

RESEARCH ARTICLE

Mechanical performance of spider orb webs is tuned for high-speed prey

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SUMMARY

Spiders in the Orbiculariae spin orb webs that dissipate the mechanical energy of their flying prey, bringing the insects to rest and retaining them long enough for the spider to attack and subdue their meals. Small prey are easily stopped by webs but provide little energetic gain. While larger prey offer substantial nourishment, they are also challenging to capture and can damage the web if they escape. We therefore hypothesized that spider orb webs exhibit properties that improve their probability of stopping larger insects while minimizing damage when the mechanical energy of those prey exceeds the web's capacity. Large insects are typically both heavier and faster flying than smaller prey, but speed plays a disproportionate role in determining total kinetic energy, so we predicted that orb webs may dissipate energy more effectively under faster impacts, independent of kinetic energy *per se*. We used high-speed video to visualize the impact of wooden pellets fired into orb webs to simulate prey strikes and tested how capture probability varied as a function of pellet size and speed. Capture probability was virtually nil above speeds of $\sim 3\text{ ms}^{-1}$. However, successful captures do not directly measure the maximum possible energy dissipation by orb webs because these events include lower-energy impacts that may not significantly challenge orb web performance. Therefore, we also compared the total kinetic energy removed from projectiles that escaped orb webs by breaking through the silk, asking whether more energy was removed at faster speeds. Over a range of speeds relevant to insect flight, the amount of energy absorbed by orb webs increases with the speed of prey (i.e. the rates at which webs are stretched). Orb webs therefore respond to faster – and hence higher kinetic energy – prey with better performance, suggesting adaptation to capture larger and faster flying insect prey. This speed-dependent toughness of a complex structure suggests the utility of the intrinsic toughness of spider silk and/or features of the macro-design of webs for high-velocity industrial or military applications, such as ballistic energy absorption.

Key words: spider silk, foraging, insect flight, kinetic energy, safety factor, organism performance, biomimicry.

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INTRODUCTION

The design of organisms, and the materials from which they are grown, often incorporates significant safety mechanisms that prevent catastrophic failure. Some safety mechanisms simply consist of using more material to strengthen a structure, such as thickening the bending axis in a plant stem or bone (Vogel, 2003). More complex safety mechanisms include the J-shaped stress–strain curves of many biological materials, such as tendon and spider capture silk, which help to limit the failure probability by recruiting more load-bearing molecules as the load increases (Vogel, 2003). The safety factor is a traditional method of quantifying how closely structures approach failure during performance. For example, the strength of a bone may be several fold higher than the forces typically encountered, but approach failure under extreme events such as falls. The safety factor is quantified as the ratio of the breaking stress of the bone to the typical stress to which it is subjected. During steady-state locomotion, the bones of small mammals have higher safety factors than the bones of large mammals, hinting at the importance of intense, non-steady state activities such as jumping in smaller mammals (Biewener, 1982; Biewener, 2005). Most mammals, including horses, have higher safety factors in more proximal bones, and hence higher breaking probability in distal limb bones (Vaughan and Mason, 1975). Cursorial mammals risk higher breakage probability in these distal bones in order to maintain high speed and

high acceleration during locomotion. Finally, at the highest level of complexity, neural mechanisms such as the Golgi tendon reflex mechanism in mammalian muscles detect dangerous levels of tension and lower the muscle force generated, preventing catastrophic tearing (Eccles et al., 1957). Thus, multiple mechanisms including material properties, shape of individual components and the overall design of complex structures interact in determining successful performance.

Spider orb webs are a likely candidate for safety mechanisms operating at multiple levels because webs are complex structures assembled from multiple materials and are exposed to prey that vary enormously in both impact energy and benefit of capture. In particular, ecological data suggest that orb webs maximize spider fitness when capturing rare, but large prey (Blackledge, 2011; Venner and Casas, 2005). Physiologically, growth of 'giant' female *Nephila* depends more on the consumption of individually large, rare insects at larger instars (Higgins and Goodnight, 2011). Mechanically, the stickiness of spider web glue droplets scales closely with the strength of the underlying axial fibers so that the glue detaches instead of the threads breaking, allowing them to repeatedly adhere to prey (Agnarsson and Blackledge, 2009), but also providing a potential safety release. Both the adhesiveness of individual glue droplets (Sahni et al., 2010) and the toughness of silk threads (Cunniff et al., 1994; Denny, 1976) increase with strain

rate. Finally, larger species of spiders also produce webs using higher quality silk (Sensenig et al., 2010).

Spider orb webs are constructed of outer frames and supporting radial spokes spun from stiff major ampullate silk, and capture spirals of highly compliant flagelliform silk covered in adhesive aggregate glue (Vollrath, 1988). The components of the spider orb web – radial silk, spiral silk and glue droplets – work together first to intercept, then to stop and finally to retain prey (Blackledge and Eliason, 2007; Blackledge et al., 2011). Thus, orb webs do not function as simple sieves, and variation in the geometric arrangement of these silks, and in their mechanical performance, can favor the capture of specific types of insect prey. Orb spiders depend on particularly large insects for most of their nutrition, even though such prey are only rarely captured (i.e. the large but rare prey hypothesis for spider orb webs) (Blackledge, 2011; Venner and Casas, 2005). Despite their abundance and ease of capture, smaller, slower flying insects simply do not provide as much biomass as these rare ‘bonanzas’. Yet, large prey are heavier and, more importantly, fly significantly faster so that they impact webs with much greater kinetic energy. Targeting large prey is a risky strategy that substantially increases the probability of webs failing without providing benefit to the spiders, but also provides a big payout when the webs function successfully.

Here, we examine the hypothesis that the design of orb webs favors the capture of larger and faster flying prey. We develop three models (fixed, improvement and safety release) for how energy absorption may scale with prey speed (Fig. 1), and apply these models to prey in both low and high kinetic energy regimes. The differences in the models hinge on the sign, rather than the magnitude, of the slope of energy absorption *versus* prey speed (e.g. zero, positive or negative). Orb webs may function with a fixed capacity to dissipate prey energy. Insects whose kinetic energy exceeds that capacity would always escape, while insects below that threshold would occasionally escape depending on the vagaries of precisely how they contact threads in the orb web. Alternatively, orb webs may improve energy absorbance when struck by faster prey. This pattern would support the strong importance of the rare,

large prey hypothesis for the evolution of spider orb webs (Blackledge, 2011; Venner and Casas, 2005). Improved performance could be caused by strain-rate-dependent properties of silk (Gosline et al., 1999) and/or emergent properties of whole web architectures (Cranford et al., 2012). Finally, orb webs may exhibit a safety release mechanism that makes it easier for larger and faster flying insects, which exceed the performance threshold, to break through webs with minimal damage (Denny, 1976). A safety release would better preserve web function for capture of future insects with lower kinetic energy, and hence higher probability of capture. While these three models predict differences in maximum web performance across all prey speeds (Fig. 1), real differences can only be observed when the speed (or size) of prey is high enough that the insect’s kinetic energy exceeds the stopping potential of silk in the orb web. Furthermore, successful captures of prey do not directly measure the maximum kinetic energy that an orb web can resist, when prey are slow or small (left side of black line in Fig. 1). The three models therefore predict observable differences in the capture success of webs under a set of intermediate speeds that are difficult to determine and quantifiable differences in the kinetic energy removed from prey that routinely break through orb webs at higher speeds.

To test these three models of spider orb web performance, we fired wooden pellets and ping pong balls into orb webs at varying speeds and filmed the impacts using high-speed video. We first measured how the capture success of orb webs changes with prey speed. We then tested whether orb webs dissipate more energy from faster moving prey by comparing the energy dissipated from prey that do escape webs across a range of speeds.

MATERIALS AND METHODS

Spiders

We collected penultimate and adult female spiders at the University of Akron’s Field Station at the Bath Nature Reserve, OH, and nearby localities. Spiders were housed in either 40×40×10 cm or 80×80×20 cm screen cages with removable plexiglass sides. Spiders were misted with tap water regularly and humidifiers were used to

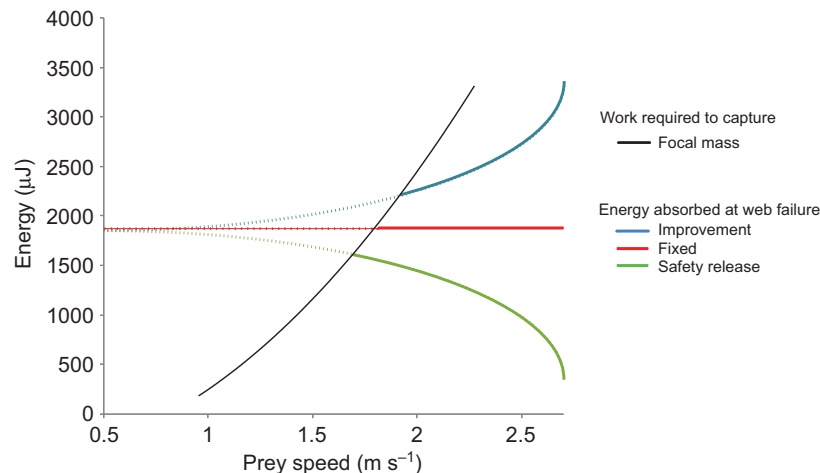


Fig. 1. Three hypotheses (models) predicting changes in web function, specifically energy absorbance, as a function of prey speed. We term the three hypotheses the improvement, fixed and safety release models. The three models are distinguished by the signs of their slopes, while their magnitudes are arbitrary in this figure. The black line indicates the work required to stop a representative 900 mg prey, calculated as its kinetic energy, $E=0.5mv^2$. In the low-speed regime (dotted colored lines), prey would easily be stopped by the web under all models, so that they are not easily distinguished. In the high-speed regime (solid colored lines), prey flying faster than 1.5 m s^{-1} with mechanical energy exceeding $2000\text{ }\mu\text{J}$ have an extremely low probability of being captured (although likely not zero probability), but the energy removed from the prey by the web differs between each model. Following from this difference in energy removal, there is thus a narrow range in prey speed (here $1.5\text{--}2\text{ m s}^{-1}$) over which the three models predict differences in capture probability. Several of our data sets support the improvement model, indicating that spider orb webs may be targeting faster prey, which characteristically have larger body mass and hence caloric value. Note that the energy required for capture increases as the square (quadratic function) of the speed.

Table 1. Spider taxa, body mass, number of webs and number of impacts

Taxa	Number of spiders	Body mass (mg; mean \pm s.d.)	Number of webs	Number of impacts			
				30 mg	100 mg	300 mg	Ping pong
<i>Metepeira</i> sp.	1	130	4	10	7	12	
<i>Verrucosa arenata</i>	3	51 \pm 5	3	6	12	3	
<i>Larinioides cornutus</i>	45	117 \pm 50	45	32	17	37	42
<i>Neoscona crucifera</i>	2	55 \pm 7	2	3	4	0	
<i>Cyclosa conica</i>	4	19 \pm 15	4	2	1	0	
<i>Argiope trifasciata</i>	14	104 \pm 25	14	20	17	8	
<i>Neoscona</i> sp.	1	47	1	1	1	2	
<i>Argiope aurantia</i>	3	375 \pm 22	3	3	3	3	
<i>Araneus trifolium</i>	6	1060 \pm 123	7	0	10	3	
<i>Araneus bicentenarius</i>	1	800	1	2	3	2	
Total	80		84	79	75	70	42

keep humidity above 60%. Some of the spider webs were examined the next day, while other spiders were allowed to build a series of webs before sampling. We used 84 webs of 10 species in the orb weaver clade Araneoidea (Table 1) in order to generalize our findings to this speciose and economically important spider group.

For nine high-energy trials, we used only *Larinioides cornutus*. The webs of these spiders were spun on thin balsa wood frames to facilitate imaging (1 \times 0.5 cm cross-section wood, 20 \times 20 cm frame). The spiders and frames were isolated in a covered pool of water in the laboratory to encourage web construction on the frames.

Projectiles representing flying prey

Webs were placed in the natural vertical position used by these spider species. Rectangular balsa wood blocks were launched at the web at velocities between 1.3 and 5.5 m s⁻¹ (Fig. 2) using a custom-made spring-loaded plastic cannon. The flying projectile kinetic energies were typical of insects that have been observed in webs (30–1500 μ J) (Blackledge and Zevenbergen, 2006). Projectiles with masses of 30 mg (6 \times 6 \times 6 mm; $N=79$), 100 mg (10 \times 7 \times 10 mm; $N=75$) and 300 mg (30 \times 7 \times 10 mm; $N=70$) were analyzed (Table 1). No one species' web was hit by particularly large or particularly fast balsa wood blocks, so that the effect of speed on capture dynamics was not confounded with taxa (Fig. 2). Individual webs were used for increasingly larger balsa projectile impacts until they were significantly damaged, which was defined as >1 broken radii or >30 broken spirals.

For very high energy intra-web comparisons (Fig. 3), we dropped a standard ping pong ball into nine different horizontal orb webs of *L. cornutus*. The mass of the ping pong ball dropped into the webs was 2609 mg and frontal surface area of the ball was 11.33 cm², several times the surface area of the 300 mg balsa blocks. The speed and energy of the ball was varied by changing the height of the drop, with zero initial speed possible by placing the ball in direct contact with the web and then releasing the ball. The ping-pong ball always broke through the webs, even at zero initial speed. The ping pong ball was aimed at a point halfway between the hub and the outer edge of the capture area, usually hitting just one radius. The order of drops for a particular web was randomized, so that some fresh webs were hit by a low energy ball while others were hit with a high energy ball as the first impact. Each web was used between two and five times depending on the size of the web and the damage from previous impacts, for a total of 42 impact events (Table 1). We confirmed the independence of drop order and impact speed with both a parametric regression of drop order *versus* speed ($F_{1,1,38}=0.54$, $P=0.46$) and a Spearman rank order test ($P=0.17$). Models also suggest that the performance of undamaged portions of orb webs are remarkably robust (Cranford et al., 2012).

Imaging methods

Images were captured with a single Fastech Troubleshooter 1268 \times 1024 pixel camera (Fastec Imaging Corporation, San Diego, CA, USA) at 500 frames s⁻¹. ProAnalyst Motion Analysis software (Xcitex, Cambridge, MA, USA) was used to digitize the projectile in each frame. Perspective calibration within ProAnalyst was used to calibrate the plane of motion of the projectile. A planar grid with 3 cm squares served as the calibration object, and was placed to within 1 cm of the trajectory plane of the projectile.

Black dots were marked on the white ping pong ball to facilitate automatic tracking by ProAnalyst, and to monitor rotation of the ball. Balls were dropped with minimal initial rotation, and possessed sufficiently high rotational inertia that rotation during impact was almost undetectable. At the highest speeds, the ball traversed approximately 15 pixels s⁻¹. Digitization accuracy for ball position was approximately 2 pixels, resulting in speed uncertainty of 0.25 m s⁻¹ at the highest speeds.

Kinetic energy of projectiles and the work performed by webs

The initial (pre-impact) kinetic energy of each event was calculated from the projectile's change in position in the video frames:

$$E_{K,initial} = 0.5mv_{initial}^2, \quad (1)$$

where $v_{initial}$ is the speed of the projectile and m is its mass. Wooden projectiles were launched at the web so that flight trajectory deviated from the plane normal to the web by 0 \pm 10 deg, as measured from a top-down or bottom-up perspective. From a lateral perspective, the trajectory varied from 45 to -45 deg from a plane normal to web. The change in kinetic energy as a projectile moved through the web was computed as:

$$\Delta E_K = E_{K,final} - E_{K,initial}. \quad (2)$$

For captured projectiles with zero velocity at the end of the interaction, $E_{K,final}$ was equal to 0.

Change in gravitational potential energy was measured as:

$$\Delta E_G = mg\Delta h, \quad (3)$$

where Δh is the drop in height from impact until final capture position or break, g is gravitational acceleration and m is projectile mass. The amount of work performed by a web was the change in total energy of the projectile during its transit through the web. Change in total energy, ΔE_{total} , was computed as:

$$\Delta E_{total} = \Delta E_K + \Delta E_G. \quad (4)$$

For the ping pong balls falling through the horizontal webs, the energy due to aerodynamic dissipation on the ball was calculated

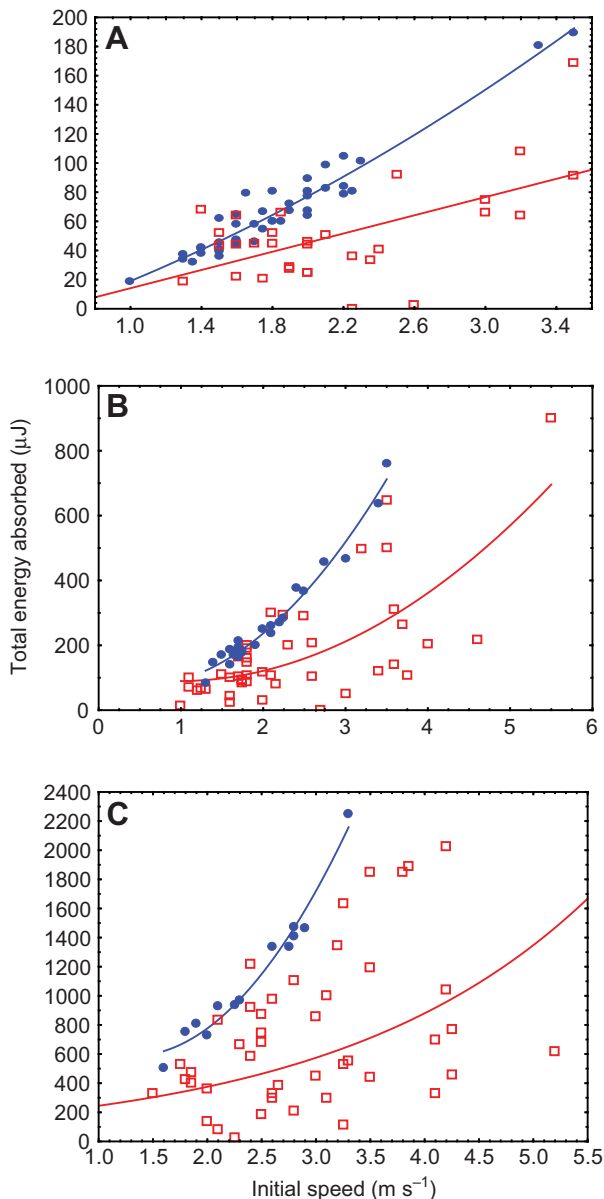


Fig. 2. Energy absorption increased with speed of projectiles. (A) 30 mg projectiles; (B) 100 mg projectiles; (C) 300 mg projectiles. Caught and escaping projectiles are indicated in blue (top line) and red (bottom line), respectively. Many factors (exact number and type of silk threads contacted, orientation of projectile at impact, etc.) help to determine whether projectiles are caught, as well as how much mechanical energy is extracted. However, we attempted to minimize this variation by using the same projectile within a weight class, which on average contacts the same number of threads on each impact. The quadratic increase of energy absorption for faster captured projectiles (in blue) is a trivial result of the kinetic energy speed dependence. The positive slope of energy absorption for the escaping projectiles (red), however, supports the improvement model rather than the fixed performance or safety release models. All regression lines are quadratic best fits.

using the ball frontal surface area, a ball drag coefficient C_d of 0.4 and instantaneous ball speed using the equations:

$$W_{\text{drag}} = F_{\text{drag}}d \quad (5)$$

and

$$F_{\text{drag}} = 0.5A_{\text{fs}}C_d\rho v^2, \quad (6)$$

where F_{drag} is the force due to air drag, d is the incremental distance fallen, A_{fs} is the frontal surface area, C_d is the drag coefficient, ρ is the density of air and v is the speed of the ball (Nagurka, 2003). Aerodynamic drag on the ball during its transit through the web represented at most $80 \mu\text{J}$, which is just 1% of the work performed by the web itself in impeding the ball's descent. Therefore, accounting for aerodynamic drag on the ball in our analysis would not change our conclusions. The aerodynamic drag on the balsa blocks was also an insignificant fraction of the web work.

Statistical methods

The effects of projectile speed on energy absorbed were tested separately for each projectile size using general linear models (GLMs) (Figs 2, 3) in STATISTICA (version 9, StatSoft, Tulsa, OK, USA), with initial impact speed and spider body mass as predictors of energy absorbed during breaking impacts. The effects of projectile speed on capture probability was tested separately for each projectile size using logistic regression in STATISTICA. A successful capture event was assigned a 1, and failure to capture was assigned a 0 value. This binomial distribution was regressed against projectile speed using the logit link function. To graph the data, bin widths of 0.33 m s^{-1} speed increments were chosen. Error bars for the capture probability within these bins (Fig. 4) representing 95% confidence intervals were calculated using the Wilson interval (Wilson, 1927) as recommended by Brown et al. (Brown et al., 2001).

Two criteria must be met in order to test the effect of projectile speed on energy dissipation. First, the speed of projectiles impacting webs must be normally distributed across spider species and body masses. Heavier spiders generally spin thicker silk threads, producing webs that would absorb more energy (Sensenig et al., 2010). A normal distribution of projectile energies across spider body size ensures that potentially higher energy webs were not hit disproportionately by higher energy projectiles. The GLM controls for the effect of body mass, even if the impacts are not normally distributed. Second, spatial calibration error must be sufficiently low, as a positive bias in the length scale would increase velocity, kinetic energy and potential energy. This would produce a positive correlation of speed and energy from calibration error alone. We found that the calibration error was on the order of 10% of the difference in energy between high- and low-speed trials, and therefore calibration error did not significantly impact the observed trends. Digitization uncertainty also produced error on the order of 10% of the observed differences.

RESULTS

We assessed the energy absorbed by webs when broken by projectiles, i.e. using only the escape events. The balsa wood projectiles comprised a lower energy regime, similar to real insects, because of lower mass. In contrast, the ping pong balls represented a very high energy regime that was unrealistic of typical prey but ideal for separating the three models of orb web performance. The energy absorption increased with the speed of the projectile for all escaping projectile sizes (30 mg, $F=14.9$, $P<0.001$; 100 mg, $F=30.5$, $P<0.001$; 300 mg, $F=10.4$, $P=0.002$; ping pong, $F=8.42$, $P=0.006$; Figs 2, 3). To verify that this trend was not caused by higher-speed projectiles hitting tougher webs, we verified using the same GLM that body mass (surrogate for web toughness) had no effect on energy absorption for any projectile size (30 mg, $F=0.09$, $P=0.77$; 100 mg, $F=0.07$, $P=0.79$; 300 mg, $F=0.73$, $P=0.40$; ping pong, $F=3.9$, $P=0.06$). The speed of the ping pong ball did not affect the distance to which webs extended at failure (four out of nine webs had positively sloped regression lines, $\chi^2=0.111$, $P=0.74$; Fig. 5),

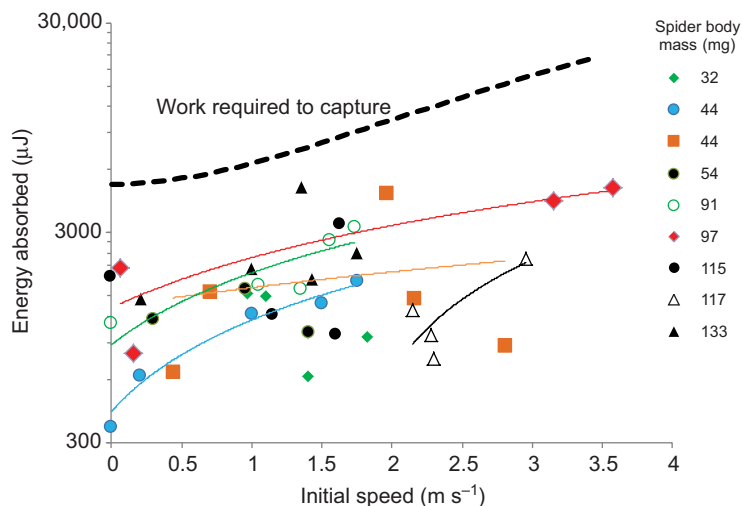


Fig. 3. Prey speed *versus* energy removed by the web for ping pong balls dropped on horizontal webs. The mass of the ping pong balls ensured that they always broke through the orb webs (e.g. the high-speed regime in Fig. 1). Energy absorbance increased with the speed of the ping pong balls (GLM with speed and body mass as predictors of energy absorbed, speed $P=0.008$, body mass $P=0.16$). Linear regression lines for five selected webs are plotted (note that the y-axis is a log scale). Seven of nine webs had a positive slope like the five slopes depicted here. Zero speed at initial contact was achieved by releasing the ball at the web surface, while speeds up to 3.5 m s^{-1} were produced by dropping the ball from a height of 30 cm. Energy required to capture is not zero at zero speed, due to the weight of the ball. This energy required to capture was computed as the potential energy associated with the average fall (web stretch) distance of 20 cm. Energy absorbance typically improved several fold over the examined speed range. Webs are identified by spider body mass (mg).

suggesting that the increased energy absorption was due to increased breaking stress at higher speeds and not due to webs maintaining contact with the ping pong balls for longer distances.

For the lower energy regime (balsa wood projectiles), we assessed probability of capture separately for the three different sizes of projectiles (Fig. 4). Capture probability decreased significantly as a function of speed only for the smallest projectiles (30 mg, Wald statistic=5.81, $P=0.016$; 100 mg, Wald statistic=1.98, $P=0.15$; 300 mg, Wald statistic=2.32, $P=0.13$).

Energy absorption of capture events is generally higher than for escape events at a given speed because not all of the kinetic energy is removed for escape events, and because capture events can include a significant change in gravitational potential energy as the projectile comes to hang in the web. Our data place upper limits on energy absorption for given sizes of prey. Specifically, we measured the highest capture energies of 200, 800 and $2200\text{ }\mu\text{J}$ for the increasing sizes of wooden projectiles (Fig. 2). Breaking energy increased with projectile size, rising as high as $5000\text{ }\mu\text{J}$ for ping ball balls. The fastest projectiles always broke the web for each size category, with webs never catching any projectile faster than 3.5 m s^{-1} . The trivial squared dependence between energy and speed of captured projectiles is plotted (Fig. 2), because this illustrates the upper limit to energy potentially absorbable for breaking events occurring at the same speed.

DISCUSSION

Our study shows that spider silk in the orb web forms a structure that exhibits improved performance with strain rate, with energy-absorbing performance improving by up to sixfold over the range of speeds applicable to flying insect prey (Fig. 3). The results from both the low energy regime (potentially stoppable prey) and the high energy regime (unstoppably heavy ping pong balls) support the improvement model in that the energy absorbed by the webs from the escaping projectiles increased with projectile speed. We failed to find evidence for the release mechanism model and the fixed performance model (Fig. 1). Larger insects generally fly faster than smaller insects. Therefore, from a kinetic energy perspective, orb webs appear to function as traps that maximize the probability of stopping the largest possible prey.

Prey capture is a complex process in orb spiders where webs first intercept insects, then stop their flight, and finally retain the insects for some period of time (Blackledge, 2012; Blackledge, 2013; Blackledge et al., 2011; Harmer et al., 2011). The struggle by kicking

and flapping prey and surface structure of the prey (e.g. silk entangling setae or Lepidoptera scale-shedding reducing silk adhesion) of the prey introduce new variables not accounted for in our simple kinetic energy model (e.g. Blackledge and Zevenbergen, 2006; Opell and Schwend, 2007). Also, if the prey oscillates in the web, our model presumes that the stickiness of the web is sufficient to hold the prey on each rebound. However, we feel that our analysis of the middle phase of capture – stopping prey kinetic energy – is a crucial step with important implications for spider fitness. The study of rare, but fitness-defining prey capture events is a challenge to spider web ecologists because rare massive prey captures are by their nature difficult to document (Blackledge, 2011; Venner and Casas, 2005). In particular, the impact of rare prey capture events for spider fitness may be determined less by how often they occur (determined in part by changes in how orb webs intercept prey) than by how effectively webs capitalize upon those events when they do occur (determined by successfully stopping and retaining prey).

Why didn't we find evidence for a safety release mechanism in orb webs that limits damage under catastrophic prey impacts? Some crucial ecological differences between spider orb webs and other foraging systems may explain our results. Many foraging decisions by animals involve cost-benefit analysis, where pursuit of prey is aborted if the prey is deemed too costly or risky (Bowen et al., 2002; Caro, 1995; Griffiths, 1980). For orb spiders, a crucial foraging step is performed by the web, substantially reducing risk to the spider itself. A web represents only approximately 0.2% of a spider's body mass (Blackledge, 1998; Gosline et al., 1986), and much of that investment can be recovered when the orb spider consumes the web and recycles the silk (Townley and Tillinghast, 1988; Townley et al., 2006). In other words, greater risks can be taken with resources that are utilized outside the organism, and that hence pose no direct mortality risk. However, spider orb webs are structurally robust to damage, with pristine regions of the web surface maintaining functionality after individual sectors are torn (Cranford et al., 2012). This suggests a 'generic' type of safety release mechanism that functions independent of prey speed or energy *per se*.

We suggest that the performance improvement in spider orb webs with strain rate is due in part to intrinsic silk material properties, although an additional role for web architecture remains to be explored. Specifically, the energy absorption increased with strain rate for both a rather small projectile size (100 mg), which usually hit only one or two threads, thereby limiting the complexity of the

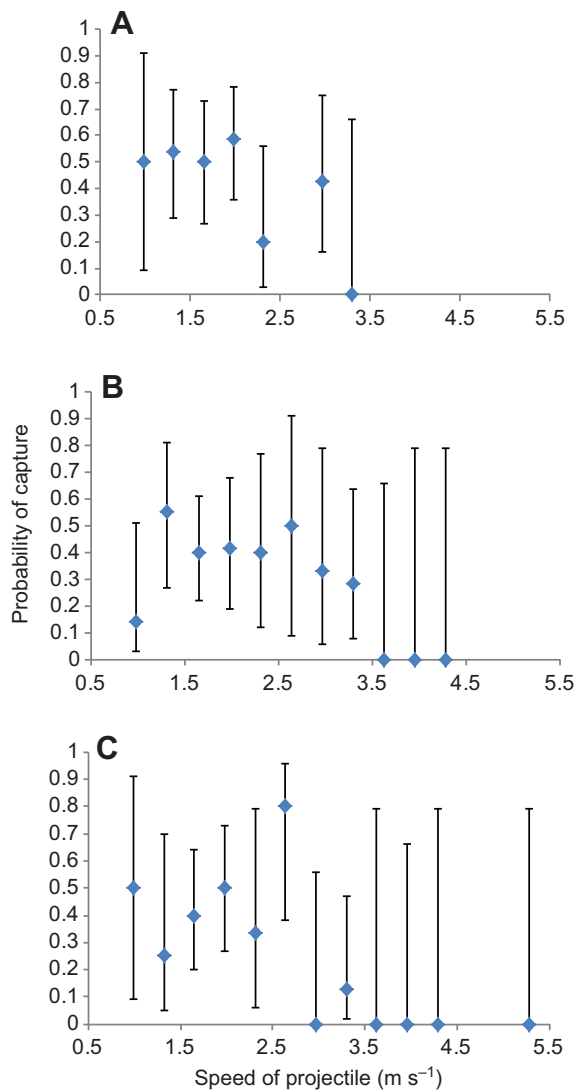


Fig. 4. Variation in capture probability as an effect of prey speed. (A) 30 mg projectiles; (B) 100 mg projectiles; (C) 300 mg projectiles. The decrease in capture probability was statistically significant only for the smallest projectile (30 mg) in a logistic regression analysis of the binomial distribution (success or failure) of the impact events (30 mg, $P=0.016$; 100 mg, $P=0.15$; 300 mg, $P=0.13$). Error bars representing 95% confidence intervals for a binomial proportion were calculated by the Wilson interval method. Bin widths are 0.33 m s^{-1} speed increments.

structure involved, and a large projectile hitting approximately seven different inter-connected threads (e.g. ping pong ball). Direct tensile tests of the material properties of individual silk threads are typically limited to relatively slow strain rates of $<10\% \text{ s}^{-1}$ (Sensenig et al., 2010; Swanson et al., 2006). Higher strain rates are derived from dropping weights onto threads. Over a 100,000-fold change in strain rate (0.05 to $5000\% \text{ s}^{-1}$), the toughness of *Araneus* single MA threads increased by approximately 10-fold (Denny, 1976; Gosline et al., 1999). Here, we generated strain rates from quasi-stationary up to $300\% \text{ s}^{-1}$, and measured at most a sixfold increase in total energy absorbed by the web. Some studies have suggested that spider silk could increase work by slightly increasing total extension at high strain rates (Gosline et al., 1999; Laible, 1980), but we found no evidence of higher extension of silk measured at the whole-web level (Fig. 5). At a given length, silk must therefore be stiffer at

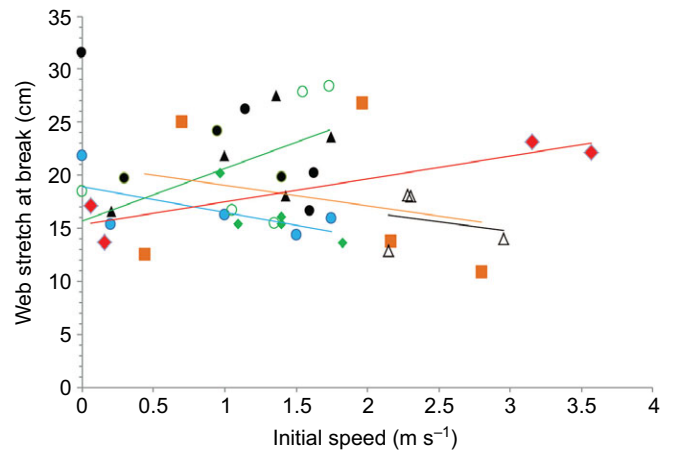


Fig. 5. Variation in web extension as a function of impact speed. Individual webs are color-coded by body mass of the spider as in Fig. 3, and only five slopes are shown, for the same spiders for which slopes are depicted in Fig. 3. Maximum web stretch did not vary with impact speed (five negative versus four positive slopes out of the nine spiders). The increased work by the web at high speeds must therefore be performed over a similar distance as at low speed, suggesting that webs do not hold onto high-value prey for longer distances.

higher strain rates. We suggest that faster extension of silk threads inhibits the entropy-driven collapse of the alpha helices, an effect not measured previously because of the low extension rates used in previous studies. Limited ballistic tests (strain $\sim 50,000\% \text{ s}^{-1}$) of pads made of spider silk show that energy absorption is similar to quasi-static tests, although it is not clear whether the ballistic impacts consist primarily of extension or compression of the material (Cunniff et al., 1994).

In summary, our findings suggest that natural selection acted upon spider orb webs to enhance capture of large, fast-flying insects. Orb webs respond to faster prey with better performance through a complex interplay of web architecture and silk material properties. We conclude that spider orb webs (particularly the individual sectors of the web) are unlikely to exhibit safety release mechanisms because the web is a 'disposable' structure optimized for a one-time impact, contrasting with many mechanical systems that are intrinsic to organisms. Instead, spider orb webs function more like human technology such as helmets and bullet-resistant armor that are designed for single impacts. Future engineering improvements to these technologies may find inspiration in the structure of spider orb webs, which have evolved for similar function at least since the early Cretaceous (Peñalver et al., 2006).

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AUTHOR CONTRIBUTIONS

A.T.S. and T.A.B. designed the study, analyzed the data and wrote the manuscript. A.T.S., S.P.K., K.A.L. and B.L. conducted the mechanical tests and performed the video analyses.

COMPETING INTERESTS

No competing interests declared.

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