Mesh Width Influences Prey Retention in Spider Orb Webs

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Abstract

Orb-weaving spiders depend upon the sticky capture spirals of webs to retain insects long enough to be captured. However, insects often escape from orb webs before the spiders can attack them. Therefore, the architectures of orb webs likely reflect strong selective pressure to increase retention times of insects. We experimentally increased the mesh width of one side of an orb web while maintaining the original mesh width on the other side as a control, and then tested the effect of this manipulation on the retention times of four different taxa of insects. We found evidence that increased mesh width of *Argiope aurantia* orb webs resulted in a general reduction in the retention times of insects. However, retention times for different taxa of insects were not predicted by any one specific morphological or flight characteristic. The influence of mesh width on the retention times of insects is very complex, but our results suggest that mesh width can act to selectively favor the capture of certain taxa of insect prey over others. This effect may help to explain both species level differences in web-building behaviors and variation in the architectures of webs spun by individual spiders on different days.

Introduction

Orb webs depend upon elastic spirals of sticky silk to capture flying insects. Supported by arrays of non-sticky radial threads, the sticky spirals of orb webs perform two important functions during prey capture. First, the sticky spirals stretch and absorb the kinetic energy of flying insects through a combination of intermolecular interactions and aerial dampening (Lin et al. 1995; Becker et al. 2003). Second, the sticky spirals adhere to insects, thereby preventing insects from escaping webs before they are captured by spiders (Eberhard 1990; Opell 1997). However, insects exhibit a variety of potential counter strategies that reduce their probability of being captured by spiders (Eisner et al. 1964). For instance, insects can bypass webs completely (Rypstra 1982; Craig 1986). Some insects employ morphological adaptations, such as the scales of moths and butterflies, that allow them to slip free from sticky webs (Eisner et al. 1964; Stowe 1986). Finally, field and experimental observations demonstrate that most insects intercepted by orb webs simply struggle free within a few seconds, long before the insects are captured by spiders (Rypstra 1982; Nentwig 1983; Uetz & Hartsock 1987; Eberhard 1989). Thus, the architectures of webs and the silk used to construct webs likely reflect strong selective pressure to increase the ability of webs to retain insects long enough for spiders to effectively subdue them.

In fact, a major diversification of orb-weaving spiders in the Araneoidea is associated with an evolutionary shift from plesiomorphic cribellate capture silk to the evolutionarily derived gluey capture silk that is used by most modern orb-weaving spiders. This evolutionary shift in capture silk is associated with an increase in the overall stickiness of webs that is hypothesized to increase the potential of webs spun by araneoid spiders to capture prey (Opell 1999).

Spiders can also alter the potential of webs to intercept and retain prey through behavioral changes in how they place sticky silk in the web. In particular, there is variation in the spacing between

individual rows of sticky silk within orb webs at both the species and individual levels (Herberstein & Heiling 1998). Intuitively, it seems obvious that orb webs with narrower mesh widths might function better than larger meshed webs at capturing smaller prey, like an aerial sieve. Alternatively, narrower meshed webs could be predicted to function better at capturing larger prey because the greater amount of sticky silk per area would increase the ability of the web to absorb kinetic energy during interception and increase retention due to the greater stickiness (Chacón & Eberhard 1980; Miyashita 1997). However, webs with widely spaced sticky spirals may benefit spiders by decreasing the overall visibility of webs to potential prey and allowing spiders to fill a given area of an orb web with sticky silk more economically (Chacón & Eberhard 1980; Rypstra 1982). These theoretical arguments clearly suggest that even small changes in mesh width should have profound impacts upon the foraging success of spiders. However, studies attempting to correlate variation in mesh width with the taxa or sizes of prey captured by spiders in the field have yielded very ambiguous and often conflicting results (see Herberstein & Heiling 1998).

One of the strengths of using orb-weaving spiders in behavioral ecology is that orb webs are themselves material manifestations of the behavioral decisions made by spiders (Blackledge 1998; Blackledge & Gillespie 2004). The architectures of webs are also amenable to direct manipulation, allowing highly controlled tests of the consequences of those behavioral decisions (e.g. Blackledge & Wenzel 1999). In this study, we experimentally increased the mesh width of one side of an orb web while maintaining the original mesh width on the other side of the web as a control. We then tested the retention times of four different taxa of insects within the experimental and control sides of webs. This protocol controlled for a variety of confounding factors that have plagued previous studies and allowed us to draw some general conclusions regarding the functional implications of mesh width for prey capture of orb-weaving spiders.

Methods

Spiders and Preparation of Webs

We obtained penultimate and adult female *Argiope aurantia* from Gainesville, FL. Although *A. aurantia* occurs naturally at the Ohio study site, this allowed us to begin the experiment at an earlier date. Spiders were housed in $40 \times 40 \times 10$ cm screen cages with removable plexiglass sides and were misted daily with tap water. We fed spiders every 2–3 d with a variety of insects collected from the surrounding fields.

We tested the effect of mesh width on prey retention by comparing the time that insects stuck in one half of a web that had been manipulated to have twice the spacing between rows of sticky silk relative to the other half of the same web, which still had the original mesh width and functioned as a control. Relative to the spider, we randomly selected either the left or right side of a web for experimental manipulation. We then gently removed the spider from the web and used a soldering iron with a fine wire tip to burn out every other row of sticky silk in the lower half of the experimental side of the web (Fig. 1). We concentrated on the lower halves of the orb webs because they are typically larger and contain more silk than the regions above the central hubs for most spiders (Masters & Moffet 1983; Nentwig 1985; Herberstein & Heiling 1999). Furthermore, more prey capture occurs within the lower halves of orb webs (Nentwig 1985). While this procedure did not remove the sticky silk from webs, it did greatly reduce the volume of viscous material and cause the remaining ends of the viscous threads to ball up tightly on the radii. Because the stickiness of viscous threads is directly related to their volume per thread length (Opell 2002), we believe that our treatment greatly diminished the stickiness of 'removed' threads and closely approximated complete removal of rows of sticky silk. Furthermore, video observation demonstrated that insects largely adhered to the intact rows of sticky silk and not to radial threads. Overall, our method controlled for any effect of variation between webs in size, stickiness, and mechanical properties of capture threads. We only tested insect retention using webs that were freshly spun on the morning of a trial and that appeared to have a high degree of horizontal symmetry.

The Insects

We tested the retention times of four types of insects: deer flies (*Chrysops* sp.), hangingflies (*Hylobittacus* sp.) and two different sizes of acridid grasshoppers (Oedopodinae). All insects were collected from the Bath Nature Preserve and the grounds of The University of Akron's Martin Field Station (Bath, Ohio) and were used within 1–2 d of collection. We quantified how each type of insect differed in body

shape and flight characteristics from the others. First, we measured the body length, body width, and length of one wing to the nearest 0.1 mm using digital calipers. We also weighed insects to the nearest 0.1 mg using a Mettler Toledo PB303-S analytical balance. Finally, we characterized the flight speed of each insect by videotaping them flying next to a ruler that was marked at 5-cm intervals. We placed a Sony DCR TRV480 digital camcorder perpendicular to the ruler at a distance of 1 m, allowing us to film approximately 5–20 cm of flight, or jumping in the case of the grasshoppers, at 30 frames/s. We performed these tests in the same location and using the same methods as we describe below for flying insects into spider webs, so that the flight characteristics we filmed are likely to represent behaviors similar to those exhibited during the experiment itself. We then used Adobe Premiere Elements 1.0 to capture the video to digital images, allowing us to measure the flight speeds of each insect across a known distance to 1/30th of a second. Finally, we estimated the kinetic energy (KE) with which insects struck webs as:

$$KE = \frac{1}{2}Mv^2$$

where M is the average mass of each type of insect and v is average flight or jumping velocity as measured from video.

The Experiment

For each web, we flew one insect of a particular prey type into the manipulated side of the web and
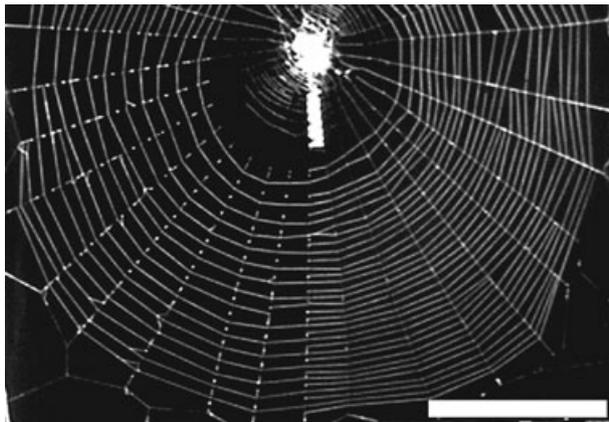
Fig. 1: Experimental web where the mesh width of the left side has been doubled by removing every other row of sticky spiral. The right side of the web was used as an experimental control. Scale = 10 cm

a second insect of the same type into the control side of the web. The experiment was performed within a patio of the Martin Field Station where black cloth was used to make a dark booth that left only a small window behind the web exposed to the sunlight. Insects typically flew or jumped toward the light and therefore directly through the spider web. We were able to induce the hangingflies and deer flies to fly into the desired side of the web with reasonable certainty by having the insects exit a dark vial through a paper cone held about 10–20 cm in front of the web. Grasshoppers were induced to jump through the webs by placing them on a hand held 10–20 cm in front of the web and then gently poking them from behind with a finger. Insects occasionally avoided webs by flying around them. We only used data from trials where the insects flew into the web near the center of the manipulated or control region of the web (i.e. we discarded data from insects that first hit the upper regions of webs or the edges of the lower regions). A random number table was used to determine whether the first insect was flown into the manipulated or control side of the web, but all insects were used only once and each web was used for only a single pair of observations (although different webs constructed by the same spider were used on as many as four different days).

Each trial was filmed using a Sony DCR TRV480 digital camcorder. The videos were then analyzed in the laboratory using Adobe Premiere Elements 1.0. We calculated the time that each insect was stuck in the web (retention time) beginning with the first frame of video where the insect struck the web, at which point threads in the web moved visibly, and ending at the first frame of the video in which the insect was no longer in contact with the sticky silk. In many instances insects remained trapped in place for long periods of time, so we stopped the timing of all trials after 180 s.

Data Analysis

We used ANOVAs to test for differences in the body shape and flight characteristics of each of the four types of prey insects. Retention time in webs was highly bimodal so we used Kruskall–Wallis ANOVAs by rank to compare retention times among different types of insects, conducting separate tests for data from the control and manipulated sides of webs. To compare the difference in retention times between control versus manipulated sides of webs, we used Wilcoxon matched pair tests, both for all insects together and separately for each type of insect prey.

Results

Each of the four types of insects differed from one another in characteristics of their body shape or flying/jumping behaviors (Table 1; univariate ANOVA comparisons at p < 0.05). Hangingflies had a larger body mass and slower flight speed than deer flies. This resulted in both hangingflies and deer flies impacting webs with similar kinetic energy. Conversely, large and small grasshoppers had similar velocities during jumping. However, the greater body mass of large grasshoppers resulted in them striking webs with twice the kinetic energy of small grasshoppers. Overall, grasshoppers had higher aerial velocity and kinetic energy than did hangingflies and deer flies.

The retention time of insects in webs varied greatly (Fig. 2). Most insects that struck the webs were either stuck for the duration of the trial (>3 min) or escaped quickly (<1 s). Eighteen percent of insects striking the control sides and 33% of insects striking the manipulated sides of orb webs escaped within the first second.

Median retention time also varied significantly among taxa for both the control halves of webs (Kruskall–Wallis ANOVA by rank, $H_3 = 24.4$, p < 0.0001) and the experimental halves ($H_3 = 14.9$, p < 0.025). These differences were primarily the result of the shorter retention times of hanging flies relative to deer flies and small grasshoppers (Fig. 3; two-tailed multiple comparisons, all p < 0.025). In general, insects struggled continuously to free themselves from webs, but behaviors differed among taxa. Deer flies rubbed their legs together or along their mouthparts in movements that appeared similar to grooming behaviors. In addition, deer flies sometimes beat their wings in an effort to fly away from the sticky silk, but often one of their wings adhered to the sticky silk thereby preventing both wings from beating effectively. Deer flies were sometimes able to struggle free from one region of entrapment in a web only to tumble down the web surface and become

entangled again. In contrast, hangingflies often freed themselves quickly from webs because hangingflies would typically contact the webs only with their long legs, leaving their wings free to beat vigorously. Individual legs would sometimes be pulled free of the web only to stick to a different spiral of silk, but the hangingflies were ultimately able to fly free of the web on the same side from which they initially encountered the web. In a few instances, the hangingflies seemed merely to tap the webs with their outstretched legs without strongly adhering to the silk. However, if their wings became entangled in the webs then the hangingflies were trapped for long periods of time and rarely freed themselves. The behaviors of the large and small grasshoppers both involved periodic vigorous kicking with their hind legs. This sometimes resulted in the grasshoppers freeing themselves from one section of the web only to tumble down the sticky spiral and become stuck to another section of capture silk. Escapes usually resulted from the grasshoppers tumbling off the bottom of the sticky spiral. In addition, the large grasshoppers sometimes jumped directly through the webs, breaking one or more strands of sticky silk, thereby avoiding being stuck for longer than a fraction of a second.

Overall, insects escaped more quickly from the sides of webs where the mesh width had been increased experimentally than from the control sides (Fig. 2; Wilcoxon matched pairs test: $T = 552$, n = 87, p < 0.005). However, this effect varied among taxa (Fig. 4). Retention time was longer in control halves of webs for deer flies (Wilcoxon matched pairs test: $T = 21$, n = 27, p < 0.05) and for large grasshoppers (Wilcoxon matched pairs test: $T = 14$, n = 16, p < 0.05), but not for hangingflies or small grasshoppers.

Discussion

Our study demonstrates that the retention time of insects in orb webs can be both extremely brief

Table 1: Morphology and aerial velocity of insect prey (mean ± SD)

|	Mass (mg)	Length (mm)	Width (mm)	Wing length (mm)	Velocity (m/s)	Kinetic energy (joules × 10^{-3})
Hangingflies (n = 17)	20.1 ± 2.8*	14.3 ± 1.3	1.9 ± 0.2	16.4 ± 1.3	0.97 ± 0.30	0.010 ± 0.006*
Deer flies (n = 11)	15.3 ± 2.9*	9.0 ± 0.6	2.5 ± 0.2	7.6 ± 0.7	1.72 ± 0.57	0.024 ± 0.015*
Small grasshoppers (n = 13)	164 ± 64	17.4 ± 2.0	3.4 ± 0.6	$-^{a}$	2.49 ± 0.75*	0.549 ± 0.322
Large grasshoppers (n = 11)	355 ± 97	24.4 ± 2.2	5.2 ± 0.7	$-^{a}$	2.43 ± 0.80*	1.153 ± 0.727

Velocity of hangingflies and deer flies indicates flight speed while velocity of the acridids indicates average forward speed during jumping. There were significant differences among taxa for all variables (ANOVAS, p < 0.05). * indicate taxa that did not differ in the mean of particular variable (post hoc comparisons at p < 0.05).
[a]All grasshoppers were immature and lacked wings.
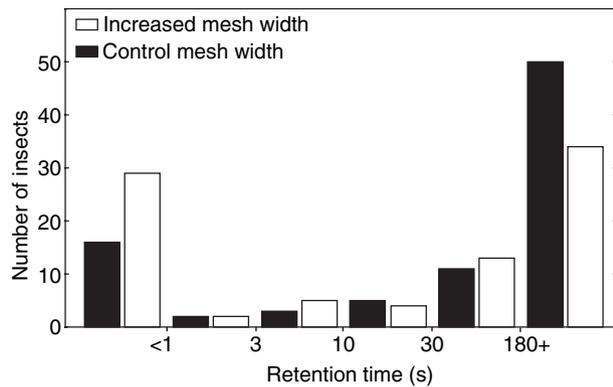
Fig. 2: Distribution of retention time of insects in webs for all prey in the study. Black bars indicate data for the unmanipulated control halves of webs and open bars indicate data for the halves of webs where mesh width was experimentally increased. Note that most insects striking webs were either retained for greater than 3 min or escaped within less than 1 s
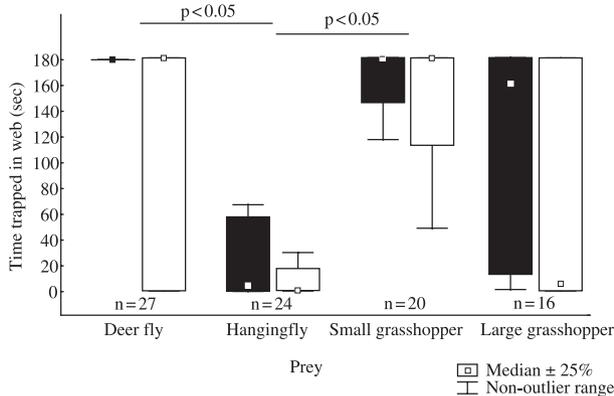
Fig. 3: Retention times of four types of insect prey in spider webs. Dark bars represent retention times of insects striking the sides of webs with the original mesh widths (controls) while open bars represent retention times of insects in the sides of webs with increased mesh widths (experimental manipulation to double the mesh width). p-values denote significant differences among species in retention times using Kruskall–Wallis anovas by rank. Differences are significant for both comparisons within the control and the experimental mesh widths

(25% of all insects were retained by webs <1 s) and highly variable within and among different taxa of insects (Figs 2 and 3). Increased mesh width reduced the retention times of deer flies and large grasshoppers while the median retention times of hanging-flies and small grasshoppers were unaffected by changes in mesh width (Fig. 4). Together, these data indicate that the influence of mesh width on the retention times of different types of insect prey is more complex than can be described by a single variable, but that mesh width can act to selectively

favor the capture of some taxa of insect prey over others.

Although orb spiders sometimes utilize specialized attack behaviors against different taxa of insects (Robinson & Olazarri 1971; Japyassu & Viera 2002), spiders usually show little discrimination among which prey are attacked within webs. Therefore, orb-weaving spiders are typically considered to be generalist sit-and-wait predators (Foelix 1996). However, this considers selectivity by spiders at only one step in the predation process. Prior to being consumed by spiders, insects must be intercepted by orb webs and retained by the sticky spirals long enough for the spiders to sense the prey, maneuver to the prey, and to successfully subdue the prey. Orb-weaving spiders often require at least 5 to 10 s to sense, to locate and to contact insects trapped in their webs (Lubin 1973; Witt et al. 1978; Eberhard 1989), but many insects are able to escape from webs before spiders reach them (Lubin 1973; Nentwig 1982; Uetz & Hartsock 1987; Eberhard 1989). Thus, any influence of the orb web itself on the probability that an insect is intercepted by the web or on the retention times of insects could act as a significant mechanism resulting in selectivity of prey.

Several studies have suggested that webs with smaller mesh widths should function better at capturing smaller insects that might otherwise fly in between the strands of sticky silk (Uetz et al. 1978; Murakami 1983; Sandoval 1994; Watanabe 2000). However, other studies have failed to find a direct correlation between intra- or interspecific variation in the mesh widths of webs and the lengths of prey captured by spiders (Nentwig 1983; McReynolds & Polis 1987; Herberstein & Elgar 1994). Moreover, a web spun from a given length of sticky silk captures insects most efficiently when the mesh width of the capture spiral is slightly larger than the size of the prey (Chacón & Eberhard 1980). Finally, webs with tighter sticky spirals may absorb greater amounts of kinetic energy and possess greater stickiness per area relative to webs with more open meshes (Craig 1987; Miyashita 1997; Opell 1999) and these are both qualities that would enhance the capture of larger, faster flying prey. Thus, given the current state of knowledge, the potential role of mesh width in prey capture is difficult to determine.

Our study found that body length per se may not predict the energy with which different insect taxa impact webs because of differences in their body shapes and flight characteristics (Table 1). Moreover, we made comparisons of the effects of mesh width
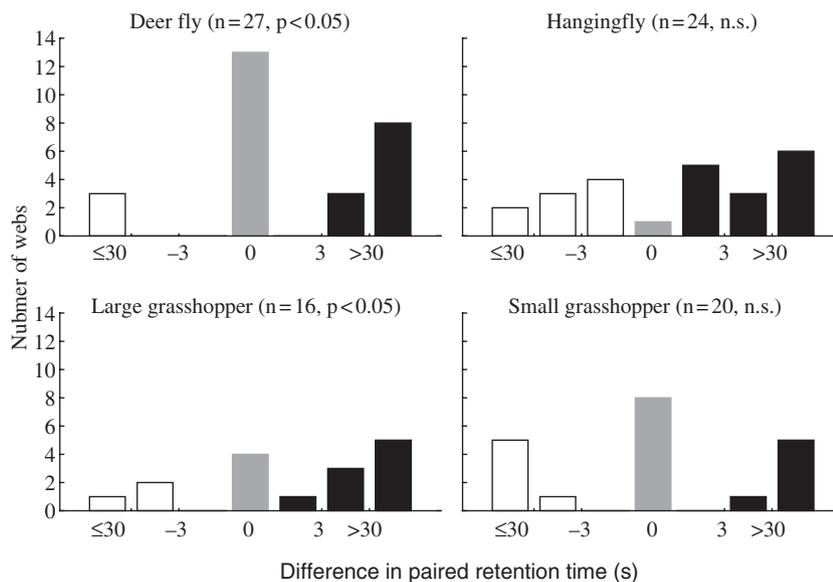
Fig. 4: Pairwise difference in retention times of insects between manipulated and control sides of webs. Positive values (dark bars) indicate that insects stuck in the control side of the web longer than in the manipulated side while negative values (open bars) indicate that insects stuck longer in the manipulated side. The gray bars indicate no difference in retention time and are entirely based on observations where insects were stuck in both sides of webs for the entire observation period. p-values are from Wilcoxon matched pair tests

within individual webs to control for other factors that might be correlated with differences in mesh width. For example, one web spun from thick silk fibers but with a very open mesh width could have the same energy-absorbing capacity as a second web spun from thinner fibers but with a more tightly packed spiral. Even two webs that appear to be identical in architecture can be expected to perform in very different ways if they differ in microhabitat location or if the silks used to construct those webs vary in their structural or material properties or adhesiveness.

Our experiment provides evidence that an increase in mesh width of *Argiope* orb webs results in a general reduction in the retention times of insect prey (Fig. 2), although the magnitude of that effect varied among taxa. Large grasshoppers and deer flies had significantly shorter retention times in the manipulated sides of webs (Fig. 4). In particular, 26% of all deer flies intercepted by the experimental sides of webs escaped in less than 1 s, while only a single deer fly escaped from the control sides of webs in less than 90 s, even though all deer flies struggled nearly continuously to free themselves. Only 50% of large grasshoppers intercepted by the experimental sides of webs were retained longer than 5 s, while 81% of large grasshoppers intercepting the control sides of webs were retained for more than 5 s. For small grasshoppers and hangingflies, there was no difference in the median retention times between

the experimental and control halves of webs (Fig. 4). However, even for hangingflies and small grasshoppers, the single shortest retention time that we observed for each type of insect occurred on the manipulated sides of webs. This effect of mesh width on the shortest retention times is particularly relevant to the evolution of spider foraging strategies because it is the prey that strike webs and escape quickly that likely produce the greatest selective pressures on web-spinning behaviors because spiders typically locate and attack prey in orb webs within 5–10 s (Lubin 1973; Witt et al. 1978; Eberhard 1989).

Our experiment also demonstrates that the retention times of different taxa of insects are not determined by any one specific morphological or flight characteristic (Fig. 3). Deer flies and small grasshoppers exhibited the longest retention times in this experiment but the velocity and kinetic energy with which they hit webs were different from each other (Table 1). These two taxa of insects also exhibited differences in their escape behaviors: deer flies attempted to groom themselves free of the sticky silk while grasshoppers generally kicked vigorously. Furthermore, the flight characteristics and body morphologies of these two taxa overlapped with large grasshoppers and hangingflies (Table 1), which were both retained by webs for much shorter periods of time. Large grasshoppers seemed to escape webs

through powerful kicking by their hind legs, which tore the sticky silk of webs. In contrast, hangingflies differed from other insects in that their escape from webs seemed to be related to their long legs, which minimized contact with the sticky silk. This suggests that efforts to construct general rules across taxa of spiders for how variation in the mesh widths of webs might target different insect prey are ultimately doomed to failure. The relationships may simply be too complex, depending on the escape behaviors of insects as much as on their morphologies and flight characteristics. However, our data do provide support for the hypothesis that spiders can target specific taxa of prey because of the effects of the mesh widths of webs on variation in the retention times of insects, even though the spiders themselves may attack any insect in their webs that is retained for a sufficient period of time.

Recently Venner & Casas (2005) developed an energetic model demonstrating that the capture of unusually large, but rare prey is necessary for orb-weaving spiders to reproduce successfully. In contrast, the capture of smaller, more common prey do not provide enough energy for successful reproduction but are essential to keep spiders alive long enough so that the spiders have the opportunity to capture the larger but rarer insects. Individual orb-weaving spiders can exhibit a great deal of plasticity in the mesh widths of orb webs spun on different days. In particular, sated spiders often spin smaller orb webs with tighter sticky spirals than do starved spiders (Sherman 1994). We suggest that the reallocation of silk resources by sated spiders into smaller orbs with tightly packed capture spirals may function to increase the likelihood that spiders capture larger prey, in part by increasing the retention times of larger insects. The small number of taxa in our study prevents us from rigorously testing this hypothesis, but Eberhard (1986) also argued that narrow-meshed webs are more likely to effectively intercept larger prey. Interestingly, the heaviest prey in our study, large grasshoppers, was best retained in the sides of webs with narrower mesh widths. Thus, variation in the mesh widths of orb webs may not only facilitate interspecific differences in the taxa of insects captured by spiders, but it may also function to allow individual spiders to spin webs that target the types of insects that most suit their energetic needs.

Acknowledgements

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