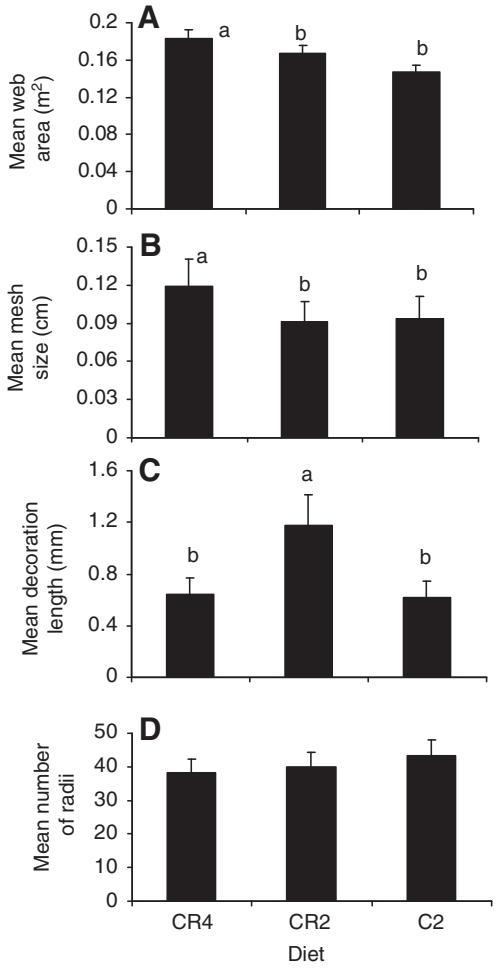


Fig. 2. The architectural parameters: web area (A), mesh size (B), decoration length (C) and number of radii (D) of *Argiope keyserlingi* webs in response to being fed either cockroaches every four days (CR4), cockroaches every two days (CR2) or crickets every two days (C2). Overall web architecture differed according to feeding regime (Wilk's $\lambda_{16,80}$=0.164; $P$<0.001). Results of Kramer–Tukey $q$-tests are shown with parameters significantly differing (at $P \leq 0.05$) identified (a>b). Parameters: L, CR4=CR2=C2; DMI, CR4=C2<CR2; ED, CR4=CR2>C2; FF, CR4<CR2=C2. L, prey length; DMI, ingested dry mass; ED, energy density (kJ g$^{-1}$); FF, feeding frequency.

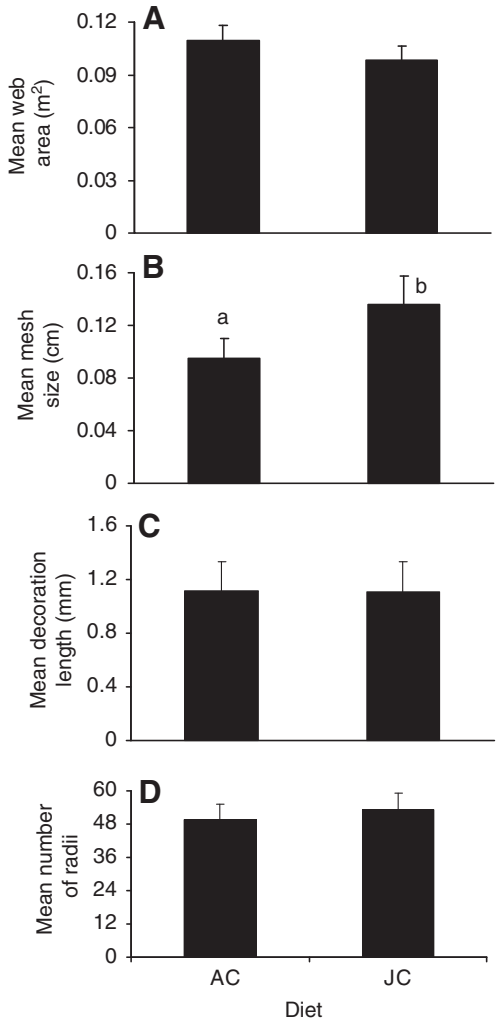


Fig. 3. The architectural parameters: web area (A), mesh size (B), decoration length (C) and number of radii (D) of *Argiope keyserlingi* webs in response to being fed either adult crickets (AC) or juvenile crickets (JC). Overall web architecture did not differ according to feeding regime (Wilk's $\lambda_{8,22}$=0.670; $P$=0.14). Results of Kramer–Tukey $q$-tests are shown with parameters significantly differing (at $P \leq 0.05$) identified (b>a). Parameters: L, AC>JC; DMI, AC>JC; ED, AC=JC; FF, AC=JC. L, prey length; DMI, ingested dry mass; ED, energy density (kJ g$^{-1}$); FF, feeding frequency.

is difficult and, consequently, previous studies have failed to control for prey type, size or nutrients. By controlling prey protein concentration while experimentally varying energy density, the size and mass of prey consumed and feeding frequency in *A. keyserlingi*, I identified feeding frequency as a prey-induced parameter influencing overall web architectural plasticity in this orb web spider, while individual web architectural parameters are responsive to other prey parameters.

*Argiope keyserlingi* alters its decoration investment according to ingested dry mass, web area according to the frequency of feeding, and mesh size according to feeding frequency and prey length. I did not find any prey-mediated factor to influence the number of radii invested in webs. *Zygiella x-notata* increases its radii investment when feeding on protein-enriched prey (Mayntz et al., 2009) but this response was not found for *A. keyserlingi* (Blamires et al., 2009). Flexibility in radii investment may thus be species specific and not mediated by any clearly identifiable cues. As the behavior associated with web building differs between *Argiope* and *Zygiella*, their responses to prey stimuli probably also differ. Radii investment in *A. keyserlingi* may be more responsive to factors such as spider body mass or wind speed (Vollrath et al., 1997) than to any prey parameters.

In the first experiment I found that decoration length was longer in the webs of spiders fed crickets every other day than it was for spiders fed cockroaches every other day; five webs in the cockroach feeding group contained decorations, one of which was fully cruciform, compared with nine webs with decorations, of which six were fully cruciform, in the cricket fed group. However, in the second experiment, decoration length was longer in the webs of spiders fed a cockroach every other day than it was for either spiders fed crickets every other day or cockroaches every four days. The results of the first two experiments, accordingly, yielded contradictory results. Feeding frequency thus cannot explain variations in decoration building in *A. keyserlingi*. Cockroaches are more energy dense than crickets; thus, even when accounting for dry mass, consuming a cockroach every fourth day provides more energy (total kJ) than consuming a cricket every other day. Therefore, variations in the mass of food items consumed (cockroaches having greater digestible dry mass than crickets) or the energy concentration of the food items may explain the web decorating responses in the second experiment, but it does not explain the contrary results found between the first and second experiment. It seems that other, unaccounted factors, e.g. temperature or wind speed variation between the two experiments may have had a significant influence over web decoration plasticity. Perhaps the response is seasonal or an anomaly of using different individuals. Many studies have shown correlations between satiation and decoration building in orb web spiders. Some studies suggest decoration building increases with satiation while others suggest it is reduced (Herberstein et al., 2000b; Seah and Li, 2002). My results suggest that for *A. keyserlingi* either could occur. Blamires et al. suggested that prey protein concentration is responsible for increasing decoration building in *A. keyserlingi* (Blamires et al., 2009). By controlling protein concentration, however, I show here that additional factors are driving decoration investment in *A. keyserlingi*. Future studies should aim to differentiate between the influential and coincidental factors influencing decoration building in *Argiope* spp. This may also provide useful insights into decoration function.

As spiders that were fed a cockroach every fourth day built webs of larger area than those fed a cockroach or a cricket every other day, feeding frequency had an influence on web area; those feeding less frequently built larger webs. Neither prey energy concentration nor total energy intake influenced web area because spiders fed a cricket every other day built webs of similar area to those fed a cockroach every other day. Web area and mesh size may be traded off against each other in spider orb webs, as only so much silk can be invested (Craig, 2003). The spider must therefore decide whether to invest its silk into webs that capture heavier prey, hence reducing mesh size, or more prey, hence increasing web area (Miyashita, 1997). I found both an increased web surface area and increased mesh size in spiders fed a cockroach every fourth day. Thus, *A. keyserlingi* builds webs that trade-off catching more prey with catching heavier prey. The spiders fed a cockroach every fourth day are therefore responding to the reduced rate of feeding by building larger webs in order to intercept more prey.

Both feeding less frequently (on a cockroach every fourth day as opposed to every other day) and on smaller prey (on juvenile

crickets as opposed to adult crickets) induced *A. keyserlingi* to build webs with increased mesh sizes. As mentioned, the influence of feeding frequency may be attributed to a trade-off between building larger webs and webs with finer mesh. I also found that *A. keyserlingi* builds larger webs when fed less frequently. Webs of finer mesh are more effective at intercepting longer and heavier prey (Venner and Casas, 2005; Blackledge and Zevenberg, 2006) so the influence of prey length and mass on mesh size may be attributed to the spiders building webs that intercept the prey on which it is predominantly feeding. Mesh size was influenced by feeding on either adult or juvenile crickets (which do not differ in nutrient concentrations) but not by feeding on a cricket every other day or a cockroach every other day (which differ in nutrient concentrations but not length). Mesh size in *A. keyserlingi* therefore is altered in response to prey size and not to prey nutrient concentration. Such a response could initiate a positivefeedback cycle; building finer meshed webs would result in larger prey being caught and/or greater prey retention, which feeds back on spider physiological state, which influences web plasticity.

Many of the architectural parameters of spider orb webs are highly plastic, and orb web spiders appear capable of exhibiting adaptive plasticity in response to immediate environmental costs such as alterations in food availability. Nonetheless, individual web architectural parameters can vary in response to changes in food energy concentration or mass without much overall shift in architecture. This is primarily because a web is the principal foraging tool available to the spider so any alteration is done under careful consideration of the costs and benefits. Orb-web architecture appears to be dichotomously plastic [i.e. appears as one of two forms (Whitman and Agrawal 2009)], and switching phenotype is induced by large-scale alterations in feeding frequency or prey retention (Nakata, 2007; Nakata, 2009). Orb-web architecture, accordingly, impacts on, and is responsive to, the physiology of the spider and the spider's niche breadth (Lehmann, 2008). It applies selective pressure on the spider and itself. Under natural conditions other feedback mechanisms, such as predators and environmental variations, may additionally interfere with or exacerbate the influences of the prey-induced plastic mechanisms. These mechanisms should be investigated further and included in future models of orb spider web architectural plasticity and models of plasticity in extended phenotypes. The implications of this study are that if the experimental manipulations performed herein account for a large part of the dietary and stimulatory variability that a spider typically encounters, then it may be also possible to estimate the genetic influence over orb-web architectural parameters.

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