Western black widow spiders express state-dependent web-building strategies tailored to the presence of neighbours

MAXENCE SALOMON
Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University

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Web-building spiders are territorial animals whose webs serve several purposes including foraging, reproduction and protection. Two factors are predicted to be of primary importance in determining a spider’s web-building strategy: (1) current nutritional state (a function of prior feeding rate), which determines the net value of a web, and (2) the presence of co-occurring spiders with whom it may have to interact and partition resources. I conducted a laboratory experiment to test whether western black widow spiders, *Latrodectus hesperus*, express state-dependent web-building strategies that vary with the presence of conspecific or heterospecific (*Tegenaria agrestis* and *T. duellica*) spiders in a microhabitat. I maintained *L. hesperus* females on two different diets (high- versus low-food) and tested their web-building behaviour in the presence or absence of neighbours. When sharing a microhabitat with cons- or heterospecific spiders, *L. hesperus* increased their web-building investment by producing higher-density webs containing more silk and by initiating web-building sooner. Web building was further influenced by nutritional state, such that well-fed spiders produced more silk and built denser webs than their poorly fed counterparts. Furthermore, microhabitat occupancy level and nutritional state showed a combined effect on the different components of web-building behaviour in *L. hesperus*. I discuss how this behavioural plasticity might optimize microhabitat settlement investments in the context of constraints on web-building activities imposed by nutritional state and cohabitation.

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Behaviours involved in the discrimination and usage of habitat components are fundamental attributes of an animal’s ecological niche. Habitats are often spatially and temporally heterogeneous, so it is essential that an animal select a suitable microhabitat in which to settle. In fact, this choice can have a major effect on several factors involved in determining an individual’s fitness, such as energy uptake, biotic interactions and reproductive output (Stamps 2001). The ability to distinguish and select among different microhabitats is contingent on the use of specific cues that provide information about the potential costs and benefits of a particular location, such as resource availability or the presence of other occupants. Use of such cues allows individuals to decide how much time and energy to invest when settling into a microhabitat. Assuming that individuals seek to maximize their fitness returns from residing in a microhabitat, they should also adjust settlement investments according to their current condition; an individual’s condition may constrain the duration or intensity of its activities during the establishment process or influence its motivation to perform these activities (Carriere & Roitberg 1996; Cuthill & Houston 1997; Bilde et al. 2002). Settlement strategies should therefore reflect an integration of perceived microhabitat suitability and an individual’s condition.

Web-building spiders are useful model organisms with which to investigate settlement decisions, because the structural properties of their webs provide a convenient measure of their investment into a microhabitat over a particular time period.

Many environmental factors influence web building, and by extension web structure, such as prey availability (e.g. Pasquet et al. 1994), prey type (Sandoval 1994; Schneider &
Vollrath 1998), the nature of the substrate for web attachment (McNett & Rypstra 2000), temperature (Barghusen et al. 1997) and predation pressure (Li & Lee 2004; Gonzaga & Vasconcellos-Neto 2005). The presence of other microhabitat occupants may also affect a spider's web-building decisions. Incoming individuals may use the webs of resident spiders as anchor points or support threads, thus permitting an economy of silk (Lloyd & Elgar 1997; Jakob 1991), and, in some cases, enhancing prey detection and capture (Uetz 1989). However, sharing a microhabitat with other spiders may depress resource availability and cause territorial disputes involving agonistic behaviours, leading to web eviction or even cannibalism (e.g. Samu et al. 1996). The presence of neighbours may thus serve as an indicator of net microhabitat profitability, and thereby greatly influence a spider’s web-building investment (e.g. Schuck-Paim & Alonso 2001). Few studies have investigated whether the proximity of conspecifics has any effect on a spider’s web-building behaviour, and those that have showed contrasting results: some failed to detect a relation between these two variables (Jakob et al. 1998; Thévenard et al. 2004), while others indicated that individuals living in aggregations with conspecifics modified web size or position, relative to those living in isolation (Leborgne & Pasquet 1987; Herberstein 1998; Harwood & Obrycki 2005). Furthermore, no study to date has explicitly examined the effect of sharing a microhabitat with other co-occurring web-building species on web construction. The balance between the costs and benefits of microhabitat sharing may vary depending on neighbour type. For example, conspecifics have overlapping foraging requirements that would cause them to be competitors, while heterospecifics may instead form predator—prey relationships.

Intrinsic individual parameters also influence web-building behaviour, such as foraging experience (Heiling & Herberstein 1999; Venner et al. 2000; Segoli et al. 2004), age (Opell 1990; Lubin & Kotzman 1991), size (Sherman 1994; Venner et al. 2003), mobility (Nakata & Ushimaru 2004) and nutritional state (Riechert 1981; Lubin & Henschel 1996; Pasquet et al. 1999; Watanabe 2000; Blackledge & Wenzel 2001). A spider’s nutritional state (i.e. its energy level, which is a function of prior feeding rate) is of particular interest, because it is one of the major determinants of body condition. For example, well-fed spiders with large energy reserves reduce their web-building efforts or even refrain from this activity altogether, whereas individuals with low reserves allocate more energy into web construction because of increased hunger, often resulting in larger webs or greater thread densities (e.g. Lubin & Henschel 1996). Such behavioural plasticity is adaptive in cases in which the marginal value of a web varies according to a spider’s nutritional state. However, certain types of webs involve significant building costs (Ford 1977; Prestwich 1977; Tanaka 1989), so a spider may be constrained in its ability to behave adaptively. Moreover, spider webs may serve several purposes, in which case the relation between nutritional state and web-building effort is not always clear.

I investigated microhabitat settlement strategies in the western black widow spider, Latrodectus hesperus, which builds spatially and temporally persistent cobwebs used concurrently for prey capture, protection and reproduction (personal observation). In particular, I examined the combined influence of nutritional state and the presence of neighbours on web-building behaviour. Because web building is a costly activity, an individual’s investment into web construction is expected to be correlated with its nutritional state. Furthermore, if the presence or absence of established spiders in a microhabitat is perceived by L. hesperus as a critical indicator of its future fitness in that site, incoming individuals may adopt specific web-building tactics that allow them to profit maximally from potential interactions with neighbours. To test the hypothesis that web-building strategies in L. hesperus depend on nutritional state and the presence of neighbours, I designed a laboratory experiment that examined whether females (1) showed state-dependent web-building strategies and (2) whether these strategies were affected by the presence of other microhabitat occupants (con- versus heterospecific spiders). I maintained individuals under two feeding regimes (high or low), introduced them into novel microhabitats that varied in their level of occupancy and the species of the occupants, and measured their subsequent investments into web construction (i.e. silk production, web architecture, weight loss and extent of building activity). I extend previous findings on state-dependent web-building strategies in spiders by characterizing the specific influence of neighbours in shaping web-building behaviours in L. hesperus, considering both con- and heterospecifics, and provide some insight into the ecology of cohabitation.

METHODS

Study Organisms

Latrodectus hesperus Chamberlin & Ivie (Araneae: Theridiidae) is an orbicularian cobweb weaver found in dry habitats of western North America, from Mexico to southern Canada (Kaston 1970). Females build large, three-dimensional webs close to the ground under pieces of wood or rocks, in rodent burrows or on rocky outcrops. These structurally complex webs are composed of a main tangled component in the centre, attached to the substrate on all sides by long radiating anchor threads. Threads anchored to the ground are supplemented with viscid glue droplets, and serve as prey capture devices (‘gumfooted lines’; see Benjamin & Zschokke 2003). These intricate webs are built over several nights and are used to intercept ground-active arthropods (M. Salomon & S. Vibert, unpublished data). Unlike some orbicularian spiders, L. hesperus females do not recycle and usually do not replace their webs, but instead repair or expand them as necessary. Cobwebs are thus enduring structures, on which adult spiders remain to forage and reproduce. Coastal British Columbia populations of L. hesperus often co-occur with two abundant nonorbicularian web-building species: Tegenaria agrestis Walckenaer, the hobo spider, and T. duellica Simon, the giant house spider (Araneae: Agelenidae). These non-native spiders build funnel-webs close to the ground on the underside of
Spider Collection and Rearing

For this experiment, *L. hesperus* females were reared from egg sacs produced in the laboratory by 17 mated adult females collected from a beach close to Cordova Spit, Saanichton, on Vancouver Island, British Columbia, Canada. All egg sacs produced (2–4 per female) were individually transferred to new dishes to allow spiderlings to emerge in isolation from their mothers. Upon hatching, spiderlings were kept together and fed *Drosophila melanogaster* prey ad libitum. After their third or fourth moult, surviving spiderlings were hosed individually and fed one blow fly (*Phaenicia sericata*) twice weekly. Once females reached the penultimate stage, they were fed four blow flies per week until their final moult to maturity, after which they were fed according to the experimental diets described below (see Feeding Regimes).

Adult female *T. agrestis* and *T. duellica* were collected from the same field location, kept in Plexiglas cages (14 × 14 × 14 cm) and fed twice weekly with blow flies. For the purpose of this experiment, *T. duellica* and *T. agrestis* were used indiscriminately because they form similar associates with *L. hesperus*. Where all three species co-occurred, field observations suggest that both species build structurally undistinguishable funnel-webs in similar locations and that adult females of either *Tegenaria* species are found during the period when female adult *L. hesperus* are most active (May–October; M. Salomon & S. Vibert, unpublished data). All spiders were maintained on a reversed 16:8 h light:dark cycle at 29 ± 1°C and 40 ± 5% RH.

Feeding Regimes

To determine whether nutritional state influences web-building behaviour in *L. hesperus*, I randomly assigned adult virgin females to one of two feeding regimes: high or low food. Females on the low-food diet (*N* = 36) received one blow fly every 12 days and those on the high-food diet (*N* = 33) received two blow flies every other day (mean blow fly weight ± SE = 30.797 ± 1.258 mg, *N* = 112). Thus, there was a seven-fold difference in feeding rate between diet groups; spiders on the high-food diet were close to satiation, whereas those on the low-food diet were food-limited but not starving. All spiders were provided with water ad libitum. Prey were placed directly onto the spiders’ webs to be consumed. I verified that all spiders had captured their prey items within 6 h; any prey that was still alive was grasped with tweezers and carefully presented to the spider until it started to wrap it in silk. Prey wrapping always led to prey capture and consumption. Spiders were maintained for 3 weeks on one of the feeding regimes before initial testing. Experimental trials using poorly fed spiders were run 12 days postfeeding and those using well-fed spiders were run 1 day postfeeding. There was no significant difference in size between spiders from the two feeding regimes (mean ± SD tibiapatellar length for the first pair of legs: well fed: 6.461 ± 0.371 mm; poorly fed: 6.426 ± 0.433 mm; Student’s *t* test: *t* = −0.366, *P* = 0.716). All spiders used as cues in the experiment (both *Tegenaria* spp. and *L. hesperus*; see Experimental trials) were well fed (i.e. two blow flies every second day) except when in the experimental units. Some test spiders within each diet group shared the same mother, but all spiders were from different egg sacs. *Latrodectus hesperus* test and cue spiders housed together in an experimental unit (see Experimental trials) always had different mothers.

Experimental Procedure

Apparatus

Each experimental unit consisted of a 75-cm-long section of black PVC tubing (inner diameter: 9 cm) cut in half longitudinally, and divided into three chambers (length: 25 cm) by means of rigid metal meshing (mesh size: 2 mm). Each unit thus had one central chamber surrounded by two side chambers. The meshing prevented spiders from moving between chambers, while still allowing spiders to reach inside and contact any silk webbing or individuals present in the adjacent chambers. The sides and base of the half-tubes were closed off with black synthetic meshing, and construction paper was fitted onto the inside walls of each chamber to provide a rough surface for web attachment (I used black paper to achieve contrast with the silk). To allow monitoring of web-building behaviours, the experimental units were placed on railings at eye level and all observations were taken from below, through the synthetic meshing covering the base. Preliminary trials confirmed that spiders readily settled and built webs in these chambers, which I was able to observe.

Experimental trials

To investigate web-building behaviours in *L. hesperus*, I conducted a 2 × 3 factorial experiment testing the relative influence of microhabitat occupancy and nutritional state. Test spiders kept on one of the two diets were introduced into the central chambers of PVC units whose adjoining chambers were either: (1) empty (control treatment), (2) occupied by one female conspecific, or (3) occupied by one female *Tegenaria* spider. Each spider was used three times, once for each occupancy treatment, and the order of treatments was randomly chosen for each spider. Consecutive trials using the same spider were separated by at least 12 days, during which time the test spider was kept on its original web in the feeding dish. ‘Cue’ spiders were introduced to the side chambers 5 days before a trial to allow settlement and the construction of a web, which I humidified every 2 days by spraying water through the meshing. These spiders were only used once. Furthermore, I used only those experimental units in which cue spiders had established a web in both of the side chambers, and whose silk threads were anchored to the metal partition...
separating them from the middle chamber. Test spiders were introduced into the units at 1200 hours, corresponding to the beginning of the dark cycle when they are most active, and allowed to settle and lay silk for 24 h. Trials were run under the same lighting, temperature and humidity conditions as for rearing (see Spider collection and rearing). Spiders were not fed while kept in the experimental units, to avoid the potentially confounding effects of prey presence on their web-building behaviours.

To establish a baseline value of weight loss for both well-fed and poorly fed L. hesperus females, laboratory-reared adult females were individually housed in petri dishes for 25 days and their body weight was compared on two consecutive days (days 25 and 26). Twenty-nine females were tested under each of the two feeding regimes outlined above (see Feeding regimes), for a total of 58 spiders. There was no significant difference in spider size between the two groups (Student's t-test; $t_{56} = -0.163, P = 0.871$). Spiders were placed inside new dishes and allowed to settle and build a web (humidified every second day) for 25 days. On day 25, I delicately removed spiders from their webs and weighed them to the nearest 0.1 mg, placed them back onto their webs for 24 h and reweighed them. In these dishes, L. hesperus females usually attach most of their webbing to the underside of the lid and build only a few gumfooted lines, which they anchor to the bottom. To minimize web damage, I used only those females that had built most of their web on the underside of a lid; thus, when removing spiders for weighing purposes, most if not all of their webs stayed intact, owing to the extensibility and high tensile strength of their capture threads (Blackledge et al. 2005). Spiders generally did not lay any silk within 2 h of the first weighing. Changes in weight result from either losses due to movement and metabolic maintenance or gains due to fluid absorption.

Data Recording

Web-building activity

To assess differences between treatments in spiders’ time to onset of web construction, I conducted hourly observations during the entire dark phase of the experiment and the first 2 h of the light phase. Preliminary trials confirmed that spiders laid silk almost exclusively during the dark phase of their cycle. The central chamber of each experimental unit was marked off into three equally sized subdivisions ($8.3 \times 11$ cm) along its length. Every hour I watched each unit for 2 min under red light (monochromatic red filters were fitted onto desk lamps with red light bulbs; white light disrupts the normal web-building process; personal observation), and rated the amount of silk present in each subdivision on a categorical scale: 0 = no silk present; 1 = spun fewer than 10 threads; 2 = spun at least 10 threads (these categories were chosen based on preliminary testing). Spiders were considered to have started building a web when one of the subdivisions contained at least 10 threads (i.e. category 2). When fewer threads were present, they were generally laid at random, without forming a web-like structure, and were used as support strands for resting. Therefore, these threads may not be considered indicative of the onset of web construction.

Material investment and web design

To examine whether test spiders modified their web-building investment (in terms of silk production and web design) under different feeding regimes and levels of microhabitat occupancy, I measured both the thread density and weight of each silken structure at the end of the trials (i.e. after test spiders had been removed). Thread density was determined by fitting a fine metal wire, three to six times, through a web in each of three orthogonal directions, and counting the number of silk strands that touched the wire, following the method of Rypstra (1982). I first sprayed each web with water to increase its visibility, and then ran wires in each of three directions: first, longitudinally (down the length of a chamber at mid-height), by introducing a 25-cm wire through the gaps in the metal meshing (three readings: one at the 1/4, 1/2 and 3/4 marks along the chamber’s width); second, vertically, in each of the three subdivisions using a 5.5-cm wire (six readings: one at each 1/4 and 3/4 mark of each subdivision along the longitudinal midline); third, through the cross section, by placing a 9-cm wire on the bottom of the web (five readings: one in the centre of each subdivision and one adjacent to each metal partition). The mean number of threads/cm was calculated for each of the three directions, and these were then multiplied together to obtain a global density value, expressed as the number of threads/cm$^3$. Subsequently, the silk was harvested by carefully winding the silk threads onto a glass rod, which were then dried in an oven at 60°C for 72 h, and weighed to the nearest 0.001 mg on a microbalance. Because of the physical constraints imposed by the walls of the chambers, this study did not allow for an exact assessment of the effect of the treatments on web size. However, I was able to examine gross differences in colonization of the available space (i.e. web size) between treatment groups by counting the number of chamber subdivisions containing silk at the end of a trial.

Energetic cost of web construction

To assess the energetic costs associated with web building, I calculated changes in spider weight and body condition (using an index; see below) and compared them across treatment groups. Before their introduction into the central chambers, I weighed all test spiders to the nearest 0.1 mg, and measured the combined length of the tibia and patella of their first pair of legs using callipers (precise to 0.01 mm), as an index of size. Spiders were then reweighed after the trials to determine the amount of weight lost during the experiment. Weight loss values were used as indicators of individual investment into web building, both in terms of silk production and web construction. Body condition was represented by an index value defined as a test spider’s residual from a regression of weight over size (both variables log-transformed) using data for all test spiders; two regressions were performed, with weight values from before and after the experiment,
respectively. Differences between initial and final body condition were compared between treatment groups.

Data Analysis

Parametric tests were used when the distribution of the data did not deviate significantly from normality (Shapiro–Wilk’s test: \( P > 0.05 \)), and nonparametric tests were used otherwise; raw data were transformed where appropriate. With respect to web-building activity, I assessed the influence of diet and microhabitat occupancy level on the time to onset of web construction by means of survival analysis, using the Cox regression method (Hosmer & Lemeshow 1999). I also assessed differences in the proportion of spiders with webs at different time points using Cochran’s Q test when comparing between microhabitat occupancy treatments and log-likelihood ratio tests (with William’s correction; Sokal & Rohlf 1995) when comparing between feeding regimes. To analyse the data on web-building investment (total and net) and its associated energetic costs, I used general linear mixed models (GLMM) with spider identity and mother identity as random factors to account for the lack of independence. I chose the best models using Akaike’s information criterion (see Burnham & Anderson 2002), starting with all factors and interactions. To examine the effect of each treatment on web-building investment (silk production and web design), I used two GLMMs, one with silk mass and another with thread density as response variables. Each model had the following predictors: diet as the between-subject factor, microhabitat occupancy level as the within-subject factor and initial body condition as the covariate. Another GLMM was then applied to evaluate the relationship between thread density and silk mass, using the same factors as in the above models, but including silk mass as a covariate. I also compared the number of subdivisions containing silk between treatments using Mann–Whitney U and Friedman tests. I used two separate GLMMs to test whether web-building costs differed between treatment groups: one with body condition (initial and final) and another with percentage weight loss as the response variable. Each model had diet as a between-subject factor and microhabitat occupancy as a within-subject factor. The body condition models included spider size (tibia–patella length of the first pair of legs) as a covariate, and the weight loss model included initial weight as a covariate. In the control experiment, the baseline values of weight change were compared between diet groups using a t test, and I examined relationships between weight loss and initial weight using linear regression. Finally, I calculated the ratio between silk mass and weight loss as a means of indexing an individual’s relative web-building investment. These ratio values were used as response variables in a GLMM to compare the relative investment between treatment groups, using diet as a between-subject factor, microhabitat occupancy as a within-subject factor and initial condition as a covariate. All statistical analyses were completed with SPSS v. 11 (SPSS, Chicago, Illinois, U.S.A.) following methods from Sokal & Rohlf (1995).

RESULTS

Web-building Activity

The time at which L. hesperus spiders started building a web (i.e. their latency to web construction) differed across microhabitat occupancy treatments but not between the two diet groups, and there was no interaction between these two factors (Table 1). In both diet groups, spiders in empty microhabitats delayed web building relative to when they were kept with conspecifics, but this delay was longer for well-fed spiders (Fig. 1). However, within each diet group, there was no difference in latency between spiders in the conspecific and heterospecific treatments. Most web-spinning activity took place during the first 8 h, when the lights were off and spiders are most active; yet a few individuals started building webs afterwards, especially when housed alone in a microhabitat.

At the end of the dark phase (after 8 h), the proportion of well-fed spiders with webs varied with the level of microhabitat occupancy (Cochran’s Q test: \( Q_2 = 19.200, N = 33, P < 0.0001 \); Fig. 1a): 93.9% of spiders that were sharing microhabitats with either conspecifics had started spinning webs, while only 57.6% of them had webs in the empty treatment. This difference was also apparent after 24 h (\( Q_2 = 12.000, N = 33, P = 0.002 \)), as all spiders in the shared treatments had built a web by then, compared to only 81.8% when housed alone. pairwise contrasts between the empty treatment and each of the two shared treatments were all significant (McNemar’s tests: after 8 h: both \( P < 0.01 \); after 24 h: both \( P < 0.05 \)), but not those between the conspecific and heterospecific treatments (\( P = 1.000 \) after 8 h and 24 h). In the poorly fed group, the proportion of spiders with webs was not significantly different between occupancy treatments after 8 h (\( Q_2 = 3.231, N = 36, P = 0.199; 77.8\% \) versus 88.9% versus 91.7%) or after 24 h (\( Q_2 = 1.600, N = 36, P = 0.449; 91.7\% \) versus 97.2% versus 97.2%). At the end of the trials a few poorly fed spiders in each of the treatment groups had failed to build a web, whereas some well-fed spiders failed to build a web only when housed alone. However, within each microhabitat occupancy treatment, there was no difference between diet groups in the fraction of spiders with webs after 8 h (adjusted log-likelihood tests: all \( P > 0.05 \)) or after 24 h (all \( P > 0.1 \)).

Material Investment and Web Design

There was an interaction between diet and microhabitat occupancy level on the mass of silk produced (GLMM

Table 1. Effect of different predictors on the time to onset of web construction during the 24-h experiment, determined by survival analysis, using the Cox regression method

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>( \chi^2 )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole model</td>
<td>5</td>
<td>36.903</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Feeding regime (FR)</td>
<td>1</td>
<td>0.189</td>
<td>0.664</td>
</tr>
<tr>
<td>Microhabitat occupancy (MO)</td>
<td>2</td>
<td>31.117</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>FR × MO</td>
<td>2</td>
<td>4.790</td>
<td>0.091</td>
</tr>
</tbody>
</table>
with square-root transformed response variable; \( F_{2,133.7} = 4.703, P = 0.011 \). Spiders spun more silk when sharing a microhabitat with con- or heterospecifics than when alone, and this difference was more pronounced in the well-fed treatment (Fig. 2a). In occupied microhabitats, well-fed spiders produced more silk than did poorly fed spiders. Furthermore, individuals with a higher initial body condition produced more silk relative to others (\( F_{1,149.0} = 11.724, P = 0.001 \)). Likewise, the silken structures built by well-fed spiders were denser than those of poorly fed spiders (GLMM with square-root transformed data; \( F_{1,79.1} = 4.902, P = 0.030 \); Fig. 2b), which was also the case for spiders in occupied microhabitats compared to those housed alone (\( F_{2,133.0} = 13.258, P < 0.0001 \)). There was no interaction between these two factors (\( F_{2,132.4} = 0.520, P = 0.596 \)), nor was there any effect of initial body condition (\( F_{1,105.2} = 0.027, P = 0.869 \)). Moreover, there was no difference in either silk mass or thread density between webs spun by spiders housed with con- versus heterospecifics.

As expected, spiders that produced more silk usually built denser web structures, as shown by a positive relationship between thread density and silk mass (GLMM: \( F_{1,142.8} = 73.794, P < 0.0001 \)), which was equivalent across diet groups (\( F_{1,73.5} = 0.852, P = 0.359 \)) and occupancy treatments (\( F_{2,109.7} = 0.403, P = 0.669 \)). This relationship was also greater (with a steeper slope) for spiders with higher initial body condition (condition: \( F_{1,125.1} = 4.764, P = 0.031 \); condition × silk mass: \( F_{1,141.1} = 10.366, P = 0.002 \)).

Within microhabitat occupancy treatments, the number of chamber subdivisions containing silk at the end of the experiment did not differ between diet groups (Mann–Whitney \( U \) test: alone: \( U = 505.5, N_1 = 33, N_2 = 36, \)
In the control trials, where spiders were kept in petri dishes, individuals in both diet groups lost weight over the 24-h period (paired t tests: well fed: $t_{28} = -8.950, P < 0.0001$; poorly fed: $t_{28} = -16.907, P < 0.0001$). However, well-fed spiders lost a larger proportion of their initial weight than did their poorly fed counterparts ($t$ test: $t_{37.451} = -10.036, P < 0.0001$); poorly fed spiders only lost, on average, $0.409 \pm 0.157\%$ (mean $\pm$ SD; range 0.2–0.7\%) of their initial weight, whereas well-fed spiders lost $1.456 \pm 0.648\%$ (range 0.3–2.7\%). For poorly fed spiders, there was an inverse relationship between percentage weight loss and initial weight (linear regression: $F_{1,28} = 10.728, P = 0.003, R^2 = 0.284$), because all spiders lost a similar amount of weight regardless of their initial weight ($F_{1,28} = 0.278, P = 0.603, R^2 = 0.010$). In contrast, there was a positive relationship between percentage weight loss and initial weight in well-fed spiders ($F_{1,28} = 10.588, P = 0.003, R^2 = 0.282$), because larger individuals lost relatively more weight ($F_{1,28} = 30.522, P < 0.0001, R^2 = 0.531$).

**Energetic Cost of Web Construction**

I compared spider body condition between treatment groups by examining the relationship between spider weight and size (both log-transformed). At the time of introduction, well-fed spiders were in better condition than poorly fed ones (GLMM: $F_{1,66.0} = 74.405, P < 0.0001$), regardless of their microhabitat occupancy treatment ($F_{2,136.0} = 0.336, P = 0.715$). Furthermore, spider weight covaried with size ($F_{1,66.0} = 19.949, P < 0.0001$). At the end of the trials, well-fed spiders remained in better condition than those that had been food-deprived (GLMM: $F_{1,66.0} = 71.827, P < 0.0001$), but there were no differences in condition across microhabitat occupancy levels ($F_{2,136.0} = 0.438, P = 0.646$); there was also a positive effect of size ($F_{2,66.0} = 20.513, P < 0.0001$). All spiders experienced a drop in condition over the course of the experiment (paired t tests: $P < 0.0001$ for all treatment groups). Well-fed spiders lost a greater percentage of weight than did poorly fed ones (GLMM with log-transformed response variable: $F_{1,78.7} = 12.932, P = 0.001$; Fig. 3), and spiders in both feeding regimes lost a greater percentage of weight when introduced into occupied microhabitats than when housed alone ($F_{2,107.1} = 3.509, P = 0.033$), an effect inversely correlated with initial weight ($F_{1,98.0} = 15.429, P = 0.0002$). However, there was no interaction between diet and microhabitat occupancy level in determining the percentage weight loss ($F_{2,106.8} = 0.773, P = 0.464$).

**Ratio of Investment to Cost**

A comparison of the ratio between the mass of silk produced and the weight loss associated with web-building activities between experimental treatment groups established that the level of microhabitat occupancy was the sole factor that had an effect on this variable (GLMM: $F_{2,134.6} = 31.309, P < 0.0001$). Spiders introduced into microhabitats with established cons- or heterospecifics produced more silk per unit loss of body weight than those in empty microhabitats (Fig. 4). Neither feeding regime ($P = 0.669$), the interaction between occupancy level and feeding regime ($P = 0.156$), nor initial body condition ($P = 0.803$) influenced this relationship.

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**Figure 3.** Percentage weight loss (least square means $\pm$ 95\% CI) in well-fed (□) and poorly fed (■) *L. hesperus* females, after residing in the experimental units for 24 h at three microhabitat occupancy levels.

**Figure 4.** Least square means (±SE) of the ratio between the quantity of silk mass produced (mg) and the associated loss in body weight (mg) in well-fed (□) and poorly fed (■) *L. hesperus* females subjected to three different microhabitat occupancy treatments.
DISCUSSION

The results of this experiment support the hypothesis that *L. hesperus* females adopt state-dependent web-building strategies when settling into novel microhabitats, and that these strategies are further determined by the presence of con- and heterospecific spiders. Both nutritional state and the presence of neighbours influenced the timing of web construction, as demonstrated by the clear differences between treatments in the latency in onset to web spinning (Fig. 1). Likewise, the diet manipulations had a direct effect on web-building behaviour, causing noticeable variation in web architecture between treatments. Overall, webs of well-fed spiders contained more silk and higher thread densities than those of poorly fed spiders (Fig. 2). These differences between diet groups were greatest for individuals that shared a microhabitat with other occupants, suggesting that *L. hesperus* perceived the presence of both con- and heterospecífics and adjusted their web-building efforts accordingly. However, I found no effect of diet on relative web-building investment (measured as the ratio between silk production and weight loss), but there was an obvious occupancy effect: individuals allocated a larger fraction of their total energy expenditure to silk production when sharing a microhabitat with other spiders (Fig. 4). The web-building behaviour of *L. hesperus* females did not differ when in the presence of con- or heterospecifics. Together, these results allow me to address one of the fundamental questions pertaining to the plasticity in web-building behaviour, which is that of its functional significance. Below, I consider how conflicting demands are managed in *L. hesperus*, and how this translates into strategic web-building behaviours, focusing on the effects of nutritional state and neighbour presence.

**State-dependent Web-building Decisions**

The classical view of optimization theory predicts an inverse relationship between an individual spider’s condition and its web-building effort (viewed as a foraging activity), which has found some support in previous research on the web-building behaviour of a diverse array of spiders (e.g. Araneidae: Sherman 1994; Venner et al. 2000; Agelenidae: Riechert 1981; Eresidae: Lubin & Henschel 1996; Pasquet et al. 1999). Hence, one would expect a spider’s web-building investment, represented here as the structural design of its web (i.e. silk mass, thread density, web size), to be proportional to the balance between the immediacy of its need for a web and the cost of web construction, weighed against its perception of habitat profitability. Contrary to this hypothesis, the results of the present experiment showed that well-fed *L. hesperus* spiders produced heavier and denser webs than their poorly fed counterparts. Two main lines of reasoning may be invoked to account for this positive correlation between feeding status and web-building investment.

First, in natural settings, *L. hesperus* spiders that build webs on the underside of logs (a microhabitat mimicked in this experiment) do not commonly construct a separate retreat, but instead use webs as both a retreat site and a foraging platform (personal observation). In fact, a recent study by Blackledge et al. (2003) provides compelling evidence in support of the hypothesis that three-dimensional webs (such as the cobwebs of *L. hesperus*) have evolved as structural adaptations to predation pressure. The presence of a web may therefore be essential for protective purposes, which may explain why well-fed individuals spent more energy building a web even though their body condition was high. Thus, when a particular structure built by an animal (e.g. a spider’s web) is tied to satisfying multiple needs (e.g. protection versus prey capture), a clear relationship between feeding status and investment into the structure is not necessarily expected. Although the return on investment for each of the possible uses of a web may be state dependent, the relationship describing each of them is likely to follow a different optimization criterion at a given state. For example, a poorly fed spider may be able to maximize its immediate foraging returns at the expense of a small and loosely woven web, whereas well-fed spiders in good condition receive optimal short-term benefits from further web-building investment that contributes primarily to protection through an improved structural design. This multifunctionality argument is consistent with my observation that all of the spiders tested spun some silk threads during the experiment, regardless of their feeding status.

Second, because cobweb weavers usually build their webs over several consecutive nights, and my study only investigated settlement behaviours during the first 24 h, the differences in web-building effort detected at this particular timescale may not necessarily reflect that of an individual’s entire web-building investment. Segoli et al. (2004) found similar results in a study with the sheet-web weaving spider *Frontinella cf. frutetorum*, where experimentally fed spiders maintained a larger web than starved ones over several days. It is likely then that in both *L. hesperus* and *F. cf. frutetorum*, for which web construction is energetically costly and web persistence is high, an adaptive strategy would be to seek a close match between building investment and current nutritional state. However, the reason underlying each of these web-building strategies may differ, because cobwebs and sheetwebs vary in their ability to capture prey or provide concealment. *Latrodectus hesperus* spiders may initially start building a web for protective purposes and progressively expand it to enhance its prey capture potential, while *F. cf. frutetorum* may directly invest into a foraging structure.

The increase in web-building activity of well-fed *L. hesperus* spiders was characterized by the production of more silk and greater thread densities, leading to the enhancement of a web’s three-dimensionality. Previous research has shown that strand density is positively correlated with prey capture rate in other cobweb-weaving spiders (Rypstra 1982; Barghusen et al. 1997). A high-food diet could thus enable a spider to maintain the integrity and prey capture potential of its web, while poorly fed spiders have to trade off a web’s design efficiency against the building costs. However, another very important feature of a *L. hesperus* cobweb that is necessary to achieve prey capture success is the presence of sticky anchor threads (gumfooted lines) at the bottom of a web used to intercept
passing prey (Benjamin & Zschokke 2003). Thus, in *L. hesperus*, an overall increase in the strand density of a cobweb may contribute more to structural resilience and protection against disturbance than to prey capture per se. Although I did not directly quantify the occurrence of gumfooted lines, viscid silk lines were commonly observed on webs spun by both well-fed and poorly fed *L. hesperus* spiders, suggesting that the production of sticky silk is unlikely to be limited by individual condition, at least not on the short term.

Rypstra (1982) measured the thread density of cobwebs spun by several species of Theridiidae (including *L. nactans*) in seminatural settings, and found values that were for the most part several orders of magnitude higher than the ones reported here. As mentioned above, *L. hesperus* spiders, like other theridiids, build their webs over several nights during which they progressively add more silk to the main structure, thereby increasing the density of threads and also web size. In the present study, *L. hesperus* females were confined to a small microhabitat and were only allowed to build a web for 24 h, which is why strand densities were low. However, strand density measurements of cobwebs spun by *L. hesperus* were similar to those reported for *Achaearanea tepidariorum* (Barghusen et al. 1997).

**Influence of Neighbours on Web Building**

An important finding of this experiment is that *L. hesperus* spiders modified their web-building behaviour in the presence of neighbours. In both diet groups, the presence of con- and heterospecifics caused spiders to build webs sooner (within the first few hours); by the end of the dark phase the majority of individuals were in the process of establishing a web. In contrast, spiders delayed web construction when housed alone relative to when they shared microhabitats. However, this delay was much greater for well-fed spiders, suggesting that their requirements for a web were lower than those of poorly fed spiders. Similarly, individuals in the shared treatments increased their silk production and built denser webs covering a larger area relative to the control groups. Although my experimental design did not allow for a precise assessment of the effects of the various manipulations on web size, the size differences observed here may reflect the interdependence of size and strand density in *Latrodectus* cobwebs. The confinement experienced by spiders in this experiment may also have biased their web-building behaviour, since they were not free to abandon a microhabitat if the conditions were deemed unsatisfactory. For instance, the greater delay in web construction shown by spiders that were housed alone, along with their lower material investment, may have been an indication of their willingness to leave. However, this alternative behaviour would not have altered the general conclusion drawn from these data, which is that the presence of neighbours increases a spider’s web-building efforts.

The ability to gather information about the distribution of previously established microhabitat occupants might influence web construction in *L. hesperus* for several reasons. First, their presence may reflect the quality of a particular microhabitat, which could preclude the need for costly habitat sampling and encourage cosettlement by conspecifics (e.g. Stamps 1988; Schuck-Paim & Alonso 2001) or even heterospecifics (e.g. Forsman et al. 2002). Second, because neighbour presence may render interactions and resource partitioning unavoidable, incoming foragers may benefit from rapidly colonizing the available space before it is taken up by others. Furthermore, spiders may build more webbing in occupied microhabitats to compensate for the potential decrease in resource availability caused by the presence of neighbours. In the orb weaver *Zygia x-notata*, constraints on space occupation associated with group living have been shown to lead to the reduction of web size, which in turn may affect foraging success (Leborgne & Pasquet 1987). *Latrodectus hesperus* spiders may also have increased their web-building efforts in the presence of neighbours as a means of limiting potentially aggressive web intrusions from conspecific neighbours. However, field observations of females sharing microhabitats do not provide strong support for this explanation, because females readily move from web to web, and the rate of cannibalism is low (personal observation). Finally, if sharing some of the microhabitat space with other spiders confers a net payoff in terms of energy return or survival, a spider may be more inclined to build a web in an occupied microhabitat. This has typically been observed in colonial spiders that form communal assemblages of individual territories, where spiders benefit from living in aggregations because of the protective, energetic or feeding advantages involved in this form of living (reviewed in Uetz & Hieber 1997). In my experiment, the presence of other spiders close to the openings of the microhabitats may have induced earlier web construction in the shared treatments because of their shielding role against potential predators, as seen in colonial orb-weaving spiders of the genus *Metepeira* (Rayor & Uetz 1990). However, further research is necessary to determine whether the presence of neighbours in a microhabitat provides any fitness benefits to *L. hesperus* females, such as facilitated prey detection, enhanced web resilience or improved protection.

My experimental design was not intended to determine whether *L. hesperus* spiders are able to distinguish between neighbouring individuals and their webs; however, the finding that spiders showed similar web construction behaviours (i.e. timing, silk production and thread densities) in the presence of conspecifics and heterospecifics (*Tegenaria* spp.) suggests that they were cued by the presence of silk in the surrounding chambers rather than by the identity of their occupants per se. The physical barriers between chambers made it difficult for individuals to interact in a ‘normal’ fashion; however, since I used only cue spiders that had attached some silk to the partitions, test spiders were able to make contact with neighbouring webs very easily (i.e. individuals were frequently observed extending their legs through the meshing to reach the other side and touch some webbing). These observations agree with the results of a previous study in an orb-weaving species suggesting that spiders are attracted to the presence of silk (*sericophily*) and settle more readily in microhabitats that contain some silk (Schuck-Paim & Alonso 2001). However, long-term settlement decisions
in *L. hesperus* living in natural settings may rely on both the interaction with neighbouring individuals (which was restricted in the experiment) and their webs.

**Net Energy Investment into Silk Production**

In contrast to the lack of difference in energy allocation across diet groups, the presence of microhabitat occupants caused *L. hesperus* spiders to channel their energy into silk production: spiders housed with con- and heterospecifics increased the fraction of energy allocated to silk production relative to spiders housed alone. The lower investment by spiders that were housed alone is consistent with their longer delay in initiating web construction, because they may have spent a greater share of their energy moving around and exploring the microhabitat before starting to spin a web. This provides further evidence that the presence of neighbours serves as an indicator of microhabitat quality, allowing individuals to rapidly and directly invest their energy into web building, rather than spending it on preliminary related activities such as site exploration. Despite the absence of an effect of diet on energy allocation, well-fed spiders lost a greater percentage of their initial weight during web construction. In the control trials, where spider weight loss reflects the basic metabolic rate under each of the two feeding regimes, weight loss due to basic metabolism averaged 0.4 and 1.5% for poorly fed and well-fed spiders, respectively. However, in the main experiment, spiders in both diet groups lost 2–2.5% of their initial weight. Relative to the values of spiders in the control trials, poorly fed spiders lost six to eight times more weight during the main experiment, whereas well-fed spiders only lost two to three times more weight. Moreover, the amount of weight lost by well-fed spiders in the experimental units was positively correlated with their initial weight, which probably reflects a higher basal metabolic rate for spiders in good condition. Overall, these results suggest that a low-food diet increases the energetic costs of web building, relative to a high-food diet.

In summary, this study provides some of the first empirical evidence showing that a cobweb weaver is capable of modifying its investment into web construction in response to the presence of other spiders, both con- and heterospecifics, when settling into a microhabitat. Moreover, these results highlight the interplay between external environmental factors and intrinsic physiological state in determining an individual’s microhabitat settlement decisions. This plasticity in web-building behaviour allows *L. hesperus* to strategically adjust its web-building efforts according to the associated state-dependent costs and benefits. Further research is needed to determine whether these strategic behaviours confer net fitness advantages to those that express them (i.e. whether they are adaptive), as well as to characterize the specific nature of these benefits.

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**References**


