



# Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*

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Animals use behavioural plasticity to cope with conflicting selective pressures. We investigated how prey availability affects the spinning of cobwebs, whose architecture influences both prey capture and defence. Fed western black widows spun cobwebs containing more silk than did fasted spiders. However, fed spiders invested relatively less silk in the sheets and sticky gumfooted threads of webs and relatively more silk in supporting threads than did fasted spiders. The material properties of silk spun by fed and fasted spiders were relatively similar, but silk threads spun by fed spiders were twice as thick as those of fasted spiders, increasing web strength by 225%. Finally, spiders fed late in the experiment did not reproduce, even though they received the same amount of food as spiders fed earlier, 43% of which reproduced. The reallocation of silk in cobwebs away from sheets and sticky gumfooted threads, which function in prey capture, to supporting threads, which surround spiders with defensive clouds of silk, is consistent with reduced foraging effort and increased predation risk avoidance by fed spiders. Furthermore, this behavioural shift occurs as spiders are reproducing, when spiders can most afford the costs of reduced prey capture and would most benefit from enhanced protection. Our results contrast with those of previous studies on orb-weaving spiders, which found reductions in the sizes of webs as spiders caught more food. Thus, the architectures of spider webs reflect many selective pressures, the effects of which may vary with physiological state.

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Animals must invest time and energy into foraging, reproduction and defence in ways that maximize fitness (Krebs & Davies 1997). Yet, seemingly optimal responses to any one of these demands are almost inevitably sub-optimal for other aspects of life history (Lima & Dill 1990; Jennions & Petrie 1997; Krebs & Davies 1997; Dukas 2002; Sih et al. 2004; Lind & Cresswell 2005). Behavioural plasticity provides animals with one mechanism to react to this conflict. By expressing alternative behaviours in different situations, organisms can maximize their fitness across diverse environments (Thornhill 1981; Maynard Smith 1982; Lima & Bednekoff 1999; Sih et al. 2000; Brockmann 2001). For instance, organisms frequently trade off the risk of predation to invest in foraging, such that the antipredator behaviours expressed by a particular

animal depend on a combination of internal physiological state, the availability of resources in the environment, and the temporal and spatial distribution of predators (Lima & Dill 1990; Lima & Bednekoff 1999; Sih et al. 2000; Lind & Cresswell 2005).

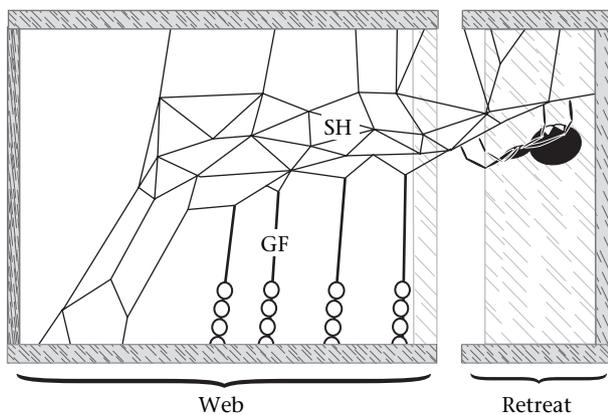
Web-building spiders provide excellent models to study how organisms respond to conflicting selective pressures, because spider webs are themselves the products of a series of behavioural decisions by the spiders (Sherman 1994; Blackledge 1998a; Heiling & Herberstein 2000). Yet, spider webs are also physical structures that are easily quantified (Eberhard 1986; Heiling et al. 1998; Blackledge & Gillespie 2004; Zschokke & Herberstein 2005). While spiders' webs are typically studied as tools used by spiders for foraging, the webs spun by most spiders are better considered to be structural modifications of the spiders' immediate environment that influence a variety of traits, in addition to prey acquisition, such as defence against predators or reproduction (Blackledge & Wenzel 2001a; Blackledge et al. 2003). Therefore, behavioural changes in how

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spiders spin webs are likely to reflect adaptive responses to predation risk or reproduction in addition to foraging (Higgins 1992; Blackledge & Wenzel 1999; Blackledge et al. 2003; Venner et al. 2006).

Cobweb spiders in the Theridiidae spin three-dimensional webs that may seem chaotic in organization but are actually constructed using stereotyped behaviours that result in discrete structural elements (Benjamin & Zschokke 2002, 2003). The basal web type within the Theridiidae is a '*Latrodectus*-style' cobweb that consists of a well-defined sheet of silk that radiates out from a retreat and is suspended within a matrix of supporting threads (Fig. 1; Benjamin & Zschokke 2003). Sticky gumfooted threads are suspended vertically from the sheet down to the substrate. These sticky gumfooted threads are gluey at their bases and function as the primary prey capture elements of most cobwebs (Blackledge et al. 2005b; Argintean et al. 2006).

The cobweb architecture evolved from a two-dimensional orb-weaving ancestor (Griswold et al. 1998). The evolutionary shift from two-dimensional orb webs to the three-dimensional webs spun by theridiids and other members of the 'araneoid sheet web weavers' is associated with increases in both species diversity and abundance in the environment (Blackledge et al. 2003). The evolution of cobwebs alters the ways that spiders forage for insect prey relative to their orb-weaving ancestors (Janetos 1986). However, it also has implications for vulnerability of spiders to their own predators. While two-dimensional orb webs provide efficient traps for the capture of flying insects, orb webs also leave spiders vulnerable to their own predators as the spiders sit on exposed planar webs (Blackledge & Wenzel 2001a). A cobweb spider, in contrast, can hunt on its web while surrounded by a matrix of supporting silk threads that provides both early warning of predators and a physical barrier against attack. In particular, the origin of three-dimensional cobwebs may be associated with the appearance of predatory mud-dauber wasps,



**Figure 1.** A cobweb constructed by the western black widow consists of four discrete regions of silk. The spider typically rests in a retreat of silk at the rear of the web. A sheet of threads (SH) is suspended above the substrate and merges with the retreat. Sticky gumfooted threads (GF) are suspended between the sheet and the substrate and function as the primary capture elements of the web. The sheet and retreat are held in place by a three-dimensional array of supporting threads.

which disproportionately attack orb-weaving spiders in many environments (Blackledge et al. 2003). This evidence suggests that the cobweb architecture may represent an evolutionary compromise in web-building behaviours that allows spiders to forage in relative safety from their own predators (Blackledge et al. 2003).

Orb-weaving spiders have a variety of behavioural strategies to alter web architectures in response to variation in the environment (Edmunds & Edmunds 1986; Higgins 1990; Heiling & Herberstein 2000). Individual orb-weaving spiders can increase or decrease the sizes of webs (Sherman 1994; Venner et al. 2000, 2006; Li & Lee 2004), spin protective barrier webs when moulting (Lubin 1975; Higgins 1992) and facultatively decorate their webs with silk stabilimenta (Kerr 1993; Blackledge 1998b; Tso 2004), in ways that can alter their prey capture, vulnerability to predators and ability to reproduce. However, the ability of cobweb spiders to alter web construction behaviours in response to their environment has not been explored, and has been investigated only rarely in other types of three-dimensional web-building spiders (e.g. Segoli et al. 2004). Furthermore, while behavioural plasticity in shapes of orb webs has been well documented (Sandoval 1994; Sherman 1994; Higgins 1995; Zschokke 1997; Schneider & Vollrath 1998; Tso 1999; Herberstein et al. 2000), none of these studies have examined how plasticity may be associated with changes in either the structural or material properties of the silk fibres used to spin orb webs (Blackledge 1998b; Tso et al. 2005; Townley et al. 2006). However, such information is critical for a comprehensive understanding of the energetic and functional consequences of architectural variation in webs. We examined how the western black widow alters its cobweb in response to changes in prey capture and we discuss the implications for understanding how these spiders trade off the selective demands of foraging, defence and reproduction. Rather than focusing simply on the shapes of webs, we also compared the total amount of silk placed in webs by the spiders as well as the structural and material properties of the capture threads in cobwebs.

## METHODS

### Maintenance of Study Organisms

We purchased 38 adult or penultimate female black widows from Hatari Invertebrates (Portal, Arizona, U.S.A.) and fasted spiders for 5 days before the start of the experiment. On the first day of the experiment, we weighed each spider and measured the length of its front right femur. Because the length of the femur does not vary within a single instar, it provides a reliable measure of the size of a spider. In contrast, body mass varies as a function of both spider growth (size) and body condition. We controlled for the effect of size per se on body mass by regressing body mass against femur length. The residuals of body mass then provided a measure of the relative body conditions of spiders.

*Latrodectus hesperus* construct cobwebs that consist of four architecturally discrete components (Fig. 1). The

entire web emanates from a retreat in which the spider hides during the day. A sheet of silk radiates out from the retreat and provides the primary substrate that black widows move upon while capturing prey. Sticky gum-footed threads are suspended vertically beneath the sheet and are coated at their bases with aqueous glue. The attachments of sticky gumfooted threads to the substrate are designed to break when prey contact them, such that tension within the web pulls the sticky gumfooted thread up, sometimes even suspending prey in the air, where they are easily attacked by the spiders. Finally, the web is suspended in place by an array of supporting threads.

We housed spiders individually in plastic terrariums ( $20 \times 35 \times 25$  cm high). We placed identical cardboard frames within each terrarium. These frames provided the spiders with substrates to which they could attach webs and were removable to allow easy analysis of the webs. The frames consisted of two parts, a retreat frame and a web frame. The retreat frame consisted of a box ( $19 \times 15 \times 9$  cm deep) that was open on one end. A triangular piece of cardboard was glued in the centre of the back of the retreat, against the ceiling, to give spiders a hiding place. The web frame consisted of a separate cardboard structure with a floor and ceiling ( $22 \times 15$  cm wide) that were held in place by three narrow cardboard supports (19 cm high). By running a hot wire between the retreat and web frames, we could free the bulk of the web for analysis while the spider was safely confined in the back retreat portion of its web.

## Experimental Design

We divided spiders into two treatment groups ( $N = 19$  each) that differed in the amount of prey they received (Fig. 2). To ensure that spiders in the two treatments were of similar size at the start of the experiment, we first ranked spiders by order of femur length. Then we randomly assorted pairs of spiders between the two treatment groups, starting with the two largest spiders and finishing with the two smallest spiders. Spiders in group 1 were each fed a single large house cricket, *Acheta domesticus* (mean mass  $\pm$  SE =  $0.24 \pm 0.01$  g), every day for 6 days, while

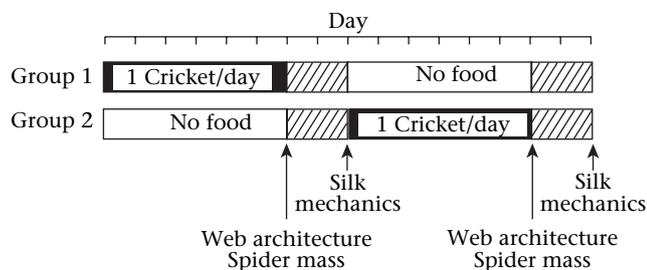
spiders in group 2 were fasted for 6 days, although their terrariums were still opened every day to provide equal levels of disturbance. We then removed the web frames and quantified the silk within them. We also weighed each spider, then returned the spiders to the terrariums and provided them with fresh web frames and their original retreat frames. Spiders were allowed to spin new webs for two additional nights before we collected the web frames to retrieve samples of freshly spun silk for structural and mechanical analysis.

We placed fresh web frames in the terrariums and reversed the feeding regimes of the spiders between groups for 6 days during trial 2. Data collection for webs, spider mass and silk biomechanics were repeated as described above (Fig. 2). Because the spiders had established webs within the retreat frames during the acclimation phase prior to trial 1 and we never removed silk from these frames, the majority of silk spinning throughout trials 1 and 2 occurred exclusively within the web frames. Five spiders moulted during trial 2 and were therefore only included in the statistical analyses for trial 1. One additional spider was removed from the trial 2 analysis because it was in the fed treatment but did not consume any prey.

## Web Architecture

We measured the mass of silk spun by spiders and how silk was allocated to different elements of the cobwebs at the end of each feeding trial. We quantified the volumes of the sheets of webs, the relative amounts of silk within the sheets and the supporting threads of cobwebs, and the total mass of silk in webs spun during the 6 days of each trial. We also counted the total numbers of sticky gum-footed threads spun during the 2 days following the end of each feeding trial (Fig. 2).

We first photographed each web in profile (as in Fig. 1) using a Nikon Coolpix 5400 digital camera to quantify the relative amount of silk invested in the sheet and supporting threads. Webs were illuminated with four 10-W fluorescent bulbs against a black shadow box background. We placed a translucent white plastic rectangle immediately in front of the webs to serve as scale for both size and illumination of webs. We then transferred the images to the computer where we traced the outline of the sheet of each web using Image J 1.34s (National Institutes of Health, Bethesda, Maryland, U.S.A.) and measured its total area. We then measured the optical density of the silk within the sheet versus the rest of the web frame by calculating the respective whiteness of each region relative to the whiteness of the scale (i.e. the mean grey value returned by the measure function in Image J). This provided a relative measure of the total amount of silk in different regions of the web, which could vary in relation to changes in either numbers or sizes of silk threads. Because we were primarily interested in the amount of silk invested in different regions of the webs, rather than web shape per se, we photographed all webs in profile to provide a maximum area over which to resolve the different web regions. In addition, we collected all of the silk within the web frame onto clean forceps and transferred the



**Figure 2.** Protocol for the feeding of spiders and data collection. During trial 1, spiders in group 1 were fed for 6 days and spiders in group 2 were fasted. Web architecture and spider mass were measured on day 7. We allowed spiders to spin fresh webs for two nights, then we collected silk samples for biomechanical analysis. During trial 2, we reversed the feeding protocol between groups, allowed spiders to construct new webs for 6 more days, then sampled web architecture, spider mass and silk, as before.

samples to small pieces of preweighed and dehydrated fishing line (Blackledge 1998b). The silk samples were then dried for 48 h in a desiccator using Drierite CaSO<sub>4</sub> and weighed to the nearest 0.1 µg using a Cahn25 Automatic Electrobalance (Blackledge 1998b). In addition to providing a direct measure of silk output, these samples also allowed us to compare our measures of silk whiteness to the total mass of silk for whole webs in trial 1.

Paired *t* tests were used to test for within-group changes in body mass and condition between trials. We used *t* tests and ANCOVAs, with the natural log of spider mass as the covariate, to test for the effects of feeding trial on the mass of silk spun by spiders. We used Mann–Whitney *U* tests to compare the relative investment of silk in different web elements between feeding regimes.

Finally, we repeated the analysis of web shape and counted the total number of sticky gumfooted threads in the freshly spun webs produced during the 2 days at the end of each trial. We then used *G* tests for goodness of fit to compare relations between feeding treatment and presence of sticky gumfooted threads in webs.

### Silk Mechanics

After we measured web architecture, we allowed spiders to spin fresh webs within the web frame for 2 days. We then collected five samples of sticky gumfooted threads from each web. This also allowed us to test for differences between foraging treatments in the mechanical performance of silk and for structural differences in fibre thickness. We collected 10-mm-long samples across the gaps in C-shaped cardboard mounts and secured them using cyanoacrylate glue (Blackledge et al. 2005b). All samples were taken from the double-stranded upper regions of the sticky gumfooted threads. We then measured the diameters of each gumfooted thread using polarized light microscopy (Blackledge et al. 2005a). Finally, the tensile properties of each sample were determined using a Nano Bionix UTM tensile tester (MTS Systems Corporation, Oak Ridge, Tennessee, U.S.A.). We extended fibres at 1% strain/s until failure, measuring four aspects of mechanical performance (Blackledge et al. 2005b, c). Young's modulus measured the initial stiffness of fibres. Ultimate strength and extensibility measured the total force generated by fibres at their maximum extension (normalized to the cross-sectional area) and the maximum lengths of fibres, respectively. Finally, toughness measured the total energy absorbed by a fibre (normalized to cross-sectional area). We calculated the mean of each of these values for each spider and used these means in a subsequent MANOVA to test for variation in structural or material properties of the silk. Univariate *t* tests were then used for post hoc tests of significant differences for individual variables.

## RESULTS

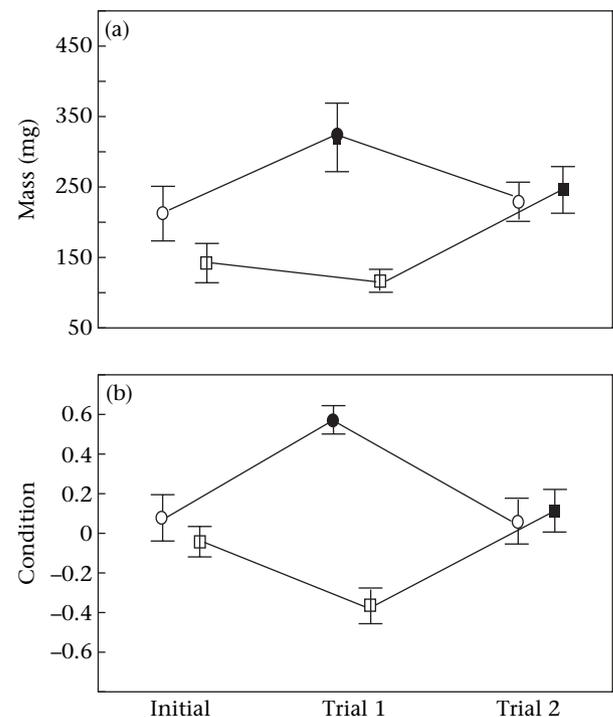
### Spider Condition

Spiders in group 1 increased both body mass and condition after being fed for 6 days (paired *t* test: body

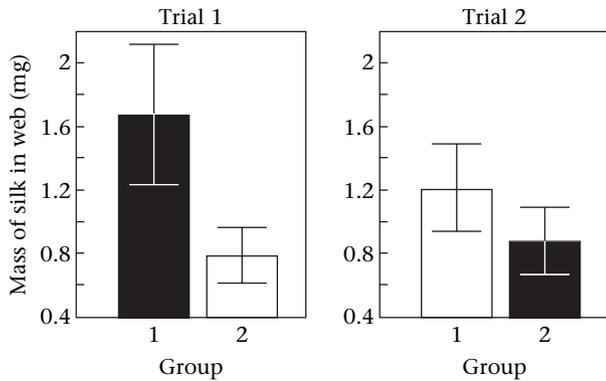
mass:  $t_{13} = 5.4$ ,  $P < 0.0005$ ; body condition:  $t_{13} = 5.4$ ,  $P < 0.0001$ ; Fig. 3). Conversely, spiders in group 2 lost body mass and condition as they were fasted (body mass:  $t_{18} = -2.4$ ,  $P < 0.05$ ; body condition:  $t_{18} = -6.0$ ,  $P < 0.00001$ ; Fig. 3). When the feeding regimes were reversed in the second trial, these trends also reversed. Spiders in group 1 displayed a significant decrease in both body mass and condition as they were fasted (body mass:  $t_8 = -2.5$ ,  $P < 0.05$ ; body condition:  $t_8 = -2.7$ ,  $P < 0.02$ ; Fig. 3). Conversely, spiders in group 2 increased body mass and condition after being fed for 6 days (body mass:  $t_{14} = 4.1$ ,  $P < 0.001$ ; body condition:  $t_{14} = 4.1$ ,  $P < 0.001$ ; Fig. 3).

### Web Architecture

During trial 1, spiders in group 1, which were fed, spun significantly more silk than spiders in group 2, which were fasted (Student's *t* test:  $t_{30} = 2.78$ ,  $P < 0.01$ ; Fig. 4). When feeding regimes were reversed during trial 2, there was no significant difference in silk production between the two groups of spiders ( $t_{24} = 1.35$ ,  $P = 0.4$ ; Fig. 4), although spiders in group 1 spun significantly less silk than when they were previously fed (paired *t* test:  $t_8 = 2.5$ ,  $P < 0.05$ ). However, the difference between groups in the amount of silk in webs could be largely explained by the effects of feeding on body mass (ANOVA:  $F_{1,29} = 23.0$ ,  $P < 0.0005$ ; Fig. 5). An ANCOVA revealed that body mass was a significant predictor of mass of silk spun ( $F_{2,29} = 18.2$ ,  $R^2 = 0.53$ ,  $P < 0.00001$ ), but that feeding

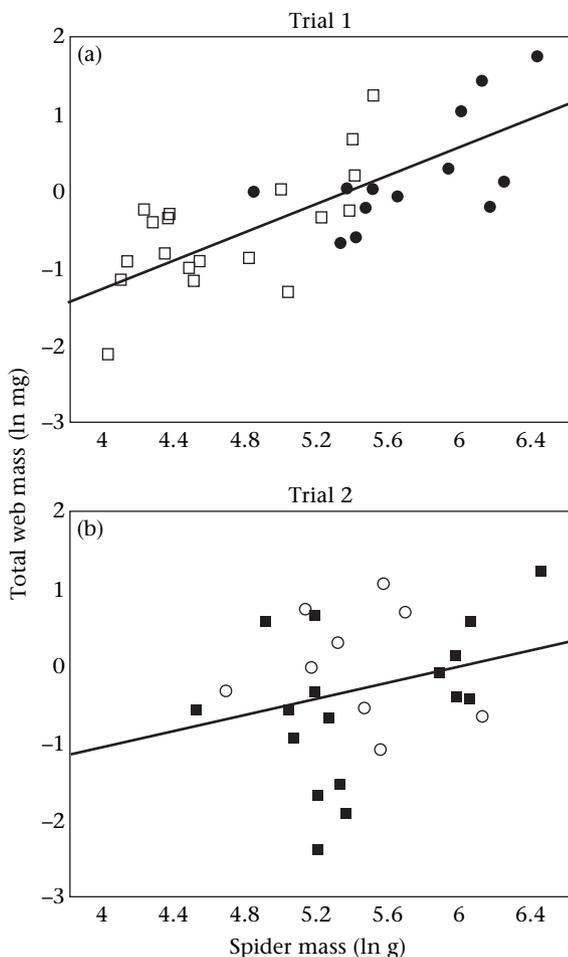


**Figure 3.** Change in (a) body mass and (b) body condition of spiders ( $\bar{x} \pm SE$ ). ○, ●: group 1; □, ■: group 2; ●, ■: spiders that were fed for the preceding 6 days; ○, □: spiders that were fasted.



**Figure 4.** Mean  $\pm$  SE mass of silk spun by spiders in groups 1 and 2 during trials 1 and 2. Spiders in each group were either fed (■) or fasted (□) during the 6-day trial.

regime per se did not influence the amount of silk spun when body mass was incorporated into the model for trial 1 ( $F_{2,23} = 2.1$ ,  $R^2 = 0.08$ ,  $P = 0.15$ ; Fig. 5). During trial 2, mass of silk was unrelated to either feeding regime or body mass.



**Figure 5.** Effect of body mass on total mass of silk in webs during (a) trial 1 and (b) trial 2. ○, ●: group 1; □, ■: group 2. ●, ■: spiders that were fed for 6 days prior to collection of webs; ○, □: spiders that were fasted.

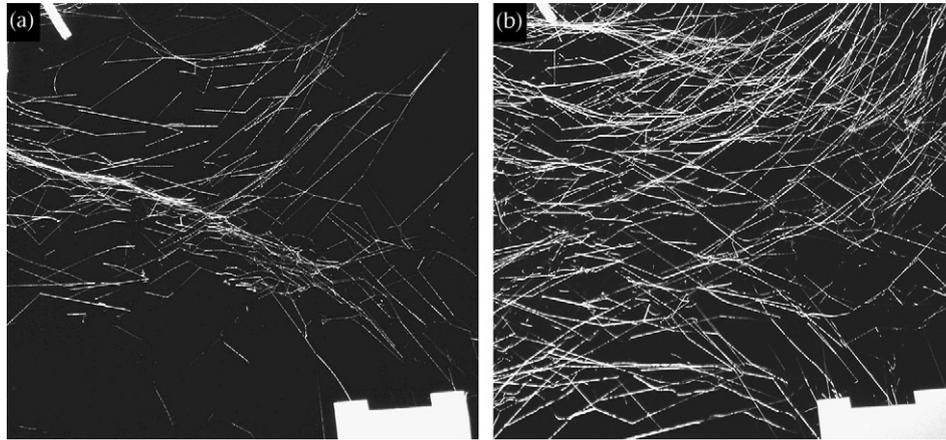
In addition to sometimes spinning more silk, black widows that were fed also changed how they invested silk in different elements of cobwebs. Starved spiders spun webs that had well-defined sheets of silk with many sticky gumfooted threads suspended beneath the sheets (Fig. 6a). In contrast, spiders that were fed increased investment in the supporting threads. In many cases, webs spun by fed spiders contained more silk than those spun by fasted spiders, but these webs lacked both defined sheets and sticky gumfooted threads (Fig. 6b).

We used digital analysis of the web photographs taken at the end of each trial to quantify these changes in the investment of silk within different elements of the webs. We first tested the utility of our measures of optical density of silk in photographs (i.e. total whiteness) to accurately predict mass of silk by comparing the actual total mass of silk collected from webs during trial 1 and the measures of total optical densities of silk from photographs. There was a high correlation between these two measures (linear regression:  $F_{1,30} = 126$ ,  $R^2 = 0.8$ ,  $P < 0.0001$ ), indicating that optical density could be used to accurately quantify the amount of silk invested in webs.

We then used Mann–Whitney  $U$  tests to compare the proportion of silk invested in capture sheets between feeding regimes (Fig. 7). For cobwebs constructed during the 6 days of each feeding regime, spiders that were fed tended to invest a lower proportion of silk in capture sheets than in the rest of the web, although this tendency was never statistically significant. However, the same analysis conducted on webs that were freshly spun over 2 days at the end of each feeding trial did show significant differences between feeding regimes (Fig. 7). Starved spiders invested more silk in capture sheets than did fed spiders both during trial 1 (Mann–Whitney  $U$  test:  $U = 3.87$ ,  $N_1 = 18$ ,  $N_2 = 14$ ,  $P < 0.0001$ ) and after feeding regimes were reversed during trial 2 ( $U = 2.42$ ,  $N_1 = 17$ ,  $N_2 = 9$ ,  $P < 0.25$ ). Furthermore, the proportion of sticky gumfooted threads in these freshly spun webs differed strongly between spiders that were fed and starved ( $G$  tests for goodness of fit: trial 1:  $G_1 = 20.71$ ,  $P < 0.00001$ ; trial 2:  $G_1 = 18.23$ ,  $P < 0.00005$ ). More than 75% of webs spun by starved spiders included sticky gumfooted threads during both trials, while fewer than 25% of webs spun by fed spiders included these gluey capture threads.

### Silk Mechanics

We also collected samples of silk from webs of spiders to examine the structural and material properties of the silk. These samples were taken from the sticky gumfooted threads of webs that were spun over the 2 days following each feeding trial to ensure that the silk was fresh and spun by spiders only after they had experienced the full feeding regime. Because sticky gumfooted threads were rarely spun by fed spiders, our sample sizes for fed spiders were relatively low. Fed spiders spun 38% thicker sticky gumfooted threads (Student's  $t$  test:  $t_{15} = 2.5$ ,  $P < 0.05$ ) than fasted spiders. However, when spider mass was included in the model, feeding treatment was no longer a significant predictor of thread diameter



**Figure 6.** Architecture of cobwebs spun by fed and fasted spiders. (a) Fasted spiders constructed webs emphasizing prey capture elements, such as well-defined sheets with many sticky gumfooted threads suspended beneath the sheets (not visible). (b) Fed spiders often spun webs that lacked prey capture structures and instead filled the available space with a highly three-dimensional matrix of supporting threads. The notch in the white scale is 2 cm.

(ANCOVA:  $F_{2,14} = 16.3$ ,  $P < 0.001$ ,  $R^2 = 0.70$ ; mass:  $F_{1,14} = 19.5$ ,  $P < 0.001$ ; treatment effect:  $F_{1,14} = 0.4$ ,  $P = 0.5$ ). Fed spiders spun marginally significantly thicker threads during trial 2 (Student's  $t$  test:  $t_8 = 1.1$ ,  $P = 0.06$ ). Again, when spider mass was included in the model, feeding treatment was no longer a significant predictor of thread diameter (ANCOVA:  $F_{2,7} = 7.9$ ,  $P < 0.025$ ,  $R^2 = 0.69$ ; mass:  $F_{1,7} = 7.1$ ,  $P < 0.05$ ; treatment effect:  $F_{1,7} = 1.6$ ,  $P = 0.2$ ).

The mechanical behaviour of the silk was similar to that described in previous studies of *L. hesperus* silk (Table 1; Blackledge et al. 2005b, c; Hu et al. 2006). We used MANOVAs to test for differences between fed and fasted spiders and found no difference between them in the material properties of the gumfooted threads spun during trial 1 (MANOVA:  $F_{4,11} = 2.7$ ,  $P = 0.08$ ) or trial 2 ( $F_{4,5} = 1.6$ ,  $P = 0.3$ ).

## Reproduction

Both groups of spiders received the same total amount of food during the experiment. However, the reproductive success of spiders in group 1, which were fed early in the experiment, was far greater than that of spiders in group 2, which were fed late in the experiment (Fig. 8). Of the 14 spiders in group 1, 43% produced a total of nine egg sacs, while only one spider in group 2 produced a single egg sac. Most of the spiders that produced egg sacs did so during trial 2, when they were being fasted. However, three spiders reproduced during the 6 days of the first feeding regime.

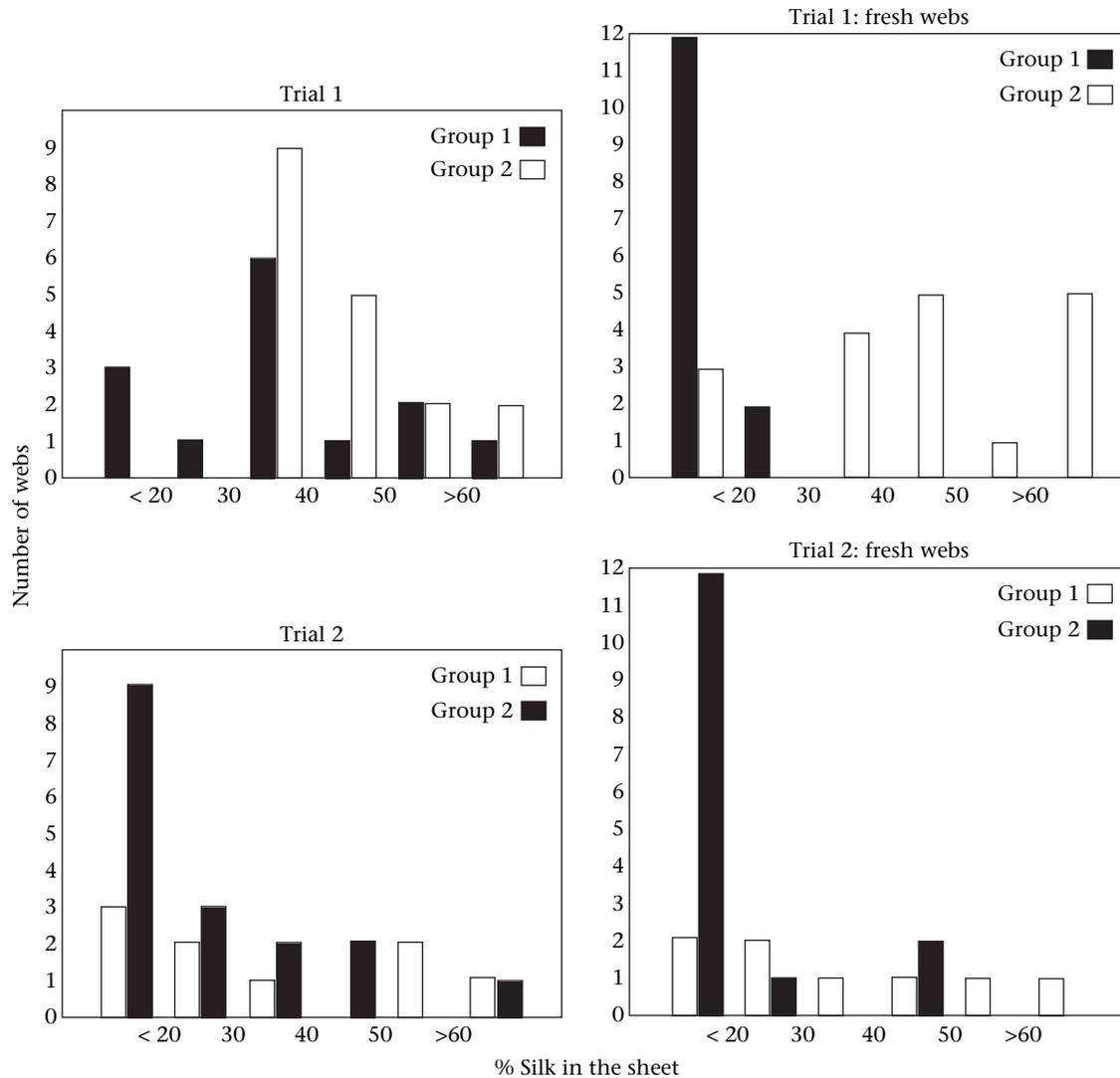
## DISCUSSION

Our study demonstrates that the western black widow changes its web-spinning behaviours in response to variation in prey capture. In particular, spiders that were sated reduced investment in regions of the web that were related to prey capture, even though they maintained or even increased the total amount of silk that they produced in

webs. This result is in contrast to earlier studies on orb-weaving spiders, which suggested that sated spiders spin smaller webs than fasted spiders (Sherman 1994; Tso 1999). In many cases, fed black widows spun cobwebs that had almost no potential to capture prey, because the webs lacked sticky gumfooted threads, the adhesive elements of cobwebs, as well as the defined sheet structure upon which spiders manoeuvre when attacking prey. Instead, fed spiders spun webs with large numbers of supporting threads that filled the space immediately in front of the retreats (Fig. 6b). This result indicates that the sated spiders did not reduce investment in prey capture structures to save the material and metabolic costs associated with spinning silk. Instead, sated spiders actively reallocated silk resources towards other structural elements within the cobwebs and in many cases increased their total energetic investment in silk in webs.

We hypothesize that the reallocation of silk resources into supporting thread structures in the cobwebs of fed spiders increases the defensive value that three-dimensional webs can have for spiders. By surrounding themselves with a matrix of silk threads, black widows may physically isolate themselves from potential predators and also receive early warnings of attacks from vibratory signals transmitted through the silk (Blackledge et al. 2003). Thus, we suggest that sated black widows are trading off different functional aspects of cobwebs, depending upon their energetic state. When starved, spiders construct webs containing large numbers of sticky gumfooted threads, which maximizes the potential to capture prey but leaves the spiders more vulnerable to predators. In contrast, sated spiders probably benefit more from avoiding predators than from capturing additional prey, and therefore spin webs that maximally fill the space between their retreats and the external environment with protective silk threads.

There are several ways in which orb-weaving spiders show behavioural plasticity in web spinning that seem to be related to physiological state, including the addition of structures such as barrier webs or stabilimenta to orb webs (Higgins 1990; Blackledge 1998a; Watanabe 1999;



**Figure 7.** Investment of silk in the capture sheets of webs relative to the total silk in webs. Data are shown both for webs that were constructed during the 6 days of the feeding regime for each trial (left) and for webs that were newly constructed over the 2 days following the feeding regime (right). ■: spiders that were fed for 6 days during a trial; □: spiders that were fasted.

Herberstein et al. 2000; Baba & Miyashita 2006). In addition, spiders can alter the shapes of orb webs in response to changes in their environment (Sandoval 1994; Schneider & Vollrath 1998; Nakata & Ushimaru 1999). In a classic study, Sherman (1994) found that *Larinioides cornutus* spun smaller orb webs after capturing prey than when starved. A similar pattern has since been found for other species of orb-weaving spiders (Tso 1999; Herberstein et al. 2000), suggesting that many orb-weaving spiders may trade off investment of silk in webs with either growth or reproduction. Alternatively, this reduction in web size by larger spiders could reflect the increased energetic costs of web spinning incurred by their heavier bodies (Venner et al. 2006). Regardless, these studies only examined the overall shapes of webs and never directly quantified the amount of silk in webs, thereby ignoring the possibility that sated spiders were maintaining high foraging effort by spinning webs that were small in area but that were spun from thicker silk threads.

In contrast to orb-weaving spiders, a study of a sheet-web weaving spider (*Frontinellina* cf. *frutetorum*), within the same evolutionary lineage as *Latrodectus hesperus*, found that food-supplemented spiders increased their foraging effort by spinning larger webs (Segoli et al. 2004). However, studies on more distantly related taxa of spiders have found either no effect of food supplementation on sizes of webs (*Dictyna volucris*; Blackledge & Wenzel 2001b) or a reduction in the sizes of webs by food-supplemented spiders (*Stegodyphus lineatus*; Pasquet et al. 1999). Again, these studies did not measure investment in silk per se, but rather focused on sizes and shapes of webs. In our experiment, we directly quantified the amount of silk that black widows invested in cobwebs. In contrast to studies on orb-weaving spiders, we found that sated black widows invested more silk in cobwebs than did starved spiders, at least in part because sated spiders spun substantially thicker silk threads. But, the most striking effect of foraging success on web architecture was that fed spiders almost completely stopped investing silk

**Table 1.** Mechanical properties ( $\bar{X} \pm SE$ ) of silk spun by fed and fasted black widow spiders

	Diameter of single fibre ( $\mu\text{m}$ )	Young's modulus (GPa)	Extensibility (ln (mm/mm))	Tensile strength (MPa)	Toughness (MPa)
<b>Day 8</b>					
Group 1 (N=3)*	3.30 $\pm$ 0.42	10.8 $\pm$ 0.6	0.46 $\pm$ 0.04	1955 $\pm$ 84	360 $\pm$ 42
Group 2 (N=13)	2.41 $\pm$ 0.14	13.3 $\pm$ 0.7	0.38 $\pm$ 0.01	2088 $\pm$ 85	336 $\pm$ 13
<b>Day 16</b>					
Group 1 (N=6)	2.56 $\pm$ 0.23	12.4 $\pm$ 0.9	0.38 $\pm$ 0.03	2122 $\pm$ 144	343 $\pm$ 23
Group 2 (N=4)*	3.21 $\pm$ 0.70	11.9 $\pm$ 1.1	0.38 $\pm$ 0.01	1985 $\pm$ 41	319 $\pm$ 15

Data were averaged for five samples of silk from each spider's web.  
\*The group was fed for 6 days before data collection.

in features of webs that are critical to prey capture, the sheets upon which spiders manoeuvre and the sticky gumfooted threads that adhere to prey. Future efforts to understand the foraging strategies of web-building spiders must incorporate information about both the structures of silk threads and how those threads are arranged within webs.

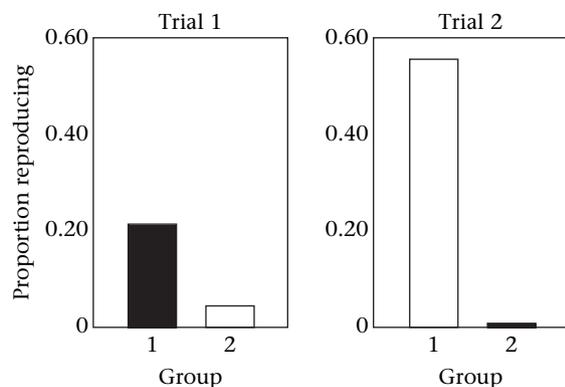
In addition to changes in how silk resources are allocated within cobwebs, we also found evidence for a potential direct trade-off between investment in the silk of webs and production of egg sacs. All of the six heaviest spiders in group 1 reproduced during the experiment (Fig. 5a). However, three of these spiders produced egg sacs during the trial 1 feeding regime, while the other three spiders produced egg sacs only during the trial 2 fasting regime. There was no difference between the body mass of the three spiders that reproduced at the end of trial 1 and the body mass of the three spiders that reproduced during trial 2 (Student's *t* test:  $t_4 = 0.47$ ,  $P = 0.6$ ). Body condition also did not differ ( $t_4 = 0.41$ ,  $P = 0.7$ ). However, the three spiders that reproduced during trial 2 spun four times more silk in their webs during trial 1 ( $4.2 \pm 0.9$  mg) than did the three spiders that reproduced during trial 1 ( $1.1 \pm 0.1$  mg) ( $t_4 = 3.6$ ,  $P < 0.025$ ). This suggests that the spiders that produced egg sacs during trial 1 reallocated some energetic and protein resources away from spinning webs and into the production of egg sacs, thereby allowing them to maintain body conditions similar to spiders that had not yet reproduced. A similar trade-off between protein resources allocated to construction of webs versus production of eggs

and spinning of egg sacs has also been suggested for orb-weaving spiders (Higgins 1990; Sherman 1994).

Spiders spun thicker silk threads when they were fed during both trials (Table 1). This increase in the diameter of silk threads could partly explain why heavier spiders spun a greater mass of silk overall. Two lines of evidence suggest that the increase in thread diameter was a direct response to changes in body mass. First, a similar increase in thread diameter has been induced in orb-weaving spiders by adding artificial weights to their bodies (Vollrath & Köhler 1996). Second, increases in the diameters of draglines spun from major ampullate silk can be closely correlated with changes in the mass of spiders as they mature, which probably tunes the strength of draglines to support the body weight of falling spiders (Osaki 1996).

In contrast to the structural change in the diameters of silk threads, we found little evidence for any physiological effect of prey consumption on the material properties of the silk (Table 1). This result suggests that black widows may be limited in their ability to respond to the environment through physiological changes in the material properties of silk, but that they can respond behaviourally with relative ease by manipulating the structures of silk threads (i.e. diameter) and how those threads are attached together (i.e. web architecture). Indeed, the increased diameters of threads spun by fed spiders could greatly affect the performance of webs. The amount of force needed to rupture a fibre scales linearly with cross-sectional area. Therefore, even when fibres are spun from silk with identical material properties, the larger diameters of threads spun by fed black widows would increase the amount of force required to break those threads by 225% relative to those of spiders in the fasted group, simply because of their larger size. Thus, the increased strength of webs spun by fed black widows would not only support the bodies of spiders but also resist predators or capture particularly large or strong prey.

The fitness consequences of these changes in the architectures of webs spun by black widow spiders have yet to be quantified. However, the reallocation of silk from sheet and sticky gumfooted threads to supporting thread elements within cobwebs seems consistent with a reduction in foraging effort and an increase in predation risk avoidance. Black widows make this change in web architecture after capturing large amounts of prey and as they are preparing to reproduce, both times when the spiders can most afford reduced prey capture and would most benefit from



**Figure 8.** Proportion of spiders that reproduced during the two experimental trials. ■: spiders that were fed daily during the 6-day trial; □: spiders that were fasted.

enhanced protection. In addition to identifying some of the proximate factors associated with behavioural plasticity, our results emphasize that spider webs cannot be considered in the context of foraging alone. Instead, the architectures of spider webs reflect many selective pressures in the environment, the effects of which may also change depending on the physiological status of the spiders.

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