

Prey protein influences growth and decoration building in the orb web spider *Argiope keyserlingi*

SEAN J. BLAMIREs, DIETER F. HOCHULI and MICHAEL B. THOMPSON School of Biological Science, University of Sydney, Sydney, Australia

Abstract. 1. Protein is important for a foraging animal to consume, as it promotes growth and enhances survival, particularly in web-building spiders, which need to invest considerable protein into web building and may trade-off growth for web investment.

2. The influence of dietary protein uptake on growth and web investment was tested in the orb web spider *Argiope keyserlingi*, by feeding them flies reared on three different media: (1) high protein, (2) low protein, and (3) standard (control) media. There was a negative correlation between protein and energy content of the flies across treatments; flies reared on the high protein media had the highest protein, but lowest energy, while flies reared on the low protein media had the lowest protein but highest energy.

3. It was found that silk investment and web architecture in *A. keyserlingi* was not affected by diet. Growth and decoration building were both enhanced when spiders were fed a high protein diet.

4. It was concluded that protein intake, rather than energy, influenced both growth and decoration building because: (1) protein intake enhances growth in other animals, (2) protein is essential for silk synthesis, especially aciniform silk, and (3) protein is a limiting factor actively sought by foraging animals in natural environments.

Key words. *Argiope*, body size, decorations, energy uptake, nutrient assimilation, orb web spider, protein uptake, radial threads, silk, spiral threads.

Introduction

As foraging influences fitness, animals regularly assess the profitability of their foraging strategy. Recent models suggest that animals that ingest the most food do not necessarily reap the greatest fitness benefits, rather the quality and balance of nutrients ingested is a better determinant of foraging profitability (Simpson & Raubenheimer, 1993; Bowen *et al.*, 1995; Mayntz *et al.*, 2005). Protein intake, for instance, has been strongly tied to growth in fish, insects, and spiders (Bowen *et al.*, 1995; Mayntz *et al.*, 2003; Lee, 2007), suggesting that selectively foraging for high protein food could result in substantial fitness benefits (Simpson & Raubenheimer, 1993; Bowen *et al.*, 1995; Lee, 2007).

Web building (araneomorph) spiders make excellent study organisms for testing foraging models, as their principal foraging cost; silk manufacture and web construction, can be readily observed and quantified (Sherman, 1994). Also, building different

webs has differential effects on fitness (Sherman, 1994; Li, 2005; Venner & Casas, 2005). Since they make their webs from biomaterials, araneomorph spiders are potentially subject to a nutritional deficiency and face the dilemma of whether to invest limited nutrients into growth and bodily functions or into web building (Craig *et al.*, 1999, 2000; Higgins & Rankin, 1999). Silk is a protein polymer with amino acid sequences and ratios that differ from other biomaterials (Craig *et al.*, 1999, 2000). As such, the availability of amino acids and protein, place limits on silk synthesis (Higgins & Rankin, 1999; Craig *et al.*, 2000). Many araneomorphs can partially overcome this limitation by re-ingesting their webs (Crews & Opell, 2006). Nonetheless, the type, quantity, and quality of silks produced vary according to diet (Higgins & Rankin, 1999; Craig *et al.*, 2000; Mayntz *et al.*, 2003). Since fitness parameters such as growth and survivorship are correlated with diet quality (Bilde & Toft, 1998; Mayntz *et al.*, 2003), silk synthesis may be additionally traded off with fitness parameters.

We performed laboratory experiments in which we manipulated the dietary protein availability for the orb web building spider *Argiope keyserlingi*. Our aims were to: (1) determine whether dietary protein or energy influences growth and silk investment,

Correspondence: Michael B. Thompson, School of Biological Sciences, Heydon-Laurence Building (AO8), University of Sydney, NSW 2006, Australia. E-mail: mike.Thompson@bio.usyd.edu.au

and (2) identify whether a trade-off between growth and silk manufacture exists. We chose *A. keyserlingi* because it builds conspicuous silk decorations derived from aciniform silk (Herberstein *et al.*, 2000; Bruce *et al.*, 2001; Blamires *et al.*, 2007a,b, 2008), which are considered profitable, in terms of prey attraction, but costly in terms of predator attraction (Bruce *et al.*, 2001; Bruce & Herberstein, 2006; Blamires *et al.*, 2008). Spiders that build decorations do so more often when satiated (Seah & Li, 2002; Tso, 2004; Bruce & Herberstein, 2005), so there appears to be an energetic trade-off associated with decoration building.

Methods

Prey types

It is unclear if spider responses to diet are a product of prey nutrient quality or are associated with feeding on different prey types, as most studies have not adequately controlled for prey type, [Mayntz & Toft (2001) and Mayntz *et al.* (2003) are exceptions]. Larval nutritional intake influences the assimilation of protein in tissue and eggs in flies (Diptera) (Reinecke, 1985). We, accordingly, controlled for prey type by exposing groups of larval houseflies (*Musca domestica*) to media of different protein constituency.

We placed *M. domestica* pupae in one of five 250 × 150 × 125 mm cotton mesh enclosures containing a water vial and Petri dish of 10 g of standard media (yeast, Nipagin, Semolina and agar; Reinecke, 1985), supplemented with 10 g of sugar. After 2 weeks, 10 g of a lecithin-based protein (68%) supplement (Reinecke, 1985) was added to the media to promote oviposition. Larvae of the second generation were placed into one of three enclosures: one in media supplemented with sugar ('low protein'), another in media supplemented with the lecithin-based protein ('high protein'), and another in standard media ('control'). The flies in each treatment were fed continuously from larvae through to adulthood. Flies were randomly selected once per week to be fed to spiders. A sample of flies was also taken once per week and sacrificed by exposure to carbon dioxide and freezing. To ensure all flies that were fed to spiders were fresh adults, any full grown flies not used within 2 weeks were sacrificed and a new allotment of larvae introduced into the enclosures.

All flies that were sacrificed were weighed to the nearest mg on an electronic balance (CP224, Sartorius, Gottingen, Germany), dried at 60°C for 24 h, re-weighed to ascertain their percentage water, and ground to <1 mm particles using a mortar and pestle. A quarter of the particles by dry mass were compressed into 10–25 mg pellets ($n = 33, 30$ and 31 for flies from the low protein, high protein, and control media respectively). Energy concentration was then determined by combusting the pellets using a microbomb calorimeter (Gentry, Aiken, South Carolina) that was calibrated using benzoic acid. Any ash remaining in the calorimeter after combustion was weighed, and accounted for in the calculation of energy concentration. The remaining 75% of the particles by dry mass were divided into 100 mg samples ($n = 19, 17,$ and 18 for flies from the low protein, high protein, and control media respectively). These were digested in 5 ml sulphuric acid at 400°C for 2 h to decompose the proteins.

A selenium buffer (Kjel-tabs®, Trecator, Honagas, Sweden) was used to prevent the acid boiling. Upon digestion, nitrogen concentration was determined for each sample using a Kjeltec direct distillation unit (2300, Trecator, Hoganas, Sweden). Percentage protein was estimated from tissue nitrogen concentration by a conversion factor ($6.25 \times \% \text{ nitrogen}$).

General procedures

We caught 36 immature female *A. keyserlingi*, of approximately equal head–cephalothorax length (7.2 ± 0.18 mm) and mass (0.14 ± 0.02 g), within the grounds of the University of Sydney, Camperdown-Darlington Campus, and housed them separately in 300 × 300 × 50 mm Perspex frames. Each spider was fed two *M. domestica* per week and *Drosophila* spp. *ad libitum*. After 2 weeks the spiders were transferred to 500 × 500 × 150 mm Perspex frames, fed two *M. domestica*, and left for 6 days to build a web. We then removed the spiders from their webs and measured their fresh body mass and their head–cephalothorax length to ensure the mass ($+0.11 \pm 0.01$ g) and length ($+0.12 \pm 0.02$ mm) of all spiders were similar.

Each spider was randomly assigned to one of three feeding regimes: 'high protein', 'low protein', or 'control' ($n = 12$ for each regime). Spiders assigned the 'high protein' regime were fed flies reared on high protein media, spiders in the 'low protein' regime were fed flies reared on low protein media, and the 'control' regime were fed flies reared on standard media. All spiders were fed twice weekly. The flies were anaesthetised using carbon dioxide to ensure they did not break free of the web and were always placed in the upper-right corner of the web. We observed each spider feeding for 1 h, noting whether the fly was accepted or rejected. All flies were weighed to the nearest milligram and measured to the nearest mm before being fed to spiders. A finite amount of undigested fly carcass was always left in the web post-consumption by the spiders. We collected these and dried and weighed them to determine the dry mass consumed. Once per week the spiders were removed from their webs, weighed and their head–cephalothorax length measured, from which a body size index was determined by principal component analyses using change in weight and head–cephalothorax length as components (Blamires *et al.*, 2007b). The webs were sprayed with water to render them visible and the number of spiral and radial threads were counted and the web capture area and mesh height of the capture spirals were estimated using calculations described by Blackledge and Gillespie (2002) and Herberstein and Tso (2000) respectively. We counted the number of decoration arms and measured the length of each arm. The webs were allowed to dry before being disassembled. The entire web was then dried, compressed into a pellet, weighed to the nearest 0.01 mg, and energy density determined by bomb calorimetry. The process was repeated over four consecutive weeks.

Analyses

We ascertained if the length, mass, dry mass consumed, water content, and energy and protein concentration differed between

flies reared on the high protein, low protein and control media by one-factor (media) analyses of variance (ANOVA). We used Kolmogorov–Smirnov and Levene’s tests to test that the data were normally distributed and variances were homogeneous, log-transforming data where appropriate. Tukey’s Honest Significant Difference analyses were carried out to determine the differing means whenever significance was detected. We determined the relationship between protein and energy concentration in fly tissue samples using correlation analysis. We compared the prey acceptance rates (scoring acceptance as 1 and rejection as 0) of spiders on each of the feeding regimes by a χ^2 log-likelihood test.

As the consumed dry mass of ‘low protein’ flies was significantly different from that of the ‘high protein’ and ‘control’ flies (Table 1), we determined the influence of feeding regime on web parameters (number of radial threads, decoration length, web area, mesh height, and silk investment) by one-factor (feeding regime) repeated measures analyses of covariance (ANCOVA), with dry mass consumed as the covariate. The mean change in body size for spiders on the three feeding regimes was also compared by a one-factor ANCOVA. Significant effects were detected by Tukey’s tests and these were subject to multiple correlation analysis, whereupon we calculated partial correlation coefficients to determine the directly- and indirectly-acting variables over the identified responses using best-fit causal models (Loehlin, 1992). We constructed causal pathways; identifying the model best fitting the data by Akaike information criterion (AIC) scores (Burnham & Anderson, 1998).

Results

Of the variables we measured (Table 1), the dry mass consumed (low protein > high protein = control), energy density (low protein > control > high protein), and % protein (low protein > control > high protein) differed significantly between fly treatments. The differences in energy and protein concentration were brought about because energy density and % protein in the dried fly samples were negatively correlated ($R^2 = 0.43$; $P = 0.04$; Fig. 1). Frequencies of prey acceptance did not differ between spiders on the ‘high protein’, ‘low protein’, and ‘control’ feeding regimes ($\chi^2 = 0.67$; d.f. = 2; $P = 0.41$).

The number of radial threads, web area, and mesh height were not influenced by spider feeding regimes (Table 2).

However, the decorations in the webs of spiders fed low protein flies were shorter than the decorations of both those fed the high protein and control flies (Table 2). Additionally, spiders fed flies reared on the high protein media grew significantly more than those fed flies reared on either the low protein or control media (Table 2). We thus constructed three possible causal pathways: (1) diet directly influences both decoration building and spider growth; (2) diet directly influences spider growth and indirectly influences decoration building via growth; and (3) diet directly influences decoration building and indirectly influencing growth via decoration building. For growth (determined by body size indices) the model best fitting the data was one predicting diet directly influencing growth, with decoration building acting indirectly (Table 3). For decoration building, the model best fitting the data was one predicting a direct influence of diet but an indirect influence of growth (Table 3). The most likely causal model for *A. keyserlingi*, therefore, is diet directly influencing both growth and decoration building.

Discussion

Both decoration building and growth are positively correlated with protein intake in *A. keyserlingi*. However, as the amount of protein and energy in their food was negatively correlated (Fig. 1), it is not clear whether it is protein or energy mediating these responses. As protein is essential for somatic growth and silk synthesis (Craig *et al.*, 1999; Higgins & Rankin, 1999) but is a limiting nutrient for most organisms (White, 1993; Mayntz *et al.*, 2005; Simpson *et al.*, 2006), we conclude that protein is the likely mediator. Additionally, spiders deprived of protein will forage specifically for high protein foods, probably to achieve a specific protein intake target (Mayntz *et al.*, 2005). Many animals forage to obtain specified protein intake targets and are willing to consume excess food in order to achieve this target when they are feeding on low protein food (Simpson & Raubenheimer, 1993). We found that *A. keyserlingi* consumed a greater amount, by dry mass, of low protein and control flies than high protein flies, suggesting that they are over-eating prey of lower protein concentration in an attempt to attain a protein intake target.

Argiope keyserlingi grows significantly more when on a high protein diet than on a low protein or standard diet, when growth was in fact negative. This is not surprising, because the promotion

Table 1. Mean (per item) \pm 1 SE length, dry mass consumed, % water, energy (kJ g⁻¹) and protein (%) of sacrificed flies reared on low protein, high protein or control (standard) media, showing the results of one-way analyses of variance *F*-scores (d.f. = 1, 41).

	Media			<i>F</i> -scores
	Low protein	High protein	Control	
Length (mm)	5.15 \pm 0.27	5.21 \pm 0.34	5.16 \pm 0.42	0.81
Dry mass consumed (g)	0.16 \pm 0.19	0.10 \pm 0.09*	0.16 \pm 0.12	2.34
% Water	76.03 \pm 1.60	76.58 \pm 2.01	76.33 \pm 1.32	0.22
Energy (kJ g ⁻¹)	24.33 \pm 1.39*	22.44 \pm 1.42	23.31 \pm 0.30	2.47*
% Protein	43.55 \pm 5.35**	66.94 \pm 4.27**	54.80 \pm 2.24	59.23**

*Indicating a significant difference from the control at $P < 0.05$.

**Indicating a significant difference from the control at $P < 0.001$ ($n = 33, 30$, and 31 for flies from the low protein, high protein, and control media respectively).

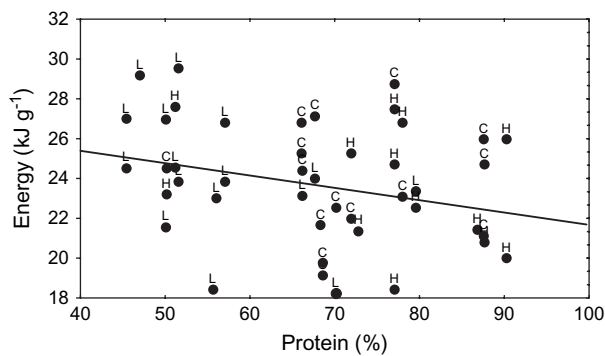


Fig. 1. Relationship between protein (%) and energy (kJ g^{-1}) in laboratory reared, sacrificed house flies, *Musca domestica*. Each point represents samples for which both % protein and energy density were determined. H, fly samples reared on high protein media ('high protein' flies); L, fly samples reared on low protein ('low protein' flies); and C, fly samples reared on standard media ('control flies'). Each sample consisted of 20+ dried adult flies of varying ages.

of growth by a high protein intake has been demonstrated in many animals (Bowen *et al.*, 1995; Ojeda-Avila *et al.*, 2003; Sandland & Minchella, 2003; Merckx-Jacques *et al.*, 2008). Under nutrient limitation, however, energy uptake becomes strongly correlated with growth (Dadd, 1985; Riechert & Harp, 1987). Spiders, however, may continue to grow under prolonged food shortages (Nakamura, 1987; Riechert & Harp, 1987; Bilde & Toft, 1998). As *A. keyserlingi* did not alter its energetic silk investment when on a low energy diet, it seems unlikely that *A. keyserlingi* was under energetic stress at any time during our study. The growth we observed in spiders fed a high protein diet, therefore, is likely to be induced by protein intake.

The web architectural parameters – number of radial threads, web capture area, mesh height, and number of sticky spirals – were not affected by the feeding regime, indicating that web architecture is strongly conserved in *A. keyserlingi*. Factors other than diet, e.g. ontogeny, predators, damage, prey size and habitat structure, are probably more influential over web architecture in this species (Herberstein & Heiling, 1998; Herberstein *et al.*, 1998, 2000; Champion de Crespigny *et al.*, 2001; Blamires *et al.*, 2007a,b). As we did not find any dietary influence over

the energetic expenditure of silk, *A. keyserlingi* is either: (1) expending a finite amount of energy on silk synthesis and web building regardless of the cost, or (2) reducing its web building activity level to conserve energy when on a low energy diet (Prestwich, 1977). In either event, they are avoiding an energetic trade-off between web building and growth.

Argiope keyserlingi reduce decoration building when protein intake is low, but the overall energetic investment in webs is not affected by diet. This suggests that factors restricting decoration building are not restricting the building of webs in general, and *A. keyserlingi* does not compensate for reduced decoration building by investing in other silks (e.g. laying down thicker radial or frame threads) when on a low protein diet. Eating more prey enhances decoration building in other *Argiope* species (Herberstein *et al.*, 2000; Tso, 2004), and the availability of dietary protein influences decoration building in *A. keyserlingi*. Dietary protein intake thus appears a key limiting factor controlling either the synthesis of aciniform gland silks or the ability of *A. keyserlingi* to build decorations. The amino acid constituency of aciniform gland silks is different than that of other spider silks (Hayashi *et al.*, 2004; Vasanthavada *et al.*, 2007), thus the synthesis of aciniform silk may be limited by dietary amino acids.

We have previously found that the temporal patterns of decoration building and antipredator behaviour are influenced by body size in *A. keyserlingi* (Blamires *et al.*, 2007a). Here we show that body size and decorations are both influenced by protein intake. Antipredator behaviours may thus change temporally according to protein uptake. Decorations attract prey (Herberstein, 2000; Bruce *et al.*, 2001; Bruce & Herberstein, 2005; Blamires *et al.*, 2008), so spiders feeding on high protein prey will build more decorations and, consequently, eat more prey, providing protein for more decoration building, and promoting a positive feedback cycle (Li, 2005).

While other studies have shown that a high protein diet promotes growth in araneomorph spiders (Mayntz & Toft, 2001; Mayntz *et al.*, 2003), this is the first study to demonstrate that a high protein diet also enhances decoration building in an orb web building spider. Although there was no energetic trade-off between web building and growth, *A. keyserlingi* builds more decorations and grows more when fed high protein prey compared to when fed low protein prey. Whether *A. keyserlingi*

Table 2. Mean (per item) \pm 1 SE body size indices, and web parameters (number of radial threads, decoration length, web area, mesh height, and silk investment) for *Argiope keyserlingi* on three feeding regimes (low protein flies, high protein flies, or control flies; $n = 12$ for each regime). One-way repeated measures analyses of covariance (with dry mass of consumed the covariate) F -scores (d.f. = 1, 22) are shown.

	Feeding regime			F -scores
	Low protein	High protein	Control	
Spider body size index	$0.47 \pm 0.13^{**}$	-0.69 ± 0.44	-0.58 ± 0.19	80.39
Radial threads	43.58 ± 4.79	41.06 ± 2.68	42.90 ± 1.79	1.10
Decoration length (mm)	$0.53 \pm 0.22^*$	1.03 ± 0.26	1.01 ± 0.14	7.06
Web area (m^2)	0.17 ± 0.01	0.14 ± 0.01	0.15 ± 0.02	0.57
Mesh height (mm)	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	0.19
Silk investment (kJ g^{-1})	25.19 ± 0.87	26.66 ± 0.69	25.92 ± 0.91	1.33

*Indicates significant difference from the control at $P < 0.01$.

**Indicates a significant difference from the control at $P < 0.001$.

Table 3. Direct and indirect effects partial correlation coefficients between the response variables Body size and Decorations, and the respective predictor variables (Diet and Decorations for Body size, and Diet and Body size for Decorations).

Response variables	Predictor variables		Direct effects	Indirect effects	AIC score
Body size	Diet	via Decorations	-0.458	0.052	0.486*
	Decorations	via Diet	0.048	-0.443	0.927
Decorations	Diet	via Body size	-0.290	0.049	0.377*
	Body size	via Diet	0.055	0.055	1.433

*Denotes the best-fit model according to Akaike Information Criterion (AIC) scores.

forages specifically for protein or attempts to attain a protein target requires further investigation, but our results suggest that they do. Any further studies should compare the role of protein against other nutrients in promoting growth or silk investment. For example salts, whose availability is strongly tied to protein (Edney, 1977; Raubenheimer & Simpson, 1999; Simpson *et al.*, 2006), may also play a role in growth and silk synthesis. Additionally, the amino acid constituency of the food may be more crucial than protein *per se* in the production of certain silks (Craig *et al.*, 2000; Tso *et al.*, 2005) and future studies should investigate the role of limited amino acids on araneomorph spider foraging strategies.

Acknowledgements

The project was funded by a University of Sydney Postgraduate scholarship awarded to SJB. We thank Naz Soran for assistance setting up and running the Kjeltec Direct Distillation Unit and Xiumei Liang for supplying *Drosophila* and fly media. Todd Blackledge, Mark Elgar, Mark Hassall, Mariella Herberstein, Daiqin Li, Stephen Simpson, and David Mayntz provided feedback on drafts of the paper. All insects were purchased from Pisces Enterprises (Brisbane).

References

Bilde, T. & Toft, S. (1998) Quantifying food limitation of arthropod predators in the field. *Oecologia*, **115**, 54–58.

Blackledge, T.A. & Gillespie, R.G. (2002) Estimation of capture areas of spider orb webs in relation to asymmetry. *Journal of Arachnology*, **30**, 70–77.

Blamires, S.J., Hochuli, D.F. & Thompson, M.B. (2007a) Does decoration building influence antipredator responses in an orb-web spider (*Argiope keyserlingi*) in its natural habitat? *Australian Journal of Zoology*, **55**, 1–7.

Blamires, S.J., Hochuli, D.F. & Thompson, M.B. (2008) Why cross the web: decoration spectral properties and prey capture in an orb spider (*Argiope keyserlingi*) web. *Biological Journal of the Linnean Society*, **94**, 221–229.

Blamires, S.J., Thompson, M.B. & Hochuli, D.F. (2007b) Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Araniidae): do they compromise foraging success for predator avoidance? *Austral Ecology*, **32**, 551–563.

Bowen, S.H., Lutz, E.V. & Ahlgren, M.O. (1995) Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology*, **76**, 899–907.

Bruce, M.J. & Herberstein, M.E. (2005) Web decoration polymorphism in *Argiope* Audouin, 1826 (Araneidae) spiders: ontogenetic and interspecific variation. *Journal of Natural History*, **39**, 3833–3845.

Bruce, M.J. & Herberstein, M.E. (2006) The influence of predator cues on orb-web spider foraging behaviour. *Ethology, Ecology and Evolution*, **18**, 91–98.

Bruce, M.J., Herberstein, M.E. & Elgar, M.A. (2001) Signal conflict between prey and predator attraction. *Journal of Evolutionary Biology*, **14**, 786–794.

Burnham, K.P. & Anderson, D.R. (1998) *Model selection and inference: A practical information-theoretic approach*. Springer, New York.

Champion de Crespigny, F.E., Herberstein, M.E. & Elgar, M.A. (2001) The effect of predator–prey distance and prey profitability on the attack behaviour of the orb-web spider *Argiope keyserlingi* (Araneidae). *Australian Journal of Zoology*, **49**, 213–221.

Craig, C.L., Hsu, M., Kaplan, D. & Pierce, N.E. (1999) A comparison of the composition of silk proteins produced by spiders and insects. *International Journal of Macromolecules*, **24**, 109–118.

Craig, C.L., Riekel, C., Herberstein, M.E., Weber, R.S., Kaplan, D. & Pierce, N.E. (2000) Evidence for diet effects on the composition of silk proteins produced by spiders. *Molecular Biology and Evolution*, **17**, 1904–1913.

Crews, S.C. & Opell, B.D. (2006) The features of capture threads and orb-webs produced by unfed *Cyclosa turbinata* (Araneae: Araneidae). *Journal of Arachnology*, **34**, 427–434.

Dadd, R.H. (1985) Nutrition: organisms. *Comprehensive Insect Physiology, Biochemistry and Pharmacology Volume 4, Regulation: Digestion, Nutrition and Excretion* (ed. by G. A. Kerkut and L. I. Gilber), pp. 313–390. Pergamon, Oxford.

Edney, E.B. (1977) *Water Balance in Land Arthropods*. Springer, Berlin.

Hayashi, C.Y., Blackledge, T.A. & Lewis, R.V. (2004) Molecular and mechanical characterization of aciniform silk: uniformity of iterated sequence modules in a novel member of the spider silk fibroin gene family. *Molecular Biology and Evolution*, **21**, 1950–1959.

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

Herberstein, M.E., Abernathy, K.E., Backhouse, K., Bradford, H., Champion de Crespigny, F.E., P. Luckcock, R. *et al.* (1998) The effect of feeding history on prey capture behaviour in the orb web spider *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Ethology*, **104**, 565–571.

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

Herberstein, M.E. & Heiling, A.M. (1998) Does mesh height influence prey length in orb-web spiders (Araneae)? *European Journal of Entomology*, **95**, 367–371.

- Herberstein, M.E. & Tso, I.-M. (2000) Evaluation of formulae to estimate the capture area and mesh height of orb webs (Aranoidea, Araneae). *Journal of Arachnology*, **28**, 180–184.
- Higgins, L.E. & Rankin, M.A. (1999) Nutritional requirements for web synthesis in the tetragnathid spider *Nephila clavipes*. *Physiological Entomology*, **24**, 263–270.
- Lee, K.-P. (2007) The interactive effects of protein quality and macronutrient imbalance on nutrient balancing in an insect herbivore. *Journal of Experimental Biology*, **210**, 3236–3244.
- Li, D. (2005) Spiders that decorate their webs at higher frequency intercept more prey and grow faster. *Proceeding of the Royal Society of London Series B*, **272**, 1753–1757.
- Loehlin, J.C. (1992) *Latent Variable Models: An Introduction to Factor, Path and Structural Analysis*. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S. & Simpson, S.J. (2005) Nutrient-specific foraging in invertebrate predators. *Science*, **307**, 111–113.
- Mayntz, D. & Toft, S. (2001) Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia*, **127**, 207–213.
- Mayntz, D., Toft, S. & Vollrath, F. (2003) Effects of prey quality and availability on the life history of a trap-building predator. *Oikos*, **101**, 631–638.
- Merkx-Jacques, M., Despland, E. & Bede, J.C. (2008) Nutrient utilization by caterpillars of the generalist beet armyworm, *Spodoptera exigua*. *Physiological Entomology*, **33**, 51–61.
- Nakamura, K. (1987) Hunger and starvation. *Ecophysiology of Spiders* (ed. by W. Nentwig), pp. 287–295. Springer, Berlin.
- Ojeda-Avila, T., Woods, H.A. & Raguso, R.A. (2003) Effects of dietary variation on growth, composition, and maturation of *Manduca sexta* (Sphingidae: Lepidoptera). *Journal of Insect Physiology*, **49**, 293–306.
- Prestwich, K.N. (1977) The energetics of web-building in spiders. *Comparative Physiology and Biochemistry*, **57A**, 321–326.
- Raubenheimer, D. & Simpson, S.J. (1999) Integrating nutrition: a geometrical approach. *Entomologia Experimentalis et Applicata*, **91**, 67–82.
- Reinecke, J.P. (1985) Nutrition: artificial diets. *Comprehensive Insect Physiology, Biochemistry and Pharmacology, Volume 4, Regulation: Digestion, Nutrition and Excretion* (ed. by G. A. Kerkut and L. I. Gilbert), pp. 391–419. Pergamon, Oxford.
- Riechert, S.E. & Harp, J.M. (1987) Nutritional ecology of spiders. *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates* (ed. by F.J. Slansky and J. R. Rodriguez), pp. 645–672. John Wiley and Son, New York.
- Sandland, G.J. & Minchella, D.J. (2003) Effects of diet and *Echinostoma revolutum* infection on energy allocation patterns in juvenile *Lymnaea elodes* snails. *Oecologia*, **134**, 479–486.
- Seah, W.K. & Li, D. (2002) *Stabilimentum* variations in *Argiope versicolor* (Araneae: Araneidae) from Singapore. *Journal of Zoology*, **258**, 531–540.
- Sherman, P.M. (1994) The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour*, **48**, 19–34.
- Simpson, S.J. & Raubenheimer, D. (1993) A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. *Philosophical Transactions of the Royal Society of London Series B*, **342**, 381–402.
- Simpson, S.J., Sword, G.A., Lorch, P.D. & Couzin, I.D. (2006) Cannibal crickets on a forced march for protein and salt. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 4152–4156.
- Tso, I.-M. (2004) The effect of food and silk reserve manipulation on decoration-building of *Argiope aetheroides*. *Behaviour*, **141**, 603–616.
- Tso, I.-M., Wu, H.-C. & Hwang, I.-R. (2005) Giant wood spider *Nephila pilipes* alters silk protein in response to prey variation. *Journal of Experimental Biology*, **208**, 1053–1061.
- Vasanthavada, K., Hu, X., Falick, A.M., Mattina, A.M.F., Jones, P.R., Yee, R. *et al.* (2007) Aciniform spidroin, a constituent of egg case sacs and wrapping fibers from the black widow spider *Latrodectus hesperus*. *Journal of Biological Chemistry*, **282**, 35088–35097.
- Venner, S. & Casas, J. (2005) Spider webs designed for rare but life-saving catches. *Proceedings of the Royal Society of London Series B*, **272**, 1587–1592.
- White, T.R.C. (1993) *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer, Berlin.

Accepted 18 February 2009

First published online 8 June 2009