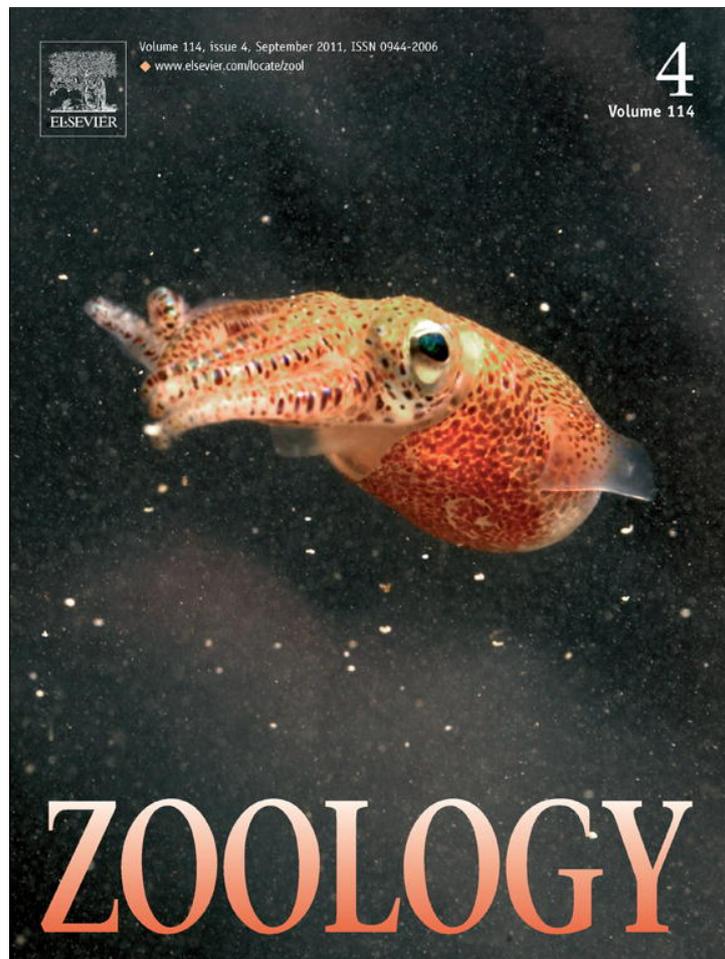


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ZOOLOGY

## Damping capacity is evolutionarily conserved in the radial silk of orb-weaving spiders

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### ABSTRACT

Orb-weaving spiders depend upon their two-dimensional silk traps to stop insects in mid flight. While the silks used to construct orb webs must be extremely tough to absorb the tremendous kinetic energy of insect prey, webs must also minimize the return of that energy to prey to prevent insects from bouncing out of oscillating webs. We therefore predict that the damping capacity of major ampullate spider silk, which forms the supporting frames and radial threads of orb webs, should be evolutionarily conserved among orb-weaving spiders. We test this prediction by comparing silk from six diverse species of orb spiders. Silk was taken directly from the radii of orb webs and a Nano Bionix test system was used either to sequentially extend the silk to 25% strain in 5% increments while relaxing it fully between each cycle, or to pull virgin silk samples to 15% strain. Damping capacity was then calculated as the percent difference in loading and unloading energies. Damping capacity increased after yield for all species and typically ranged from 40 to 50% within each cycle for sequentially pulled silk and from 50 to 70% for virgin samples. Lower damping at smaller strains may allow orb webs to withstand minor perturbations from wind and small prey while still retaining the ability to capture large insects. The similarity in damping capacity of silk from the radii spun by diverse spiders highlights the importance of energy absorption by silk for orb-weaving spiders.

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### 1. Introduction

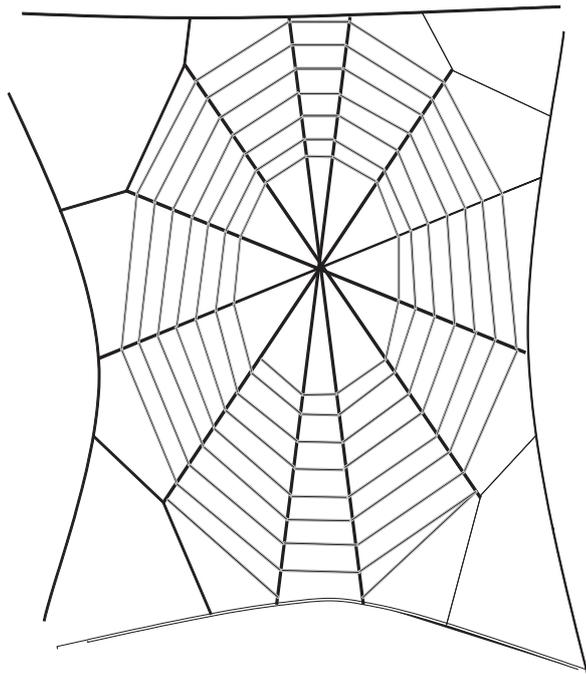
More than 4000 species of spiders use orb webs to trap prey (Blackledge et al., 2009). The success of orb-weaving spiders is due in part to the extraordinary properties of the silks that these spiders use to construct their orb webs and how those silken networks dissipate the kinetic energies of flying insect prey (Denny, 1976; Bond and Opell, 1998). The silk used to construct the radii and supporting frames of orb webs (Fig. 1) is produced by the major ampullate gland and is extraordinarily stiff and strong (Swanson et al., 2006). In contrast, the capture spirals of orb webs are extremely compliant and extensible (Swanson et al., 2006). Capture spirals are spun from fibers produced by the flagelliform glands that are coated with glue from aggregate glands. Although both of these materials are extraordinarily tough, the capture spiral fibers can be ten times more extensible than the radii (Denny, 1976; Blackledge and Hayashi, 2006a).

Large insect prey typically contact at least one radius and several rows of capture spiral when they impact webs (Eberhard, 1986; Blackledge and Zevenbergen, 2006). The kinetic energy of

their flight is then transferred to adjoining threads in the web as the web stretches (Lin et al., 1995; Ko and Jovicic, 2004; Alam et al., 2007; Aoyanagi and Okumura, 2010). While highly extensible and tough, the capture spiral is so compliant that it generally plays little role in energy absorption during prey impact (Sensenig et al., unpublished data). The thin diameters and correspondingly low Reynold's numbers for silk threads in orb webs suggest that friction of threads moving through the air might dissipate a significant amount of energy as webs stretch (Lin et al., 1995). However, both theoretical modeling (Ko and Jovicic, 2004; Alam et al., 2007) and calculation of energy budgets of actual webs deforming under impact (Sensenig et al., unpublished data) demonstrate that friction of threads moving through the air, or "aerial damping" plays a significantly smaller role in energy absorption than previously hypothesized by Lin et al. (1995). Thus, for many prey impacts, the radii do most of the work of stopping flying insects and the major ampullate silk used to construct those radii is both significantly stronger and tougher in orb weaving spiders as compared to other taxa (Swanson et al., 2006). However, radial silk must do more than simply resist breaking under the high energy impacts of prey. The silk must also minimize internal storage of energy to prevent a "trampoline" effect where insects bounce out of oscillating webs. Radial silk should therefore minimize the amount of energy that is stored internally as it extends. Damping capacity measures

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**Fig. 1.** Typical spider orb web. An elastic spiral of sticky capture silk, in gray, is suspended upon a network of comparatively stiff and strong major ampullate radial and frame threads, in black.

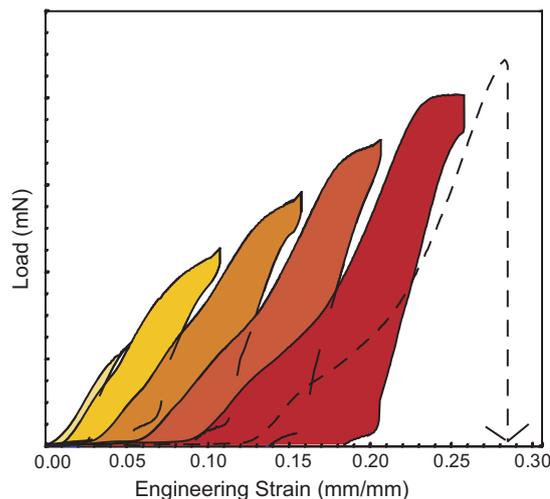
the proportion of energy input into silk that is dissipated through the breaking of molecular bonds, increases in entropy, and the production of internal heat, such that the energy will not be returned to prey as orb webs oscillate. Here, we calculate damping capacity using “specific damping capacity”, or the ratio of dissipated energy to stored energy per volume of silk. This measure of material performance has been called various names in other studies, including loss tangent ( $\tan \delta$ ), hysteresis, and the inverse of resilience (e.g., Martz et al., 1996).

Our goal is to understand the integrative function of webs during prey capture. Because of the inherent importance of damping for orb webs, we predict that it should be a strongly conserved trait among different evolutionary lineages of orb-weaving spiders, even though other material properties, such as tensile strength and extensibility, can vary greatly among taxa (Swanson et al., 2006). In this study, we calculate the damping capacities of radial threads taken from the orb webs of six evolutionarily diverse species of orb-weaving spiders and place the data into a phylogenetic context.

## 2. Materials and methods

### 2.1. Silk collection

We compared the damping capacity of radial silk from webs spun by six orb-weaving spiders: *Argiope aurantia*, *Argiope trifasciata*, *Larinioides cornutus*, *Cyclosa conica*, *Caerostris darwini* and *Leucauge venusta*. While the choice of these species was largely opportunistic, they also span much of the evolutionary diversity of orb-weaving spiders (Scharff and Coddington, 1997). Most belong to the Araneidae, the most speciose family of orb spiders, and include large (*A. aurantia* and *A. trifasciata*), medium (*L. cornutus*) and small-bodied (*C. conica*) species. *L. venusta* is a member of Tetragnathidae and tends to construct horizontal rather than vertical orb webs. All five species occur broadly across the US and were collected from Akron or Bath, OH. In contrast, *C. darwini* is endemic to Madagascar and was included because of its unique ecology. These spiders spin giant orb webs that are suspended across rivers



**Fig. 2.** Load–strain curve for a single radial thread pulled in 5% strain increments until failure. Damping energy is indicated by the filled area under each curve and is significantly lower for the first 5% strain compared to all other increments. Note that the absolute magnitude of load generated by a particular silk fiber depends largely upon its diameter but that damping energy measures the relative difference in loading and unloading.

and lakes using silk that is significantly tougher than any other known biomaterial (Agnarsson et al., 2010). Silk was collected from webs spun in the laboratory.

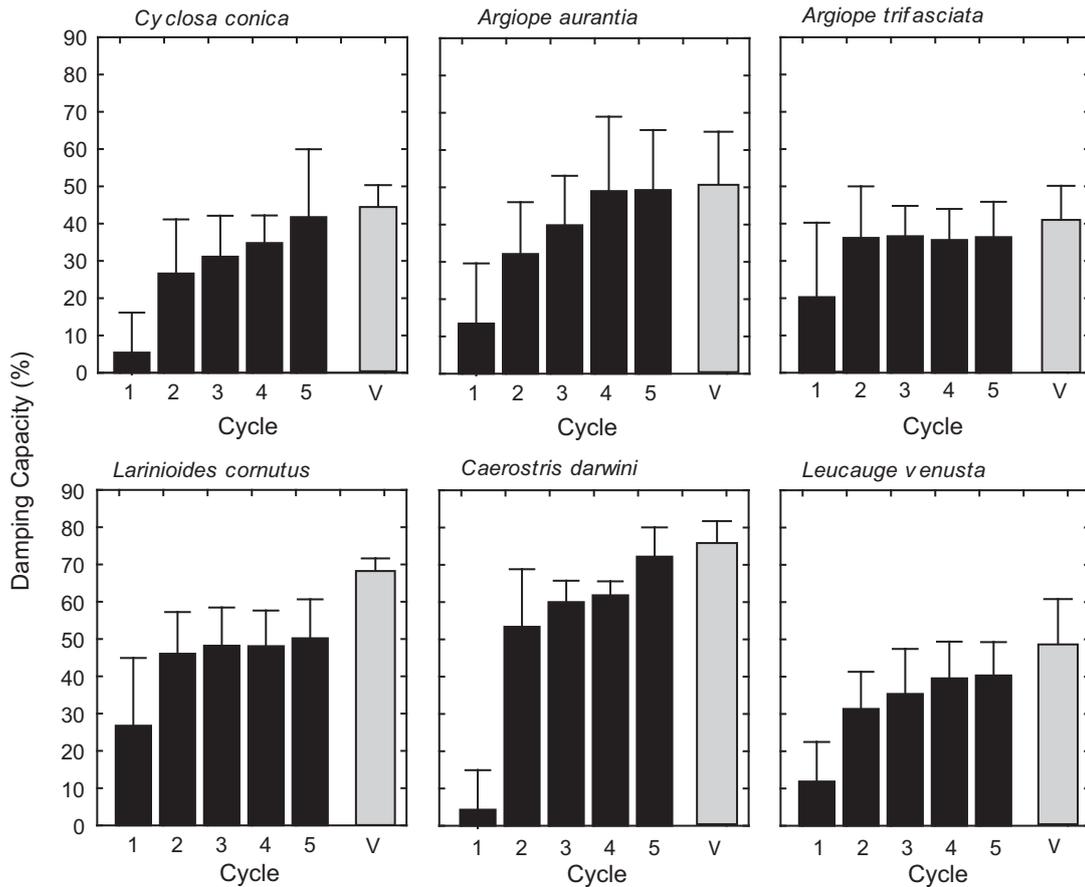
Most species were housed in 40 cm × 40 cm × 10 cm cages with removable sides described by Sensenig et al. (2010a). However, *L. venusta* suspends its horizontal orb within a three-dimensional framework of threads such that they only spun webs in a greenhouse. The large size of *C. darwini* webs also meant that they only spun webs within the greenhouse.

Radial silk was collected from webs using standard methods (Sensenig et al., 2010a). A single radius was secured across a 16 mm gap on a cardboard mount using cyanoacrylate. The sample was then cut free from the web using a hot soldering iron to avoid straining it. For each web, we collected four samples—one each from the north, south, east and west quadrants. At least three different individual spiders' webs were sampled per species. For three spiders, two different webs each were sampled. A small number of silk samples were lost during testing. Total sample sizes ( $N$  = number of spiders and  $n$  = number of silk samples) were therefore: *A. aurantia*:  $N=5$ ,  $n=23$ ; *A. trifasciata*:  $N=6$ ,  $n=30$ ; *L. cornutus*:  $N=6$ ,  $n=20$ ; *C. conica*:  $N=6$ ,  $n=20$ ; *C. darwini*:  $N=3$ ,  $n=14$ ; *L. venusta*:  $N=5$ ,  $n=18$ .

### 2.2. Silk testing

Tensile tests of the radial silk were then conducted using a Nano Bionix test system (Agilent Technologies, Inc., Santa Clara, CA, USA), as described by Blackledge et al. (2005), Blackledge and Hayashi (2006a), and Agnarsson and Blackledge (2009). We used two different protocols. First, we subjected 16 mm gauge lengths of radial silk to a sequential series of hysteresis cycles, starting at 5% engineering strain and progressing in 5% intervals up to 25% strain (Fig. 2). For each cycle, the fiber was extended at a strain rate of 10% gauge length/s, followed by immediate relaxation back to the mounting extension, at the same rate. Major ampullate silk often breaks at 25% strain; thus, some fibers failed before completing this final strain loop. For other tests, we pulled virgin fibers, with no previous straining, to 15% engineering strain for comparison to samples pulled sequentially to that same strain.

For each sample we calculated loading and unloading energies (Nmm) from the areas under the force–extension curves. Damping capacities were then calculated for each silk sample



**Fig. 3.** Mean ( $\pm$ SD) damping capacity of major ampullate silk fibers for each species. Cycle 1=5% strain, Cycle 2=10% strain, Cycle 3=15% strain, Cycle 4=20% strain, and Cycle 5=25% strain. Final column “V” shows a virgin silk, with no prior extension, pulled to 15% strain.

from the difference in loading versus unloading energies using the formula:

$$\text{damping capacity} = \frac{(\text{loading energy} - \text{returned energy})}{\text{loading energy}}$$

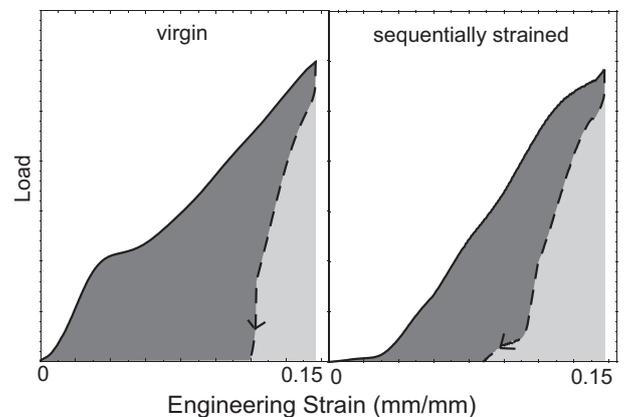
Damping capacity was calculated for each cycle for sequentially pulled samples. We then used a two-way ANOVA to compare damping among the six species, using cycle number and species as categorical factors. We used a second two-way ANOVA to compare the damping of virgin silk to the 15% strain cycle of sequentially pulled silk across species. Tukey's HSD tests were used for post hoc pair-wise comparisons.

### 2.3. Phylogenetic comparison

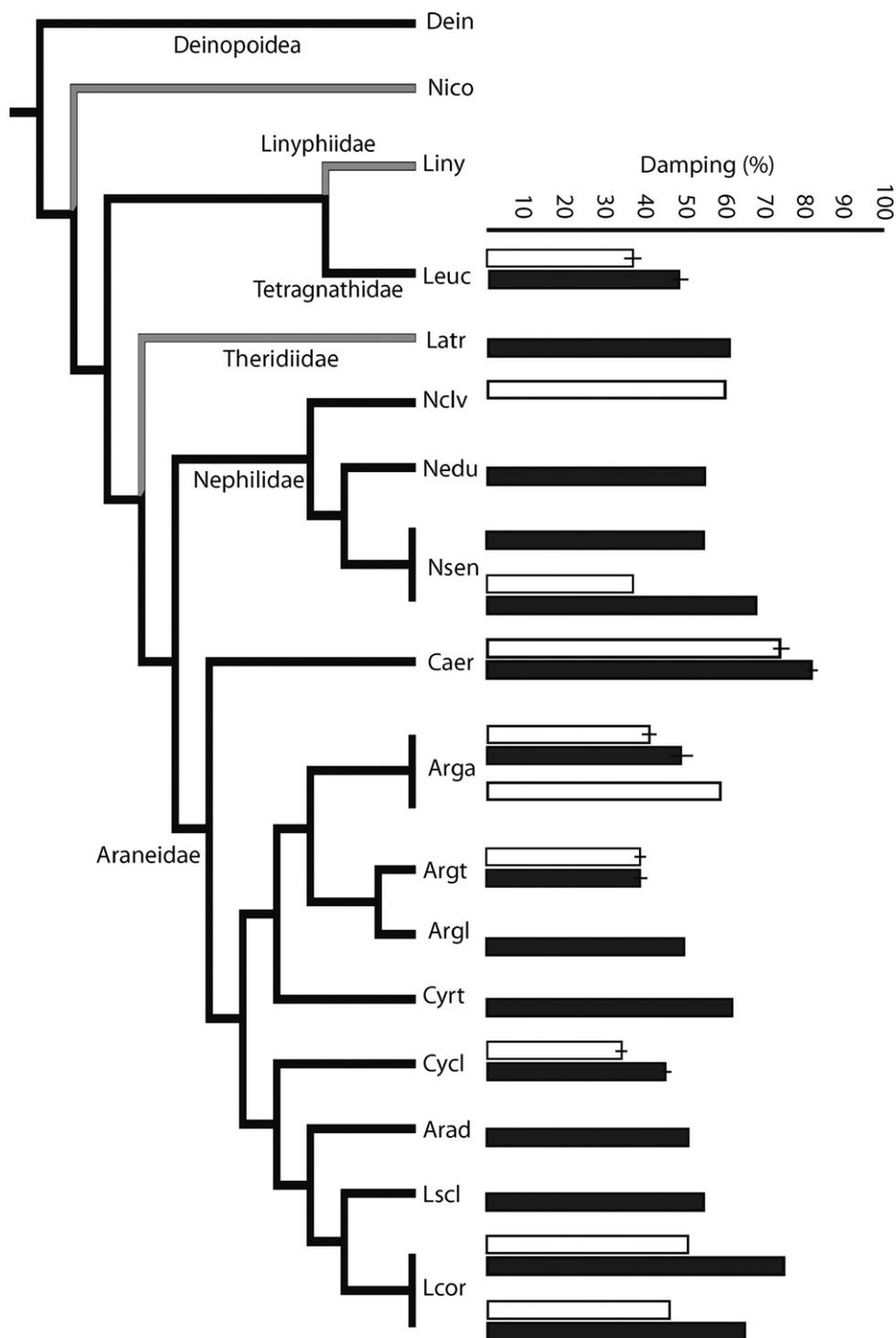
Finally, we compared our results to existing data in the literature, placed in a phylogenetic context. We assembled a composite phylogeny because no single study includes all of the taxa for which damping capacity data are available. Higher level relationships of orbicularian spiders were taken from Blackledge et al. (2009) and Sensenig et al. (2010a). Kuntner et al. (2008) was then used to infer relationships within *Nephila* and Elices et al. (2009) to infer relationships within *Argiope*. Data on silk damping were taken directly from Denny (1976) for *Larinioides sclopetarius*, which has changed taxonomically from *Araneus sericatus* (Platnick, 2010), from Brooks et al. (2007) for *A. aurantia* and *Nephila clavipes*, and from Vehoff et al. (2007) for *Nephila senegalensis*. We also inferred the mean damping capacity from graphs in Liu et al. (2008) for *Araneus diadematus*, *Argiope argentata*, *Argiope lobata*, *Cyrtophora citricola*,

*Latrodectus hesperus*, *Nephila edulis*, *Nephila senegalensis*, and *Nuctenea sclopetaria* whose current taxonomy is *Larinioides sclopetarius* (Platnick, 2010). The methodologies of these studies were generally similar to our own in terms of how far, how fast, and how often silk samples were strained. However, we refer the reader to the original publications for exact details.

Comparative data were included for all major clades of orb-weaving spiders, with three exceptions: (i) Cribellate orb spiders in the Deinopoidea use a radically different type of adhesive silk



**Fig. 4.** Load–strain cycle comparison for virgin versus sequentially strained major ampullate silk. Dark gray indicates the damping energy, while total gray area represents the loading energy. Load for the two samples, which is diameter-dependent, was normalized to the same height on the y-axes to facilitate the comparison of the relative areas under the stress–strain curves.



**Fig. 5.** Phylogenetic distribution of dragline silk damping among orb spiders. White bars indicate damping of silk stretched sequentially to ~15% strain, while black bars indicate virgin silk stretched to ~15%. Standard error is reported only for silk tested in the current study and not all studies collected both types of data. The three “apical polytomies” indicate species for which two studies presented data. Gray branches in the phylogeny indicate clades that spin derived, non-orb-shaped webs (e.g., cobwebs and sheet webs). Phylogenetic relationships for Orbiculariae are from Blackledge et al. (2009) and from Sensenig et al. (2010a). Relationships within Nephilidae are inferred from Kuntner et al. (2008) and within *Argiope* from Elices et al. (2009). Arad: *Araneus diadematus*; Arga: *Argiope aurantia*; Argl: *Argiope lobata*; Argt: *Argiope trifasciata*; Caer: *Caerostris darwini*; Cycl: *Cyclosa conica*; Cyrt: *Cyrtophora citricola*; Dein: Deinopoidea; Latr: *Latrodectus hesperus*; Lcor: *Larinioides cornutus*; Leuc: *Leucauge venusta*; Liny: Linyphiidae; Lscl: *Larinioides sclopetarius*; Nclv: *Nephila clavipes*; Nedu: *Nephila edulis*; Nico: Nicodamidae; Nsen: *Nephila senegalensis*.

that alters the way orb webs function mechanically (Blackledge and Hayashi, 2006b). This dry adhesive silk is ancestral for orb spiders but there are relatively few extant species left in this lineage (Opell, 1998). (ii) The Linyphiidae are a speciose clade that spin three-dimensional sheet webs using behaviors derived from an orb-weaving ancestor. Despite their diversity, almost nothing

is known about the biomechanics of their silks or webs. (iii) The Symphytognathoidae are a diverse group of enigmatic orb weavers whose tiny size has largely precluded mechanical analysis of their webs and silk. Despite these gaps, the species in this analysis define a clade that constitutes ~2/3 of the total diversity of orbicularian spiders.

### 3. Results

#### 3.1. Silk damping

Damping capacity varied significantly, both among species and across cycles during sequential straining (ANOVA, species  $F=17.7$ ,  $P<0.0001$ ; strain cycle  $F=67.7$ ,  $P<0.0001$ ). There was also a significant interaction between species and strain cycle (interaction  $F=2.5$ ,  $P<0.0005$ ). Damping capacity increased significantly after the initial 5% strain for sequentially strained silk in all species (Figs. 2 and 3). In contrast, there were no statistical differences in damping capacity between the last three cycles within species. Damping capacity varied among species by as much as 36% within any one cycle (Fig. 3). In particular, *C. darwini* silk exhibited higher damping capacity for later cycles than all other species, although the difference was not statistically significant for *L. cornutus* ( $P<0.25$ ).

Damping capacity was higher for virgin fibers pulled to 15% strain compared to sequentially pulled fibers in the 15% strain cycle for all species (Figs. 3 and 4; ANOVA, strain cycle  $F=34.3$ ,  $P<0.00001$ ).

#### 3.2. Phylogenetic comparisons

Data on the damping capacity of the major ampullate silk were available for 15 species of spiders within the Orbiculariae (Fig. 5). Damping capacity generally ranged from 40 to 60%, but was always lower for cyclically strained silk compared to virgin fibers from the same species.

### 4. Discussion

The damping capacity of spider silk plays a critical role in how orb webs stop flying insects without them ricocheting out of the web (Denny, 1976; Vehoff et al., 2007). More than 4000 species of spiders construct orb webs using the same basic design—a compliant spiral of glue-coated silk suspended upon a stiff framework (Blackledge et al., 2009). However, these webs vary immensely in size (>800 cm<sup>2</sup> for *C. darwini* and less than 90 cm<sup>2</sup> for *C. conica*) and in architectural details (Craig, 1987; Sensenig et al., 2010a). The tensile properties of major ampullate silk also vary significantly among orb-weaving spiders, by up to 100% (Swanson et al., 2006; Sensenig et al., 2010a). Despite this variation, the damping capacity of major ampullate silk is relatively similar among diverse species of spiders (Figs. 3 and 5). The phylogenetic distribution of species in our study suggests that energy damping by major ampullate silk was largely conserved during the evolution of orb-weaving spiders. Most species exhibited damping capacities of ~40–50% at high strain under repeated loading (Fig. 5). An obvious exception was *C. darwini*, whose silk showed a much higher damping capacity of about 60% under repeated loading. The high damping of *C. darwini* silk might be explained by phylogenetic inertia because the golden silk orb spider *Nephila senegalensis* also shows very high damping, up to 68% (Vehoff et al., 2007). While *Caerostris* is currently in a different family, Araneidae, recent phylogenetic analyses suggest that it is much more closely related to *Nephila* (Sensenig et al., 2010b). However, the phylogenetic inertia hypothesis is weakened by the observation that the damping of *N. senegalensis* silk drops to 37% under sequential straining (Vehoff et al., 2007), which is comparable to other species in our study rather than to *Caerostris*. In addition, *C. darwini* exhibits an extraordinary ecology, spinning giant orb webs across rivers in Madagascar that are suspended upon bridge lines exceeding 20 m in length. *C. darwini*'s major ampullate silk is also tougher than all other known spider silks (Agnarsson et al., 2010). Perhaps these attributes result in differences in how

*C. darwini* webs oscillate during prey impact, accounting for the silk's higher damping capacity. For instance, it is possible that the same molecular mechanisms that promote high energy absorption by silk may also facilitate rapid energy dissipation.

The reduced damping of silks at 5% strain (cycle 1) compared to subsequent cycles (Fig. 3) is easily explained by the viscoelastic behavior of spider silk. Until yielding at 2–3% strain, the silk proteins deform primarily through straining of hydrogen bonds, in an entirely elastic manner such that no damping occurs (Termonia, 1994). Might this have a functional benefit for webs? Damping capacity is higher in virgin fibers (Fig. 4). Thus, webs should function optimally, in terms of maximizing energy dissipation, when they are first loaded beyond yield. However, orb webs are subjected to two very different types of loading in nature. The rapid, concentrated loading of discrete web regions during prey impact contrasts strongly with the dispersed loading caused by wind, which generally results in significantly lower strains. Low damping at the small strains caused by wind loading might allow webs to recover elastically from such repeated perturbations while still retaining maximum functionality during prey impact. In addition, particularly small insects are common prey of spiders, but are of little energetic value (Venner and Casas, 2005; Blackledge, 2011). Such small prey may also fail to strain the silk past yield due to their low kinetic energies. Again, initially low damping allows orb webs to retain the full functionality of their silk until the impact of larger, energetically valuable prey.

The relative similarity in damping capacity of silk from the radii spun by diverse spiders (Fig. 5) highlights the importance of energy absorption by silk for orb-weaving spiders. Like other material properties, damping capacity appears strongly shaped by natural selection. The high damping of major ampullate spider silk contrasts with the characteristics of other durable biomaterials such as collagen, elastin, and resilin, which exhibit damping capacities as low as 3% (Wainwright et al., 1976; Vincent, 1990). The low damping of these biomaterials can be explained by their function to store and return energy during a stride or wingbeat, thereby enhancing the efficiency of locomotion. Spider silk is selected for the opposite extreme of energy damping, and instead functions to stop locomotion of insect prey. Similarly high damping is found in functionally analogous biomaterials such as the byssal threads of mussels, which affix the mussels to rocks in the high energy surf zone (Brazee and Carrington, 2006).

Many questions remain. In particular, major ampullate silk evolved long before the origin of aerial orb webs and was used primarily to spin lifelines and the frames of terrestrial webs capturing pedestrian arthropod prey (Swanson et al., 2006). Will comparative studies of damping in the silk of these non-orb-weaving species yield evidence for selection on the damping capacity of major ampullate spider silk associated with the origin of the aerial orb, and the use of silk to capture flying insects?

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