

## RESEARCH ARTICLE

# Wet webs work better: humidity, supercontraction and the performance of spider orb webs

Cecilia Boutry\* and Todd A. Blackledge

University of Akron and Integrated Biosciences Program, University of Akron, Akron, OH 44325-3908, USA

\*Author for correspondence (cb54@zips.uakron.edu)

### SUMMARY

Like many biomaterials, spider silk responds to water through softening and swelling. Major ampullate silk, the main structural element of most prey capture webs, also shrinks dramatically if unrestrained or develops high tension if restrained, a phenomenon called 'supercontraction'. While supercontraction has been investigated for over 30 years, its consequences for web performance remain controversial. Here, we measured prey capture performance of dry and wet (supercontracted) orb webs of *Argiope* and *Nephila* using small wood blocks as prey. Prey capture performance significantly increased at high humidity for *Argiope* while the improvement was less dramatic for *Nephila*. This difference is likely due to *Argiope* silk supercontracting more than *Nephila* silk. Web deflection, measured as the extension of the web upon prey impact, also increased at high humidity in *Argiope*, suggesting that silk softening upon supercontraction explains the improved performance of wet webs. These results strongly argue that supercontraction is not detrimental to web performance.

Key words: silk, water, humidity, web mechanics, prey capture.

Received 14 December 2012; Accepted 3 June 2013

### INTRODUCTION

When exposed to water, natural and artificial polymers swell (Mark and Erman, 2007). Water also induces a softening in biological structures made of polymers such as keratin (Aksakal and Alekberov, 2009; Puthoff et al., 2010; Taylor et al., 2004) and chitin (Kim et al., 1996; Vincent, 2002). These changes can impact material properties and hence ultimately organism performance (e.g. Puthoff et al., 2010; Shawkey et al., 2011). Spider major ampullate (MA) silk is the main structural element in most prey capture webs and responds to humidity over 70% by supercontracting (Work, 1977). During supercontraction, water infiltrates the silk and disrupts the hydrogen bonding that maintains much of the ordered tertiary structure in the amorphous regions of silk proteins (Eles and Michal, 2004; Grubb and Ji, 1999; Parkhe et al., 1997; Termonia, 1994). Unrestrained MA silk fibers consequently shrink by up to half their length, while restrained fibers instead develop high tension (Bell et al., 2002; Boutry and Blackledge, 2010; Savage et al., 2004). Supercontracted silk is also up to 1000 times more compliant and several times more extensible than dry silk (Guinea et al., 2005; Pérez-Rigueiro et al., 2003; Savage and Gosline, 2008a; Shao et al., 1999). Such changes in material properties could substantially affect how spider webs interact with prey.

Orb webs are composed of two main types of fibrous silk (Fig. 1). The capture spiral is composed of elastic flagelliform silk that is coated by hygroscopic glue droplets. The glue droplets swell and shrink in response to changing humidity, affecting their adhesiveness (Opell et al., 2009; Sahni et al., 2011; Vollrath et al., 1990), while water in the glue droplets also maintains flagelliform silk in a continuously supercontracted state at all but the lowest humidity (Guinea et al., 2010; Savage and Gosline, 2008b; Vollrath and Edmonds, 1989). MA silk forms the radii and frame threads that support orb webs and contrasts with flagelliform silk in qualitatively

changing from dry to supercontracted at ~70% relative humidity (RH). Supercontraction in radii tenses up the web at high humidity. Radii also dissipate most of the kinetic energy of prey (Sensenig et al., 2012). Thus, the greatest influence of environmental humidity on energy absorption by webs during prey capture is likely to manifest through changes in the radii.

At least two functions for supercontraction of MA silk are hypothesized. First, supercontraction of MA silk could prevent orb webs from sagging under the weight of dew drops by keeping the webs tense (Work, 1977). This hypothesis is consistent with the observation that, within Orbiculariae, orb-weaving spiders' silk supercontracts slightly more than silk from taxa that secondarily lost orb-weaving (Boutry and Blackledge, 2010). An alternative hypothesis argues that supercontraction plays an important role during the spinning of silk from liquid dopes by facilitating the alignment of molecules along the fiber axis, such that the water responsiveness of dry threads might be a 'non-adaptive by-product' for webs (Guinea et al., 2005). This second hypothesis is supported by the observation that spiders using MA silk in a greater variety of contexts (e.g. in different web structures, as dragline and as safety lines *versus* only trailing draglines) produce silk that supercontracts more (Boutry and Blackledge, 2010).

However, direct tests of how supercontraction affects orb web performance are still lacking. Bell and colleagues (Bell et al., 2002) calculated that supercontraction caused tensions in orb webs of 300 MPa. They concluded that supercontraction would limit the ability of orb webs to resist future stresses, such as the ones due to prey impact, and was thus detrimental to orb web function. Later, Savage and colleagues (Savage et al., 2004) found that supercontraction only created tensions of 50 MPa in webs, far below the yield point of MA silk, and hence too small to permanently impair web function. Although valuable, these two studies are limited by the fact that they

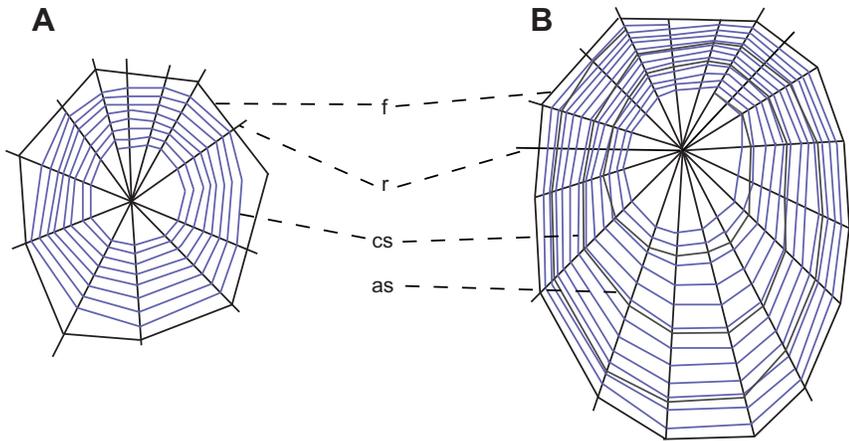


Fig. 1. Diagram of an *Argiope* (A) and a *Nephila* (B) orb web indicating radii ( $r$ ), auxiliary spiral ( $as$ ) and frame threads ( $f$ ) made of major ampullate silk, as well as the capture spiral ( $cs$ ) made of flagelliform silk.

used isolated threads. In orb webs, threads are interconnected and form a complex, geometrical network. Furthermore, threads in webs are already under some tension (Wirth and Barth, 1992), while studies of isolated silk typically start with fully relaxed threads. The stress generated by supercontraction declines strongly with initial tension (Boutry and Blackledge, 2010). Thus, it is difficult to predict the behavior of a whole orb web from isolated threads.

We propose that supercontraction, by softening silk, may improve orb web prey capture performance. Orb webs dissipate the energy of prey impact through radii deformation (Sensenig et al., 2012) and aerodynamic damping (Lin et al., 1995). Thus, more compliant silk may allow webs to absorb more prey energy. For instance, softening of MA silk as it extends past the yield point, followed by subsequent stiffening, helps to maximize the energy an orb web can resist and also localizes damage when webs fail during prey capture (Cranford et al., 2012). Increased compliance of MA silk may also interact with the capture spiral by reducing the forces generated as prey decelerate over longer distances so that they are more easily retained by the web. Synergistically, web spiral stickiness increases with humidity, at least until glue droplets become over-lubricated by water (Sahni et al., 2011). Alternatively, wet MA silk becomes rubberlike, reducing elastic hysteresis at high humidity (Gosline et al., 1984; Plaza et al., 2006) (C.B., unpublished data). This drop in hysteresis may return more energy to the prey during web oscillations, thereby ricocheting prey off webs (Denny, 1976). Thus, there is a clear need to empirically test how water-induced changes in silk properties affect whole orb web performance.

Here, we investigated how humidity affects prey capture success in orb webs from two spider genera, *Nephila clavipes* (Linnaeus, Araneae: Nephilidae) and *Argiope trifasciata* (Forsskål, Araneae: Araneidae). These two genera both spin orb webs, but differ in their silk properties and web architecture. *Nephila* silk supercontracts ~30% less than *Argiope* silk when exposed to high humidity (Liu et al., 2008; Work, 1981a). Furthermore, *Nephila* orb webs have ~50% more radii and their capture area is ~60% larger than *Argiope* webs (Sensenig et al., 2010) so that they likely deform less under the same impact energy (Fig. 1). *Nephila* webs also retain their auxiliary spiral, a temporary structure that is removed upon web completion in *Argiope* and likely functions to mechanically stabilize the closely packed capture spirals in *Nephila* webs (Foelix, 1987; Hesselberg and Vollrath, 2012; Kuntner et al., 2008). While it has sometimes been assumed that the temporary spiral is made of minor ampullate silk, evidence suggests it is actually made of MA silk (Hesselberg and Vollrath, 2012; Work, 1981b). Based on these differences, we expect *Nephila* webs to remain stiffer at high humidity compared with

*Argiope* webs. We propose that high humidity improves capture success by increasing web deflection upon prey impact. Therefore, the performance of *Argiope* orb webs should improve more under high humidity compared with that of *Nephila* webs. We tested this hypothesis by comparing capture success and web deflection at high and low humidity for both *Nephila* and *Argiope*.

#### MATERIALS AND METHODS

Six *Nephila* spiders were purchased from Tarantulaspiders.com (www.tarantulaspiders.com) and four *Argiope* spiders were collected from Bath and Akron (OH, USA). The spiders were housed in 40×40×10 cm cages at ~20°C and 35% RH and fed crickets daily.

Trials took place at either 30–35% RH for dry webs or >70% RH (in most cases, >80% RH) for wet webs. Supercontraction usually happened nearly instantaneously, but the webs were exposed to the trial humidity for at least 15 min before the start of the experiment. To verify that the silk in wet webs was indeed supercontracted during the experiment, supercontraction measurements were performed as described previously (Agnarsson et al., 2009) on 12 threads from *Argiope* webs, immediately after the trials. Supercontraction is a one-time response in restrained silk, unless ‘reset’ by subsequently straining the thread. Thus, silk that had supercontracted during the prey capture trials would display little additional supercontraction. As expected, silk samples from webs exposed to high humidity exhibited half as much supercontraction stress as silk from webs kept at room humidity (9.3±2.2 MPa for high humidity versus 18.2±3.0 MPa for low humidity), confirming that MA silk in wet webs was indeed supercontracted during the prey capture trials.

The trials were recorded with a Troubleshooter high-speed video camera (Fastec, San Diego, CA, USA) at 500 frames s<sup>-1</sup>. The camera was oriented within the plane of the web, which was illuminated from both sides by 250 W halogen lights. A black background was used to maximize contrast with the back-lit silk threads of the web. An 8×8 cm cardboard square was used for calibration. Balsa wood blocks, weighing 90–300 mg and measuring ~10×10×5 to 20×10×10 mm, were used to simulate prey. Blocks were thrown by hand, perpendicular to the webs, at speeds ranging from 2 to 4 m s<sup>-1</sup>. These masses and speeds correspond to relatively large prey, such as honeybees or crickets (Blackledge and Zevenbergen, 2006; Denny, 1976). Each web was hit by several blocks in succession. Hit number was recorded as first versus subsequent because web damage could influence performance. However, most thread deformation is highly localized within orb webs, making them robust to damage, so that they can still effectively stop prey in pristine regions of the web (Cranford et al., 2012; Sensenig et al., 2012).

The behavior of the block was recorded using the following rubric. (1) Caught: the block was effectively stopped by the web and remained suspended in the capture spiral. (2) Broke through: the block passed through the plane of the web, breaking at least one row of capture spiral or radial thread. This indicated that the kinetic energy of the block exceeded the orb web's ability to stop it. In three cases, the block was still held by a thread after breaking through the web, then was pulled back and stuck to the web. We did not code these events as captures because they indicated that the block still exceeded the energy-absorbing capacity of the MA radial silk. However, coding them as 'caught' did not change the significance of any relationships (see below). (3) Bounced off: the block hit the web and ricocheted from the impact side of the web.

Trials where the block passed through the web but did not visibly damage any threads were discarded because we assumed that the block did not contact any silk. The behavior of the block in the web was compared using a mixed effect model with humidity and hit number as co-factors and web as random factor, independently for *Argiope* and *Nephila*. As few blocks bounced off the web (4 out of 91 trials), we only used trials where the block was caught or went through the web in our subsequent analysis.

Stills were taken from the video using VirtualDub 1.9.9 (A. Lee, <http://virtualdub.org>, 1998–2009) just before the block impacted the web (frame 0) and at the web's maximum extension (frame max.). Web deflection was calculated as the distance between the point of impact at frame 0 and frame max. using ImageJ (W. S. Rasband, US National Institutes of Health, Bethesda, MD, USA, <http://rsb.info.nih.gov/ij/>, 1997–2007) (Fig. 2). Kinetic energy of the block over 25 frames before impact was also calculated as:

$$\text{Kinetic energy} = \frac{1}{2}mv^2, \quad (1)$$

where  $m$  is the mass of the block and  $v$  is its velocity, calculated as:

$$v = \frac{\sqrt{(\delta_x + \delta_y)^2}}{t}, \quad (2)$$

where  $\delta_x$  is the displacement of the block on the  $x$ -axis,  $\delta_y$  is the displacement on the  $y$ -axis and  $t$  is time.

Deflection of the web was compared between high and low humidity using a nested ANCOVA with humidity, hit number and kinetic energy as co-factors and with web as random factor. ANCOVA were run independently for *Argiope* and *Nephila*. Kinetic energy was added as a co-factor because we expected webs to deform more under high-energy impacts.

All statistical tests were conducted in SAS (SAS Institute, Cary, NC, USA).

## RESULTS

Mean ( $\pm$ s.e.m.) kinetic energy before impact was  $1.12 \pm 0.09$  mJ for blocks caught by wet *Argiope* webs versus  $0.82 \pm 0.10$  mJ for blocks that broke through, and  $0.73 \pm 0.11$  mJ for blocks caught by dry *Argiope* webs versus  $0.86 \pm 0.14$  mJ for blocks that broke through. It was  $0.90 \pm 0.09$  mJ for blocks caught by wet *Nephila* webs versus  $1.07 \pm 0.07$  mJ for blocks that broke through, and  $1.19 \pm 0.14$  mJ for blocks caught by dry *Nephila* webs versus  $1.25 \pm 0.12$  mJ for blocks that broke through.

Wet webs captured more blocks compared with dry webs in *Argiope* (77% versus 38%,  $P=0.0073$ ,  $N=55$ ). In *Nephila*, wet webs caught 83% of the blocks and dry webs caught 53% of the blocks. Despite this increase of over 50% in capture success, this difference was only marginally significant ( $P=0.0691$ ,  $N=31$ ). Hit number did

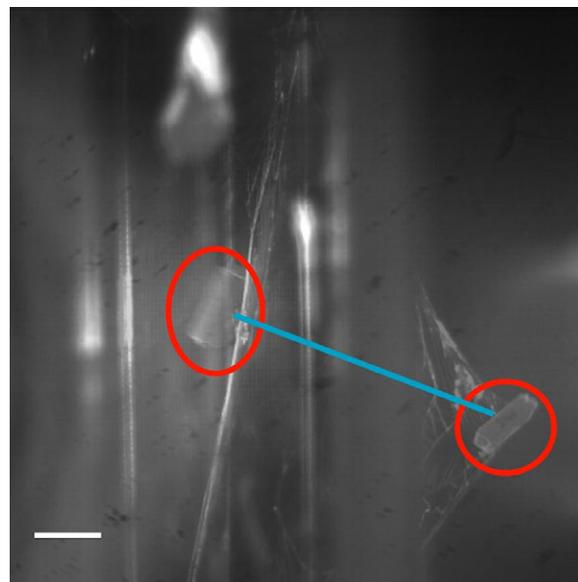


Fig. 2. Superimposed stills of a web before impact (left) and at its maximum deflection (right). The block is circled in red on both stills and the web deflection is represented by a blue line. Scale bar is 30 mm.

not affect capture success ( $P=0.3795$  for *Argiope* and  $P=0.0931$  for *Nephila*) (Table 1). The results are similar if the three cases where the block broke through webs, but were still retained by the capture silk, are coded as 'caught' instead of 'broke through'.

Web deflection was higher for wet webs in *Argiope* ( $P=0.0029$ , mean  $\pm$  s.e.m.  $97 \pm 5$  mm for wet webs versus  $68 \pm 4$  mm for dry webs) (Fig. 3). Deflection also increased with initial kinetic energy ( $P=0.0421$ ). In *Nephila*, web deflection depended on initial kinetic energy ( $P=0.0141$ ) but not on humidity ( $P=0.4754$ ).

## DISCUSSION

Contrary to Bell and colleagues' (Bell et al., 2002) suggestion, supercontraction does not impede orb web performance. Instead, capture success nearly doubles at high humidity for *Argiope* webs, despite the higher impact energy sustained by wet webs in our experiment. The effect of humidity on web performance was weaker in *Nephila* and likely reflects that *Nephila* silk reacts to humidity weakly compared with *Argiope* silk (Liu et al., 2008; Work, 1981a). Moreover, the higher number of radii and presence of a temporary spiral in *Nephila* webs suggest that *Nephila* webs are structurally stiffer than *Argiope* webs, so that softening of silk by water may alter mechanical performance less in *Nephila*. It is also worth noting that the sample size was smaller in *Nephila*, which may affect our statistical results.

Several factors could explain why wet orb webs are better at capturing prey. The first one is stickiness. Stickiness increases with

Table 1. Capture behavior for wet and dry orb webs

No. of blocks	<i>Argiope</i>		<i>Nephila</i>	
	Wet webs	Dry webs	Wet webs	Dry webs
Caught	<b>23</b> (6)	<b>10</b> (3)	<b>10</b> (4)	<b>10</b> (4)
Breaking through	<b>7</b> (4)	<b>15</b> (4)	<b>2</b> (0)	<b>9</b> (1)
Bouncing off	<b>0</b> (0)	<b>1</b> (1)	<b>3</b> (0)	<b>0</b> (0)

Data for all hits are in bold, and data for first hits only are indicated in parentheses.

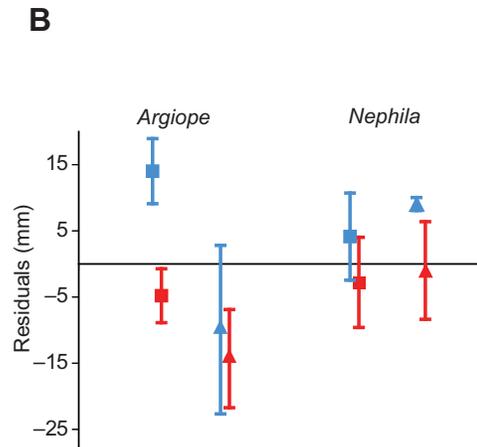
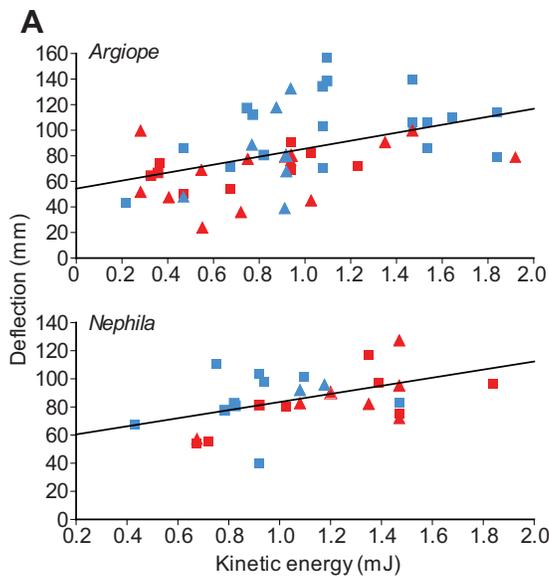


Fig. 3. (A) Web deflection as a function of kinetic energy for wet (blue) and dry (red) webs of *Argiopo* and *Nephila*. (B) Residuals from the web deflection versus kinetic energy regression for wet (blue) and dry (red) webs of *Argiopo* and *Nephila* spiders. Errors bars show s.e.m. In A and B, squares represent successful capture events; triangles represent failed capture attempts. Both panels suggest that wet *Argiopo* webs deflect more than expected while dry webs deflect less than expected.

humidity as water lubricates the adhesive glycoproteins, at least until reaching an optimum, such that wet webs may be better at retaining prey (Sahni et al., 2011). Thus, the increased deflection of wet webs and their ability to stop higher kinetic energy projectiles may be due in part to the silk simply maintaining contact with the prey for more time. However, the lower capture success of dry orb webs compared with wet webs is mainly due to more blocks breaking through dry webs. This suggests that, in this study at least, humidity primarily affected capture success through changes in web mechanics and not stickiness. However, we observed three cases where the block broke through the web and damaged threads, but was still held by a single capture thread, demonstrating the importance of web adhesion for capture success.

A second factor that could play a role in explaining why wet orb webs work better is elastic hysteresis, or energy damping. Hysteresis represents the proportion of energy dissipated by a material. As orb webs rely on radial silk to dissipate the energy received during prey impact, capture success should increase with hysteresis for silk of a given toughness (Sensenig et al., 2012). However, as silk becomes rubberlike when wet, it is likely that hysteresis decreases at high humidity (Gosline et al., 1984; Plaza et al., 2006) (C.B., unpublished data). Therefore, if anything, water-induced changes in hysteresis should decrease capture success. Yet, we observed the opposite.

Finally, we believe that our results are due in part to changes in silk tensile properties resulting from supercontraction. The MA silk forming the radii and frames of orb webs supercontracts strongly. The flagelliform silk forming the capture spiral also becomes softer at high humidity, but because the surrounding glue coating already hydrates the silk, these changes are small compared with how MA silk interacts with water (Guinea et al., 2010; Savage and Gosline,

2008b). Deformation of radial threads is the main mechanism of energy dissipation in orb webs, and thus contributes to capture success (Cranford et al., 2012; Denny, 1976; Lin et al., 1995; Sensenig et al., 2012). In *Argiopo*, unrestrained supercontracted MA threads are 250 times less stiff than and nearly twice as extensible as dry threads (Table 2). Because of that, wet threads will extend more under a given force than dry threads, and as a result, should dissipate more incoming energy.

However, the previous reasoning assumes wet threads are allowed to fully contract. Silk threads are inter-connected in webs and thus restrained and unable to shrink in length. This leads to tension developing in the thread. At first, restrained threads in wet webs seem to correspond to fully supercontracted threads that are extended back to their original dry length and are consequently under substantial stress. Based on this assumption and the fact that thread length does not change between dry and wet webs (C.B., unpublished data), we calculated the tension due to supercontraction in wet radial silk by measuring the stress in an unrestrained supercontracted fiber re-extended to reach its original dry length. The tension due to supercontraction is 70 MPa in *Argiopo* ( $N=7$ ). This figure is close to that reported by Savage and colleagues (Savage et al., 2004) in *Nephila*, and to what we reported previously (Boutry and Blackledge, 2010) in several orb-weavers including *Araneus*, *Nuctenea* and *Verrucosa*. However, stress due to restraining supercontracted threads may be lower than stress due to re-extending supercontracted threads back to their original length (Work, 1985). In this case, the tension due to supercontraction may be only 25% of our calculated value; that is,  $\sim 18$  MPa. This is exactly the value we measured in webs (see Materials and methods). If restrained threads behaved like supercontracted and re-extended threads,

Table 2. Tensile properties of three types of *Argiopo* silk threads: virgin dry threads, threads that were supercontracted then re-extended while wet to their original length, and unrestrained wet supercontracted threads ( $N=7$ )

Thread type	Stiffness (GPa)	Ultimate strength (MPa)	Extensibility	Toughness (MPa)
Dry	5.2 $\pm$ 2.3	1584 $\pm$ 288	0.29 $\pm$ 0.06	163 $\pm$ 46
Supercontracted (re-extended)	1.8 $\pm$ 0.3	1020 $\pm$ 261	0.2 $\pm$ 0.01	119 $\pm$ 23
Supercontracted (unrestrained)	0.02 $\pm$ 0.0	1545 $\pm$ 237	0.53 $\pm$ 0.04	204 $\pm$ 40

Stiffness was measured as Young's modulus. Toughness was measured as the energy absorbed at break. Data are means  $\pm$  s.d. Data for dry threads come from Sensenig et al., 2010. All values use true stress and strain.

supercontracted threads within orb webs would be only three times less stiff and about as extensible as dry threads (Table 2). The energy they could absorb before breaking would also be similar to that of dry threads. But if tension in restrained threads is only 25% of tension in supercontracted and re-extended threads, as suggested by Work (Work, 1985), then supercontracted threads within orb webs are even less stiff, probably nearly 12 times less stiff than dry threads. As their stiffness and strength are low, the energy that restrained supercontracted threads can absorb before breaking is likely much lower than that for dry threads, suggesting that increased prey capture is not due to thread toughness *per se*. As their radii are less stiff, *Argiope* wet webs deform over 40% more upon prey impact than dry webs. This extra deformation may decrease the deceleration of the prey and the force sustained by the web during prey impact. In contrast, high humidity does not affect web deflection in *Nephila* (Fig. 3). This is likely because *Nephila* MA silk reacts to water less than *Argiope* MA silk, and the higher radii density and presence of the auxiliary spiral in *Nephila* may make *Nephila* webs stiffer and limit web deflection compared with *Argiope* webs.

While the effect of hydration on the tensile properties of biomaterials is well known, the functional consequences of these changes for the organism are important (e.g. Puthoff et al., 2010; Shawkey et al., 2011). Improved prey capture performance of wet orb webs shows how water-induced molecular changes in biomaterials have dramatic macroscopic consequences at the whole-organism level. Supercontraction of MA silk likely plays a strong role in wet webs' greater ability to stop prey, although the effects are difficult to disentangle completely from water-induced changes in web adhesion. However, how water influences other aspects of wet orb web performance, such as the ability to detect a struggling prey, remains to be investigated. Regardless, our findings suggest that improving orb web performance could have been a potential selective pressure for the evolution of spider silk supercontraction, interacting with its other proposed functions (Guinea et al., 2005; Work, 1977).

#### ACKNOWLEDGEMENTS

We thank Andrew Sensenig and Sean Kelly for advice on the high-speed videos. Sam Evans, Vasav Sahni and two anonymous reviewers provided helpful comments on the manuscript. This is publication no. 34 of the University of Akron Field Station.

#### AUTHOR CONTRIBUTIONS

T.A.B. and C.B. designed the experiment, interpreted the results and wrote the article. C.B. collected and analysed the data.

#### COMPETING INTERESTS

No competing interests declared.

#### FUNDING

This work was supported by the National Science Foundation [award IOS-0745379].

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