



Fine dining or fortress? Functional shifts in spider web architecture by the western black widow *Latrodectus hesperus*

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Spiders alter web architecture in response to many environmental factors. Yet, the functional implications of this behavioural plasticity are poorly understood, especially for spiders that spin long-lasting webs such as cobwebs. The western black widow spins a three-dimensional web that captures terrestrial prey and can persist for many days. However, the shape of the cobweb depends upon changes in the spider's body condition. Starved spiders invest more silk in sticky gumfooted threads, whereas sated spiders invest more silk in supporting threads. We tested the hypothesis that the increased investment in sticky gumfooted threads by starved spiders functions to improve the prey capture of their webs. Regardless of intrinsic foraging motivation, both fed and starved spiders captured more prey, more quickly and more efficiently, when hunting on a web that was spun by a starved spider. Our study shows that cobweb spiders actively manipulate web-spinning behaviours in ways that alter the functions of their webs and that even spiders spinning relatively long-lasting webs may use behavioural plasticity to respond to changing selective pressures in their environment.

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Behavioural plasticity allows animals to alter resource allocation when confronted by temporal or spatial variation in selective pressures (Lima & Bednekoff 1999; Lind & Cresswell 2005). For instance, many animals shift time and energy away from foraging and into defensive behaviours as body condition improves because the relative fitness gain from procuring additional food becomes small compared to the costs of predation (Lima & Dill 1990). Many animals can continuously fine-tune such behavioural responses, within the limits of their ability to gather accurate information about their environment. In other situations in which behavioural decisions have more persistent consequences, fine-scaled responses to the environment may be constrained. For instance, many spiders spin webs that alter the local environment for the

duration of the web's existence. Variation in spider web architectures therefore reflects behavioural responses to many environmental factors such as prey capture, thermoregulation and protection from the spider's own predators.

The basic architectural pattern of a particular species of spider's web is largely determined genetically (Eberhard 1990; Foelix 1996). However, spiders also alter their spinning behaviours in response to many environmental factors (Heiling & Herberstein 2000). For instance, some orb-weaving spiders change the size of their web or the spacing between the rows of sticky silk in response to variations in prey capture (Higgins & Buskirk 1992; Sherman 1994), which may alter the number or size of prey captured by the spider (Blackledge & Zevenbergen 2006; Blackledge & Eliason 2007). Orb-weaving spiders can also reduce the frequency with which they decorate their web with stabilimenta in response to increased prey density (Blackledge 1998; Herberstein et al. 2000). Furthermore, orb-weaving spiders sometimes increase investment

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in barrier webs, which surround the orb and may protect the spider from predators during developmental changes such as moulting (Higgins 1992). Yet, the orb is only one of many types of web spun by spiders and the functional implications of spinning plasticity in spiders that spin other web architectures are largely unknown.

The western black widow spins a three-dimensional cobweb on which it resides for most of its life, frequently modifying the web but only rarely abandoning it. A typical western black widow web consists of a sheet of silk threads held in place by a three-dimensional array of supporting silk (Fig. 1a; Benjamin & Zschokke 2003; Agnarsson 2004; Blackledge & Zevenbergen 2007). The sheet emerges from a retreat, usually located in a crevice, in which the spider rests. The black widow typically moves out onto the sheet when hunting at night. The supporting threads maintain the basic web structure, but may also play a variety of other roles in how spiders interact with their environment. Sticky gumfooted threads are suspended between the sheet and the substrate. These threads are coated with 1–2 cm of glue droplets at their base and are held under tension (Blackledge et al. 2005). The sticky gumfooted threads break away from the substrate when prey contacts the glue, thereby physically restraining the prey and providing vibrational cues of its presence in the web to the spider (Argentean et al. 2006).

Black widows change the architecture of their webs in response to variations in body condition (Fig. 1; Blackledge & Zevenbergen 2007; Salomon 2007). Spiders in poor body condition spin cobwebs with ‘typical’ architectures, including well-defined sheets and many sticky gumfooted threads. Conversely, spiders in good condition because they have recently fed on prey often spin webs that lack sheets and sticky gumfooted threads. Instead, they produce ‘tangle-based’, highly three-dimensional clouds of nonsticky silk threads around their retreats. This architectural shift does not result from a simple reallocation of resources away from web production and into reproduction or growth. Instead, black widows in good condition produce more silk overall compared to those in poor condition, which spin the ‘typical’ architecture (Blackledge & Zevenbergen 2007; Salomon 2007). It seems

likely that black widows vary the architecture of their webs in response to the fitness consequences of different architectural elements. Sticky gumfooted threads and sheets may facilitate prey capture, which is particularly advantageous for starved spiders. In contrast, the three-dimensional tangle-based webs spun by sated spiders may better protect them from their own predators as the supporting threads function to isolate spiders physically or provide early warning of a predator’s approach. Here, we test the hypothesis that spiders in poor body condition spin webs that are more effective at capturing prey than the webs spun by spiders in good body condition, providing a functional benefit to behavioural plasticity in these spiders.

METHODS

We used a total of 112 juvenile female western black widow spiders, *Latrodectus hesperus* (Araneae: Theridiidae), obtained from Riverside, California, U.S.A., to compare the foraging success of spiders hunting on webs spun under two different energetic conditions. Spiders were approximately two moults from maturity and weighed (mean \pm SD) 125 ± 82 mg. Prior to the experiment, we lightly anaesthetized spiders using CO₂ and photographed them under a stereomicroscope. We also weighed the spiders to the nearest 0.1 mg and measured their front right femurs to the nearest 0.1 mm using digital photographs and ImageJ software (National Institutes of Health, Bethesda, MD, U.S.A.). We then calculated body condition as the residual of a regression of body mass against femur length (Jakob et al. 1996).

We placed spiders in individual acrylic cages ($l \times w \times h$; $30 \times 20 \times 20$ cm). Each cage contained cardboard frames that allowed webs to be removed and measured easily. A frame consisted of a 30×20 cm top and bottom and was divided into a 7 cm deep rear retreat area, enclosed on three sides, and a 23 cm deep foraging arena supported on the opposite end by a thin piece of wood (similar to Fig. 1). A small flap cut into the rear of the retreat allowed us to prod spiders out of their webs easily with minimal disturbance to the webs themselves.

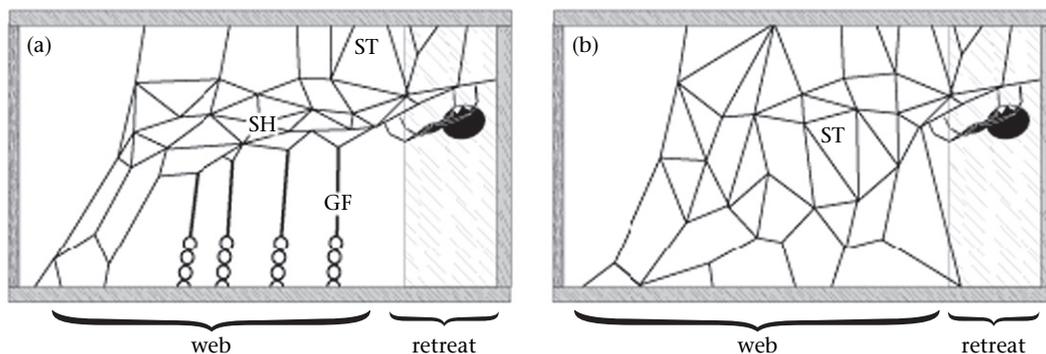


Figure 1. Western black widow cobwebs consist of up to four regions of silk. The spider manoeuvres on a sheet of silk (SH) that is supported by an array of threads (ST). Sticky gumfooted threads (GF) run from the sheet to the substrate and are coated with glue near their base. Spiders typically hide in a retreat during the day and move out onto the sheet when actively hunting at night. (a) Starved spiders spin webs that contain all four components. (b) Satiated spiders spin webs that typically contain more supporting threads and lack both sticky gumfooted threads and defined sheets of silk.

We assigned spiders to one of two treatments ($N = 56$ each). Fasted spiders received no prey for 7 days prior to the experiment. Fed spiders were offered one small cricket, *Acheta domestica* (230 ± 40 mg), for each of 7 days prior to the experiment. We intentionally assigned smaller spiders to the feeding treatment and heavier spiders to the fasting treatment so that the final sizes of the spiders in each treatment would be as similar as possible during the subsequent prey-capture trials. As a result, the body condition of spiders did not differ between feeding treatments at the start of the prey-capture trials (t test: $t_{93} = -0.4$, $P = 0.67$). Regardless of treatment, we opened all cages each day to provide similar levels of disturbance to the treatments. After 7 days, we destroyed all the webs and allowed the spiders to spin new webs for 2 days. This ensured that web architectures largely reflected the spiders' current foraging condition.

Prior to the prey-capture trials, we coaxed the spiders out of their webs. We then counted the total number of sticky gumfooted threads in each web and photographed the webs using a Nikon Coolpix 5400 digital camera to measure later the ratio of silk in the sheet versus supporting regions of the webs. We photographed webs against a shadow box illuminated by two 20-W fluorescent lights. We then used ImageJ (National Institutes of Health) to measure the total whiteness of the area of each photograph delimiting the sheet versus the rest of the web. This area consisted primarily of supporting threads because sticky gumfooted threads did not appear in the photographs due to their unique orientation. The ratio of whiteness of the sheet to that of the surrounding web provided a measure of the relative investment of silk in sheet versus supporting threads. Our previous work showed that this technique correlates strongly with silk mass and, more important, did not damage webs (Blackledge & Zevenbergen 2007).

We returned the spiders to their webs 1 h before conducting prey-capture trials. However, we expected the overall motivation of spiders to hunt, determined by their recent feeding history, to affect prey capture strongly regardless of any influence of web architecture per se. Therefore, we randomly selected half of the spiders in each treatment group and placed them on webs spun by spiders of the opposite foraging motivation. This allowed us to compare directly the prey-capture performance of spiders with similar foraging motivation when hunting on different types of webs (e.g. how fasted spiders hunt on their own webs versus how fasted spiders hunt on webs spun by fed spiders).

Once the spiders had acclimated to the webs for 1 h, we added six small crickets, *A. domestica*, to the cages and filmed prey capture for 3 h in the dark using the infrared night-shot feature of Sony Handycam DCR-HC42 video cameras. We recorded the total number of crickets captured, latency until capture of the first cricket, and total number of capture attempts. We defined a capture attempt as any noticeable movement towards a cricket, with successful attempts ending with the cricket securely wrapped in silk by the spider. We made separate comparisons between pairs ($N = 28$) of fasted spiders foraging on both types of webs and pairs ($N = 28$) of fed spiders foraging on both types of web. Each spider and each web was used for only a single trial, for a total of 112 spiders.

We used chi-square goodness-of-fit tests to compare the proportions of spiders capturing prey when foraging on each type of web. When data were normally distributed, we used two-way ANOVAs to test whether foraging motivation or web architecture influenced prey capture. When data could not easily be transformed to meet assumptions of normality, we analysed the data separately for fed and fasted spiders because our primary interest was in the effect of web architecture on prey-capture performance. In these cases, we used Mann–Whitney U tests to compare the total number of prey captured, the number of attempted captures of prey, and the overall success rate of spiders.

RESULTS

Juvenile black widows altered their web architecture in response to foraging history in a manner similar to that previously seen in adult spiders (Blackledge & Zevenbergen 2007). Fed spiders spun webs with more silk in supporting threads than in sheets (Mann–Whitney U test: $Z = 5.1$, $P < 0.00001$). Fed spiders ($N = 56$) also spun sticky gumfooted threads less often than fasted spiders ($N = 56$) (46 versus 88% of webs, respectively; $\chi^2_1 = 61.0$, $P < 0.000001$). Even when sticky gumfooted threads were included in webs, fed spiders spun fewer of them than fasted spiders (20.5 versus 31 median sticky gumfooted threads, respectively; Mann–Whitney U test: $Z = 7.4$, $P < 0.0001$).

Spiders hunting on webs built by fasted spiders (sheet-based webs) were able to capture at least one prey more often than the same type of spider foraging on webs built by fed spiders (tangle-based webs) (Fig. 2; fasted spiders: $\chi^2_1 = 4.5$, $P < 0.05$; fed spiders: $\chi^2_1 = 4.7$, $P < 0.05$). Both fasted and fed spiders tended to capture more prey when foraging on sheet-based webs, but this was significant only for fasted spiders (Fig. 3; Mann–Whitney U test: $Z = -2.7$, $P < 0.01$; $Z = -1.8$, $P < 0.08$, respectively). The time until first capture of prey was also shorter for spiders

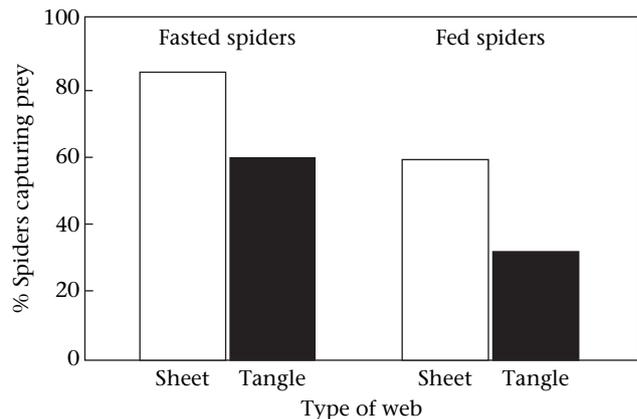


Figure 2. Percentage of spiders capturing prey in each trial ($N = 28$). Capture depended upon both intrinsic foraging motivation (feeding history) and the architecture of the web on which the spider was hunting. All spiders were more likely to capture prey when hunting on webs spun by fasted spiders.

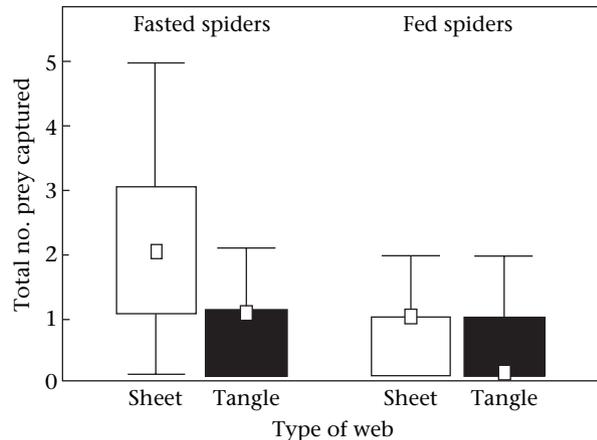


Figure 3. Number of prey captured by spiders foraging on different webs. Fasted spiders captured more crickets when they were on webs spun by fasted spiders (sheet) than when on webs spun by fed spiders (tangle). Box denotes median and 25–75% intervals while bars denote nonoutlier range.

foraging on sheet-based webs compared to spiders of the same motivation foraging on tangle-based webs (Fig. 4; two-way ANOVA: web type: $F_1 = 5.1$, $P < 0.05$; spider motivation: NS).

Fasted spiders also attempted to capture prey (i.e. moved towards prey) more often when foraging on sheet webs than on tangle-based webs (Fig. 5; Mann–Whitney U test: $Z = -2.2$, $P < 0.05$). Capture success was greater for fasted spiders when foraging on sheet webs compared to tangle-based webs (Fig. 6; Mann–Whitney U test: $Z = -2.2$, $P < 0.05$). Fed spiders also tended to attempt to capture prey more often when foraging on sheet webs than when foraging on tangle-based webs, but the difference was just above statistical significance (Fig. 5; Mann–Whitney U test: $Z = -2.2$, $P = 0.0503$). We did not detect an effect of web architecture on the percentage of successful capture attempts for fed spiders (Fig. 6).

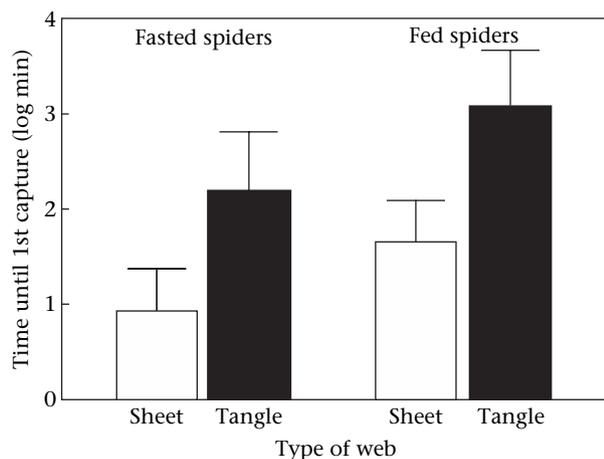


Figure 4. Time until capture of first prey (mean \pm SE) based upon foraging motivation and web architecture. Spiders captured prey more quickly when hunting on the sheet webs spun by fasted spiders.

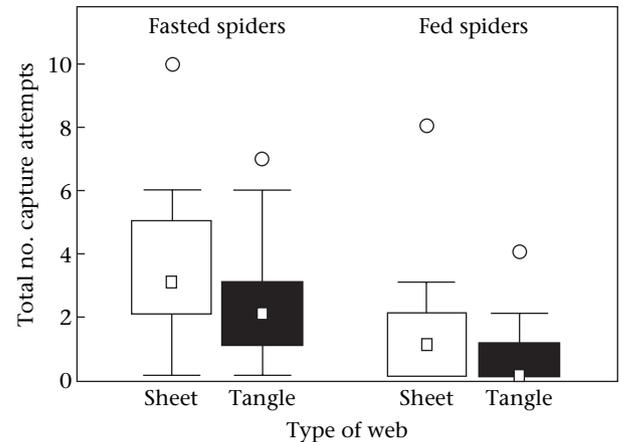


Figure 5. Number of attempts to capture prey during 3 h. Spiders attempted to capture prey more often when hunting on the sheet webs spun by fasted spiders. Box denotes median and 25–75% intervals, bars denote nonoutlier range, and points indicate outliers.

DISCUSSION

Our study shows that spiders can change the architecture of cobwebs in ways that can alter the prey capture function of the webs and better meet the spiders' energetic needs. Fasted spiders spin webs that function better for a variety of measures of prey-capture performance than webs spun by well-fed spiders. The improved prey-capture performance of these webs is expressed regardless of the intrinsic foraging motivation of the spiders hunting on the webs.

Adult western black widows display a remarkable degree of plasticity in web spinning, altering the amount of silk in their webs in response to potential competitors (Salomon 2007) and shifting between two different web architectures when starved versus sated (Blackledge & Zevenbergen 2007). The precise shape of cobwebs often varies in relation to the substrates on which the webs are constructed (e.g. Agnarsson 2004; Jorger & Eberhard 2006; Eberhard

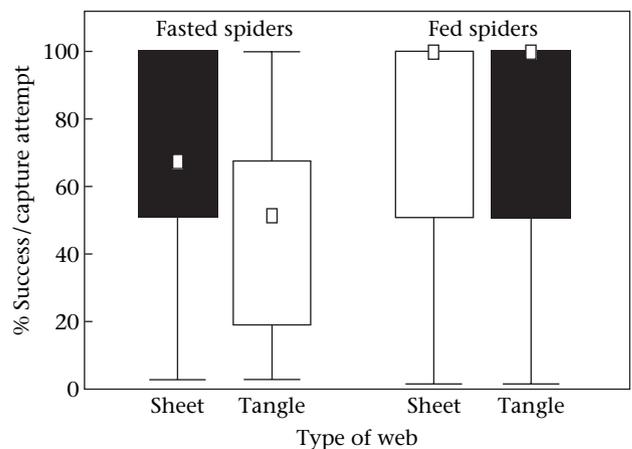


Figure 6. Median probability of capture success for spiders. Box denotes median and 25–75% intervals, bars denote nonoutlier range.

et al., in press). However, the behavioural plasticity displayed by western black widows differs in that they are altering the basic structural elements included their webs, rather than simply changing the overall size or shape. This degree of plasticity is so far known in only one other species of cobweb spider (Agnarsson & Coddington 2006). Previous research on web-spinning plasticity by adult orb-weaving spiders suggests that it may allow spiders to shift resources away from silk in webs, used for foraging, and into development of eggs, used for reproduction (Sherman 1994; Venner & Casas 2005; Venner et al. 2006). Moreover, the functional implications of such changes in web investment have rarely been tested. Here, we found that immature black widows display a pattern of behavioural plasticity remarkably similar to that of adults. This suggests that, at least for the parameters that we measured, the plasticity displayed in web shape and silk investment may not be directly related to reproduction, but rather to other life-history traits such as foraging or defence.

Another crucial difference between our study and past work is that those studies used experimental designs resulting in groups of spiders that differed in both final body condition and recent change in body condition. In nature, any given body condition could result from either a decline or an increase in body condition so that it can be difficult to determine to which proximate cues the spiders are responding. We deliberately chose to feed the smallest spiders and fast the largest spiders in this study to achieve overall similar body sizes and body conditions between treatments. Thus our spiders differed primarily in their recent change in body condition. Yet, we found behavioural shifts in web architecture similar to past studies. This suggests that recent change in body condition or perhaps even the perception of prey availability, rather than absolute body condition per se, may be the proximate cue used by spiders when making decisions about web architecture.

We found support for the hypothesis that behavioural plasticity in web architecture is adaptive for spiders, allowing black widows to spin webs that function best for their most immediate ecological needs. The fitness of spiders whose body condition is declining due to lack of prey consumption could clearly benefit from spinning webs that enhance prey capture. We found substantial evidence that the architecture of webs spun by fasted spiders increased the probability and speed of capturing prey, as well as the total number of prey captured. This is probably caused by two factors. First, sheet-based webs contain many sticky gumfooted threads that can adhere to prey, absorbing kinetic energy and making it difficult for insects to escape from webs. These webs also have a clearly defined sheet upon which the spider manoeuvres to the prey. This increases the overall success rate of spiders attacking prey (Fig. 6). Second, we hypothesize that the sticky gumfooted threads connected to a defined sheet of silk probably transmit more precise vibrational information about prey location than does a diffuse network of supporting threads. This increases the overall likelihood that the spider will attempt to attack the prey. We found that all spiders were more likely to respond to prey when hunting on sheet-based webs. Lamoral (1968)

determined that *Latrodectus mactans* and *Latrodectus geometricus*, close relatives of *L. hesperus*, depend upon 'leading threads' to transmit vibrations that the spiders use to locate prey. These leading threads are among the first threads spun by the spiders when constructing cobwebs and we suggest that the leading threads may be more precisely arrayed within the flat sheets of webs spun by starved western black widows. This is similar to the radial threads of orb webs, which transmit vibrational signals directly to the spider at the centre of the web (Suter 1978; Masters & Markl 1981). In contrast, most supporting threads in cobwebs connect through a network of other threads, allowing attenuation of vibration and possibly obscuring the directionality of signals.

The effect of web architecture on prey capture occurred regardless of the intrinsic foraging motivation of the spiders. Even fed spiders captured more prey more easily when hunting on webs spun by fasted spiders compared to their own type of web (Figs 3, 4). Moreover, they attempted to capture prey more often when hunting on fasted spiders' webs (Fig. 5; marginally significant). Yet, these fed spiders probably had little to gain by consuming additional prey and this effect was likely due to improved transmission of information about prey location through the sticky gumfooted threads. Thus, the web itself can act as an important regulator of the foraging behaviours of spiders (e.g. Watanabe 2000). Many types of web-spinning spiders engage in superfluous killing—capturing prey that are never consumed (Smith & Wellington 1986; Riechert & Maupin 1998; Maupin & Riechert 2001) or even 'overeating' to the point of death (Higgins & Rankin 2001). This may reflect behavioural syndromes resulting from strong selection for prey capture when spiders are food-limited, which may override weaker selection against the 'negative' expression of prey-capture behaviours in other ecological contexts (Sih et al. 2004). Our results suggest that the black widow's shift in web architecture may also function to alter the way in which webs transmit information to spiders. The lack of sticky gumfooted threads in fed spiders' webs potentially limits the expression of prey-capture behaviours by spiders that have little to gain from additional food, reducing superfluous killing of prey.

The more three-dimensional web architecture spun by fed spiders may have benefits in addition to modulating the attack behaviours of spiders. Protection against predators probably played a key role in the evolutionary origin of cobweb spinning from ancient orb-web-weaving ancestors (Blackledge et al. 2003). Reduced foraging activity by fed spiders, resulting from decreased transmission of vibrational cues, would reduce exposure to predators. More important, Blackledge & Zevenbergen (2007) suggested that fed black widows may be reallocating silk away from prey-capture elements of webs into supporting threads because this part of the web can provide physical protection and early warning of attack. This hypothesis has yet to be tested empirically but is consistent with the hypothesized function of the three-dimensional barrier webs that are sometimes spun around orb webs (Lubin 1975; Higgins 1992). Unfortunately, direct tests of the effects of three-dimensional silk arrays on predation of spiders are mostly

lacking for both orb and cobweb spiders, but are clearly desirable.

Our study shows that cobweb spiders actively manipulate web-spinning behaviours in ways that alter the function of their webs. These functional shifts are congruent with adaptive responses to the external prey environment because they are associated with changes in the body condition of spiders. This shows that even spiders spinning relatively long-lasting webs may use behavioural plasticity to respond to changing selective pressures in their environment.

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