

## Foraging strategies and feeding regimes: Web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae)

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### ABSTRACT

The principal foraging cost for web-building spiders is the amount of silk invested in their webs. Spiders in the genus *Argiope* additionally decorate their orb webs with conspicuous UV-white silk bands, called web ‘decorations’ or ‘stabilimenta’, which enhance foraging success by attracting prey to the web. We subjected *Argiope keyserlingi* Karsch to different feeding regimes and measured their foraging response with respect to the size and design of the orb-web, and the number and length of decorative silk bands. Spiders experiencing low prey encounter rates constructed larger webs and incorporated more silk but fewer web decorations than spiders experiencing high prey encounter rates. When the rate of prey encounter was constant, the spiders increased the amount of silk per web but with little change in the number of decorative bands. In contrast, when prey supply was variable, spiders increased the number of decorative silk bands but not the amount of silk invested in the web.

**Keywords:** foraging behaviour, orb web, optimal foraging, spiders, stabilimenta, web decorations, web investment.

### INTRODUCTION

Animals are predicted to balance the costs and benefits of foraging in an adaptive manner (Emlen, 1966; MacArthur and Pianka, 1966) and to make foraging decisions based on their previous experiences, physiological condition, and the distribution and variation of available resources (Stephens and Krebs, 1986; Bateson and Kacelnik, 1997). Consequently, food-deprived animals may invest more energy in foraging to increase the probability of prey capture. In contrast, food-satiated animals may reduce foraging investment by redirecting energy into growth, reproduction or predator avoidance (Abrams, 1991). Animals may also adjust their foraging behaviour in response to the variation in prey availability (Caraco *et al.*, 1980; Caraco, 1981).

Foraging theory and its tests have been largely developed for active foragers that move through the environment searching for food, rather than sit-and-wait foragers that typically invest little energy in prey search (Shafir and Roughgarden, 1998). Web-building spiders are

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an interesting class of sit-and-wait foragers because silk synthesis (Peakall and Witt, 1976; Prestwich, 1977; Opell, 1997) and web construction, the primary costs of their foraging investment (Higgins and Buskirk, 1992), are analogous to the search costs of an active forager. ‘Searching’ by these spiders can be measured accurately by the amount and arrangement of silk (e.g. Vollrath, 1992; Heiling *et al.*, 1998). Relatively little metabolic energy is spent in prey apprehension after the web is constructed (Uetz, 1992).

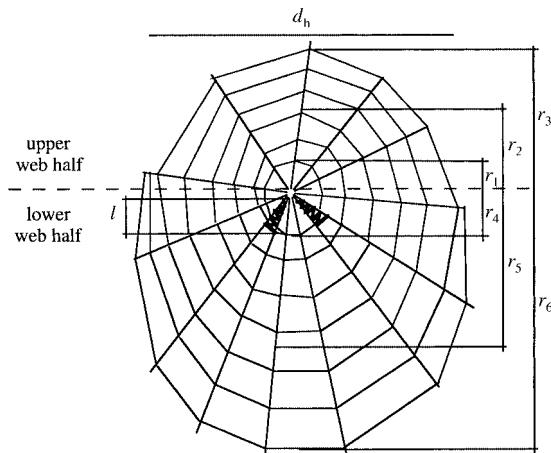
Most studies that have investigated the foraging decisions of web-building spiders have focused on orb-web spiders, which can influence their prey capture success in several ways. First, they may locate their webs in an area of high prey abundance. For example, the nocturnal orb-web spider *Larinoides sclopetarius* builds its webs near artificial lights, which also attract numerous flying insects (Heiling, 1999). Selecting web sites in conspecific aggregations may also ensure high rates of prey capture, when prey supply is low or unpredictable (Uetz, 1988; Craig, 1991; but see Lloyd and Elgar, 1997). In contrast, a spider that constructs a web in a non-productive site is likely to be penalized because of the high costs of the silk invested in web construction (Janetos, 1986; Uetz, 1992) and of moving between sites (Janetos, 1982; Vollrath, 1985; Lubin *et al.*, 1993).

Second, spiders may adjust the size and design of their orb-webs in ways that increase prey capture rates. For example, *Larinoides cornutus* (Sherman, 1994) and *Nephila clavipes* (Higgins and Buskirk, 1992) spun larger orb-webs when insect capture rates dropped, and *Parawixia bistriata* dramatically altered mesh height and web size in response to the presence of unusually large termite prey (Sandoval, 1994). These field studies, while strongly suggestive, could not control for the potentially confounding influences of variation between sites, life-history stage, previous foraging investments and/or weather patterns. Here, we report on a series of laboratory tests designed to eliminate these effects and test more precisely the role of prey encounter rates and variability on spider foraging behaviour.

Following a model developed for web-building spiders (Higgins, 1995) that is consistent with classical foraging models (e.g. Stephens and Krebs, 1986), we expect spiders to decrease investment in foraging as food levels increase. When food levels decrease to an intermediate level, spiders should increase their foraging investment. However, when the reduction of food resources results in weight loss, spiders should reduce their foraging effort to conserve resources (Higgins, 1995; see also Sherman, 1994).

Most studies that have investigated risk-sensitive foraging have examined how animals choose between patches that contain either a constant or a variable food supply (e.g. Kacelnik and Bateson, 1996; Smallwood, 1996). In web-building spiders, the relationship between variation in prey abundance and web site tenacity has previously been examined: the web relocation patterns of *Tetragnatha elongata* may either reflect risk-sensitive foraging strategies (Caraco and Gillespie, 1986; Gillespie and Caraco, 1987) or intense conspecific interactions (Smallwood, 1993). However, few studies have predicted how much energy animals should invest while foraging in patches characterized by constant or variable prey encounter rates. Nevertheless, Caraco and Gillespie (1986) suggested that spiders should change their foraging site more frequently with increasing variation in prey capture rates. Assuming that changing foraging sites is costly and dangerous (e.g. Janetos, 1982; Lubin *et al.*, 1993), we argue that spiders experiencing sporadic prey supply may also increase the resources they invest in web construction.

Spiders in the genus *Argiope* add conspicuous zig-zagged silk bands (see Fig. 1) to their orb-webs called ‘decorations’ (McCook, 1889) or ‘stabilimenta’ (Simon, 1895). The size and arrangement of these decorations (0–4 bands of a diagonal cross, a vertical line, a



**Fig. 1.** Schematic representation of an orb-web (modified from Heiling *et al.*, 1998; Herberstein and Tso, in press) defining the parameters used to calculate the capture thread length, mesh height and web area. The web contains two decorative silk bands in the lower web half ( $l$  = length of silk band).

circular band or doily) can vary greatly, and their function remains controversial. For example, they may act to camouflage the spider by obscuring its outline (Eberhard, 1973; Tolbert, 1975; Edmunds, 1986; Schoener and Spiller, 1992), advertise the web to larger animals, such as birds, which may otherwise damage it (Horton, 1980; Eisner and Nowicki, 1983), or provide a sunshield for the spider (Humphreys, 1992).

Recent experiments suggest that the web decorations spun by *Argiope argentata* (Fabricius) reflect UV-light in patterns similar to those that attract flower foraging insects (Craig and Bernard, 1990), thereby drawing prey to the web site (Craig and Bernard, 1990; Craig, 1994a,b; Craig and Ebert, 1994; Tso, 1996, 1998a; Hauber, 1998). Here, we examine whether the St. Andrew's Cross spider, *Argiope keyserlingi* Karsch, increases the number and size of web decorations during periods of food deprivation.

## METHODS

### Animals and maintenance

Juvenile female *A. keyserlingi* were collected in Brisbane, Queensland, in October 1996 and transported to Melbourne, Victoria. The spiders were individually maintained in small plastic cups ( $13.5 \times 9 \times 9$  cm) in which they constructed webs containing only a few silk threads. This ensured that the energetic expense of silk production and web-building behaviour before the experimental trials were both uniform and minimal. Spiders were provided with water and an *ad libitum* diet of blowflies (*Lucilia cuprina*; Diptera) until they reached maturity. After maturation, the spiders were weighed, their carapace width measured, and they were randomly assigned to a feeding treatment. The spiders were hand-fed flies (mean weight  $\pm$  s.d. =  $0.022 \pm 0.004$  g,  $n = 50$ ) during the experiments to ensure that all prey were ingested, in contrast to similar studies that did not include this control (e.g. Blackledge, in press). In the experimental trials, the spiders were placed into individual, three-dimensional perspex frames ( $40 \times 50 \times 8.5$  cm) where they were able to build a

complete orb-web. A small plastic cup containing five blowflies and covered by mesh was also placed in each frame, since the presence of potential prey stimulates web construction (see Pasquet *et al.*, 1994).

### **Measuring the effects of prey encounter rates**

The first experiment examined the effects of prey encounter rates on web building and decorating behaviour. The spiders were maintained in the cups during the pre-experimental feeding period of 14 days. Spiders assigned to a low-prey diet ( $n = 24$ ) received one fly every 3 days (four flies in total) and spiders assigned to a high-prey diet ( $n = 19$ ) received one fly every day (14 flies in total). After 14 days, all spiders were weighed and transferred to individual frames in which a web could be built. The first web spun by each individual was measured and used as the benchmark for evaluating the effects of the prey treatments. This helped reduce the effects that previous foraging investment (previously constructed webs) or experience may have on web size and design. Although the first web constructed by a spider was sometimes smaller than consecutive webs, this effect is expected to be the same for spiders in both treatments.

### **Measuring the effects of variation in prey encounter rates**

The second experiment examined the effects of prey predictability on spider behaviour. Here, the spiders were maintained in individual frames. In the field, orb-webs spun by *A. keyserlingi* suffer high rates of damage due to wind, rain and prey capture events and, as a result, spiders rebuild them daily. In contrast, webs spun in the laboratory by spiders that are hand-fed are rarely damaged and thus are not renewed regularly. Therefore, daily web construction was ensured by destroying the webs after the spiders were fed and watered. The lateral support threads of each web were uniformly cut, causing the web to collapse into the middle while still being suspended in the frame. Thus, the spider was able to consume the silk and recycle it.

Under conditions of constant food availability, spiders ( $n = 34$ ) were fed two flies every day for 10 days. Under conditions of variable food availability, spiders ( $n = 31$ ) received either no or four flies in a random order (from day 1 to day 10: 4, 0, 4, 4, 0, 4, 0, 4, 0, 0 flies). After 10 treatment days, both groups had received a total of 20 flies. Regardless of whether the spiders built a new web, they were fed according to their treatment and their webs were measured every day. Erratic feeding may affect the efficiency with which spiders digest prey. However, it is unlikely that the feeding regimes used in this experiment had any affect on the physiology of the spiders because the average weight gain was the same for spiders in both treatment groups (constant: weight gain =  $0.198 \pm 0.07$  g; variable: weight gain =  $0.202 \pm 0.01$  g; two tailed  $t$ -test:  $t_{36} = 0.352$ ,  $P > 0.05$ ). The data for spiders that did not construct a minimum of seven webs throughout the 10 day experimental period (12 of 31 spiders in the variable food treatment and 15 of 34 spiders in the constant food treatment) were excluded from the analyses to reduce the variation in web-building behaviour.

### **Measuring web parameters**

We estimated foraging investment by the amount of sticky silk in the web (see Heiling *et al.*, 1998) because the various silk types used in constructing an orb-web have different costs

(Opell, 1997). The length of the sticky spiral (capture thread length = CTL) was calculated following Heiling *et al.* (1998):

$$\text{CTL} = \pi/2[n_1(r_1 + r_2) + n_2(r_2 + r_3) + n_3(r_4 + r_5) + n_4(r_5 + r_6)] \quad (1)$$

where  $r_1$  is the radius length from the hub to the innermost spiral and  $r_3$  is the radius length from the hub to the outermost spiral in the upper web half;  $r_4$  is the radius length from the hub to the innermost spiral and  $r_6$  is the radius length from the hub to the outermost spiral in the lower web half;  $r_2$  ( $r_2 = (r_3 - r_1)/2 + r_1$ ) and  $r_5$  ( $r_5 = (r_6 - r_4)/2 + r_4$ ) represent the half points of the upper and lower radii covered by the sticky spirals;  $n_1$  is the number of capture spirals between  $r_1$  and  $r_2$ ;  $n_3$  is the number of capture spirals between  $r_4$  and  $r_5$ ;  $n_2$  is the number of capture spirals between  $r_2$  and  $r_3$ ; and  $n_4$  is the number of capture spirals between  $r_5$  and  $r_6$  (Heiling *et al.*, 1998; Fig. 1).

The mesh height (average distance between spirals; (2)) and the web capture area (the area covered by the sticky spirals; (3)) were calculated following Herberstein and Tso (in press).

$$\text{Mesh height} = \frac{1}{2} \left( \frac{r_3 - r_1}{(S_u - 1)} + \frac{r_6 - r_4}{(S_l - 1)} \right) \quad (2)$$

where  $S_u$  and  $S_l$  are the number of capture spirals in the upper and lower web halves respectively, counted in the vertical sector directly above and below the hub (Fig. 1).

$$\text{Capture area} = \left( \frac{1}{2}\pi(r_7)^2 - \frac{1}{2}\pi(r_1)^2 \right) + \left( \frac{1}{2}\pi(r_8)^2 - \frac{1}{2}\pi(r_4)^2 \right) \quad (3)$$

where

$$r_7 = \frac{r_3 + d_h/2}{2} \quad r_8 = \frac{r_6 + d_h/2}{2}$$

and  $d_h$  is the horizontal web diameter (Herberstein and Tso, in press; Fig. 1).

*A. keyserlingi* spun up to four bands of zig-zag silk that meet at the hub of the web. The arrangement of the decorative bands and their width vary; spiders frequently change the pattern of the decorations and the bands increased in width from the centre of the web. Therefore, we used the length and number of the bands as an approximation of silk investment (Fig. 1).

### Statistical analysis

All statistical analyses were performed using SYSTAT 5.2 (Wilkinson, 1992) and SPSS for Windows, Version 6.0 (Norušis, 1993). Data that were not normally distributed (Kolmogorov-Smirnov test) were analysed using non-parametric procedures. All values are reported as the mean  $\pm$  standard error unless stated otherwise. In the first experiment (prey encounter rates), the number of zig-zag bands was correlated with length of the capture thread (low-prey diet:  $r = 0.554$ ,  $n = 19$ ,  $P < 0.01$ ; high-prey diet:  $r = 0.686$ ,  $n = 24$ ,  $P < 0.01$ ). Therefore, the length of the capture thread was introduced as a covariate when comparing the cumulative length of zig-zag bands between the two treatments. The data from the second experiment (variation in prey encounter rates) were analysed using the daily

arithmetic mean for the constant and variable treatment. The regression slopes created by the arithmetic means over the 10 day feeding period were compared between the two treatments using a modified *t*-test (Zar, 1984).

## RESULTS

### Prey encounter rates

Varying the prey encounter rates significantly affected the weight gain of spiders. Spiders that were fed daily gained significantly more weight than spiders that were fed every third day (two tailed *t*-test:  $t_{14,2} = 6.7$ ,  $P < 0.001$ ; Table 1). Feeding treatment also affected the size and the structure of the web. Spiders that received fewer flies spun a significantly longer capture thread than well-fed spiders (ANCOVA:  $F_{1,42} = 4.3$ ,  $P < 0.05$ ; covariate: spider mass; Table 1). The increase in the length of the capture thread resulted in webs that covered a significantly larger area (ANCOVA:  $F_{1,42} = 10.4$ ,  $P < 0.01$ ; covariate: spider mass; Table 1). The different feeding regimes also influenced the design of the web. Spiders that were maintained under the high-prey diet spun webs with a significantly smaller mesh than those on the low-prey diet (ANCOVA:  $F_{1,42} = 6.5$ ,  $P < 0.02$ ; covariate: spider mass; Table 1). Well-fed spiders decorated their webs with more zig-zag bands (measured as number of bands per unit length of capture thread) than spiders maintained under the low-prey regime (Mann-Whitney:  $U_{24,19} = 85$ ,  $P < 0.01$ ; Table 1), resulting in a significant difference in the cumulative length of zig-zag bands between the two feeding groups (ANCOVA:  $F_{1,42} = 9.4$ ,  $P < 0.01$ ; covariates: spider mass, capture thread length; Table 1).

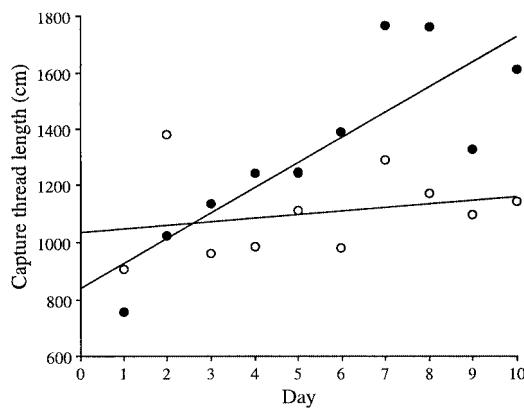
### Variation in prey encounter rates

Spiders fed the same amount of food but at different rates showed no significant difference in weight at the start (constant:  $0.20 \pm 0.04$  g; variable:  $0.21 \pm 0.05$  g; two-tailed *t*-test:  $t_{37} = 0.78$ ,  $P > 0.05$ ) or end of the experiment (constant:  $0.40 \pm 0.05$  g; variable:  $0.42 \pm 0.06$  g; two-tailed *t*-test:  $t_{36} = 1.29$ ,  $P > 0.05$ ). Furthermore, the spiders did not differ significantly in size, as estimated by carapace width (constant:  $0.44 \pm 0.03$  cm, variable:  $0.45 \pm 0.04$  cm; two-tailed *t*-test:  $t_{37} = 0.46$ ,  $P > 0.05$ ). However, the predictability of prey encounter had a significant effect on silk investment. Spiders that received food on a predictable schedule gradually increased the amount of sticky silk invested in

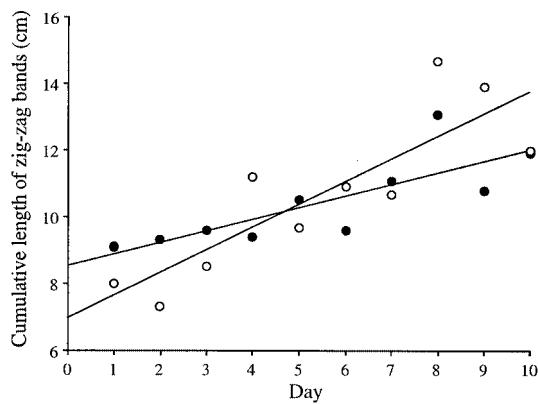
**Table 1.** Body weight and web characteristics (mean  $\pm$  s.e.) for *A. keyserlingi* on a high-prey diet ( $n = 19$ ) and a low-prey diet ( $n = 24$ )

	Low-prey diet	High-prey diet
Weight change (g)	$0.035 \pm 0.005$	$0.122 \pm 0.012$
Capture thread length (cm)	$1502.0 \pm 144.9$	$1008.5 \pm 119.3$
Web area ( $\text{cm}^2$ )	$553.3 \pm 47.2$	$325.4 \pm 40.0$
Mesh height (cm)	$0.52 \pm 0.015$	$0.43 \pm 0.026$
Number of zig-zag bands	$2.04 \pm 0.3$	$2.63 \pm 0.3$
Cumulative length of zig-zag bands (cm)	$6.1 \pm 0.98$	$8.0 \pm 1.20$

the web over the 10 day experimental period, whereas spiders that received prey sporadically did not, resulting in significantly different regression slopes ( $t_{16} = 3.82$ ,  $P < 0.001$ ; Fig. 2). Feeding regime also affected the decorating behaviour. Spiders fed sporadically spun more zig-zag bands, resulting in a steeper increase in the cumulative length of the zig-zag bands over the 10 days compared with the constant food group ( $t_{16} = 3.067$ ,  $P < 0.01$ ; Fig. 3).



**Fig. 2.** The mean capture thread length of webs built by spiders in the constant (●;  $y = -4.9 + 0.02x$ ;  $R^2 = 0.698$ ;  $P < 0.01$ ) and sporadic (○;  $y = -1.0 + 0.006x$ ;  $R^2 = 0.093$ ;  $P > 0.05$ ) food group over the 10 day feeding period. The slopes of the regression curves are significantly different ( $P < 0.0001$ ), as the capture thread length in the constant food group increases over time, whereas it remains stable for the sporadic food group.



**Fig. 3.** The mean cumulative length of zig-zag bands in webs built by spiders in the constant (●;  $y = -14.0 + 1.9x$ ;  $R^2 = 0.65$ ;  $P < 0.01$ ) and sporadic (○;  $y = -5.7 + 1.0x$ ;  $R^2 = 0.751$ ;  $P < 0.01$ ) food group over the 10 day feeding period. The slopes of the regression curves are significantly different ( $P < 0.001$ ), as the cumulative length of zig-zag bands in the sporadic food group increases with a much steeper slope compared with the constant food group.

## DISCUSSION

Our results show that the web-building spider *Argiope keyserlingi* adjusted its foraging behaviour by modifying the size and design of the web according to changes in the overall rate of prey encounter and the variability in prey encounter rates.

### Effects of prey encounter rates on spider foraging performance

The response of animals to food availability can vary according to the life-history strategy of the animal, the possibility of starvation and various costs including exposure to predators or the metabolic costs of food ingestion (Abrams, 1991, 1993). As a consequence, the response to changes in prey encounter rates might be variable (see Abrams, 1991). Here, the foraging response of *A. keyserlingi* was generally consistent with foraging theory (e.g. Higgins, 1995). Spiders that were fed more prey decreased their foraging investment in terms of silk material and foraging time by constructing smaller webs with less sticky silk. The response of spiders in the low-prey diet appears to contradict the prediction that spiders experiencing low food levels should reduce their foraging efforts to conserve energy (Higgins, 1995). However, individuals in the low-prey diet still gained weight during the feeding treatment. This means that these spiders were not food-limited, but rather were relatively food-deprived compared with the spiders on the high-prey diet.

Changing the size and design of the web may influence the prey capture success of spiders in several ways. For example, spiders building larger webs may increase their rate of prey encounter (Chacón and Eberhard, 1980). Additionally, adjusting the size of the web-mesh may allow spiders to target prey of particular types and sizes. For example, webs with a large mesh may intercept large-sized prey more efficiently (Murakami, 1983; Sandoval, 1994; Herberstein and Heiling, 1998; Schneider and Vollrath, 1998), while small-meshed webs may arrest prey in the web more successfully (Vollrath, 1992). A high number of spirals and radials also increase the ability of the web to absorb insect kinetic energy (Craig, 1987). However, a smaller mesh is more costly to build, because it requires more silk (Sherman, 1994). Similarly, a small mesh may reflect more light than a large mesh, and hence the web may be more visible to some approaching prey (Craig, 1986). Perhaps *A. keyserlingi* on a low-prey diet increased the mesh size to reduce the amount of silk incorporated into the web and/or to reduce web visibility, but at a cost of greater retention capabilities.

### Effects of variation in prey encounter rates on spider foraging performance

Our results indicate that *A. keyserlingi* is sensitive to variation in the rate at which prey arrive at the web and adjust their foraging investment accordingly. When insect encounter was predictable, the spiders increased the amount of silk produced per web. When prey encounter was unpredictable, the amount of silk synthesized per web remained at a low level. This result contradicts our initial prediction. However, the spiders in both feeding treatments were on a positive energy budget, gaining weight throughout the experiment. In general, animals on a positive energy budget are more often risk-averse, preferring to exploit food resources that are predictable (e.g. Kacelnik and Bateson, 1996). The results of our experiment may therefore reflect risk-averse behaviour in a more derived form: well-fed

*A. keyserlingi* prefer patches with constant food supply and consequently invest more resources to forage in those patches. If this is the case, *A. keyserlingi* on a negative energy budget should show the reverse effect, investing more energy when prey encounter rates are highly unpredictable.

The potential cost of additional foraging investment was not detected in the present study. There was no difference in the rate of weight gain between the two treatments, although spiders in the constant food treatment consistently invested more resources in terms of silk length and time. This is probably because, under laboratory conditions, all spiders were able to ingest all silk at the end of each day and therefore recycle a substantial part of their foraging investment. In the field, however, the entire web or considerable parts of it are frequently lost to rain, wind, detritus and prey interception.

A common assumption of foraging theory is that animals are able to perceive the quality of a foraging patch and that they possess sufficient memory capabilities to incorporate this information in long-term foraging gain decisions (Smallwood, 1993). Some foraging decisions appear to be 'paradoxical' (*sensu* Real, 1996) and do not seem to maximize the long-term energy return, which may be caused by a memory constraint or simply a conceptual constraint of foraging theory (Bateson and Kacelnik, 1997). Although the effective memory of a forager can affect its foraging behaviour, Bélisle and Cresswell (1997) showed that, in theory, animals with limited memory capacity forage approximately as efficiently as animals with infinite memory capacity. Web spiders have been assumed to lack long-term memory or 'perception' of habitat quality and make foraging decisions irrespective of habitat quality (Vollrath and Houston, 1986). Our results show that web-building spiders can perceive differences in habitat quality, and that they modify the webs they build on the basis of their previous experience, such as variability in the rate of prey encounter.

### Effects of food availability on web decorating behaviour

There is increasing evidence to suggest that web decorations function to attract prey to the web (Craig and Bernard, 1990; Craig, 1991; Craig and Ebert, 1994; Elgar *et al.*, 1996; Hauber, 1998; Tso, 1996, 1998a,b; Watanabe, 1999). In *A. keyserlingi*, the rate of prey encounter affected the number and size of web decorations added to the webs, which is apparently inconsistent with this idea. Spiders that were fed more prey added more zig-zag bands to their smaller webs, while spiders that were fed less food spun fewer decorative bands but larger webs. Nevertheless, these patterns may reflect a trade-off between two alternative foraging strategies. Previous field observations showed that *A. argentata* (Nentwig and Rogg, 1988) and *A. appensa* (Hauber, 1998) also built small webs with decorations or large, undecorated ones. While decorated but smaller *A. appensa* webs achieved similar foraging success as larger, undecorated webs, the decorated webs suffered greater damage due to increased prey interception (Hauber, 1998). Consequently, *A. appensa* may be trading off the benefits of prey attraction with the higher costs of web damage (Hauber, 1998). Our results suggest that *A. keyserlingi* may trade off the amount of resources allocated to the capture area of the web with those allocated to web decorations. This trade-off may also be reflected in our second experiment: spiders either increased the web size or the web decorations in response to constant or sporadic prey encounter rates. Clearly, the precise function of web decorations in *A. keyserlingi* and the apparent trade-off need to be addressed directly.

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