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The Form and Function of Spider Orb Webs: Evolution from Silk to Ecosystems

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- 1 Introduction 176
 - 1.1 Origin of orb webs 177
 - 1.2 Orb web structure and characterization 179
 - 1.3 What is silk? 184
 - 1.4 Orb web spinning behaviours 197
 - 1.5 Is web spinning innate? 199
- 2 Orb web function during prey capture 201
 - 2.1 What prey are spiders targeting? 201
 - 2.2 Prey interception 203
 - 2.3 Prey stopping 204
 - 2.4 Prey retention 206
 - 2.5 Vibration transmission 208
 - 2.6 Web visibility and stabilimenta 209
- 3 How costly are orb webs? 214
 - 3.1 Energetic costs 215
 - 3.2 Web relocation 216
- 4 Plasticity and response to the environment 216
 - 4.1 Responsiveness to microhabitat 217
 - 4.2 Response to prey 217
 - 4.3 Predator induced plasticity 220
 - 4.4 Chemically induced webs 220
 - 4.5 Supercontraction: maintaining function of wetted webs? 221
- 5 Beyond prey capture: orb webs as habitats 222
 - 5.1 Webs as predatory defences 222
 - 5.2 Kleptoparasitism 223
- 6 Evolution of orb webs 223
 - 6.1 The cribellate/ecribellate transition 223
 - 6.2 Evolution within the orb architecture 225
 - 6.3 Stepping stones to new web architectures 226
- 7 New horizons 235
 - 7.1 Whole web function and biomechanics 235

7.2	Can webs drive speciation?	236
7.3	Molecular ecology of silk production	236
7.4	Biomimicry	237
	Acknowledgements	237
	References	238

Abstract

Spiders are the preeminent silk craftsmen among arthropods and are best known for producing aerial orb webs that snare flying insects. Orb web spiders are ubiquitous predators in terrestrial ecosystems and are popular models for behavioural and ecological research, in part due to the ease of characterizing the shapes of orb webs. Orb webs are composite structures built from multiple types of silks, each with its own unique molecular structure and mechanical function, such that orb webs also link together evolutionary research from the genes coding for silk proteins to whole web function in the environment. Yet, orb webs are only intermediate structures in the evolutionary diversification of silk use among spiders, acting as stepping stones facilitating the origin of new web types and increased spider diversification. Here, we review the current research on the form and function of spider orb webs. We provide a comprehensive introduction to all aspects of orb web biology, suitable for any new investigation into orb web biology. While other reviews exist individually for webs, silk, and spider evolution, we hope that the synthetic nature of this review will facilitate a more integrated approach by future investigators. Finally, we explore in more detail some of the most dynamic areas of orb web biology to suggest promising venues for the next decade of research on these fascinating creatures and their silken snares. In particular, we discuss how spider webs might drive speciation, the dramatic growth in our understanding of the molecular ecology of spider silk, and the importance of a greater role for spider biology *per se* in silk biomimicry.

1 Introduction

Silk production evolved many times in arthropods (Craig, 1997). Yet, spiders are the preeminent silk craftsmen, utilizing multiple types of silk threads to construct a dizzying array of structures ranging from simple lifelines to shelters for moulting and protective egg sacs to webs. No group of spiders exemplifies this strategy better than the orb web spiders. More than 4600 species of spiders currently construct orb webs (Platnick, 2011). They are ubiquitous predators in most terrestrial ecosystems (Turnbull, 1973; Wise, 1993) and are common subjects of behavioural and ecological research (Herberstein, 2011). In particular, there is relatively extensive knowledge of how orb web spiders produce silk. The diverse toolkits of silk fibres produced by orb web spiders rank among the strongest, stretchiest, and toughest biomaterials known and are assembled nearly instantaneously from liquid protein feedstock inside the spiders' bodies. While this sets the stage for a highly integrative understanding of the form and function of orb webs, from molecules to whole webs to how webs function in

ecosystems, such synthesis largely has yet to be realized (Craig, 2003; Harmer et al., 2010). Here, we explore the functional morphology of spider orb webs from these different perspectives with three goals: First, to provide a comprehensive introduction to all aspects of orb web biology that is suitable for a general audience and can act as a 'launching pad' for new investigations into orb web biology. Second, we hope that this review will facilitate researchers in specialized fields of orb web and silk biology to incorporate more integrated approaches for future investigations. Finally, we explore in more detail some of the most dynamic areas of orb web biology to suggest promising venues for the next decade of research on these fascinating creatures and their silken snares.

1.1 ORIGIN OF ORB WEBS

Orb web-weaving occurs within a single evolutionary lineage of spiders, the Orbiculariae (Griswold et al., 1998), and seven families currently produce stereotypical orb webs that are easily recognized due to their round, 'wagon wheel'-shaped architectures. Orb webs are more appropriately distinguished from other types of spider webs in their suspension in the air column upon discrete networks of frame threads, their two-dimensional (2D) capture surfaces comprised of continuous spirals of sticky silk, and the high degree of stereotypic motor patterns during web spinning (Blackledge et al., 2009c; Coddington and Levi, 1991). Orb webs range in size from < 2 cm (Anapidae) to almost 2 m (*Caerostris darwini*) in diameter, and the spider species spinning those webs also range orders of magnitude in body size (Blackledge et al., 2009b; Gregorič et al., 2011). Despite the orb web's elegance and unique capacity to capture flying insects, it represents a stepping stone in the evolution of spider webs and many families within the Orbiculariae no longer spin orb webs (Griswold et al., 1998). In particular, orb web spiders gave rise to two major radiations of three-dimensional (3D) web spinning spiders—the cobweb spinning Theridiidae (Agnarsson, 2004; Arnedo et al., 2004) and the aerial sheet-web spinning Linyphiidae (Arnedo et al., 2009; Miller, 2007).

Spider orb webs can be divided into two architectural categories that differ mainly in the type of silks used for the adhesive capture spiral—viscid spiral consisting of flagelliform fibres coated with aggregate glue or cribellate spiral consisting of pseudoflagelliform fibres surrounded by dry cribellar threads (Opell and Schwend, 2009; Fig. 1). The production of different types of capture silk has many functional consequences. For instance, cribellate silk is combed out in a labour-intensive manner such that cribellate orb webs take a long time to build, although they may also be longer lasting (Kawamoto and Japyassu, 2008). In contrast, orb webs made with gluey spirals of viscid capture silk can be built rapidly, but typically do not last long and are rebuilt daily or when the glue dries out. The glands producing these silks also differ radically (see Section 1.3.3). These rather fundamental differences led authors to propose the spider orb as a classical example of convergence, hypothesizing that spiders

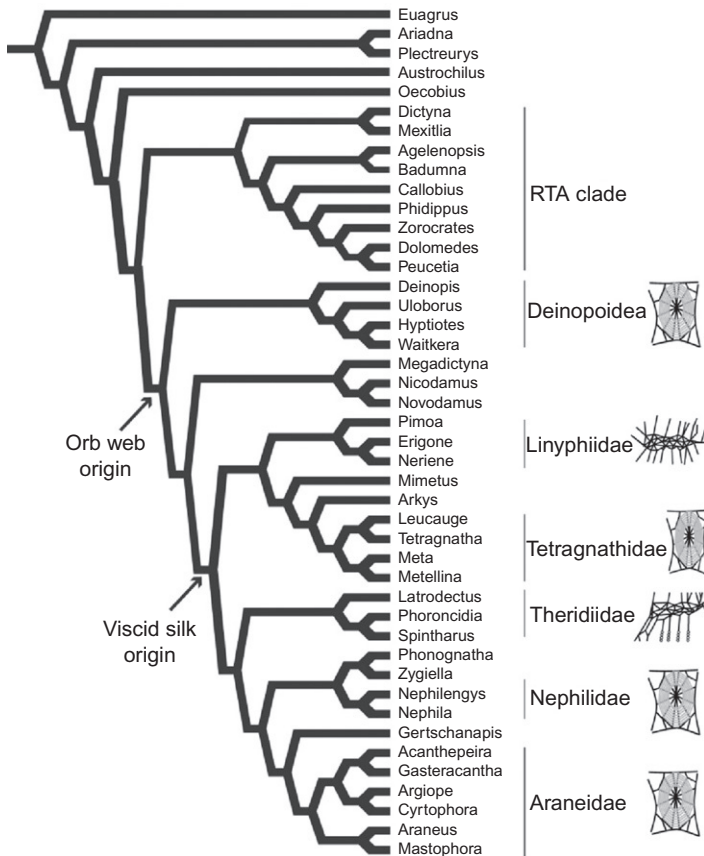


FIG. 1 Phylogeny of orb-weaving spiders based upon total evidence analysis. Modern orb web spiders belong to the Araneoidea, defined here by the origin of the viscid silk glue. However, orb spinning arose much earlier in the cribellate ancestor of all Orbicularia (Deinopoidea + Araneoidea). After Blackledge *et al.* (2009c).

utilizing cribellate capture silk and viscid capture silk each evolved the orb architecture independently (Eberhard, 1987; Kaston, 1964; Tsychenko, 1986). However, other authors argued that shared derived similarities between cribellate and viscid orb instead suggested a single, monophyletic origin of the spider orb (Coddington, 1982, 1986a; Griswold *et al.*, 1998). Coddington, in particular, argued that the similarities were not simply the web architectures, but also included details in the behavioural sequences and motor patterns used during web construction.

Evidence for or against each hypothesis can be gathered at various levels—from detailed comparison of architecture, to comparison of behaviour, to developmental pathways. However, these hypotheses must ultimately be evaluated in

a phylogenetic framework. The earliest quantitative phylogenies based on morphology and behaviour supported monophyletic origin of orb webs (Coddington, 1982, 1986a). Yet, these studies could be criticized for relying heavily on the observed similarities under testing—the architecture of the orb itself and the behavioural sequences of orb web spinning formed the strongest character systems in these character poor phylogenies. Subsequent tests that included more data, primarily morphology, all supported the monophyletic Orbiculariae, a clade grouping cribellate and ecribellate orb web spiders (Álvarez-Padilla et al., 2009; Griswold et al., 1998; Hormiga et al., 1995; Kuntner et al., 2008a; Lopardo and Hormiga, 2008; Scharff and Coddington, 1997). However, most of these phylogenies were not entirely independent from one another, as they used largely overlapping cladistic matrices. Therefore, independent testing of orb web monophyly using independent, that is, molecular, data became an urgent priority (e.g. Hausdorf, 1999). The most conclusive study to date recovered the orb web as monophyletic (Blackledge et al., 2009c; Fig. 1), such that there is currently little evidence supporting the convergence hypothesis.

We explore some of the functional implications for the evolution of viscid capture threads in orb web spiders in Section 2 and examine the controversy over the evolutionary sequence of events for this transition in Section 6.

1.2 ORB WEB STRUCTURE AND CHARACTERIZATION

1.2.1 Terminology

The rich history of research on orb web spiders results in a diversity of sometimes contradictory terminology describing web structures so that we start with a brief review. The older literature was summarized by Zschokke (1999) and we follow his nomenclature, except in the cases where the current literature has settled upon alternatives.

The main structural elements of an orb web are the bridge line, which anchors to the substrate, the frame lines, which may connect directly to the substrate or to other lines in the web, the radii (or radius lines), which connect the frames with the central web termed the hub, and the capture spiral, which is a continuous thread that is attached to the radii as it spirals from the periphery to the hub and is constructed using either cribellate or viscid adhesive silks (Fig. 2). An auxiliary, non-sticky spiral is constructed prior to the capture spiral. The auxiliary spiral acts as a physical guide for the placement of the adhesive capture spiral and is typically removed during the web-building process. However, auxiliary spirals are retained in the finished webs of Nephilidae (Fig. 3; Kuntner et al., 2008a) and *Cyrtophora* (Lubin, 1973).

Orb webs may include additional features such as 3D networks of threads on either side of the orb plane, termed barrier webs (e.g. *Nephila*, *Leucauge*, and *Argiope*; Fig. 3), or silken retreats above or to the side of orb webs that are

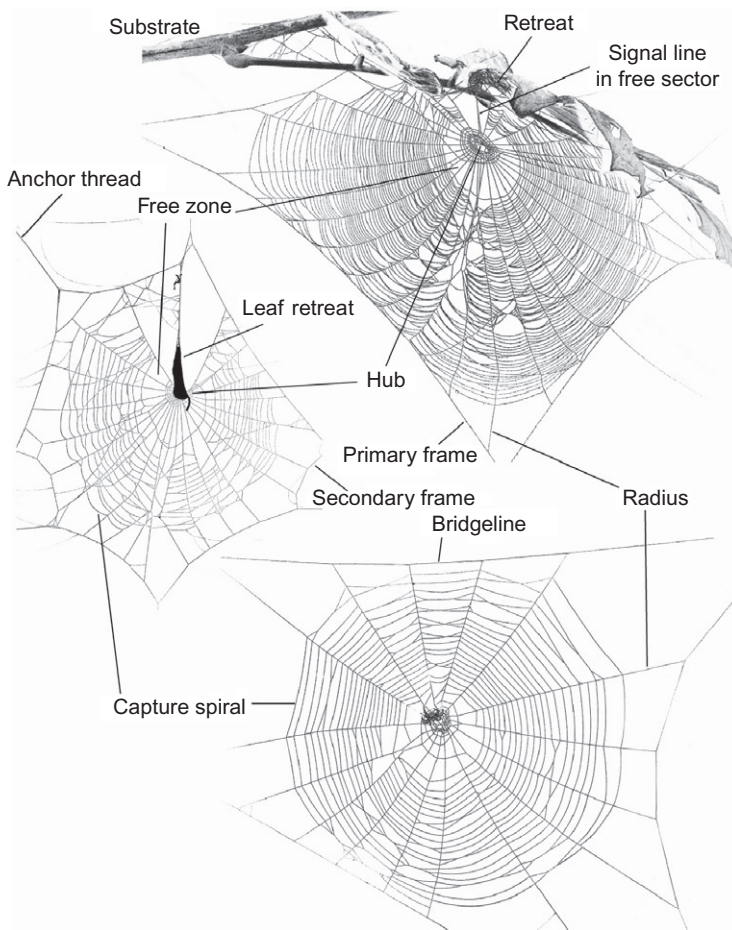


FIG. 2 Orb web terminology showing renderings of diverse araneid webs: an unknown juvenile from India (top), *Acusilas* sp. from China (middle) and *Caerostris darwini* from Madagascar (bottom).

connected to the hub via a signal line (e.g. *Nephilengys*, *Zygiella*, some *Araneus* and some other araneids; Fig. 2). More highly modified orb webs possess elements that deviate from the common form—for instance, the relatively small but highly stretchy sticky webs held by the legs of deinopids (Coddington, 1986c), vertically elongated sticky spirals in ladder webs, the pseudoradii found in arboricolous ladder webs of *Herennia* (Kuntner, 2005), the 3D mesh ‘tents’ made from modified radii and non-sticky spirals in *Cyrtophora* and *Mecynogea* (Lubin, 1973), and various types of stabilimentum ‘silk decorations’ or leaves added to webs (see Sections 2.6 and 6.2 for more details).

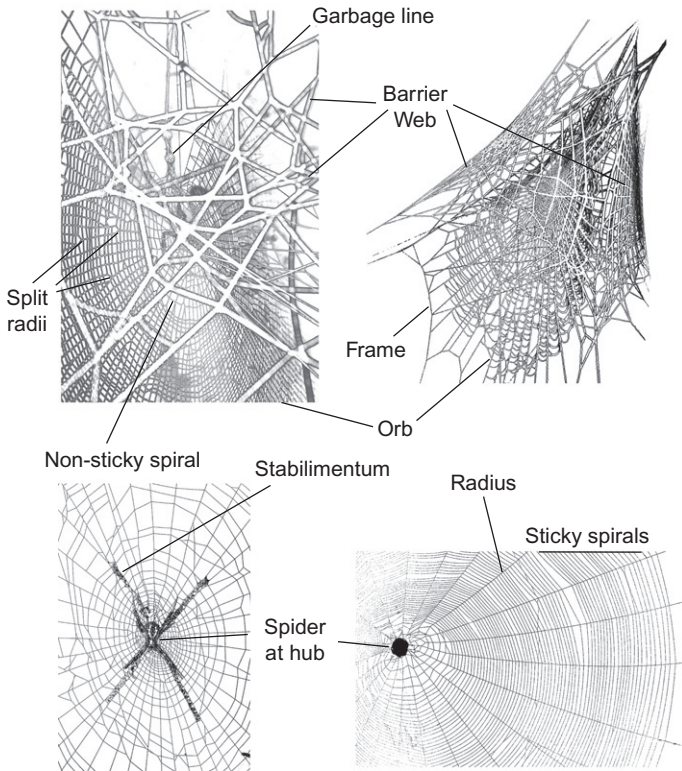


FIG. 3 Orb web terminology showing renderings of diverse nephilid and araneid webs: web of *Nephila clavipes* from Belize (top left), juvenile *Nephila pilipes* from Singapore (top right), *Argiope* sp. from China (bottom left) and *Polys* sp. from China (bottom right).

Web reduction is common within the Orbiculariae (see Section 6.3.1) and some orb webs contain free sectors where a signal line leading to a retreat replaces the capture spiral and radii. The best known are webs of *Zygiella* and relatives (referred to as *Zygiella sensu lato*; Gregorič et al., 2010), although similar architectures exist in some araneid and tetragnathid exemplars including *Araneus*, *Eriovixia*, *Dolichognatha*, and *Chrysometa* (Kuntner, personal observation). The function of the free sector is unclear, but it may be related to signalling, as the free sector provides open space for the signal thread connecting the retreat with the hub. However, numerous other spiders hide in retreats and connect signal lines to hubs without a sector of the webs lacking capture spirals.

Finally, some orb-weavers have further reduced or changed the orb architecture so much as to be barely recognizable (see Section 6.3.1). Indeed, most species within the Orbiculariae now produce highly modified 3D sheet and cobwebs (see Section 6.3.2).

1.2.2 Quantifying web shape and investment

A variety of metrics quantify the sizes and shapes of orb webs (reviewed in part by [Herberstein and Tso, 2000](#)). The name 'orb' is somewhat misleading in that the webs are rarely fully symmetric circles. Orb webs are instead typically elliptical. The total capture area of an orb web, delimited by the outside of the capture spiral, is best measured directly from photographs, but can also be estimated through a variety of formulae. [Blackledge and Gillespie \(2002\)](#) argue that the most efficient formula to estimate capture area is:

$$\text{Capture area} = \left(\frac{d_v}{2}\right)\left(\frac{d_h}{2}\right)\pi - \left(\frac{H}{2}\right)^2\pi,$$

where d_v is the vertical diameter of the web measured from the outermost row of capture spiral, d_h is the horizontal diameter measured from the outermost row of capture spiral, and H is the average diameter of the hub and free zone, measured along the vertical axis ([Fig. 4](#)).

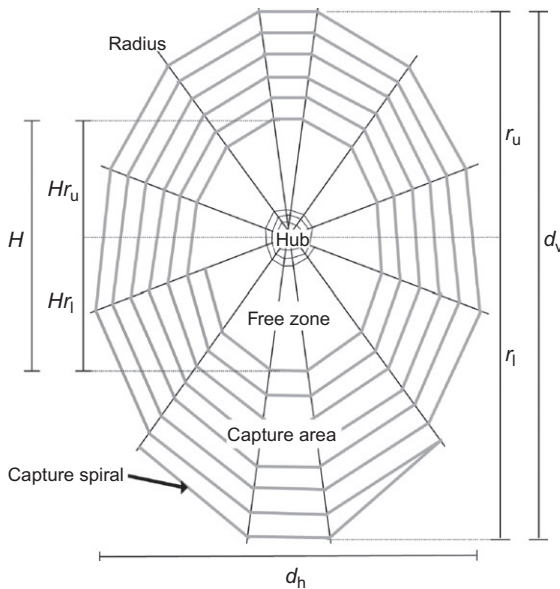


FIG. 4 Parameterization of the capture surface of an orb web. See [Section 1.2.2](#) for explanation.

Blackledge and Gillespie (2002) term the departure of the shape of the web from a circle as *web asymmetry*, which is calculated as:

$$\text{web asymmetry} = 1 - \frac{d_h}{d_v},$$

where d_h is the diameter of the web along the horizontal axis and d_v is the diameter along the vertical axis (Fig. 4). This index, also used by Gregorič et al. (2010), departs from a value of zero and tends toward one in asymmetric webs, but may show negative values in horizontally exaggerated webs. Kuntner et al. (2008b, 2010a,b) and Kuntner and Agnarsson (2009) termed a similar formula the *ladder index* (calculated as the ratio of web height to web width; Peters, 1937 named this Große Achse/Kleine Achse), which tends to the value of one in symmetrical webs, but may reach values above five in strongly vertically elongated webs (e.g. *Herennia*; Kuntner et al., 2010b).

The *hub asymmetry* of an orb web quantifies the displacement of the hub from web's geometric centre (Blackledge and Gillespie, 2002) and is calculated as:

$$\text{hub asymmetry} = 1 - \frac{r_u}{r_l},$$

where r_u is the length of the upper radius along the vertical axis and r_l is the length of the lower radius (Fig. 4). The values of the hub asymmetry index are close to zero in symmetric webs, slightly above zero in upwardly eccentric webs, or below zero in the less common, downward eccentric shaped web (e.g. *Cyclosa* or *Deliochus* in Kuntner et al., 2008a; Nakata, 2010b). Similar indexes were termed *hub displacement* (Kuntner et al., 2008b, 2010b) and *asymmetry index* (Nakata and Zschokke, 2010). The former index show values of 0.5 in webs with a symmetric hub, and correspondingly closer to 1 in upward, and closer to zero in downward eccentric webs, and the latter equals zero in webs with a symmetric hub, but shows differently scaled values to hub asymmetry in asymmetrical ones. Other hub displacement indexes were proposed by Masters and Moffat (1983) and ap Rhisiart and Vollrath (1994), but these are less intuitive because their values decrease with increased hub asymmetry. All of the above measures of web geometry take into account only the actual capture area that is delimited by the inner and outermost rows of the capture spiral, even though the radii extend beyond them all the way to the frame.

Venner et al. (2001) reviewed formulae for calculating the capture thread length (CTL) of an orb web, and concluded that the most appropriate, consistent, and straightforward formula was:

$$\text{CTL} = (1 - a) \frac{\pi}{16} (N_v + N_h) (D_{ov} + D_{iv} + D_{oh} + D_{ih}),$$

where the correction factor $a = 0$ for most species except the free sector of *Zygiella* (and similar genera), N is the number of spiral turns, D_o and D_i are the outermost and innermost diameters of the capture area, and suffixes v and

h denote vertical and horizontal, respectively. Note that D_{ov} is equivalent to H in Fig. 4. This formula does not take into account varying mesh width across the web, but nevertheless provides a good estimation of the total length of capture spiral in an orb web.

The mesh width (also called mesh height or mesh spacing) varies between closely related spiders. Mesh width is believed to greatly influence prey retention, and thus the sizes of prey targeted by webs, although these relationships are difficult to estimate (Blackledge and Zevenbergen, 2006; Eberhard, 1986). A tight mesh provides more silk per unit area for kinetic energy absorption as well as more stickiness per area, and may well result in more effective snare for relatively larger prey compared to a wider meshed web. However, this generality could easily change if threads differ in diameters or material properties. Thus, a complicated combination of factors in web architecture as well as thread characteristics influences the functionality of the orb (see Section 2). Mesh width is typically measured as the average distance between rows of capture spiral along a particular axis of the web (usually the vertical) and is calculated as:

$$\text{mesh width} = \frac{1}{2} \left(\frac{r_u - Hr_u}{S_u - 1} + \frac{r_l - Hl_l}{S_l - 1} \right),$$

where r_u is the upper radius length, Hr_u is the distance from hub to innermost upper capture spiral, S_u is the number of rows of capture spiral in the upper half of the web, r_l is the lower radius length, Hl_l is the distance from hub to innermost lower capture spiral, and S_l is the number of rows of capture spiral in the lower half of the web (Herberstein and Tso, 2000; Fig. 4). While commonly used, this mesh width index ignores that spacing between rows of capture spiral is rarely constant within an orb web and instead tends to increase from the hub outward.

One final consideration is that all of these formulae are designed to measure the geometries of orb webs. Capture area and CTL are often used as proxies for material or energetic investment in orb webs (e.g. Sherman, 1994). However, this approach entails a critical assumption that the numbers and diameters of threads are identical between webs of different geometries. Given that spiders actively control both parameters during web spinning (see Section 4), this assumption is likely often violated. Energetic or material investment in webs is instead much better characterized as the total volume or mass of a particular type of silk in a web (Sensenig et al., 2010).

1.3 WHAT IS SILK?

Silk is loosely defined as fibrous proteins that are extruded outside an organism's body and that are composed of semi-crystalline molecular structures (Craig, 1997). This simple definition belies the dizzying complexity of different

types of silks produced by most spiders. Individual spiders spin ‘toolkits’ of seven to eight different types of silks, each of which comes from its own discrete gland(s) and spigot(s) (Blackledge and Hayashi, 2006a). Each type of spider silk has a unique chemical composition, molecular structure, and material properties. Most, if not all, spider silks appear to be coded for by a family of genes whose evolutionary history was punctuated by bouts of gene duplication followed by strong diversification (Gaines and Marcotte, 2008; Garb et al., 2010; Gatesy et al., 2001).

Silk fibres are ‘spun’ from liquid feedstock (dope) through spigots on the spinnerets of spiders (Vollrath and Knight, 2001). In orb web spiders, the spinnerets are three paired appendage-like organs on the abdomen, each of which contains dozens to hundreds of spigots connected to their own internal silk-producing glands (Fig. 5). Cribellate spiders also possess an additional, unpaired spinning field termed the cribellum just anterior of the main spinnerets (e.g. Foelix, 2011). A single spider is therefore capable of simultaneously producing multiple silk threads of many kinds, and the arrangement of spigots

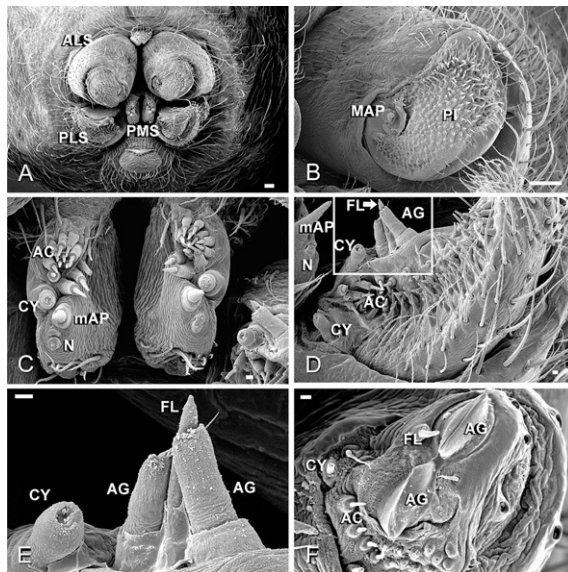


FIG. 5 Spinneret morphology of typical orb web spiders showing all three pairs of spinnerets. (A), anterior lateral spinnerets (B), posterior median spinnerets (C), and two details of posterior lateral spinnerets (D–E) in female nephilid *Nephilengys papuana* from Australia; detail of posterior lateral spinnerets in the theridiid *Parasteatoda tepidariorum* (F). Scale bars A–B = 100 μm , C–F = 10 μm . Abbreviations: AC, aciniform gland spigot(s); AG, aggregate gland spigot(s); ALS, anterior lateral spinneret; CY, cylindrical gland spigot(s); FL, flagelliform gland spigot(s); MAP, major ampullate gland spigot(s); mAP, minor ampullate gland spigot(s); N, nubbins; PI, piriform gland spigot(s); PLS, posterior lateral spinneret; PMS, posterior median spinneret.

on the spinnerets appears to relate functionally to how different silks are used together (Eberhard, 2010a). The spinnerets are vestigial legs and still retain segmentation and musculature, such that spiders can exert control over the placement of threads, which is particularly important for creating the connections between threads and for anchoring threads to the substrate (Eberhard, 2010a).

1.3.1 *Silk production*

Most spider silk proteins consist largely of internal regions of highly repetitive amino acid 'motifs'. These motifs are short sequences of amino acids hypothesized to form the specific secondary structures that ultimately determine the overall shapes of individual proteins, and therefore how silk proteins interact to form whole fibres (Guerette et al., 1996; Hayashi et al., 1999; Fig. 6). Amino acid motifs are combined into larger repetitive units, sometimes called ensemble repeats or repetitive modules, that range from < 50 to over 200 amino acids in length (Ayoub et al., 2007). Ten to 100 of these repetitive modules are linked together, forming ~90% of the total protein, and are flanked on either end by *n* (amino) and *c* (carboxyl) terminal runs of 100–200 amino acids (Ayoub et al., 2007; Fig. 6). The high degree of conservation in the amino acid sequences of the termini among different types of silk, some of which diverged hundreds of millions of years ago, argues for conserved function of the termini in the production of different silks (Rising et al., 2006; Spenner et al., 2004). The amino acid sequences of these terminal regions also provide the primary data to describe the evolutionary origin of silks (Garb et al., 2010). In contrast, the ensemble repeats of different types of silks are incredibly divergent, to the degree that they cannot be easily homologized (Gatesy et al., 2001).

All spider silks begin as liquid protein solutions, termed dopes. Solid silk fibres form through a phase transition as the liquid silk is pulled through the spinning duct due to rearrangement of the molecular structure of individual silk proteins such that they interlock to form the solid fibres (Vollrath and Knight, 2001; Fig. 6). In particular, β -sheets form and stack together into nanocrystals. Well characterized in major ampullate silk, these crystals are $2 \times 5 \times 7$ nm in size (Grubb and Jelinski, 1997) and bind fibroins together through hydrogen bonds. While individual hydrogen bonds are relatively weak, they are closely confined in the hydrophobic β -sheet crystals resulting in very uniform deformation and consequently high strength (Keten and Buehler, 2008; Keten et al., 2010). Silk dopes are initially stored in the lumens of silk glands in highly saturated form with concentrations up to 50% wt/vol (Vollrath and Knight, 2001). This high concentration appears essential for fibre formation and is facilitated in part by the proteins forming micelles where the hydrophilic termini of the molecules comprise the outer layers of the spheres (Hagn et al., 2010; Jin and Kaplan, 2003; Knight and Vollrath, 1999). The micelles isolate the repetitive crystal forming domains in an alternative secondary structure,

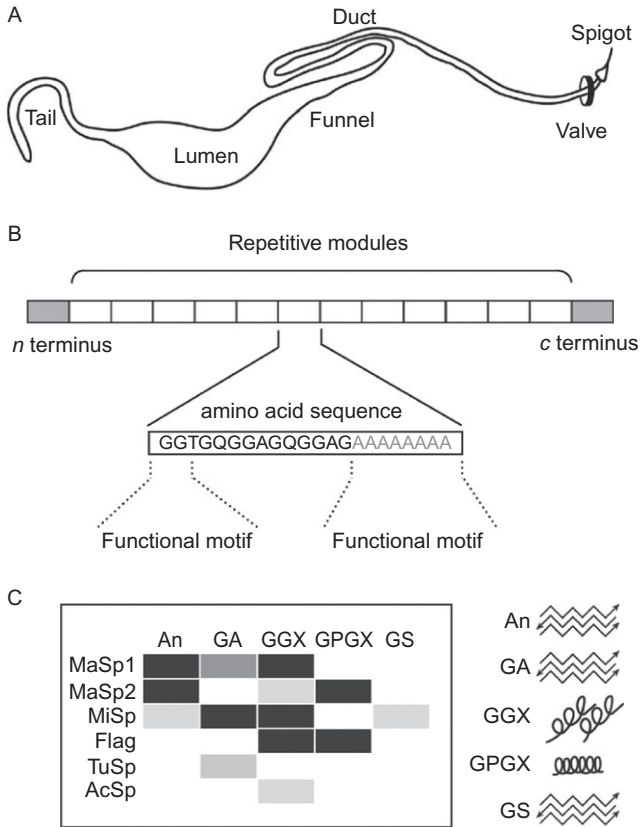


FIG. 6 Structure of spider silk glands and silk proteins. (A) Major ampullate glands in orb spiders are composed of at least six functional elements. The tail contains secretory cells that excrete silk fibroins into the gland. The fibroins are stored as micelles in a concentrated liquid solution in the lumen. The micellar configuration of the fibroins is squeezed as they pass through the narrowing of the funnel and into the duct where counter-current exchange allows for ion uptake and water resorption. The now solid fibre passes through a muscled valve that can further control molecular alignment until the fibre passes out of the spigot. (B) Most spider silk fibroins have a modular structure consisting of ~ 12 – 20 modular units or ‘ensemble repeats’ whose amino acid sequences are largely similar to one another. Each repetitive module is composed of short runs of amino acids, termed functional motifs, which are often predicted to form specific secondary structures in the silk fibre. (C) At least five different functional motifs are identified in various spider silks. The relative abundance of each type of functional motif (black = common and white = absent) are indicated for each of the five fibrous silks spun by orb spiders (MaSp, major ampullate; MiSp, minor ampullate; Flag, flagelliform; TuSp, tubuliform; and AcSp, aciniform). Secondary structures are indicated to the right and include various β -sheets that stack to form crystals, 3_1 helices that can link molecules together (GGX) and elastic nanosprings that bond intra-molecularly (GPGX). Amino acid abbreviations are A, alanine; G, glycine; P, proline; Q, glutamine; and S, serine.

until a phase shift is caused by shear forces within the narrowing of the duct of the gland (Knight et al., 2000; Knight and Vollrath, 1999; Lefevre et al., 2008) and a drop in pH (Askarieh et al., 2010; Vollrath et al., 1998) together trigger the self assembly of the β -sheet crystals. Fibre assembly primarily occurs within an 'S'-shaped duct that likely allows for counter-current exchange of water and ions and provides an internal draw down that aligns silk proteins along the fibre (Vollrath and Knight, 2001). The process of β -sheet formation is at least partially stabilized by the c-termini (Hagn et al., 2010) and further control over fibre assembly is likely exerted by a pH sensitive dimerization of the n-termini (Gaines et al., 2010). The final processing of the fibre occurs at the distal end of the duct where the crystallites are further aligned along the axis of the fibre. A muscled valve near the end of the duct allows spiders to control the force applied to the fibre, thereby providing control of the final properties of the silk through the overall alignment of molecules (Ortlepp and Gosline, 2004; Pérez-Rigueiro et al., 2005; Vollrath and Knight, 1999). This valve is also used as a friction brake by spiders dropping on draglines.

Significant micro- and nano-structuring may occur internally within at least some types of silk. The best studied is again major ampullate dragline silk. Some studies suggest that a single fibre consists of a core surrounded by a thin sheath containing lipids and glycoproteins (Augsten et al., 2000; Frische et al., 1998; Sponner et al., 2007). The structure of the core may also be heterogeneous, composed either of nanofibrils or containing elongate cavities that may distribute energy and help contribute to the high performance of the fibres (Frische et al., 1998; Li et al., 1994).

1.3.2 *Understanding mechanical performance*

Adult female araneoid orb web spiders produce seven to eight discrete types of silk that have diverse mechanical properties (Blackledge and Hayashi, 2006a). Most types of silk are produced throughout spiders' lives, with the exception of specialized silks used in reproduction (see Section 1.3.3). Some adhesive silks are also not produced by the youngest instars of spiders, and adult male spiders often produce fewer silk types (Coddington, 1989). Silks are viscoelastic, such that their mechanical performance changes as threads are stretched and several different parameters are required to describe their performance (Blackledge and Hayashi, 2006a; Denny, 1976; Elices et al., 2009; Gosline et al., 1999; Köhler and Vollrath, 1995; Swanson et al., 2006b; Fig. 7). Silk mechanics is normally described in terms of stress, strain, and toughness (work of fracture). Stress measures pressure—simply the amount force applied to a fibre divided by its cross-sectional area, to normalize comparison of fibres differing in diameter. Strain is a dimensionless measure of how far a material has been stretched—the ratio of the current to original length of a fibre, again to normalize comparisons of fibres differing in length. Two different 'flavours' of stress and strain are common in silk literature. Engineering values normalize fibre performance to

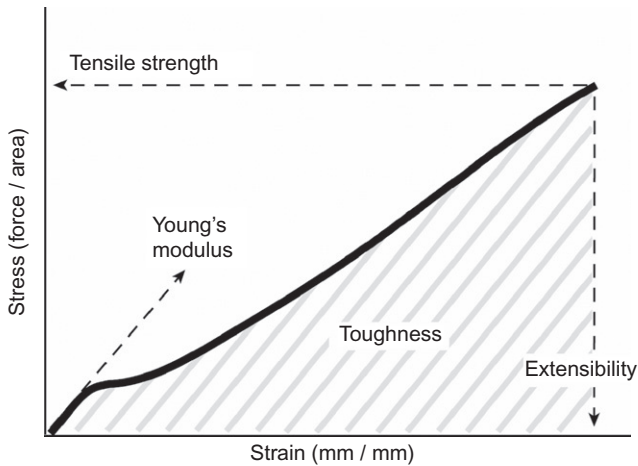


FIG. 7 Stress–strain curve typical of most dry spider silks. Five parameters are usually measured to characterize the material properties of spider silks. Young’s modulus is the initial stiffness of the silk. Yield occurs when the stress–strain curve departs from the linear slope of Young’s modulus and indicates plastic deformation of the silk. Tensile strength and extensibility are the stress and strain respectively at the breaking point. Toughness is the total work required to extend the silk to the breaking point normalized to the volume of the fibre and is measured as the area under the stress–strain curve.

the original cross-sectional area (engineering stress) and length (engineering strain) while ‘true’ values normalize performance to the instantaneous cross-sectional area (true stress) and length (true strain) because both of these values change substantially as highly extensible materials like spider silks are stretched. Thus, most current research on silk mechanics report the true breaking stress and true breaking strain of fibres at failure (Guinea et al., 2006). Finally, toughness is a measure of the total amount of work, or energy, required to stretch a fibre until it breaks and is normalized to the volume of material tested.

Dry silks initially behave as elastic materials, deforming linearly in direct proportion to the amount of stress applied to them and then recovering completely if relaxed. Young’s modulus describes the slope of this elastic region and it indicates straining and rupturing of reversible bonds, such as hydrogen bonding, in localized regions. Silks with higher Young’s modulus are stiffer and therefore harder to stretch. Yield occurs once silk is pulled far enough that the proteins begin to permanently deform, around 2–3% strain for typical major ampullate silk (Denny, 1976). This is a critical parameter because it defines a performance limit for silks after which their behaviour in webs is altered, whether in response to repeated environmental perturbations like wind or future prey capture events (Boutry and Blackledge, 2008). There is substantial variation in the behaviour of different types of spider silks after yield (Blackledge and Hayashi, 2006a; Denny, 1976). Some become very soft and

extend greatly under loading while others remain relatively stiff. Others are in between, initially soft but then becoming stiffer as they are stretched close to failure, a process termed 'strain-hardening'.

The material properties of individual types of spider silks differ by 100% or more across various taxa of spiders (Agnarsson *et al.*, 2010; Elices *et al.*, 2009; Sensenig *et al.*, 2010; Swanson *et al.*, 2006b, 2007), suggesting ample variation for natural selection to shape silk performance in different webs. However, natural selection acts only indirectly on the material properties of silk. Survival, and ultimately fecundity, of spiders is affected not by the tensile strength or toughness of a particular thread, but rather by whether or not a thread breaks and how much work it can perform stopping prey or acting as a safety line. Thread performance is therefore determined at least as much by its structural properties—the total numbers and sizes of fibres in a thread, as by intrinsic material properties (Fig. 8). These structural properties are likely easier for the spiders to control and hence likely to be the most responsive to selective factors in the environment (Boutry and Blackledge, 2008).

1.3.3 *Silk toolkits*

Major ampullate, or 'dragline', silk is the best known type of spider silk and is produced by both sexes and at all life stages. Major ampullate silk is used as a lifeline by most spiders moving through the environment (Osaki, 1996) and forms the backbones of most webs (Blackledge *et al.*, 2009c; Coddington, 1989; Fig. 9). It is also used for dispersal by ballooning (Bell *et al.*, 2005; Suter, 1991). The spinnerets of most spiders contain only a single set of major ampullate spigots such that the silk is always produced as a single thread consisting of paired fibres (Fig. 5B). However, a few taxa such as *Deinopis* have multiple major ampullate spigots (Coddington, 1989). Curiously, a secondary set of major ampullate glands is used to produce moulting threads in at least some araneid spiders, as the cuticle lining of the primary major ampullate gland is shed (Townley *et al.*, 1993). Major ampullate silk evolved early in the history of spiders and is produced by all extant taxa except for the basal liphistiimorphs and mygalomorphs (Craig, 1997), although at least one recent study suggests that homologous proteins occur in mygalomorph silk (Bittencourt *et al.*, 2010). While comparative data are relatively sparse, there are several key differences in the major ampullate silk of orbicularian spiders (i.e. all orb spiders and their derived descendents) compared to other spiders. Their major ampullate silk is significantly stronger and tougher, but slightly more compliant (lower Young's modulus) compared to other taxa (Agnarsson *et al.*, 2010, Swanson *et al.*, 2006a). Moreover, their silk is composed of two distinct types of fibroins (Guerette *et al.*, 1996; Hinman and Lewis, 1992; Sponner *et al.*, 2005) that are distinguished by their repetitive regions and appear to have resulted from relatively recent gene duplication (Ayoub and Hayashi, 2008; Gatesy *et al.*, 2001). Major ampullate spidroin 1 (MaSp1) has a repetitive region dominated

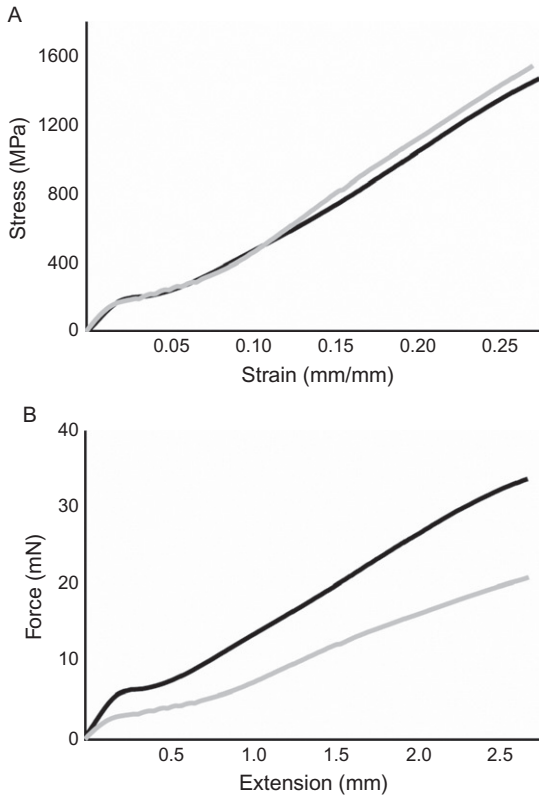


FIG. 8 Comparison of material properties (A) and mechanical performance (B) of dragline silk from the radii of spider orb webs. In this experiment, *Nephila pilipes* were fed either crickets (black line) or flies (grey line). The treatment had little effect on the material properties of the major ampullate silk *per se*, but the greater diameters threads spun by cricket-fed spiders meant that the radii in their orb webs could support twice as much loading without breaking. Adapted from ‘Does the giant wood spider *Nephila pilipes* respond to prey variation by altering web or silk properties? Tso, Chiang & Blackledge. *Ethology* 113 © 2007’.

by two types of motifs (Fig. 6). Poly-alanine and glycine-alanine units are predicted to fold silk fibroins into the β -sheet configuration necessary for formation of the nanocrystals that interlock molecules (Gosline et al., 1999; Hayashi et al., 1999; Knight et al., 2000; Xu and Lewis, 1990). The second motif, glycine-glycine-X (where X is a small subset of amino acids), is relatively poorly understood but might form a second level of crystal structure where 3_1 helices can bond inter-molecularly (Hayashi et al., 1999; Kümmerlen et al., 1996). Major ampullate spidroin 2 (MaSp2) appears to be derived from a gene duplication event in orb web spiders (Ayoub and Hayashi, 2008) and is similar to MASp1 with one key exception. The glycine-glycine-X motifs are

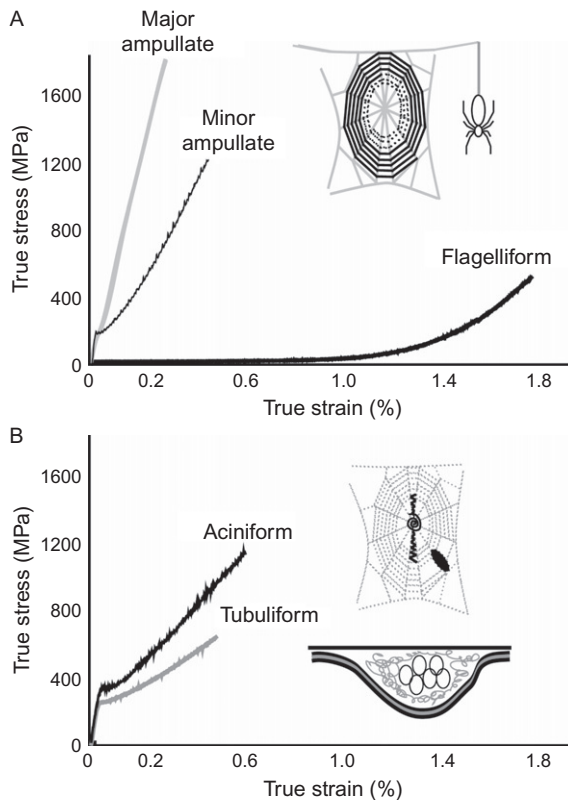


FIG. 9 Material properties of spider silk ‘toolkits’. Orb spiders produce seven chemically and mechanically distinct silks. (A) Three types of fibrous silks are used to spin orb webs. Major ampullate silk (grey) is the strongest spider silk and forms the backbones of webs as well as draglines. Minor ampullate silk (dashed line) is sometimes added to major ampullate threads and may comprise the temporary auxiliary spiral that guides the placement of the finished capture. Flagelliform silk (grey) is the rubbery core of the capture spiral, which is coated with a viscid aggregate silk glue. Connections between threads and to the substrate are made using piriform silk secretions. (B) Two additional fibrous silks are produced by orb spiders. Aciniform silk is used to produce many stabilimentum web decorations and to wrap prey. Tubuliform silk (grey) comprises the fluffy inner layers of egg sacs and is mixed with aciniform silk, as well as ampullate fibres to form the hard outer coat.

replaced by a glycine-proline-glycine-XX motif (Gatesy et al., 2001). The presence of the proline kinks the amino acid chains and forms a molecular nanospring that is predicted to enhance the elasticity of the silk (Becker et al., 2003). The relative ratio of MaSp1 and MaSp2 varies among different taxa of orb web spiders, and possibly within individual spiders, but the functional implications are only recently receiving attention (Elices et al., 2009; Liu et al., 2008b; see Section 4.2.2).

Minor ampullate silk is so named because the structure of its gland resembles a smaller version of the major ampullate silk. Orb web spiders possess a single pair of minor ampullate glands on their median spinnerets (Fig. 5C) that produce a thread that is sometimes added to major ampullate draglines (Coddington, 1989). It may also form the aerial bridging threads released by spiders and the temporary spirals of orb webs (Peters, 1990). The repetitive elements of minor ampullate fibroins mostly consist of β -sheet forming poly-alanine and glycine-alanine repeats, as well as the glycine-glycine-X motif (Colgin and Lewis, 1998; Gatesy et al., 2001; Hayashi et al., 1999). However, these motifs are often interrupted by non-repetitive spacer regions (Colgin and Lewis, 1998). Minor ampullate silk has a crystalline structure that is relatively similar to major ampullate silk (Dicko et al., 2004; Rousseau et al., 2009). However, the resulting fibres are significantly more extensible, but also weaker and less tough (Fig. 9; Blackledge and Hayashi, 2006a). The thinner diameters of minor ampullate fibres also means that they have significantly less load bearing capacity compared to major ampullate fibres.

Aciniform silk is likely similar to the earliest types of spider silks, such as the relatively undifferentiated sheets of threads produced by mygalomorphs (tarantulas and their relatives) (Vollrath and Selden, 2007). Orb web spiders have varying numbers of aciniform spigots on their posterior median and posterior lateral spinnerets (Fig. 5C, D, and F) and even on the cribellum (Coddington, 1989). The silk is used primarily for prey wrapping and egg case construction (Fig. 9; Vasanthavada et al., 2007). It is also used by some orb web spiders to produce stabilimenta or 'web decorations' (see Section 2.6). The amino acid sequence of aciniform silk is far less homogeneous than major ampullate silk, with significantly more complex repetitive elements—both longer and containing a greater diversity of amino acids (Hayashi et al., 2004). This results in reduced crystallinity and lower alignment compared to major ampullate silk (Rousseau et al., 2009). The resulting fibres are far stretchier than most major ampullate silks and correspondingly tougher, consistent with their use by many spiders to wrap and resist the struggles of prey prior to biting (Fig. 9; Blackledge and Hayashi, 2006a; Hayashi et al., 2004).

Flagelliform silk is unique to araneoid orb-weaving spiders and is produced solely by a single spigot on the posterior lateral spinneret (Fig. 5D–F; Coddington, 1989). It is used in the production of the capture spiral of orb webs (Fig. 10a). The function of flagelliform silk in many derived taxa, with highly modified webs, is unclear, but the spigot producing flagelliform silk is often vestigial in these taxa (Peters, 1993). However, the flagelliform spigot is present in many other derived taxa, such as most cobweb spinning theridiids (Agnarsson, 2004), where it is likely used in sticky prey wrapping (e.g. Eberhard, 2010a). The repetitive region of flagelliform fibroins is dominated by long stretches of the glycine-proline-glycine-XX motif and it lacks β -sheet forming poly-alanine motifs (Hayashi and Lewis, 2000, 2001). This results in a highly extensible, relatively disorganized molecular structure (Dicko et al.,

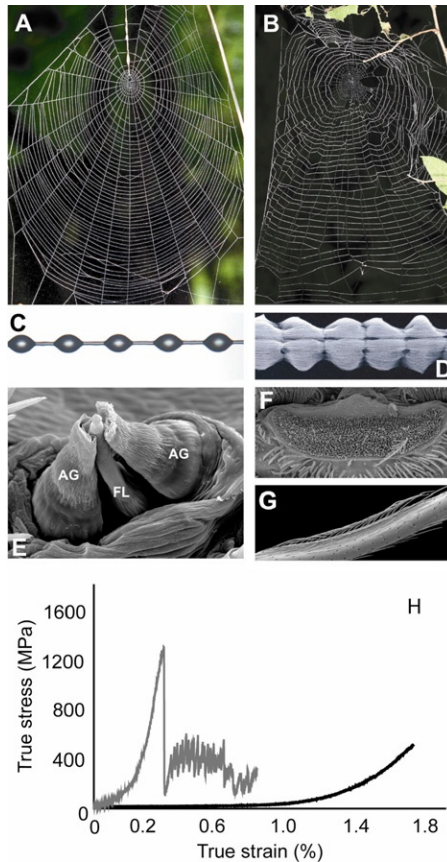


FIG. 10 Comparison of modern viscid glue orb webs and cribellate orb webs. Webs spun by (A) *Cyclosa* and (B) *Uloborus* are similar in overall architecture. However, they utilize radically different adhesive silks. (C) Araneoid orb webs use capture threads coated in viscous glue droplets while (D) cribellate deinopoid spiders coat their capture threads with puffs of tiny dry silk fibrils. The spinning organs used to produce these silks are quite different. (E) Viscid glue from a pair of aggregate glands (ag) is secreted directly onto the flagelliform (fl) axial fibre as it is spun. (F) Deinopoid spiders use a field of spigots called a cribellum, anterior of the main spinnerets, to produce adhesive silk and (G) a calamistrum on their hindlegs to physically comb the silk into shape. (H) The mechanical performance of these two types of capture threads also differs greatly (grey = cribellate silk from *Uloborus diversus* and black = viscid capture silk from *Argiope argentata*). A–G reproduced from Blackledge et al. (2009c). H produced from data in Blackledge and Hayashi (2006b).

2004; Hayashi and Lewis, 1998; Rousseau et al., 2009). The motif itself folds into a spiral structure that can act as a molecular ‘nanospring’ (Becker et al., 2003). Flagelliform silk is an order of magnitude stretchier than most other silks and is ~ 1000 times less stiff (Blackledge and Hayashi, 2006a). Functionally,

it is similar to a rubber and initially extends greatly under very little load (Savage and Gosline, 2008). Near failure, the increased alignment of flagelliform fibroins stiffens the fibres and ultimately results in a toughness that approaches major ampullate silk (Fig. 9; Blackledge and Hayashi, 2006a; Denny, 1976). The mobility of the molecules within the fibre is highly dependent upon water, which is normally supplied by its surrounding glue coating that contains hydrophilic salts (see Section 6.1).

Aggregate silk is the glue coating on viscid capture threads and is unique to araneoid spiders. It is excreted by paired spigots on the posterior lateral spinnerets (Fig. 5D–F) that flank the single flagelliform spigot in typical orb-weavers, forming a characteristic ‘triad’ of spigots (Araneidae, Nephilidae: Figs. 5D–E, 10E). In derived taxa, the aggregate glands may be positioned separately and exaggerated in size (e.g. Theridiidae in Fig. 5F). Aggregate silk contrasts strongly with most other silks in containing a complex cocktail of low molecular weight hydrophilic molecules (Vollrath et al., 1990), as well as glycosylated proteins (Vollrath and Tillinghast, 1991). This complexity plays a critical role in the function of aggregate silk as glue (see Section 6.1). Recently described cDNA corresponding to the glycoproteins suggests two proteins that are curiously encoded by opposite strands of the same DNA sequence, resulting in identical repetitive regions for the two proteins (Choresh et al., 2009). These proteins contrast greatly with other spider silk cDNAs and currently cannot be homologized. The proteins do contain glycosylation sites and possible chitin binding domains that could help account for the glue’s adhesion. In contrast, a second study found evidence for a totally different protein in the glue of the cobweb spinning black widow (Theridiidae) that had metal chelating properties that could function as a microbicide (Hu et al., 2007). The origin and control of the production of salts in the glue are unknown, but they play two critical roles in facilitating the adhesiveness of the threads by attracting atmospheric water to hydrate the axial fibre and by chemically solvating the glycoproteins themselves (see Section 6.1).

Pseudoflagelliform silk is used to produce the axial fibres of the capture threads in cribellate orb webs (Coddington, 1989; Opell, 1997a). It is likely homologous to the flagelliform silk of modern orb web spiders because it is produced from spigots in the same position (Blackledge and Hayashi, 2006b) and contains some of the same proteins (Garb et al., 2006). However, its mechanical properties are quite different and present an important challenge in understanding the evolution of modern orb webs (Blackledge and Hayashi, 2006b; see Section 6.1).

Cribellar fibrils provided some of the earliest adhesive silk for spiders and are still used by ~300 species of orb web spiders in two extant families, Uloboridae and Deinopidae (Coddington, 1989; Sahni et al., 2011). The fibrils are produced from a field of spigots on the cribellum just anterior of the spinnerets (Opell, 2002) and are among the thinnest silks, ranging down to ~10 nm diameter. The small size of cribellate fibrils facilitates van der Waals interactions with

surfaces allowing dry adhesion much like the tarsal pads of wandering spiders (Hawthorn and Opell, 2003) and also physically entangling the surface features of insect prey (Opell, 1994a). A comb, termed the calamistrum and located on the fourth leg metatarsus, is used to draw the fibrils onto the pseudoflagelliform axial fibres of capture threads (Fig. 10G). There is currently no information about the molecular structure or genetic control of this silk.

Piriform silk is used to cement threads to the substrate as well as to form silk junctions by forming attachment disks (Coddington, 1989; Eberhard, 1976). Attachment disks consist of numerous threads produced from a field of ~ 10 – 100 spigots on the anterior lateral spinneret (Fig. 5B) that are secreted on top of a thread with a zigzagging motion of the spinneret. They are embedded in a matrix that cements the threads to the substrate. The overall structure of the amino acid sequence of piriform silk is similar to that of other fibroins, but the ensemble repeat units are relatively large and contain diverse amino acids (Geurts et al., 2010; Perry et al., 2010). Moreover, they include two unique 'functional motifs' (Perry et al., 2010). One is a glutamine rich sequence, glutamine–glutamine–serine–serine–valine–alanine. The second motif contains proline alternating with other amino acids (proline–X–proline–X–proline–X). A second study reported a substantively different, alanine and glutamine rich, amino acid sequence, suggesting that piriform secretions may be a cocktail of different proteins (Blasingame et al., 2009). Unfortunately the difficulty of collecting large samples of attachment disks means that nothing is known about either their molecular structure or their mechanical properties. However, when threads break, failure tends to occur along the length of the fibre rather than at the attachment disk. Whether this is due simply to the structure of the disks (relatively large quantities of small fibres) or inherent superiority of their material properties is not known. However, it at least argues that the strength of attachments is not normally limiting to the performance of orb webs and suggests a fruitful area of research for strong and adhesive biomaterials (Geurts et al., 2010). The role of more specialized attachments, particularly the sliding junctions of orb webs is explored in Section 2.3.

At least three additional types of spider silks are described in the literature, but are not typically used in webs. Tubuliform silk, also called cylindrical silk, is produced by adult female spiders, typically from three cylindrical spigots, two on their posterior lateral and one on the posterior median spinneret (Fig. 5C–F), during the production of their egg sacs (Casem et al., 2010; Hu et al., 2005b; Van Nimmen et al., 2005). Egg sacs themselves are complex, layered structures containing fibres from several different glands (Fig. 9; Gheysens et al., 2005; Hajer et al., 2009; Vasanthavada et al., 2007). This complexity creates confusion about how tubuliform silk is utilized. However, the morphology of the silk is quite distinctive because the glands produce large fibres with an irregular surface that is unlike any other silk. Moreover, the left and right fibres are coated with a gluey secretion that causes them to adhere together (Gheysens et al., 2005). The mechanical behaviour of the silk is quite distinct in displaying

a very prominent yield followed by a long low modulus extension (Blackledge and Hayashi, 2006a; Van Nimmen et al., 2006). Tubuliform silk proteins appear to contain more serine than most other silks (Garb and Hayashi, 2005; Hu et al., 2005a). Tubuliform silk has weaker intermolecular connections and its crystalline fraction consists of twisted structures, both of which contrast with the classic major ampullate silk structural model (Barghout et al., 1999; Dicko et al., 2004).

Adult male spiders produce epiandrous silk utilizing glands and associated spigots that are restricted to sexually mature males. The epiandrous spigots are immediately anterior to the genital furrow (e.g. Kuntner, 2005: Fig. 24C–D) and are present, albeit sporadically, in most spider lineages (Marples, 1967). Epiandrous silk function is poorly understood, but it is used during the building of the sperm web and sperm droplet induction (Knoflach, 1998, 2004). Knoflach (1998) suggests that epiandrous silk is deposited just prior to ejaculation, when many male theridiids display intense rubbing movements of the epigaster against the bridge of the sperm web. At the end of sperm induction a silken line can be seen between the sperm droplet and the epiandrous glands (Knoflach, 1998). The epiandrous silk may ‘reinforce’ the sperm web (Knoflach, 1998), or may possibly play a role in maintaining the sperm droplet as it is being taken up by the male palpal organs because epiandrous silk is mostly limited to the zone where the sperm drop is deposited (B. Knoflach, personal communication). However, the sperm web is initiated using silk from the spinnerets, and ‘typical’ silks are clearly also involved in both processes (Fig. 10E–F in Knoflach, 1998). Further, many male spiders, especially small spiders such as erigonine linyphiids (Miller, 2007) and small theridiids (Agnarsson, 2004), lack epiandrous spigots (see also Marples, 1967). Hence, the function of epiandrous silk seems readily replaced by other spigot types, but we are unaware of studies showing sperm web construction in males lacking epiandrous spigots.

Finally, a recent study suggested that mygalomorphs may produce silk threads through spigots in their tarsi and that these threads could be used to facilitate locomotion, especially climbing (Gorb et al., 2006). However, these findings were disputed due to the lack of any morphological evidence for tarsal silk production in the diverse literature on taxonomy and morphology (Perez-Miles et al., 2009 but see Gorb et al., 2009). More recently, Rind et al. (2011) provided new evidence for tarsal silk spigots and their role in climbing vertical surfaces.

1.4 ORB WEB SPINNING BEHAVIOURS

The production of an orb web begins with web site exploration, a period of laying draglines that precedes those threads that will eventually form the finished web (Eberhard, 1990a; Zschokke and Vollrath, 1995a,b). The spider either crawls around the substrate or releases a silk bridging thread that is carried on air currents until the thread is entangled at some other point. Like all spider silk ‘threads’, the bridge thread actually consists of a pair of fibres

produced from the bilaterally symmetric spinning organs, but it is sometimes reinforced with additional fibres such that bridge line is a better term. The initial bridge line is then replaced by the spider with a line that will ultimately be pulled down to form the beginning of the hub, or web centre, as the spider establishes a third attachment point below the soon to be orb (Fig. 11). This 'Y junction' usually establishes the centre of the orb. The spider then begins to construct primary frames, which are those that connect anchor threads (Zschokke, 1999), and radii by moving from the hub back to an anchor point, spinning a new radius, and along the substrate to establish more of the frame. At the same time the spider may reinforce the hub by adding blobs and lines of silk around it. Eventually a complete outer frame is established and the primary frames are connected with secondary frames, where needed (Figs. 2 and 11D). At the same time, the initial Y junction in most orb webs is typically broken by secondary frames (Fig. 11D), and additional radii are suspended (Fig. 11). Both the frames and radii are spun using dragline silk from the major ampullate glands.

The spider then moves back to the central hub and produces a non-sticky auxiliary spiral (sometimes called a temporary spiral) by moving from the centre of the web toward the outer frame (Fig. 9). The non-sticky spiral is usually stated to be composed of silk from the minor ampullate gland. However,

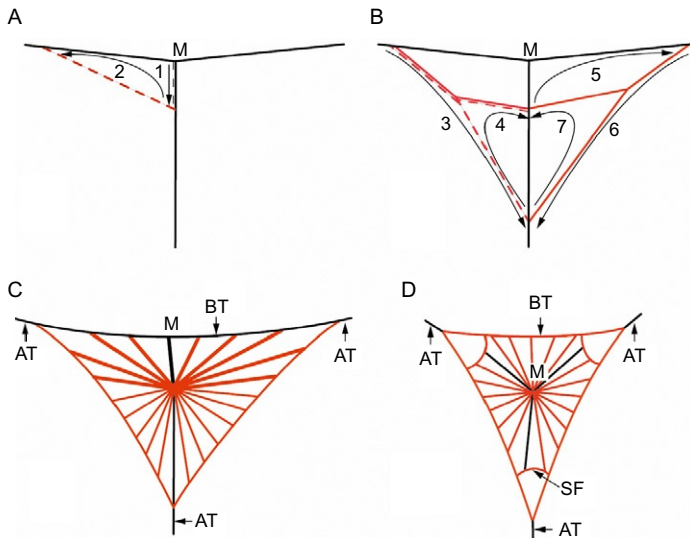


FIG. 11 Web building in *Caerostris darwini* (A–C) compared to the 'classical' araneid web (D), shown without capture spirals. The classical web contains a Y-junction formed by the initial bridge line, which later becomes the hub, whereas *C. darwini* webs depart from the typical architecture in maintaining the initial bridge line intact above the capture part of the web (M). AT, Anchor thread; BT, Bridge thread; M, Connection point of the initial bridge thread and vertical anchor thread; SF, Secondary frame. Numbered arrows show building sequence of web frame. Thicker lines in 'C' indicate doubled radii.

this assertion is likely incorrect because the auxiliary spiral's morphology and mechanical properties are similar to the rest of the web's major ampullate framework (Blackledge, personal observation). The non-sticky spiral functions as a guide for the final capture spiral, and is subsequently taken down during the production of the sticky spiral with notable exceptions including *Nephila*, *Nephilengys*, *Herennia*, *Clitaetra*, *Cyrtophora*, *Mecynogea*, and *Scoloderus* (Kuntner et al., 2008a).

'Late', or split radii describes those radii that are added at this point, and thus originate later than at hub (Fig. 3). They usually start from a junction between an existing radius (primary or late) and a loop of the non-sticky spiral. Kuntner (2005, 2006) and Kuntner et al. (2008a) referred to these late radii as secondary, tertiary, etc. Nephilid webs may contain late radii that split many times, for example, up to five times in *Nephilengys* (Kuntner, 2007: Fig. 34C) and up to nine times in *Nephila* (M. Kuntner, personal observation).

The sticky spiral (also called capture or viscid spiral) of an orb web is typically a continuous double-stranded thread of elastic silk produced from the flagelliform gland that is covered with glue secretions from paired aggregate glands. The spider begins producing the sticky spiral at the outer edge of the web, moving toward the central hub in the opposite direction to that when building of the non-sticky spiral, and attaches the spiral at each junction with a radius using a piriform disc. These connections are either stiff (e.g. Tetragnathidae) or flexible, the so called 'sliding connections' found in araneids and nephilids (Eberhard, 1976; Kuntner and Agnarsson, 2009).

Finally, the spider adds silk to the central hub of the web as it adjusts the final tensioning of the radii. Some spiders also eat out their hub, and renew it or leave it open. Many orb web spiders then modify their webs with silk decorations called stabilimenta (see Section 2.6), external barrier webs (see Sections 2.3 and 5.1), or even by adding non-silk elements to the web. For example, *Phonognatha* and *Acusilas*, as well as some *Araneus*, *Cyclosa*, and *Cyrtophora* pull a leaf from the ground into the web and position it at the hub to form an in-web retreat. Other *Cyclosa* and some *Nephila* decorate their webs with plant debris and/or prey remains (e.g. garbage line in Fig. 3; see Section 2.6).

The final architecture of the web includes a central hub of non-sticky threads upon which the spider rests, or at least moves to, while hunting (Figs. 2 and 3). The hub is encircled by the free zone, a region consisting of only radii (Fig. 4) that allows the spider to freely shuttle from front to back of its web. Finally, there is the capture area, delimited by the inner and outermost rows of the capture spiral (Fig. 4).

1.5 IS WEB SPINNING INNATE?

Eberhard (1982) first documented the precise leg movements of spiders during capture spiral construction, which are stereotypical and define clades roughly around the family level boundary. During capture spiral construction, araneids

use their outer first leg to locate the previous loop of the auxiliary spiral, while tetragnathids use the inner first leg, and nephilids use their outer fourth leg. Other stereotypical web-building behaviours summarized by Eberhard (1982) that define major clades include the details of how spiders keep contact with the auxiliary spiral while laying the capture spiral, how radii are spun (araneids and tetragnathids lay a single radius using cut-and-reel behaviour, uloborids lay a radius with a double thread, and nephilids lay two radii on a single trip from hub), the transition between the hub loop and capture spirals, and how spiders remove and rebuild the hub (see characters 206–219 in Kuntner *et al.*, 2008a). Most of Eberhard's generalizations still hold and these behaviours are routinely used as phylogenetic characters defining major araneoid spider clades (Griswold *et al.*, 1998; Hormiga *et al.*, 1995; Kuntner *et al.*, 2008a; Scharff and Coddington, 1997). However, there are exceptions. For example, combinations of different leg movements at various proximities to the hub can occur (Kuntner, personal observation in *Leucauge* and *Deliochus*).

Most phylogenetic studies using these behavioural traits implicitly assume that these behaviours are innate. Web-building behaviours, and web architecture itself are only rarely subjected to tests for ecological or ontogenetic plasticity (see Section 4). However, there are clear exceptions to the stereotypy of web spinning behaviours within a species. For instance, Gregorič *et al.* (2010) found that the free sector, usually cited as a defining trait of *Zygiella* (e.g. Wunderlich, 2004), in fact is only present in 40–90% of webs spun by individual spiders within populations, for several different species of *Zygiella* *sensu lato*. Second, Harmer and Herberstein (2009) showed that the Australian ladder web spider, *Telaprocera*, adapts the architectures of their webs to optimize use of the available space on tree trunks so that their webs are sometimes highly asymmetric and other times relatively ordinary. Similar modification of web architecture to the available space occurs in some theridiids, such as *Achaearanea* (e.g. Eberhard *et al.*, 2008a; Jorger and Eberhard, 2006). However, this does not seem to be the case in other elongate, ladder web-building spiders. The extreme aerial ladder web of *Scoloderus* is an adaptation to prey specialization on moths and does not vary intraspecifically (see Section 6.3.1; Eberhard, 1975; Stowe, 1986; Traw, 1995). The ladder webs of nephilid spiders, on the other hand do vary greatly, but this is determined ontogenetically. Small instar juveniles make tiny symmetric orb webs. Web shape then changes allometrically as the spiders mature, becoming increasingly ladder shaped in adults (Japyassu and Ades, 1998; Kuntner and Agnarsson, 2009; Kuntner *et al.*, 2008b, 2010b).

In conclusion, most of the basic motor patterns used to spin orb webs seem innate, and result in consistent differences in the architectures of orb webs spun by different species of spiders. However, spiders also modify their web spinning in response to a variety of environmental parameters, as well as ontogenetically. The interplay between spider ecology and the plasticity of web-building behaviours remains largely unstudied (see Section 4 and review in Herberstein and Tso, 2011).

2 Orb web function during prey capture

Orb web spiders are often considered generalist predators that consume all insects entering their webs (Foelix, 2011). However, dramatic differences between the prey consumed by spiders and the abundance of different insects in the environment demonstrate that webs are far from passive sieves (Blackledge et al., 2003a; Nentwig, 1983; Uetz and Hartssock, 1987; Wise, 1993). Instead, orb webs allow spiders to select specific types of prey from the environment. Understanding this selectivity requires answering three questions about the 'interception', 'stopping', and 'retention' of prey by orb webs: What determines the type of prey intercepted by a particular orb web? Can an orb web dissipate the kinetic energy of a particular flying insect prey (stopping)? And, finally does an insect stick to the web long enough to be captured (retention)? The answers to these questions involve a complex interplay between the web spinning behaviours of spiders and the physiological production of silk.

2.1 WHAT PREY ARE SPIDERS TARGETING?

2.1.1 *Is common really better?*

Ecological studies that seek to understand how orb web architecture influences prey capture often compare frequencies of different taxa of prey to infer functional variation among webs, but this approach may be substantially misleading. The morphologies of most spiders facilitate a boom or bust lifestyle that is necessitated by their sit and wait foraging strategies. The extensible abdomens of spiders allow them to double their body mass in a single meal (Foelix, 2011), which sets up the opportunity for spiders to capitalize upon the capture of exceptionally large insect prey. A single large prey could represent more consumable biomass than dozens, or even hundreds of tiny insect prey. Thus, despite their rarity, large insect prey play a disproportionate role in determining fitness. Venner and Casas (2005) called this the 'rare, large prey hypothesis' when they found that biomass in the diet of *Zygiella x-notata* was contributed almost entirely by rarely captured, but large insects. Subsequently, a meta-analysis by Blackledge (2011) extended these findings to a much broader sampling of orb web spiders in four different families. Across a study of 31 taxa that included 18 genera in four different families of orb web spiders, 74% of the biomass captured by orb web spiders in field studies was contributed by large insects that accounted for only 15% of the total number of prey captured (Fig. 12). This suggests that orb webs target prey that are both exceptionally difficult for researchers to observe and also exceptionally challenging for orb webs to capture (Blackledge, 2011). Moreover, the 'rare, large prey' hypothesis predicts that the design of orb webs should reflect the

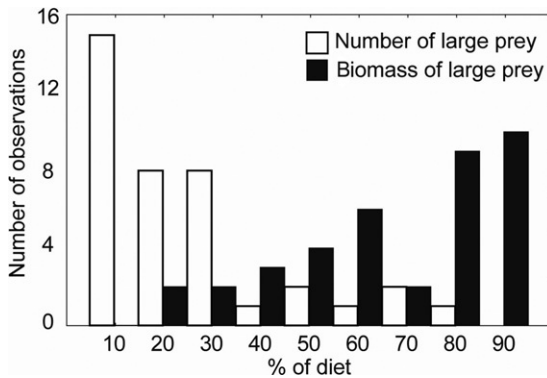


FIG. 12 Comparison of the relative frequency and biomass of larger prey in diets of orb spiders. Large prey were defined as insects at least 66% of the body length of the spider capturing them. Reproduced from Blackledge (2011).

importance of these large and difficult to capture prey (Blackledge, 2011; Venner and Casas, 2005).

2.1.2 Nutrient constraints

There is growing evidence that prey selection in spiders is driven in part by nutrient constraints on development (Mayntz et al., 2009; Mayntz and Toft, 2000, 2001). Such constraints may extend to the production of silk (see Section 4.2). Although spider silk proteins are largely composed of non-essential amino acids that are unlikely to be in short supply in these carnivores, differences in the costs of synthesizing amino acids may constrain silk production (see Section 4.2.2). Thus, silk production and web spinning behaviours may respond to specific nutrients in the diets of spiders, which we explore more fully in Section 4.2.

2.1.3 Non-traditional 'foraging'

Spider webs function as snares for insect prey, but the webs may also catch other consumable 'food'. Many orb-weavers drink water from their webs as moisture condenses on the silk in the early morning (Edmonds and Vollrath, 1992; Walter et al., 2009; Zheng et al., 2010). The stabilimentum spun by some species retains water especially well and may, in part, serve to secure a water supply for the spider (Walter et al., 2009). Although it remains to be tested, the water gathered by these webs may play an important role in the water balance of at least some species of orb web spiders.

In addition to insect prey and water, webs also entangle plant material of various kinds. For most species this represents nothing but debris that impairs web functionality and is generally cut out of the web. For at least a few species, however, such plant material is a source of food. Consumption of pollen is best documented (Carrel et al., 2000; Linskens et al., 1993; Ludy and Lang, 2006; Peterson et al., 2010; Smith and Mommsen, 1984; Vogelei and Greissl, 1989) and is an important food source for at least some spiders, particularly linyphiids (Peterson et al., 2010). Interestingly, symphytognathid spiders have fused chelicerae that appear ill adapted to bite prey which has led to the speculation that they may be predominantly or entirely vegetarian (Coddington et al., 2005).

2.2 PREY INTERCEPTION

Selecting foraging patches is critical for most animals. At the macroscale, patch selection in spiders is likely determined primarily through random dispersal (Bell et al., 2005; Janetos, 1986). However, there is some evidence that orb web spiders can utilize prey cues in the environment when locating webs (Herberstein et al., 2000; Nakata, 2007). The mechanisms that spiders use to determine how long to stay in a patch, and the degree to which those decisions are determined by prey capture are more controversial. A number of studies suggest that spiders relocate webs in response to low prey availability (Caraco and Gillespie, 1986; McNett and Rypstra, 1997; Riechert and Luczak, 1982; Rittschof and Ruggles, 2010). And, spiders may reduce investment in the silk of orb webs when they first build in a new site as a type of bet hedging (Nakata and Ushimaru, 1999). However, variance in prey resources can be so high among patches that other studies argue that spiders could not effectively evaluate the relative quality of different patches, even after several days of spinning a web in the same location (Edwards et al., 2009; Janetos, 1986). Thus, web relocation decisions in orb web spiders may instead be governed more strongly by responses to proximate factors in the environment such as predation pressure, interference competition (Rypstra, 1981; Smallwood, 1993), accumulation of kleptoparasites (Grostal and Walter, 1997; Rittschof and Ruggles, 2010; Rypstra, 1981), and web destruction (Chmiel et al., 2000).

Within a particular habitat, different species, and even different developmental stages, of spiders clearly select discrete microhabitat locations for webs (Janetos, 1986; Wise, 1993). Sympatric species show clearly differentiated preferences for heights of webs, openness of web sites, and types of substrates to which webs are attached (Blackledge et al., 2003a; Brown, 1981; Richardson and Hanks, 2009). These are correlated with differentiation of the bridge lines and frame threads of orb webs. Webs located higher in the vegetation have longer bridge threads, while larger webs are located in more open areas in the vegetation. This suggests that the exploratory behaviours of spiders that precede web construction, in particular, the release of bridging threads play a critical role in microhabitat selection. Microhabitat choice might be limited by how

much bridging silk a spider releases before reeling it back in (Peters, 1990), or even by the degree to which such bridges sag under the spiders' weight (Rodríguez-Girones et al., 2010). Perhaps the most spectacular example of how the early stages of web spinning define microhabitat choice comes from Darwin's bark spider (*C. darwini*), which only locates orb webs over streams, rivers, and small lakes (Agnarsson et al., 2010). This microhabitat is accessible only because the spiders use specialized behaviors to bridge gaps reaching 25 m (Gregorič et al., 2011; Kuntner and Agnarsson, 2010).

The overall size of the orb plays a clear, direct role in defining the total number of insects interacting with the web. Here, bigger seems better. However, orb web spinning is limited in large part by the total amount of capture spiral that a spider can produce (Eberhard, 1988). Thus, any change in web size necessitates alteration either in the spacing between rows of the capture spiral or in the thickness of the capture spiral and its glue coating. Thus, the larger the size of a web produced from a given volume of capture silk, the greater probability that smaller insects will fly through the plane of the web without contacting capture silk. Modelling suggests that the most efficient spacing of capture threads is slightly larger than the body size of the 'target' prey (Chacón and Eberhard, 1980; Eberhard, 1986). However, these geometry-based assessments assume that contact with a single silk capture thread subsequently determines whether or not prey are captured (e.g. ap Rhisiart and Vollrath, 1994; Eberhard, 1986). There is ample reason to doubt this simplistic assumption because prey often escape from webs and the assumption ignores the importance of the stopping and retention powers of webs (Blackledge and Eliason, 2007). In general, there is likely strong evolutionary tension between architectural changes in webs that enhance prey interception and those that facilitate prey stopping and retention (Sensenig et al., 2010). Finally, web visibility is another critical mediator of insect interception that we investigate more fully in Section 2.6.

2.3 PREY STOPPING

Orb webs interact mostly with flying and jumping insects that cannot be captured unless the webs successfully dissipate their kinetic energy without breaking. Indeed, the importance of stopping insect flight is often cited as a major selective factor favouring the evolution of the impressive material properties of the silks in orb webs (e.g. Denny, 1976). Radial silk toughness and glue droplet stickiness are highest under very rapid strains (Cunniff et al., 1994; Sahni et al., 2010, respectively), suggesting that web performance is maximized under conditions such as the explosive impact of a flying insect. The material properties of single silk threads are easily measured in the laboratory, but their interconnections within webs are complex. Thus, it is no surprise that understanding how orb webs operate at the 'whole structure' level to dissipate prey energy is among the least investigated aspects of prey capture (see Section 7).

The kinetic energy of flying insects can be dissipated through at least four routes in orb webs: internal molecular deformation in either the major ampullate silk of radii or the flagelliform silk of capture spirals, the breaking of thread junctions, and aerodynamic damping as webs stretch through the air. To date, no study has quantified and compared the importance of each route. Colloquially, webs are referred to as composite architectures of stiff, strong major ampullate silk in radii that resist breaking under prey impact, and compliant stretchy flagelliform silk in capture spirals that cradles insects during impact, sticks to the insects, and prevents them from ricocheting out of webs. In reality, both types of silk exhibit exceptionally high damping capacities compared to other energy absorbing biomaterials such as tendon and insect resilin that store up to 95% of the energy input into their deformation and then return it. In contrast, both major ampullate silk and viscid glue-coated flagelliform silk dissipate more than 50% of the energy imparted to them when stretching as heat, such that the energy is not returned to prey as webs oscillate under impact (Brooks et al., 2007; Kelly et al., 2011; Liu et al., 2008a). Moreover, the radii in orb webs are extremely stiff relative to capture silk, with $\sim 1000\times$ higher Young's modulus (Denny, 1976). This means that even minor stretching of radii requires a significant input of energy. In contrast, capture spirals begin to stiffen only after they have extended further than the breaking capacity of major ampullate silk. Thus, except in instances where insects only contact capture silk, prey stopping is likely dominated by radii (Sensenig and Blackledge, unpublished).

Cribellate orb web spiders present an exception because of the very different mechanical behaviour of their capture spirals. Cribellate capture silk consists of a dry 'yarn' of nanofibers laid down on an axial core of paracribellar fibres (Hawthorn and Opell, 2002; Opell et al., 2000). These paracribellar fibres are analogous to the flagelliform silk of ecribellate spiders (Blackledge and Hayashi, 2006b). They likely even contain some of the same proteins (Garb et al., 2006). However, they are dry and significantly stiffer than viscid capture silk, which may allow cribellate capture spiral to contribute more to the work of stopping prey (Blackledge and Hayashi, 2006b).

Spiders typically interconnect threads in webs using piriform secretions, creating extremely durable bonds. However, capture spirals are attached to radii using a unique 'sliding connection' first described by Eberhard (1976). Sliding connections break under loading in such a way that adjacent segments of the capture spiral are freed to slide through the junction before the thread breaks. This distributes energy across a greater volume of capture spiral and prevents the capture thread from breaking, unless its loading continues to increase. To date, no study has quantified the breaking load of the junctions, nor their role, if any, in dissipating flight energy. However, sliding connections appear confined to Araneidae and Nephilidae (Eberhard, 1976; Kuntner and Agnarsson, 2009). Cribellate orb webs do not contain sliding connections. They do, however, use an analogous mechanism to distribute loading across multiple segments of capture spiral. At least some species, such as *Uloborus diversus*, skip

attachments between some radii and their capture spirals (Eberhard, 1976). This may be facilitated by the typically horizontal orientation of cribellate webs, which does not allow rows of capture spiral to sag and adhere to one another.

Silk threads are extremely thin, with the largest spiders producing threads only a few microns in diameter and many spiders producing sub-micron fibres (Blackledge et al., 2005a; Sensenig et al., 2010). Silk therefore has an intermediate Reynold's number, which characterizes the relative importance of inertial versus viscous forces for objects when interacting with fluids such as air. In other words, much as tiny insect wings 'swim' through a viscous solution of air, spider silk threads can potentially interact with air as though it were thick and viscous rather than thin gas (Lin et al., 1995). This led to the hypothesis that aerial damping, or friction between silk and air molecules, plays a significant role in how webs dissipate prey energy. Lin et al. (1995) characterized the retardation of webs oscillating with and without the capture spiral intact and concluded that aerial damping, particularly by the capture spiral, accounted for half of the work performed by webs. However, several recent computer models challenge this assertion (Alam and Jenkins, 2005; Ko and Jovicic, 2004) and more recent high speed video studies of web deformation under simulated prey impacts found that aerial damping was negligible for most orb webs (Sensenig and Blackledge, unpublished). Instead, dissipation of prey energy still appears to be mediated primarily by radial silk.

Some spiders may enhance the stopping potential of their webs by reducing the flight energy of prey before the insects contact the surface of the orb. For instance, some orb web spiders are colonial and many species aggregate in rich prey environments (Uetz, 1989). In these instances, the capture surfaces of some orb webs are shadowed by orb webs in front of them (Rao, 2009). While reducing the overall number of prey that might be intercepted, these spiders gain access to larger insects that would normally break through a web as the insects either ricochet off or slow down as they pass through exterior webs (Uetz, 1989). Even solitary spiders could take advantage of the 'ricochet' effect by adding 3D barriers of silk around their orb webs. Barrier webs (Fig. 3) are commonly added to many orb webs by *Nephila*, *Argiope*, *Cyrtophora*, *Metepeira*, etc. (Higgins, 1992; Lubin, 1975). For some genera, barrier webs are a ubiquitous feature of all orb webs, while other genera such as *Nephila* mostly add barriers at juvenile stages (Higgins, 1992). Blamires et al. (2010b) showed that barrier webs interact with old carcasses in webs to increase overall retention of prey.

2.4 PREY RETENTION

Many insects escape from webs before being attacked by spiders (Nentwig, 1982; Rypstra, 1982). This places a premium on the ability of webs to adhere to insects and on rapid response by spiders (Blackledge and Zevenbergen, 2006). Two key innovations that facilitate prey retention are associated with the origin of modern orb web spiders (Araneoidea) compared to the Deinopoidea, viscid

glue and vertical capture surfaces (Bond and Opell, 1998; Opell et al., 2006; Zschokke et al., 2006).

The capture spiral of a modern orb web is a remarkably complex structure. It is produced from a triad of spigots on the posterior spinneret of the spiders (Coddington, 1986a, 1989). A central flagelliform gland spigot produces the axial fibre as an aqueous glue coating is simultaneously laid down by two adjoining aggregate gland spigots (Fig. 5D–F; Peters, 1995). The axial fibre is extremely soft and compliant, with material properties more similar to rubber than dry spider silks (Bonhronne et al., 1992; Vollrath and Edmonds, 1989). The viscid glue rapidly self assembles into a series of regularly arrayed droplets that act as the fundamental units of adhesion. Each droplet consists of a core of fibrous glycoproteins surrounded by an aqueous coating (Vollrath and Tillinghast, 1991). The glycoproteins granules likely act as anchors for a more diffuse adhesive region of transparent glycoproteins (Opell and Hendricks, 2010) and the entire structure is suspended within an aqueous cocktail of low molecular weight compounds (Vollrath et al., 1990). These mostly consist of hydrophilic molecules including amino acids, neurotransmitters, and salts (Townley et al., 2006; Vollrath et al., 1990). Salt concentration, in particular, determines water uptake by the glue droplets while the sugars on the glycoproteins likely provide the surface adhesion (Sahni et al., 2011). The complex morphology of viscid glue droplets appears to serve multiple functions by anchoring the droplets to the axial core fibre, but also by allowing the droplets to stretch when adhering to surfaces—the glue droplets act as extensible viscoelastic solids (Sahni et al., 2010). Droplet adhesion increases with pulloff rate allowing glue droplets to generate more adhesive force as insects try to pull away faster, but also to retain adhesion under static loading without creep (Sahni et al., 2010). This ability to stretch is critical because most adhesive surfaces face a serious constraint in that adhesion is generated primarily at the edges of surfaces during pull off. The elasticity of the glue droplets themselves and the high compliance of the underlying axial fibre overcome this constraint through an unusual ‘suspension bridge effect’ (Opell and Hendricks, 2007, 2009; Opell et al., 2008). As a capture thread begins to peel off of a surface, droplets stretch and continue to contribute adhesive force even as interior droplets are recruited to resist pull off. The resulting viscid capture thread is ideally suited for retaining a variety of insects (Opell and Schwend, 2007) in that it can generate more adhesion under faster pulloff rates and more adhesion on larger surfaces, both of which should enhance retention of fast moving, bigger insect prey. Yet, at the same time the silk can still retain insects even after they have ceased struggling. Finally, adhesiveness of aggregate glue varies manifold across spider species, generally increasing with spider size (Opell and Hendricks, 2009). Agnarsson and Blackledge (2009) found that stickiness increased linearly with capture spiral strength, maintaining a significant safety factor where thread stickiness was always less than the force required to break the capture

thread. They suggested that this safety factor enhanced web function by allowing the silk to repeatedly release and readhere to struggling prey in webs.

Prey retention is ultimately determined by a strong interaction between the adhesive force of individual viscid threads, the architectures of webs, the features of insect surfaces, and insect escape behaviours making it difficult to predict how effectively various types of insects will be retained by webs (Blackledge and Zevenbergen, 2006). In particular, mesh width, or the spacing between rows of capture spiral is one of the most variable features of orb webs among species but directly influences the total adhesive force applied to an insect by a web (Blackledge and Eliason, 2007; Blackledge and Zevenbergen, 2006). The vertical orientation of most araneoid orb webs likely increases insect retention because prey that escape are very likely to tumble down under the force of gravity and re-entangle themselves (Opell *et al.*, 2006). The importance of tumbling is evidenced by the vertical trails left in many webs by insects and has selected for the repeated evolution of highly elongate ladder webs in at least two separate lineages of orb web spiders (Stowe, 1986). Lepidoptera normally escape quickly from most orb webs when their detachable scales gum up the viscid silk (Eisner *et al.*, 1964; Stowe, 1986). Ladder webs enable these genera to capture moths once they have tumbled down the webs and lost most of their scales (see Section 6.3.1).

2.5 VIBRATION TRANSMISSION

Given the relatively short time that spiders have to recognize and subdue prey (see Section 2.2), there are likely significant tradeoffs in the evolution of the geometries of webs and material properties of silk for how webs function mechanically versus how webs function as information transmitting devices. The radial threads of orb webs transmit vibrations to the central hub, thereby allowing spiders to localize trapped insects and to determine their identity (Landolfa and Barth, 1996) in a manner that differs strongly with ground-based sheet webs (Naftilan, 1999). Orb web spiders use vibrational information to actively hunt on the surfaces of their webs, selectively responding to prey through a suite of different attack behaviours (Japyassu and Viera, 2002; Robinson, 1969; Robinson and Mirick, 1971). Vibrations are transmitted most effectively along the longitudinal axis of radii, reaching the hub with almost no attenuation in empty webs because the capture spiral is so compliant (Masters, 1984). However, significant attenuation does occur in webs that retain the auxiliary spiral as energy is lost to it (Landolfa and Barth, 1996).

Spiders use the difference in amplitude among radii to localize prey and are effective at transmitting a broad range of frequencies (Landolfa and Barth, 1996). Information about prey size can be provided by differences in the frequency of oscillation of webs (Landolfa and Barth, 1996), with larger prey typically producing lower frequencies (Suter, 1978; Watanabe, 2000). Spiders can tune the responsiveness of orb webs by manipulating the tension in radii during the final stages of hub construction. This allows spiders to alter the

frequencies of vibrations that are transmitted effectively such that webs can 'exclude' smaller prey from being perceived by well-fed spiders (Watanabe, 2000) and to 'focus' the attention of spiders on regions of webs that are more likely to intercept prey (Nakata, 2010a).

Significantly less is known about how spiders receive information about prey taxa. Many orb web spiders employ different attack behaviours for prey that differ in their risk for spiders and their propensity to escape from webs (Robinson, 1969; Robinson and Mirick, 1971). While spiders clearly gain chemotactile cues once they have reached an entrapped insect, at least some of these behavioural strategies are initiated prior to contact arguing that they are mediated by vibratory cues (Suter, 1978).

2.6 WEB VISIBILITY AND STABILIMENTA

Orb webs depend upon low visibility to prey for successful capture, and the thin diameters of silk threads ($\sim 4 \mu\text{m}$ and less) means that individual silk threads are below the visual resolution of most flying insects (Craig, 1986). However, the larger glue droplets in the viscid capture threads may increase visibility of webs (Craig, 1988). Many spiders also add seemingly conspicuous decorations of silk to webs, termed stabilimenta, whose function has proved quite controversial.

A rich literature exists on the functional implications of stabilimenta in orb webs (Blackledge, 1998a; Bruce, 2006; Eberhard, 1990b; Herberstein et al., 2000a; Starks, 2002; Thery and Casas, 2009). Despite these extensive reviews, the function of stabilimenta is still contested. Our goal here is not to provide a comprehensive survey of this literature, but rather to focus on the current state of the field. The term 'stabilimentum', now often called 'web decorations', was first coined by Simon (1864) to refer to the ribbon-like zigzags of silk that *Argiope* place in the centres of webs. Stabilimentum has since been used to refer to a variety of silk and detritus structures added to spider webs (Fig. 13). Despite the name, little evidence supports the antiquated hypothesis that stabilimentum decorations somehow stabilize webs because the silk is typically too loosely attached to structural threads. The pattern of stabilimenta is species specific (Cheng et al., 2010; Hingston, 1927; Lubin, 1986) and the decorations are built by over 22 genera of spiders, primarily in the Araneidae and Uloboridae but also in the Nephilidae and Tetragnathidae (Herberstein et al., 2000a; Scharff and Coddington, 1997). Virtually every species in some genera, such as *Argiope*, *Cyclosa*, *Gasteracantha*, and *Uloborus*, include silk stabilimenta in some webs. However, the behaviour is extremely plastic with individual spiders usually decorating only some of their webs and shapes of stabilimenta changing from web to web in correlation with a variety of environmental factors (Fig. 13; Bruce et al., 2001; Elgar et al., 1996; Herberstein and Fleisch, 2003; Neet, 1990; Seah and Li, 2002; Uhl, 2008).

Recent phylogenetic analyses suggest nine origins of this behaviour in the Araneoidea (Herberstein et al., 2000a; Scharff and Coddington, 1997), although

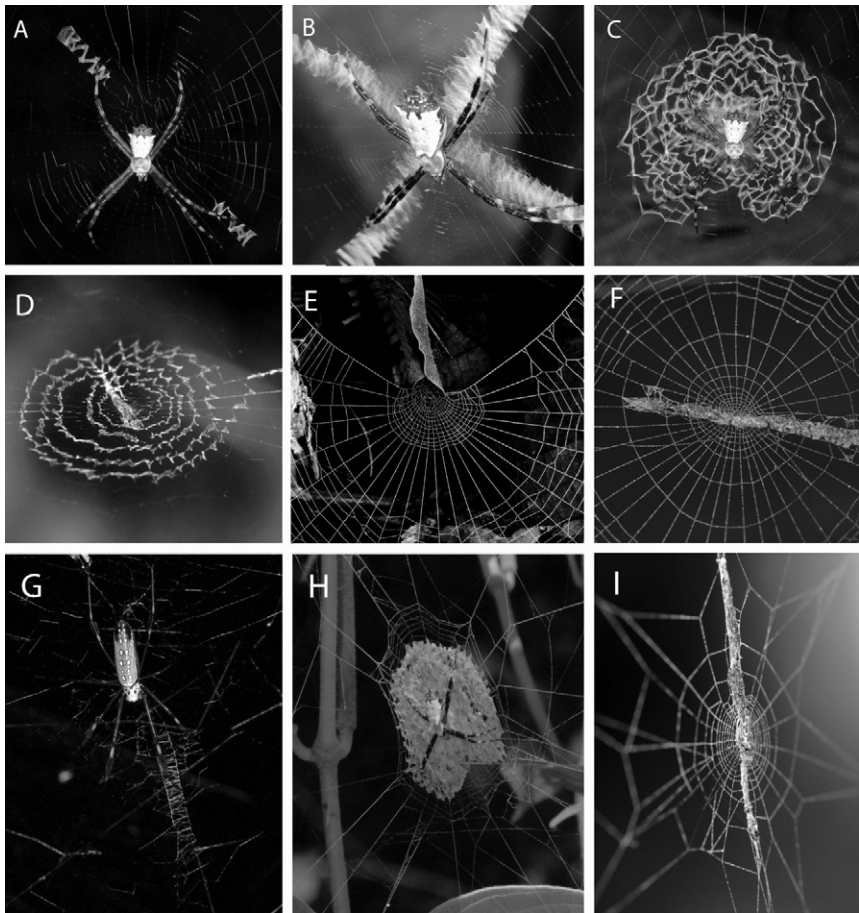


FIG. 13 Stabilimenta in spider orb webs. (A–C) various morphologies of silk stabilimenta in the webs of *Argiope argentata* (Costa Rica). (D) Spiral silk stabilimentum in the horizontal orb web of *Uloborus glomosus* (USA). (E) Curled leaf ‘stabilimentum’ in the web of an unidentified araneid (New Britain). (F) Debris stabilimentum at the hub of the web of *Cyclosa caroli* (Costa Rica). The spider is sitting at the centre of its hub and its horizontal orientation matches that of the stabilimentum. (G–I) Stabilimenta are commonly included in the resting webs built by spiders preparing to moult or lay eggs. (G) *Nephila clavipes* (Costa Rica). (H) *Argiope argentata* (Costa Rica). (I) *Cyclosa caroli* (Costa Rica).

many taxa known to build stabilimenta could not be included in these studies. More important, these analyses strongly support early observation that construction of stabilimenta is always associated with diurnal spiders that sit on the hubs of webs while hunting (Eberhard, 1973; Edmunds, 1986). Neither species that rest in retreats during the day nor exclusively nocturnal species decorate webs. The decorations therefore likely serve either a visual or thermoregulatory

function. While some stabilimenta may act as 'sun shields' (Humphreys, 1992), many of these spiders build webs in sheltered sites and the shapes of most decorations cannot shade spiders so that, like the 'stability' hypothesis, thermoregulation cannot explain the repeated origin and maintenance of these enigmatic structures for the vast majority of spiders. Instead, two classes of vision-based hypotheses are usually considered—that the decorations lure prey to webs or act as defences against a spider's own predators.

2.6.1 *Prey attraction*

Stabilimenta may provide visual cues that attract insects to webs by mimicking flowers or light gaps (Elgar et al., 1996; Ewer, 1972; Gawryszewski and Motta, 2008; Gertsch, 1949). The prey attraction hypothesis gained strong favour after an innovative study by Craig and Bernard (1990) in which they showed that stabilimentum silks retain the strong reflectance of ultraviolet (UV) light found in a variety of primitive spider silks (Craig et al., 1994). This UV component is lost in the derived silks used to construct orb webs, but can be an important cue for insect navigation (Goldsmith, 1961; Wehner, 1981) and floral signals (Chittka et al., 1994; Kevan et al., 1996; Menzel and Shmida, 1993). Craig and Bernard (1990) reasoned that UV reflectance by stabilimenta could mimic these cues and attract prey to webs (Craig, 1995; Kiltie, 1996). Support for this hypothesis rapidly grew from a variety of laboratory choice chamber experiments showing insect attractance to UV reflecting spider silks (Blamires et al., 2008; Bruce et al., 2001; Li et al., 2004; Watanabe, 1999) and field correlations between presence of stabilimenta in webs and prey capture (Bruce et al., 2004; Craig and Bernard, 1990; Herberstein, 2000; Humphreys, 1992; Li et al., 2004; Tan et al., 2010; Watanabe, 1999). Even the bodies of spiders, which may reflect UV light, have been hypothesized to attract prey to webs (Bush et al., 2008; Craig and Ebert, 1994; Hauber, 1998; Tso et al., 2007a), but see contradictory evidence from Vanderhoff et al. (2008). Finally, the yellow-pigmented silks produced by *Nephila* are argued to function similarly (Henaut et al., 2010).

Despite apparent strong support, the prey attraction hypothesis faces several serious challenges. Most critical, it does not fit the ecological pattern of which species add stabilimenta to webs. There is no obvious explanation for why diurnal, but retreat-dwelling spiders, such as *Araneus*, *Metepeira*, and *Zygiella* do not build stabilimenta, as they would certainly benefit from visual attraction of prey too. All laboratory choice experiments are incredibly difficult to extrapolate to the field because they rarely replicate the complex background and light environments common in nature. Early field studies on prey attraction inferred prey capture from patterns of web damage (Craig and Bernard, 1990; Hauber, 1998). To our knowledge, there is no empirical demonstration that this technique accurately measures prey consumption. Observations that decorated webs in the field capture more prey are not universal (Baba, 2003; Prokop and Gryglakova, 2005), and these observations might be better explained by the effect that prey capture has on

decorating behaviours (Blackledge, 1998b). High prey consumption rates make spiders more likely to decorate future webs with larger stabilimenta (Blackledge, 1998b; Herberstein et al., 2000b; Tso, 2004), although these effects are not universal (Nakata, 2009; Tso, 1999). This means that correlations between prey capture and presence of stabilimenta in webs are likely caused by high prey capture influencing the inclusion of stabilimenta in webs rather than the reverse (Blackledge, 1998b). Finally, direct manipulation of the presence of stabilimenta in webs in the field shows that these decorations cost spiders a 30% reduction in prey capture (Blackledge and Wenzel, 1999). A last argument against the prey attraction hypothesis, at least for some webs, is that stabilimenta are often more common and larger in moulting webs that do not contain sticky silk and do not act as prey capture devices (Fig. 13; Eberhard, 2007b; Ewer, 1972; Robinson and Robinson, 1973a,b; Nentwig and Rogg, 1988; Walter et al., 2008).

The focus on UV reflectance *per se* by stabilimenta and other spider silks is also problematic. Visual conspicuousness is determined by an interaction between *all* colours of light reflected by an object, its background, the ambient environment, and the visual physiology of the perceiver (Endler, 1993a,b). Stabilimentum silk reflects large amounts of blue and green light (Zschokke, 2002), resulting in a flat, achromatic coloration to many insects that blends with the background and is cryptic (Blackledge, 1998a; Chittka et al., 1994; Kevan et al., 1996). Honey bees trained to associate 'flowers' made of spider silk with nectar rewards could learn to find flowers made from primitive tarantula silk, which has a UV reflective peak, but not learn to find flowers made from stabilimentum silk, whose UV + blue + green reflectance gave poor colour contrast against the natural grass background where the experiment took place (Blackledge and Wenzel, 2000).

2.6.2 *Predator defence*

Spiders resting on their webs in daylight are particularly exposed to visually hunting predators, suggesting the hypothesis that stabilimenta act as defences against predators of spiders. Various proximate mechanisms include camouflaging the spiders outline, distracting attackers and advertising the presence of noxious or potentially dangerous webs.

2.6.2.1. Camouflage Stabilimenta may provide camouflage for spiders, or in some cases physically hide spiders from predators (Eberhard, 1973, 2003; Lubin, 1975; Marples, 1969; Marson, 1947a,b; Robinson and Robinson, 1973b). The coloration of many spiders blends well with their stabilimenta (Fig. 13). Some *Cyclosa* change from a silvery to brown coloration as they develop and this is accompanied by a change from stabilimenta made largely from silk to mostly debris (i.e. light to dark coloured designs; Bristowe, 1939; Marson, 1947a) while ontogenetic changes in body colour of *Allocyclosa* correlate with a shift from silk to egg sac stabilimenta (Eberhard, 2003), and

the silvery hairs on the dorsum of *Argiope*, particularly juveniles, blend with the bright white silk of their stabilimenta. The resting postures of spiders in webs are highly stereotyped (Kuntner et al., 2008a; Opell and Eberhard, 1984) and match stabilimentum shape. Uloborids, which build linear stabilimenta, rest in small gaps in the stabilimenta with their legs tightly appressed to the designs while *Argiope*, which build cruciate stabilimenta, hold their legs in tight alignment with their x-shaped designs (Eberhard, 1972; Ewer, 1972; Hingston, 1927; Kuntner et al., 2008a; Robinson and Robinson, 1974). All of these spiders were observed relaxing the positions of their legs after sunset, when visual predators were presumably no longer hunting. Finally, populations of spiders exposed to higher predation pressure also decorate webs more often (Kerr, 1993; Lubin, 1975), as do individual spiders exposed to 'predator mimicking' cues in the laboratory (Nakata, 2009). Despite substantial support from natural history, there is only sparse experimental evidence for the camouflage function. Juvenile *Argiope trifasciata* are more likely to survive sphecid wasp attacks in decorated webs (Blackledge and Wenzel, 2001), and clay models of *Cyclosa* are bitten less often when placed in decorated webs (Gonzaga and Vasconcellos-Neto, 2005).

In criticism, some field surveys found decreased long-term survival of spiders that decorate webs most frequently (Craig et al., 2001). But, those spiders may simply have matured quickly because they were in web sites with high prey density, which also caused their higher frequency of decorations (see Section 2.6.1). The apparent conspicuousness of stabilimenta may also provide cues that predators use to locate spiders (Robinson and Robinson, 1970), which is supported by laboratory choice experiments for both jumping spider (Seah and Li, 2001) and mantid predators (Bruce et al., 2001). Again, extrapolating from these results to how predators locate prey in nature is difficult (see Section 2.6.1). Moreover, at least one study found higher overall survival of spiders employing stabilimenta despite higher rates of attacks by predators (Tseng and Tso, 2009; see Section 2.6.2.2).

2.6.2.2. Predator confusion The bright silk of stabilimenta may increase the probability of spiders surviving attacks by startling or confusing predators (Marples, 1969). Many spiders vibrate or pump their webs when disturbed, causing the outlines of spiders and stabilimenta to blur (Cloudsley-Thompson, 1995). This may make it more difficult for predators to attack spiders (Schoener and Spiller, 1992; Tolbert, 1974). Also, the bright silk of stabilimenta may simply draw the attention of attacking predators away from spiders (Bristowe, 1939; Hingston, 1927) or increase the apparent size of the spiders to gape-limited predators (Schoener and Spiller, 1992; Tolbert, 1975). Finally, salticid spiders will attack wrapped prey bundles in webs in preference to *Argiope* (Robinson and Valerio, 1977), suggesting that detrital stabilimenta could act as similar 'decoys'. A recent test of the predator confusion hypothesis (Tseng and Tso, 2009) showed that spider employing conspicuous self-mimicking decoys in their webs suffered higher number of wasp attacks, but nevertheless reduced predation through predator confusion. Further, most of the experimental evidence for camouflage

(see [Section 2.6.2.1](#)) could also be explained through predator confusion—for instance the higher rates of survival of spiders with stabilimenta in webs when exposed to wasp predators ([Blackledge and Wenzel, 2001](#)).

2.6.2.3. *Web advertisement* The sticky silk of webs can be dangerous to many predators such as wasps and small vertebrates including lizards, birds, and bats ([Cloudsley-Thompson, 1995](#); [Edmunds, 1986](#); [Rayor, 1997](#)), and it is an irritant to birds, which may spend up to an hour grooming after sticky silk adheres to their feathers ([Eisner and Nowicki, 1983](#); [Horton, 1980](#)). Thus, stabilimenta may function as aposematic signals ([Gawryszewski and Motta, 2008](#)). Experimental support for web advertisement comes largely from laboratory experiments ([Horton, 1980](#)), the addition of artificial stabilimenta to webs ([Eisner and Nowicki, 1983](#)) and the placement of webs around bird feeding stations ([Blackledge and Wenzel, 1999](#)). These studies clearly demonstrate that web advertisement by stabilimenta can be beneficial to spiders, but do not address how important it is to the overall fitness of spiders. Because bird ‘fly-through’ is probably rare, preventing it may not offset the cost of signalling presence of webs if insect prey detect stabilimenta ([Blackledge and Wenzel, 1999](#)). Furthermore, many taxa that build stabilimenta do so in relatively sheltered areas such as deep in tall grass or around tree buttresses, where birds are unlikely to fly into webs ([Eberhard, 1990b](#)).

2.6.3 *Summary*

The debate over the function of stabilimenta is likely to continue. Our goal here is to highlight the strengths and weaknesses for current hypotheses. A recent trend has developed in literature to explain conflicting studies simply as evidence for multiple functionality and inter-specific variability in stabilimenta. While plausible, this approach should not be used as an excuse to avoid examining the implications of newly gathered data for alternative hypotheses. We encourage any experiment on stabilimentum function to consider the implications of its evidence for all hypotheses in the ultimate hope of stabilizing on a coherent functional explanation. Yes, stabilimentum-construction evolved many times among orb web spiders, but always in diurnal, hub dwelling spiders. This similarity in ecology suggests convergent evolution for similar function across orb web spiders rather than a hodgepodge of explanations that vary down to the population level.

3 **How costly are orb webs?**

While orb web spiders employ a sit and wait foraging strategy, they are sometimes considered active foragers because of their greater mobility compared to spiders spinning other types of webs. Most orb web spiders rebuild their

webs daily, providing ample opportunity to move to new locations. What rules govern movement to new websites and how costly are webs to produce? Three energetic costs are associated with web spinning: (1) the metabolic costs of synthesizing silk proteins, (2) the caloric energy contained in the silk itself, (3) the behavioural costs of assembly. Additionally, orb web spiders face exposure to predators when exploring potential websites and spinning webs.

3.1 ENERGETIC COSTS

Spinning webs dominates the daily energy budgets of many orb web spiders (Tanaka, 1989). The relative importance of the cost of producing silk versus the movements of spiders for the production of webs is critical to understanding constraints on web architecture (Eberhard, 1986), although precise data are unfortunately lacking. Because silk consists predominately of protein, the caloric energy in dry silk is relatively constant among spiders (Lubin, 1973; Prestwich, 1977) and therefore proportional to the amount of silk in an orb web. However, the cost of synthesizing the actual amino acids in silk varies depending upon the metabolic pathways involved (Craig, 2003). Thus, variation in the amino acid sequences of silk, particularly due to differential expression of proline poor MaSp1 versus proline rich MaSp2 in dragline silk, could alter the cost of synthesis by up to 22% (Craig, 2003). Decreasing the cost of silk synthesis may itself play an important role in shaping the evolution of the amino acid composition of silks, as major ampullate silk in derived orb web spiders appears less costly to synthesize compared to major ampullate silk in ancestral taxa (Craig, 2003). Unfortunately, the viscid glue of orb webs is far more complex and we know little about either its caloric content or the cost to synthesize it.

Spiders are renowned for their low metabolic rates (Anderson, 1970), with anecdotal accounts of some spiders surviving more than 200 days without food (Anderson, 1974). However, the metabolic rates of many web-building spiders are significantly higher compared with cursorial spiders (Prestwich, 1977), suggesting that the behavioural costs of spinning orb webs are not trivial. The movement costs associated with web spinning can account for $\sim 1/3$ of the total energy of web production in derived sheet-web spiders (Ford, 1977) as well as the sheet-web spinning wolf spider *Sossipus* (Prestwich, 1977). However, these taxa produce silk-intensive webs compared to orb web spiders, whose webs can weigh less than 0.2% of the spider's mass (Blackledge, 1998b). Thus, it is not surprising that the only estimate of an energy budget for an orb web spider places the behavioural costs of spinning at nearly 78% (Peakall and Witt, 1976).

3.1.1 *Silk recycling*

Despite the relatively 'cheap' cost of producing orb webs compared to other web architectures, reductions to the material and behavioural costs of web spinning still play an important role in the evolution of orb webs. Most notable

is the transition from cribellate silk to viscid glue, which reduces the overall cost of web production by 34%, in part because it is significantly quicker to produce (Opell, 1998). Along with the many ways in which viscid silk adheres better (Opell and Schwend, 2009; Opell et al., 2008; Sahni et al., 2010), this economization was likely key to the explosive diversification of araneoid spiders, which now account for 95% of all orb web spiders. Most araneoid orb web spiders also digest the silk from webs, recycling the amino acids into new silk with an efficiency approaching 95% (Peakall, 1971), although other studies suggest a much more modest rate of 32–50% (Breed et al., 1964; Townley and Tillinghast, 1988). This recycling of silk reduces the cost of spinning orb webs by up to 32% (Opell, 1998). Curiously, web recycling occurs primarily in viscid orb-weaving spiders rather than cribellate orb web spiders or derived web builders. This suggests that the primary ‘target’ of recovery may be some of the compounds in the viscid glue droplets themselves rather than silk proteins (Townley et al., 2006). Indeed, at least one component of the glue, GABamide, might be more efficiently recycled than the protein in major ampullate silk (Townley and Tillinghast, 1988).

3.2 WEB RELOCATION

Despite an overall lack of empirical data, viscid orb webs are relatively cheap traps for spiders to build and this appears to facilitate an active hunting strategy where spiders can more frequently change websites from day to day compared to other web builders (Kawamoto and Japyassu, 2008; Tanaka, 1989). Thus, many authors suggest that orb web spiders behave similar to active searching predators, sampling their environment on a daily basis until a suitable web location is found (Heiling, 1999) and potentially even building ‘exploratory’ webs with reduced amount of silk (Nakata and Ushimaru, 1999). This optimality-based understanding of how spiders locate webs is challenged by the extreme stochasticity of insect prey resources in many environments because it requires spiders to sample prey at a location for many days to adequately compare resource richness among patches (see Section 2.2). Instead, orb web spiders may abandon web locations primarily due to negative stimuli such as destruction of webs, parasitism, and interference from conspecifics. Regardless of the rules governing web relocation, it often appears to be a relatively ‘last resort’ decision associated with reduced reproductive output (Wherry and Elwood, 2009) and a significant risk of predation (Vollrath, 1985).

4 Plasticity and response to the environment

The basic motor patterns used by spiders to construct webs are largely innate and result in species specific differences in web architecture (see Section 1.5; Reed et al., 1970; Risch, 1977). However, spiders also clearly alter details of

individual webs in response to both their internal physiology and the external environment (Herberstein and Tso, 2011). While such behavioural plasticity is often adaptive, linking variability in web spinning to web function is surprisingly difficult, in part due to the disjunction between research on silk *per se* versus webs (Harmer et al., 2010). The ease and simplicity of designing experiments to manipulate the environment in the laboratory or field and study orb webs sometimes contrasts with the difficulty of interpreting the meaning of the data garnered from them.

4.1 RESPONSIVENESS TO MICROHABITAT

The mechanical integrity of the substrates to which orb webs are attached can vary greatly and spiders may shift their web spinning behaviours in response to a variety of cues such as wind, light, and temperature. Spiders actively explore their web-building sites and can also alter the early stages of web construction under severe spatial constraints, resulting in abnormally shaped webs that maximize capture areas (Krink and Vollrath, 2000). Spiders in windier microhabitats consistently build smaller orb webs (Hieber, 1984; Liao et al., 2009; Vollrath et al., 1997). This alteration likely reduces the chances that webs are damaged, although it is typically unclear whether the smaller sizes of the webs are due to decreases in the total amount of silk used, or increases in thread diameters. Similar variation among spiders constructing webs in open versus secluded microhabitats might also be explained more by predation pressure than by physical differences in those habitats (Blamires et al., 2007).

Spiders that decorate their webs with stabilimenta are particularly responsive to microhabitat, changing the frequencies and sizes of decorations in response to light levels (Herberstein and Fleisch, 2003) and position in the vegetation (Blackledge and Wenzel, 2001; Blamires et al., 2007; Elgar et al., 1996), although the relationships often contrast from study to study. The propensity of *Nephila* to incorporate yellow pigments into their 'golden' silk is similarly malleable (Putthanarat et al., 2004) and responsive to different light environments (Craig et al., 1996).

4.2 RESPONSE TO PREY

4.2.1 *Web architecture*

The architectures of orb webs clearly influence the types of prey ultimately captured and consumed by spiders (see Section 2). But, do spiders target specific prey by altering the designs of orb webs? Many studies find clear changes in web architectures from spiders fed different diets or in different microhabitats.

The simplest question to ask is how do spiders respond to low prey density or starvation? Several early studies suggested that starved spiders increase the

overall sizes of orb webs (Higgins and Buskirk, 1992; Sherman, 1994; Witt et al., 1968), although this effect was not universal (Vollrath and Samu, 1997; Witt et al., 1968). Regardless, larger orb webs might be interpreted as increased foraging effort (e.g. Eberhard, 1986; Venner et al., 2000, 2006; Watanabe, 2001) because of the direct influence of the size of capture area on the potential number of prey intercepted by orb webs. However, prey stopping and prey retention do not necessarily scale linearly with shifts in web architecture (see Sections 2.3 and 2.4). Instead, starved spiders may target fundamentally different prey from satiated spiders by spreading silk resources more thinly in a larger space, thereby increasing the probability of intercepting prey at the expense of stopping and retaining the largest insects (e.g. Blackledge, 2011; Miyashita, 1997). Unfortunately, such implications are rarely tested in the field (e.g. Watanabe, 2001).

Spiders also clearly respond to higher levels of prey consumption by increasing the frequency and/or size of stabilimentum web decorations in orb webs (Blackledge, 1998b; Herberstein et al., 2000b; Tso, 2004), although this effect is again not universal (Blamires, 2010). They may also be more likely to spin barrier webs around their orb webs (Baba and Miyashita, 2006). The implications of this variation are discussed in Section 2.6.

Perhaps the most dramatic example of web spinning plasticity in response to prey density comes from laboratory studies on the western black widow *Latrodectus hesperus*, which is derived from an orb web ancestor but now produces 3D cobwebs. These spiders spin two radically different types of webs depending upon prey abundance. Starved spiders produce a classic cobweb, a sheet of dry silk from which descend gumfoots, all suspended in a 3D network of dry supporting threads. Satiated spiders rapidly shift behaviours and instead produce webs consisting of only a greatly elaborated network of the supporting threads (Blackledge and Zevenbergen, 2007). As predicted, the webs produced by starved black widows function better at capturing prey, regardless of the motivation of the spider foraging upon them (Zevenbergen et al., 2008).

The degree to which spiders manipulate web architectures in ways that may target the capture of specific types of prey is much more difficult to assess. A clear example in the field comes from *Parawixia*, which radically enlarges the spacing between rows of capture spiral in orb webs by 300% during termite emergences compared to the smaller webs that they normally spin (Sandoval, 1994). Because termites are relatively weak fliers, increased mesh width likely allows the spiders to spin larger orb webs without compromising the orb web's ability to absorb their low kinetic energy (see Section 2). While Sandoval did not explicitly test the functional implications of these two web geometries, this example is compelling because the variation in web architecture occurred diurnally—the large, open webs were constructed during the middle of the day when reproductive termites emerged while the smaller webs were crepuscular, thereby excluding many alternative causal explanations. Similarly,

Araneus diadematus in the laboratory increases mesh width when fed longer-bodied insects, compared to more compact prey, of equal mass (Schneider and Vollrath, 1998). When starved, the cribellate orb web spider *Octonoba sybaitides* decreases mesh width and adjusts the tension of threads in webs in ways that may target smaller, more abundant insects (Watanabe, 2000, 2001).

An important complication for any of these studies is to determine precisely what environmental cues a spider responds to when attacking and consuming prey. Do spiders pay attention to mechanical and vibratory cues when physically capturing prey (Herberstein et al., 2000c; Nakata, 2009; Pasquet et al., 1994)? Are spiders responding to the total energy gained from consuming prey and/or ontogenetic shifts toward reproduction or moulting (Higgins, 1990, 2006)? Or, might the influence come from a more subtle nutrient constraint such as protein or lipid content (Blamires et al., 2009; Mayntz et al., 2009) or specific nutrients that limit silk production (Higgins and Rankin, 1999)? Finally, do spiders alter web spinning simply in response to the mechanical necessities of supporting heavier or lighter bodies as food consumption varies (Kuntner et al., 2010a; Vollrath and Köhler, 1996)?

4.2.2 *Plasticity in silk production*

Orb web spiders possess a number of physiological mechanisms by which they could potentially manipulate the material or structural properties of silk threads, and even its biochemical composition (see Herberstein and Tso, 2011). These range from altering the ratio of specific fibroins in silk to controlling the molecular orientation of the fibroins to altering the numbers and diameters of threads composing specific elements of orb webs (Boutry and Blackledge, 2008). Mechanical performance of major ampullate silk typically differs between silk from orb webs and silk collected directly from spiders (Agnarsson et al., 2010; Ortlepp and Gosline, 2004). Rapid variation in the mechanical performance of silk is well demonstrated along single threads of major ampullate dragline collected from restrained spiders (Garrido et al., 2002b; Madsen et al., 1999; Ortlepp and Gosline, 2004; Vollrath et al., 2001). Structural variability appears to facilitate the function of dragline silk as a lifeline, allowing it to sustain loading by larger or smaller spiders (Garrido et al., 2002a; Ortlepp and Gosline, 2008; Vollrath and Köhler, 1996).

Manipulation of amino acid availability in the diets of spiders can also result in changes in the chemical composition of dragline silk (Blamires et al., 2010a; Craig et al., 2000) and ultimately its mechanical performance (Zax et al., 2004). Biochemical variation occurs in both the viscid glue of the capture spiral and major ampullate radial silk in orb webs in response to starvation (Townley et al., 2006) or variation in type of prey fed to spiders (Tso et al., 2005). At least three studies found similar biochemical variation among populations of spiders in webs in the field (Craig et al., 2000; Higgins et al., 2001; Tso et al., 2005). Some of these changes may simply reflect shifts toward

metabolically cheaper pathways in silk synthesis (Guehrs *et al.*, 2008), but others correlate with variation in the structure and properties of silk, as well as whole web performance (Guehrs *et al.*, 2008; Tso *et al.*, 2007b).

The mechanisms by which such biochemical variation arises are unknown, but may involve changes in the regulation of MaSp1 and MaSp2 expression for major ampullate silk (e.g. Guehrs *et al.*, 2008). An important caveat is that such changes are unlikely to have an immediate effect on silk performance because the major ampullate gland has a large reserve of material and the viscous nature of liquid silk precludes silk in the lumen from mixing with newly synthesized fibroins. Thus, most detectable variation in silk performance over short time periods likely involved 'spinning effects' rather than biochemical variation (Boutry and Blackledge, 2008). Finally, as was the case with web geometry, it can be difficult to determine precisely what cues from prey spiders are responding to in these studies and complex interactions are possible (e.g. Blamires *et al.*, 2010a).

4.3 PREDATOR INDUCED PLASTICITY

Orb webs are in essence microhabitats constructed by spiders that influence how spiders interact with their environment well beyond prey capture (see Section 5). Thus, it is not surprising that spiders will alter web spinning in response to cues of predation risk (Bruce and Herberstein, 2006; Li and Lee, 2004), although such links are rarely explicit. For instance, the barrier web in *Nephila clavipes* functions as a predatory deterrent, and its relative size is influenced by predation load (Higgins, 1992).

4.4 CHEMICALLY INDUCED WEBS

4.4.1 *Drug webs and non-target effects of pesticides*

In an initial attempt to change the timing of web construction in *Argiope* garden spiders P. N. Witt explored the effects of various chemicals on orb web spiders. Instead of altering when webs were constructed, the various drugs induced changes in the architectures of orb webs (see summary in Witt *et al.*, 1968). This classic set of experiments produced results that played a critical role in dispelling the notion that web spinning behaviours were solely innate and immutable. The 'drug web' experiments are still conducted today (Hesselberg and Vollrath, 2004), and importantly set the stage for modern research on non-target effects of pesticides on these potential agents for biological control in agriculture (Riechert and Lockley, 1984). For instance, the large surface areas of orb webs means that they can absorb large amounts of airborne chemicals that spiders ingest when recycling webs (Samu *et al.*, 1992). Sub-lethal doses of common insecticides received this way reduce web spinning frequency and disrupt web architecture (Samu and Vollrath, 1992).

4.4.2 *Spider manipulation by parasites*

Parasitoids affect spiders in many ways, including altering spider behaviour (Schlinger, 1987). An exquisite example of the influence of parasitoids on their spider hosts' behaviours comes from the ichneumonid wasp *Hymenoepimecis* sp. Just prior to killing its host, the wasp larva induces the spider to build a unique type of web that serves as a support for the wasps' cocoon (Eberhard, 2000b, 2001b; Nielsen, 1932). The 'cocoon web' is constructed using repetitions of one stereotypical behavioural subroutine in the early stages of normal orb web weaving. Thus, the spider is chemically manipulated to repeat an innate behavioural pattern, resulting in a structure that is useful for the wasp (Eberhard, 2000b). Recently, further polysphinctine wasp species (*Poly-sphincta* clade sensu) have been shown to induce various types of cocoon webs in their host spiders (Gonzaga and Sobczak, 2007; Gonzaga et al., 2010; Matsumoto, 2009; Weng and Barrantes, 2007). These range from highly specialized supportive structures (Eberhard, 2000b, 2001b) to relatively minor changes in the normal orb (Gonzaga et al., 2010). In all cases, these behavioural manipulations seem to result in web architectures that help to protect the wasp's cocoon. The chemicals involved and their exact effects on the spiders remain to be studied, and discovering how such chemicals interact with or control behavioural pathways may help understanding the natural control and organization of normal orb web construction behaviour (Eberhard, 2010b).

4.5 SUPERCONTRACTION: MAINTAINING FUNCTION OF WETTED WEBS?

Spider dragline silk absorbs water at high humidity, altering its material properties and shrinking up to 50% of its original length, if unrestrained, a property referred to as 'supercontraction' (Blackledge et al., 2009a; Work, 1981). Supercontraction is broadly distributed across spiders, but the silk of orb web spiders contracts more strongly than other taxa (Boutry and Blackledge, 2010). One hypothesis suggests that it evolved as a mechanism to allow tailoring of silk properties as wet fibres emerge from the spinning ducts (Guinea et al., 2005) and that it is largely a byproduct in webs. However, supercontraction generates substantial stress in silk when it is restrained, such as in the frames and radii of orb webs. Thus, supercontraction is hypothesized to provide a mechanism that tensions webs as they become loaded with dew or rain (Elices et al., 2004; Guinea et al., 2003). This could potentially help maintain the structure and function of webs (Savage et al., 2004). However, this hypothesis remains to be tested and at least one experiment argues that enough stress would be generated in webs to permanently impair silk function (Bell et al., 2002). Furthermore, many spiders remove their orb webs during rain (personal observation, Blackledge Kuntner and Agnarsson). Direct tests of the effect of supercontraction on whole web mechanics are therefore needed.

5 Beyond prey capture: orb webs as habitats

Spider orb webs not only serve as snares for their owners, the webs also represent shelters against predators. Certain web types may also regulate environmental stressors, such as temperature and rain. Specialized resting webs are built for protection during the fragile stages of moulting. Webs also are used as protective habitats by a diversity of organisms and certain insects while some spiders utilize webs built by others as a way of obtaining food via stealing. Thus, orb web spiders are really constructing their own micro-environments when they spin webs.

5.1 WEBS AS PREDATORY DEFENCES

While spider webs are examined primarily for their role as prey capture devices, webs also provide protection against predators. The classical orb webs, with their 2D architectures where resting spiders are exposed at the hub, seem to offer little protection from flying predators such as birds and wasps. However, many orb-weavers add protective elements to their webs, such as rolled leaves or detritus cups in the centres of the webs of *Deliochus*, *Acusilas* (Fig. 2), *Phonognatha*, *Spilasma*, and others (Eberhard, 1986, 2008; Eberhard et al., 2008a; Kuntner et al., 2008a; McKeown, 1952) and silk stabilimentum ‘web decorations’ (see section 2.6.2 and Fig. 13). Some orb-weavers such as *Nephila* commonly add a ‘barrier web’ to at least one side of the web (Fig. 3), and this 3D structure may represent a protective shield against larger predators such as birds and mud-dauber wasps (Higgins, 1992). Many spiders are also cryptic or manipulate webs defensively by shaking the webs to confuse predators and shuttling rapidly from side to side of the web through the freezone (Edmunds and Edmunds, 1986; Kuntner et al., 2008a). Some spiders resemble plant material such as buds or bark, for example, *Poltya*, *Caerostris*, *Deinopsis*, and *Miagrammopes*. Finally, many species (e.g. many *Araneus*, *Zygiella*, and *Nephilengys*) spend their days hiding in a silken retreat at the web periphery, and only forage openly at night.

Predation pressure is proposed to have played a critical role in the transition from planar orb webs to the 3D webs of the derived orb web families Linyphiidae and Theridiidae (Blackledge et al., 2003b). Blackledge et al. demonstrate that, while linyphiids and theridiids are the most diverse and abundant ‘guilds’ of aerial web-building spiders worldwide, they comprise only a minor component of the prey taken by the spider-specialist mud-dauber wasps. Many theridiids and linyphiids rest at the centres of their 3D webs completely surrounded by silken threads that could act as effective barriers to major predators such as mud-dauber wasps (Fig. 16) and that are chemically ‘distasteful’ to at least some predatory wasps (Uma and Weiss, 2010). However, 3D webs may be ineffective against smaller parasitoids (e.g. Eberhard et al., 2008a), which may explain why many theridiids include additional predator deterring structures in their 3D webs or add peripheral retreats. The webs of social spiders seem to offer particularly

good protection against larger predators, with their extremely dense 'cloud' or basket webs containing both silken compartments and a myriad of leaves and detritus within which the spiders rest whenever they are not feeding or performing other colony tasks (e.g. [Agnarsson et al., 2006](#); [Aviles, 1997](#); [Bilde and Lubin, 2011](#)). Again, social spider webs seem less effective against smaller parasitic wasps. Regardless, predation pressure has clearly been an important factor in the evolutionary diversification of orb-weaving spiders and their relatives.

5.2 KLEPTOPARASITISM

Many organisms use spider webs as shelters and some spiders routinely use other individuals' webs for structural support when building their own webs. Parts of giant *Nephila* webs, for example, are routinely used as anchoring points for individual orb webs by *Leucauge*. However, other spiders are kleptoparasites that utilize host's orb webs for prey catching, and effectively pilfer or steal prey from the host. Kleptoparasites in spider orb webs include insects, such as mirid bugs ([Agnarsson, 2006](#); [Henry, 1999](#); [Nentwig, 1985](#)), as well as other spiders including some mysmenids and theridiids (reviewed by [Elgar, 1993](#); [Vollrath, 1984](#); [Whitehouse, 2011](#)). Certain theridiids, particularly the argyrodines *Argyrodes* and *Faiditus*, are obligate kleptoparasites and feed exclusively in host webs ([Agnarsson, 2002, 2003b](#); [Henaut and Machkour-M'Rabet, 2010](#); [Whitehouse et al., 2002](#)). These spiders pilfer tiny prey ignored by the host, but also steal larger prey, may feed simultaneously on the same prey item as the host, and sometimes even prey on the host's offspring ([Whitehouse, 2011](#)). Finally, the kleptoparasites may eat silk directly from webs ([Miyashita et al., 2004](#)). Several studies show that *Argyrodes* and *Faiditus* spiders reduce growth rate and induce web abandonment of their *Nephila* ([Grostal and Walter, 1997](#); [Rittschof and Ruggles, 2010](#); [Rypstra, 1981](#)) or *Metepeira* ([McCrate and Uetz, 2010](#)) hosts. Accordingly, *Nephila* sometimes shake webs and chase the kleptoparasites. For spiders such as *Argyrodes* and *Faiditus*, host orb webs are natural habitat patches that experience similar dynamics of immigration, emigration, extinction, and recruitment as more classical habitat patches ([Agnarsson, 2003b, 2011](#); [Elgar, 1994](#)).

6 Evolution of orb webs

6.1 THE CRIBELLATE/ECRIBELLATE TRANSITION

The single origin of the orb web implies a transition in capture spiral composition from cribellate silk to viscid gluey silk. How and when that transition took place is poorly understood. Throughout spider evolution cribellate silk has been lost repeatedly ([Miller et al., 2010](#); [Spagna and Gillespie, 2008](#)). However, there

are very few examples of cribellate silk being replaced by a functionally similar yet morphologically distinct silk, such as viscid capture spirals. Phylogenetic evidence leaves little doubt that the switch to viscid glue occurred once within orb web spiders, with cribellate silk primitively present in Deinopoidea and replaced with a new system composed of the araneoid spigot 'triad' (flagelliform and aggregate spigots) in the common ancestor of Araneoidea. However, it is not possible to deduce the sequence of events using available phylogenetic data. Did spiders first lose the cribellum and subsequently evolve viscid glue? Did viscid glue evolve first, thus rendering the cribellum 'obsolete'? Or did these events occur simultaneously? Although we may never be able to answer these questions, data bearing on them might be gathered from fossils, or even possibly, through developmental biology.

Recent investigations into the expression of spider silk genes and the material performance of capture threads provide new insights into these questions. There are two key differences in the function of cribellate versus viscid capture threads. First, the tensile mechanics of the two threads are quite different and second they produce adhesion through radically different mechanisms. The extensibility of both cribellate and viscid threads is significantly greater than most other silks. However, the cribellate threads depend upon their composite structure. First, a relatively stiff pseudoflagelliform axial fibre initially extends until it breaks after stretching approximately 50% of its original length (Blackledge and Hayashi, 2006b). However, the surrounding halo of cribellate fibrils maintains the integrity of the capture thread and allows it to continue to stretch up to 500%, in the case of *Deinopis spinosa*, as the capture thread continues to dissipate energy through the rupturing of individual cribellate fibrils (Köhler and Vollrath, 1995). For some species, the adhesive cribellate fibrils account for 70–90% of all the work of extension (Blackledge and Hayashi, 2006b). In contrast, the axial flagelliform silk determines tensile performance of viscid capture spiral. The flagelliform silk acts like a rubber, initially extending under loads that are orders of magnitude less than cribellate silk, before undergoing strain hardening as the fibroins align along the fibre axis until the thread fails at extensions that are significantly greater than cribellate silk (Denny, 1976; Opell and Bond, 2001). This elasticity is enabled in large part by the GPGGX motif that dominates flagelliform silk proteins (Becker et al., 2003). Interestingly, Garb et al. (2006) found that flagelliform silk genes were also expressed in cribellate spiders. However, because cribellate spiders' 'glue' is dry, such proteins would not be predicted to provide the same level of molecular mobility and they are not expressed to the same high level. Thus, a simple increase in the expression of the flagelliform silk gene, coupled with plasticization of the axial fibres by the addition of water (see below) could explain the evolutionary transition to modern orb web spiders' axial fibres.

The second key difference, transitioning from dry cribellate adhesive to the wet, viscid glue of araneoid spiders, is a much greater puzzle in part because the two adhesives are produced using very different glands in different body

locations. Cribellate silk depends upon the tremendous surface area of the tiny cribellar fibrils for sufficient van der Waals forces to generate adhesion and the force of adhesion varies linearly with surface area (Opell, 1994b). When wetted, these fibrils mat together, permanently inhibiting adhesion. In contrast, the stickiness of viscid silk rapidly declines when it dries out (Opell and Schwend, 2008). Simply put, an intermediate glue seems likely to be non-functional because it would either be too wet for the cribellate fibrils to function or too dry for viscid glue to adhere. However, the hydrophilic salts in the aqueous coating of glue droplets may do more than simply attract water to hydrate viscid silk. The salts may themselves act to directly increase the adhesion of the glycoproteins. While still speculative, this suggests that the transition from dry cribellate silk may have begun with the incorporation of salts that first facilitated adhesion and then quickly set up a situation where their hydrophilic properties selected for aqueous glue droplets and plasticization of axial fibres. Opell et al. (2011) combined cribellate and viscid capture threads to produce 'composite' glue droplets of liquid viscid glue encasing cribellate fibrils. These composite threads were stickier than either type of silk alone. Opell et al. hypothesize that viscid glue may have evolved initially in very young cribellate spiders, whose undeveloped cribellum could not produce adhesive capture threads, as a mechanism to provide adhesion for their webs until the fully functional cribellum developed in the next instar. Secondly, the hydrophilic glue would also provide these small spiderlings increased access to water from their webs.

Regardless of the mechanisms, the evolutionary transition from cribellate to viscid capture silk is associated with an explosive diversification of orb web spiders (Blackledge et al., 2009c; Bond and Opell, 1998). Araneoid orb web spiders produce capture threads that are stickier per unit of volume compared to cribellate orb web spiders and do so at significantly greater speed and material economy (Kawamoto and Japyassu, 2008; Opell, 1997b, 1998). Coupled with other advantages, such as thicker axial fibres, this equips araneoid orb web spiders to spin vertical orb webs that can intercept and stop significantly faster moving insect prey (Opell et al., 2006; Opell, 1997a, 1999).

6.2 EVOLUTION WITHIN THE ORB ARCHITECTURE

6.2.1 *Orb webs and spider body size*

Spider size has evolved rapidly and diversely throughout the evolutionary history of spiders, both in terms of absolute size and relative sexual size dimorphism (SSD; Head, 1995; Prenter et al., 1999). In general, there seems to be a trend towards increased spider body size, especially for females, across the phylogenetic tree. This trend has been demonstrated clearly in orb-weavers with multiple origins of female gigantism and female-biased SSD (Coddington et al., 1997; Hormiga et al., 2000). However, SSD is a complex phenomenon

that can arise through ecological or evolutionary changes in each gender. Thus, SSD may evolve through female gigantism (Coddington et al., 1997; Higgins, 2002; Kuntner and Coddington, 2009), male dwarfism (Moya-Laraño et al., 2002; Vollrath, 1998; Vollrath and Parker, 1992), or both. For orb web spiders, the most common explanation is likely fecundity-based female gigantism because clutch size, the most commonly used proxy for spider fecundity, generally strongly correlates with female body size both intra- and inter-specifically (Blackledge et al., 2009b; Head, 1995). However, sexual selection mechanisms may play an important role in male body size evolution at various hierarchical scales as well (Corcobado et al., 2010; Kuntner and Coddington, 2009; Moya-Laraño et al., 2002; Vollrath, 1998). Regardless, SSD and sexual selection may play a role in orb web biology through their mediation of spider size (Craig, 1987b).

Conversely, might the function of orb webs also play a role in spider size evolution? We believe the answer is yes. In general, orb web architecture determines the type of prey intercepted and retained that could be consumed by the spider (see Section 2). Thus, spider size evolution may occur under selection for how webs might fill ‘empty niches’. For example, tiny anapid and mysmenids build orb webs that capture insects ignored by larger orb-weavers, and theridiosomatids specialize on mosquitoes that are too small to be relevant to the diets of large spiders but also such specialized fliers that they are rarely captured by the webs of other, less-specialized spiders. Symphytognathids may primarily aim their small and incredibly dense webs at capturing small plant pollen. Similarly, the largest orb-weavers make webs powerful enough to retain the largest insects, which are simply not available to smaller spiders, and their webs can sometimes even subdue vertebrate prey (Cox and NeSmith, 2007; Graham, 1997; Ross, 1950; Timm and Losilla, 2007). Orb webs may place an upper limit on the maximum size achievable by orb web spiders due to increases in the costs of producing webs in larger spiders (Venner et al., 2003) and due to differences in how the kinetic energy of insect prey versus the stopping powers of orb webs scale with size (Blackledge et al., unpublished).

6.3 STEPPING STONES TO NEW WEB ARCHITECTURES

Early evolutionary spider biologists upheld the spider orb web as the ‘pinnacle’ in web evolution. Orb webs were depicted as highly organized and efficient traps with thrifty use of material maximizing the interception of prey and providing unique access to prey in the air column that were not available to other types of webs. Such thought mirrored the view that cribellate and ecribellate spiders independently converged on the ‘ideal’ orb web architecture (see Section 1.1). However, phylogenetic evidence undermined this view of orb webs, and rather depicts orb webs as stepping stones to other novel architectures, some highly specialized, that include some of the most diverse spider radiations—the sheet-web spinning Linyphiidae and the cobweb spinning Theridiidae.

6.3.1 Specialist webs: the minor radiations

Many small lineages of orb web spiders evolved a variety of highly derived odd 'orb' architectures, which are nevertheless homologous with the archetypical orb. Our survey of them is not exhaustive and does not follow a phylogenetic order of events, but rather begins with slightly modified architectures and continues to lineages whose webs have lost all resemblance to the orb architecture.

Some orb webs are vertically elongated, and referred to as 'ladder webs' because their side frames are often parallel and their capture 'spirals' resemble ladders rather than rounded spirals (Fig. 14). Kuntner et al. (2010b) proposed to

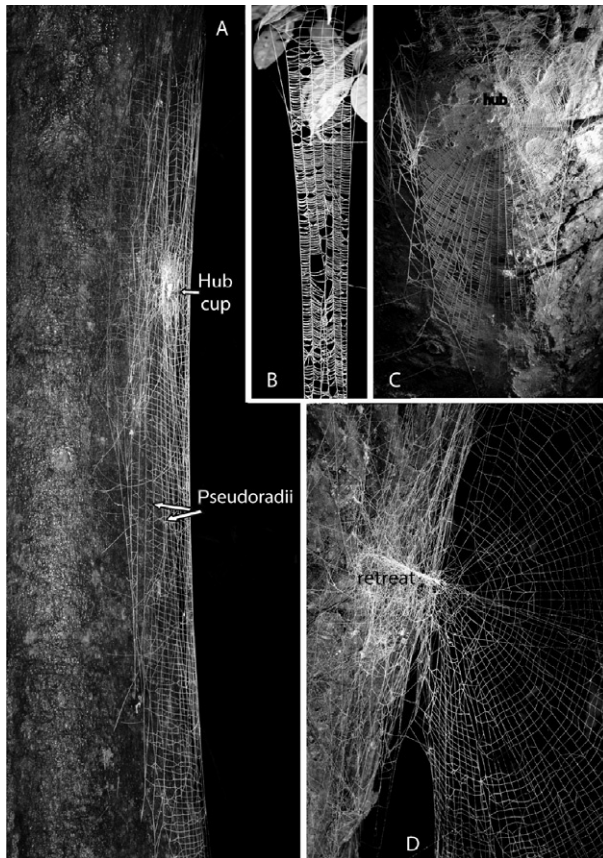


FIG. 14 Ladder webs in nephilid and araneid spiders. (A) Arboricolous ladder in *Herennia multipuncta* from Singapore, (C) *Clitaetra episinoides* from Mayotte, (D) *Nephilengys malabarensis* from Singapore, (B) and aerial ladder in *Scoloderus* sp. from French Guiana, only showing the upper web part extended above the orb.

apply this name to any webs that are more than twice as high as they are wide. Typical ladder webs have evolved independently in Araneidae, Nephilidae, and Tetragnathidae (Eberhard, 1975; Harmer, 2009; Kuntner et al., 2010b; Robinson and Lubin, 1979; Stowe, 1986). In Araneidae and Tetragnathidae, ladder webs are confined to sporadic genera such as the neotropical *Scoloderus* (Fig. 14B; see Eberhard, 1975), the Australian *Telaprocera* (Harmer, 2009; Harmer and Framenau, 2008), the New Zealand *Cryptaranea* (Forster and Forster, 1985), and the New Guinean *Tylorida* (Robinson and Robinson, 1972). While at least some of these lineages are clearly convergent, the lack of detailed phylogenetic hypotheses within these families precludes precise interpretation of their origins. On the other hand, recent morphological and behavioural phylogenies suggest that the ladder architecture is ancestral for Nephilidae as a moderately ladder-like orb web (as in extant *Clitaetra*, Fig. 14C) has been modified into a more extreme ladder web (as in *Herennia*, Fig. 14A), but then gradually reversed back to less extreme ladders (as in *Nephilengys*, Fig. 14D) and relatively symmetric orb web (as in *Nephila*) (Kuntner et al., 2010b). Because nephilid ladder webs all show developmental shifts from round juvenile orb webs to extreme elongation in adults, the specialized architecture is likely an adaptation to arboricolous lifestyles. By developing elongate webs, growing spiders do not need to find increasingly larger diameter trees on which to spin larger webs (Kuntner et al., 2008a, 2010b). Together, ontogenetic and phylogenetic patterns in nephilids may fit the biogenetic law, where ontogenetically derived traits mirror evolutionarily derived ones (e.g. Eberhard et al., 2008b). In other lineages, ladder webs likely function as specialized traps for specific prey. For instance, the most extreme ladder web, built by *Scoloderus*, is a moth capturing device (Eberhard, 1975; Stowe, 1978), and this is also likely the case for the poorly studied webs of *Tylorida* (Robinson and Robinson, 1972). Finally, the Australian *Telaprocera* spider's behaviour is quite plastic. Harmer and Herberstein (2009) convincingly showed that the web is not specialized for a certain prey type; rather, the spiders may adapt its architecture to fit the given web space. When the spiders were given limited horizontal space, they constructed a ladder, and when given ample space, their web was less elongated (Harmer and Herberstein, 2009).

The web of Synotaxidae, described by Eberhard (1977) as a 'rectangular orb', fundamentally differs from orb webs in being built as series of approximately rectangular modules, rather than a single unit organized around a central hub (Agnarsson, 2003a; Eberhard, 1977, 1995). The interplay between the height of each module, and the number of modules built in sequence determines the ultimate shape of a *Synotaxus* web. The arrangement of dry and sticky silk in *Synotaxus* webs is also unique. Each module includes vertical frame threads on both sides, between which are suspended a series of horizontal non-sticky lines. The sticky lines are then laid vertically between the horizontal non-sticky lines, typically in sets of three (Agnarsson, 2003a; Eberhard, 1977).

The 'asterisk' webs spun by *Wixia ectypa* present a different kind of specialization as they lack capture spiral and are instead composed solely of radially arranged dragline threads (Levi, 1993; Stowe, 1986). The spider actively preys on insects that come in contact with the web close to the attachment of the radii at hub (Stowe, 1978).

In contrast, 'sector' webs reduce the total size of the capture area such that they consist of only portions of an orb. The uloborid genus *Hyptiotes* constructs such a cribellate sector that resembles a triangle, consisting of four radii converging on a single mooring line. Cribellate sticky silk is suspended between the radii and spider uses the mooring line to hold the web under tension at one end. The spider releases the taut web when prey contact it, helping to entangle the insects (Lubin, 1986; Opell, 1982). This tension also provides an escape mechanism for *Hyptiotes*, allowing it to catapult away from attacking predators. Another uloborid, *Miagrammopes* exhibits even more extreme reduction, producing only a single vertical capture thread that it holds in its legs (Lubin et al., 1978). Within cribellate spiders, web reduction is accompanied by a dramatic increase in the adhesive force generated by individual capture threads (Opell, 1994b,c). This increased stickiness helps to compensate for the reduced capture areas of the webs (Opell, 1996).

A similar pattern of web reduction occurs within the ecribellate family Araneidae where a variety of partially to strongly reduced webs are spun within the Cyrtarachninae (Stowe, 1986). Some representatives such as *Cyrtarachne* spin more or less complete orb webs while others such as *Poecilopachys* exaggerates one side of the web such that capture spiral is completely lacking elsewhere. *Pasilobus* spins a web that consists of only two sectors of the orb. All of these webs are unusual for Araneidae in their horizontal orientation and their very slack capture threads, each of which is produced as a discrete unit between radii and are termed 'spanning threads', rather than a continuous spiral (Robinson and Robinson, 1975). The glue droplets are also atypically large and sticky. These features appear to facilitate predation on moths, which normally slip free from most orb webs (Eisner et al., 1964). The related bolas spiders (*Mastophora* and relatives) produce even more reduced webs, typically single threads, tipped by large glue droplets, which are held in the legs of the spiders and twirled or tossed at passing moths (Eberhard, 1980). One genus, *Celaenia* even captures moths by grabbing the insects out of the air with its forelegs. While *Cyrtarachne* is a generalist predator with a web proficient at retaining moths (Cartan and Miyashita, 2000), the more extremely reduced web builders rely upon aggressive chemical mimicry of female moth pheromones to attract male moths of specific species (Gemeno et al., 2000; Haynes et al., 2002; Stowe et al., 1987; Yeargan, 1994). The similarities among these varyingly reduced webs suggest a possible sequence for a gradual reduction of the orb web coupled with increased specialization on moths (Robinson and Robinson, 1975). However, a strong phylogenetic test is currently lacking and at least one genus, *Kaira*, also hunts moths without a capture web (Stowe, 1986), but

appears morphologically distant from the Cyrtarachninae (Piel and Nutt, 1997; Scharff and Coddington, 1997). Regardless, these reduced webs present an opportunity to investigate how silk evolves during web reduction, as the silk of *Cyrtarachne* appears significantly stronger and stickier than the silk of other araneids (Cartan and Miyashita, 2000) and the axial fibre has an unusual morphology within the glue droplet of *Mastophora* (Eberhard, 1980).

Several other araneoid genera also no longer produce prey capture webs and instead function as cursorial hunters. The Asian *Chorizopes* invades other spiders' webs while the Australian *Arkys* sits on vegetation and attacks prey with its spiny legs, a behaviour that resembles crab spiders (Stowe, 1986). Tetragnathidae shows several spectacular instances of web reduction within the Hawaiian archipelago that appear to be caused by niche expansion (Gillespie, 1991, 2004; Gillespie et al., 1994). Finally, the family Mimetidae, which has recently been shown to belong to Orbiculariae as possible relatives of Tetragnathidae (Blackledge et al., 2009c; Schütt, 2000), similarly abandoned web building and are now specialized predators on other spiders (Jackson and Whitehouse, 1986).

The webs produced by deinopid spiders bear so little resemblance to the classic orb that they were not even considered homologous until detailed investigation by Coddington (1986a,c). These cribellate spiders spin a small net that is held in the front pairs of legs (Fig. 15C), then stretched out to several times its size when the spider casts the web over prey (Coddington, 1986a,c; Coddington and Sobrevila, 1987; Getty and Coyle, 1996). This behavioural strategy may help to explain why the capture silk of *Deinopis* is so much more extensible than other cribellate orb web spiders (Blackledge and Hayashi, 2006b).

Theridiosomatid spiders show a variety of modifications in orb architectures. The standard architecture in this family, exemplified by *Theridiosoma*, *Naatlo*, and *Epeirotypus*, is a small loose orb web that contains all familiar elements such as radii and spirals, but is pulled out of the vertical plain with the spider holding it in position with a tension line (Fig. 15A; Coddington, 1986b). Other genera show different levels of web reduction. *Epilineutes* sometimes and *Baalzebub* always lack the tension line, *Ogulnius* constructs further reduced webs with little resemblance to orb webs, and *Chthonos* apparently abandoned web building altogether (Coddington, 1986b). Finally, *Wendilgarda* is an extreme specialist building relatively simple webs in an unusual habitat—attached to the surface of water at the edges of rivers and lakes (Fig. 15B; Coddington, 1986b; Coddington and Valerio, 1980; Eberhard, 1989, 2000a, 2001a). Most *Wendilgarda* construct a few approximately horizontal suspension lines, attached to twigs or rocks, from which they drape up to 20 vertical sticky lines that are attached at their lower ends to the water surface. The sticky lines trap insects on the surface of the water, such as water striders. At least one species builds an even simpler web, often with only a single vertical line, which it may actively drag back and forth over the water surface, in effect 'trolling for

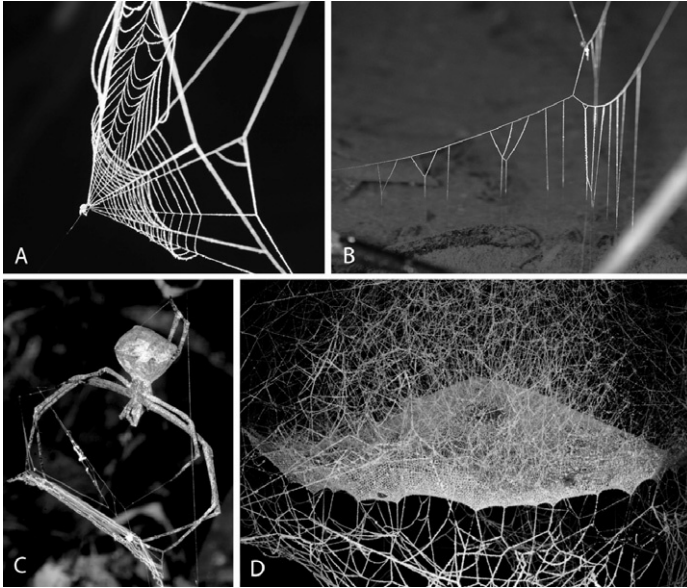


FIG. 15 Specialized orb web architectures. (A–B) two members of the Theridiosomatidae with dramatically differing web architectures, (A) *Theridiosoma* sp. from French Guiana and (B) *Wendilgarda* sp. from Costa Rica with attachment points on water; (C) A specialized deinopid casting web held in front legs by *Menneus capensis* from South Africa; (D) A highly three-dimensional tent web of *Mecynogea* sp. from French Guiana.

water striders' (Eberhard, 2001a). *Wendilgarda* are extremely variable in both the behaviours that they use to build the webs and the final architectures of those webs, both within and between species (Eberhard, 2000a, 2001a). For example, the number and arrangement of both the suspension lines and the vertical sticky lines are highly variable, and some species including *W. galapagensis* sometimes build webs with threads attached to water surface, but may also build webs in forests far from water (Shinkai and Shinkai, 1997). These observations support the hypothesis that behavioural imprecision in web spinning has helped to drive diversification of web architectures within Orbiculariae (Eberhard, 2000a, 2007a).

An extreme modification of the archetypal orb are the 3D 'tent webs' of *Cyrtophora* and *Mecynogea* (Fig. 15D). These large webs lack capture spirals, but instead possess an extensive and finely meshed non-sticky spiral on a horizontal plane (Lubin, 1973). Flying or jumping prey is intercepted by an exaggerated mesh of trip lines extending above and below the 'orb', and the spider may hide in a leaf retreat or simply hangs from the tent. Such web architecture may entangle large prey and perhaps as a consequence, the genus *Cyrtophora* is known for species with extremely heavy bodied females (Levi, 1997).

We have summarized only some of the best known instances of highly specialized or reduced versions of the orb web here. With the current understanding of spider phylogeny, evolutionary interpretations are still preliminary, but most of the cases outlined above were likely derived independently. These diverse examples therefore illustrate just how labile web spinning behaviours can be over evolutionary time and suggest significant costs associated with the production of classic orb webs (Blackledge *et al.*, 2009c).

6.3.2 *Adaptive radiation through novel architecture: Cobwebs and sheet webs*

As seen in Section 6.3.1, orb web spiders (Orbiculariae) in fact construct a wide variety of web types, including many highly specialized forms that seem to have little in common with the ancestral orb. But alternative web forms are not restricted to ‘minor radiations’ of tens or dozens of species. Some of the largest groups of orbicularians do not build orb webs, but instead novel web architectures that are secondarily derived from the orb (e.g. Blackledge *et al.*, 2009c; Griswold *et al.*, 1998). Most notable among these are the linyphiid sheet-web weavers and the theridiid cobweb spiders, which together comprise well over half of the diversity within the Orbiculariae (Blackledge *et al.*, 2009c; Bond and Opell, 1998). Web architecture, and especially web-building behaviours, are rather poorly studied in linyphiids (Benjamin *et al.*, 2002), despite the abundance of linyphiids in most ecosystems. A few studies provide illustrations of linyphiid webs (e.g. Arnedo *et al.*, 2009; Eberhard *et al.*, 2008a; Nielsen, 1932) and a single study has revealed some of the web-building behaviours (Benjamin and Zschokke, 2004). In sum, most linyphiids spin ‘sheet webs’ that may have relatively few substrate-attachment threads with a clearly suspended aerial sheet or webs that are more or less laid upon the substrate and may not resemble a planar sheet (Arnedo *et al.*, 2009; Fig. 16). In general, linyphiid webs are spun in a much less stereotypical manner than classical orb webs (Benjamin and Zschokke, 2004), though detailed comparative studies are yet lacking. Pimoid webs are similar in appearance but almost completely unstudied (Hormiga, 1994).

The cobwebs of theridiids are better studied architecturally (Agnarsson, 2004; Benjamin and Zschokke, 2002, 2004; Eberhard *et al.*, 2008b; Jorger and Eberhard, 2006; Madrigal-Brenes and Barrantes, 2009; Nielsen, 1932; Zevenbergen *et al.*, 2008), for review see (Eberhard *et al.*, 2008a). However, understanding of their building behaviours is still rudimentary and limited to only a couple of studies (e.g. Benjamin and Zschokke, 2002, 2003; Madrigal-Brenes and Barrantes, 2009). Theridiid web architecture is highly variable, both within and among species (Eberhard *et al.*, 2008a). ‘Cobweb’ refers to irregular 3D webs such as those made by the common house spider (*Parasteatoda tepidoriarum*) and commonly found in corners of buildings. However, ‘cobweb’ is an imprecise category that refers to a variety of

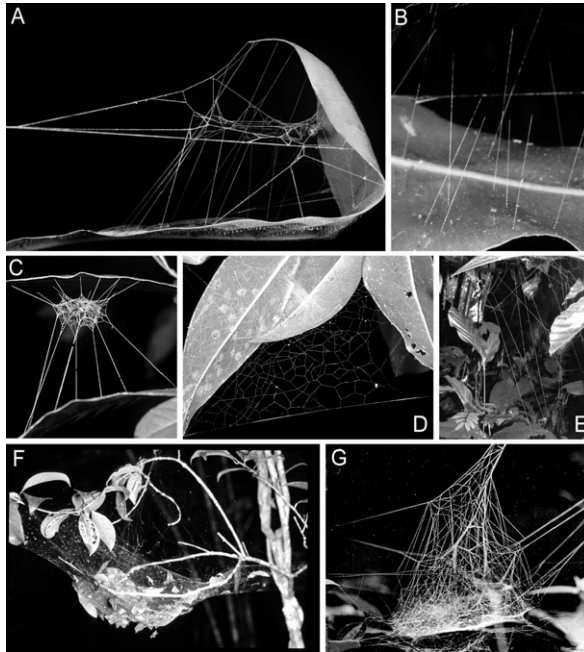


FIG. 16 Theridiid cobwebs and linyphiid sheetwebs. (A–B) the cobweb of *Parasteatoda (Achaearanea) valoka* from New Britain. The web is unique in how a leaf is bent over and used as the substrate for the entire web, yet it illustrates common themes of typical cobwebs—a central to peripheral irregular sheet forming a retreat for the spider with sticky gumfooted threads radiating from it and attached to the substrate (A), with sticky globules restricted to the lower part of the gumfoot lines (B). (C) a ‘star web’ (*Achaearanea* sp. juvenile) as built by many *Achaearanea/Parasteatoda* species, with a semi-global central retreat, and radiating gumfoot lines. The spider rests in the centre of the ‘globe’ and seems well protected from larger predators. (D) *Theridion* sp. that spins a simple two-dimensional sheet with sticky globules distributed throughout the sheet. The spider has a silk retreat under the leaf. (E) *Helvibis* cf. *thorelli*, with long gumfoot lines radiating from a silk retreat under a leaf. (F) subsocial web of *Anelosimus may*, a ‘basket’ shaped sheet web with knockdown lines above the sheet. No sticky silk seems to be employed. The spiders rest under leaves in the basket area and seem well protected from larger predators. (G) sheet web of *Dubiaranea* sp. (Linyphiidae) (photograph courtesy of W. Eberhard).

architecturally different 3D webs. Perhaps the best known feature of many cobwebs is the gumfoot (Fig. 16), which consists of a major ampullate dragline thread with viscid glue droplets along its length where it attaches to the substrate (Blackledge et al., 2005b; Boutry and Blackledge, 2009; Hu et al., 2007). At least some nesticids and many theridiids place gumfoots, radiating from their mesh retreats, web centres, or periphery. These threads are attached to the substrate and in at least some species are under high tension. When pedestrian prey walks into these threads they release from the substrate and the prey is

pulled up where it dangles helplessly until the spider arrives to deliver a bite (Argentinean *et al.*, 2006; Boutry and Blackledge, 2008). However, the function of gumfoots has been studied in only a few species (e.g. Zevenbergen *et al.*, 2008). Many theridiids do not place their glue on gumfoot threads, but instead may place it throughout the web, on a sheet, on a single thread, or may not use glue at all (Eberhard *et al.*, 2008a). Theridiid web architecture includes webs with distinct linyphiid-like sheet webs, sometimes ‘basket’ shaped, simple sheets, irregular tangles, ‘star webs’ with a retreat in the centre with gumfoot lines radiating from it, H-shaped webs, single lines, and a variety of other architectures (Fig. 16; Eberhard *et al.*, 2008a). Theridiid web-building behaviour has been characterized as less stereotypical than seen in typical orb web spiders (Benjamin and Zschokke, 2002, 2003). Again, this supports the hypothesis that the behavioural precision needed to construct symmetric orb confines the evolution of web architecture and that loss of this precision might be an initial step in the evolution of new web forms (Eberhard, 2000a).

The hypothesis of the monophyletic origin of the orb web implies that sheet webs and cobwebs evolved from an orb ancestor (Blackledge *et al.*, 2009c; Coddington, 1986a). The main evidence for this transition is phylogenetic, as both linyphiids and theridiids nest within Orbiculariae (e.g. Blackledge *et al.*, 2009c; Griswold *et al.*, 1998). However, both theridiids and linyphiids use some behavioural patterns in web construction that appear homologous to those seen in true orb-weavers, particularly the cutting and reeling of threads. Furthermore, recent behavioural studies on *Latrodectus* reveal vestiges of orb webs in the web of young instars, consistent with the ‘biogenetic law’ where ontogeny repeats phylogeny (Eberhard *et al.*, 2008b). Such continued investigations should ultimately reveal the shifts in web spinning behaviours that are keys for releasing spiders from the stereotyped orb architecture thereby facilitating the evolution of novel types of webs.

The number of extant species in a given group provides evidence for the rate of diversification and is therefore often used as a measure of evolutionary ‘success’. Strictly speaking, comparing any two clades is a rather arbitrary exercise unless they are of similar age and, ideally, sister groups. Nevertheless, two of the most ‘successful’ lineages, or web types, within Orbiculariae are linyphiids (sheet webs) with 4378 extant species, and theridiids (cobwebs) with 2310 extant species (Blackledge *et al.*, 2009c; Coddington and Levi, 1991; Platnick, 2011). Hence the evolutionary transition from orb webs to these novel 3D web types has apparently led to increased diversification rates. This suggests that these novel web types may somehow be more ‘efficient’ than the classical orb web. One suggestion is that these webs facilitate escape from predation (Blackledge *et al.*, 2003b; see Section 5.1). A second possible explanation for the diversity of theridiids lies in the immense variety of webs they spin, which may facilitate exploitation of a variety of new habitats and types of prey. Eberhard *et al.* (2008a) suggest that loss of stereotypical web-building behaviours and behavioural imprecision has facilitated the diversification of

spider web architectures, and in turn, also speciation of theridiids, termed the 'behavioural imprecision' hypothesis (see also [Agnarsson, 2004](#); [Eberhard, 1990b, 2000a](#)).

Finally, the 'hyper-diverse' theridiids and especially linyphiids are typically much smaller-bodied than araneid and nephilid orb-weaving spiders ([Blackledge et al., 2009b](#); [Head, 1995](#)). We speculate that, while the orb web architecture may facilitate the capture of large flying insect prey that facilitate growth of large body sizes, the resulting increased fecundity ([Blackledge et al., 2009b](#)) is not necessarily advantageous for lineage diversification. The smaller body sizes and likely accompanying shorter generation times of sheet-and cobweb spiders may increase their evolvability, and consequently their diversity in most ecosystems.

7 New horizons

Spider webs have fascinated scientists and laymen for centuries and are the subjects of a myriad of scientific studies. With the relatively recent discoveries of the amazing biomechanical properties of spider silk, studies of spider webs and silk will continue to expand in the foreseeable future. Here, we outline a few promising horizons.

7.1 WHOLE WEB FUNCTION AND BIOMECHANICS

Recent advances have been made in integrating information from ecological studies of web function and the biomechanical properties of the silks comprising those webs ([Harmer et al., 2010](#)). However, most studies of silk biomechanics still primarily characterize single threads in isolation from webs and the complex interactions of the myriad of threads comprising any given web are poorly understood (e.g. [Argintean et al., 2006](#)). Evolutionary shifts in both web architecture and silk biomechanics have 'improved' the function of orb webs through evolutionary time ([Opell, 1999](#); [Sensenig et al., 2010](#)). The cribellate/ecribellate transition has been investigated most intensively and the focus is now shifting to understanding patterns within the Araneoidea ([Craig, 1987a](#); [Sensenig et al., 2010](#)). We can only dream of the insights to be gained from extending this approach to the derived web architectures nested with orb web spiders (see [Section 6.3](#)).

The growing availability of apical clades for which species level phylogenies exist provides a second promising venue. For instance, Hawaiian *Tetragnatha* show a strong pattern of convergence in web architectures among unrelated species on different islands ([Blackledge and Gillespie, 2004](#)). Might such convergence be accompanied, or even facilitated, by similar shifts in silk biomechanics? Nephilids exhibit even greater ecological diversification of webs within a single, well-characterized evolutionary lineage. Roughly 40

species are grouped into four genera with highly predictable web architectures and life histories that span from small arboricolous ladder webs to gigantic aerial orb webs (Kuntner and Agnarsson, 2009; Kuntner et al., 2008a). Evolution of nephilid web architecture is coupled with a monotonic increase of female size towards true gigantism (Kuntner and Coddington, 2009). Does that shift go hand in hand with the evolution of silk properties, as might be the case among araneoids in general (Sensenig et al., 2010)? Other fascinating clades wait within the Araneidae, where several cases of dramatic web reductions may have been accompanied by the evolution of superior silks (Cartan and Miyashita, 2000) and unique glues within the bolas spiders (Eberhard, 1980). Unfortunately, lack of species level phylogenies within araneids, a hugely species diverse group, currently precludes such endeavours. Regardless, integrating whole-web function with silk biomechanics is challenging, but promises a more complete understanding of how webs have facilitated evolutionary diversification of spiders.

7.2 CAN WEBS DRIVE SPECIATION?

Mating in many orb web spiders depends intimately on webs because males often court females directly on webs (Barth, 1997; Foelix, 2011; Scheffer et al., 1996). Males sometimes modify webs by cutting or adding threads and certain courtship behaviours directly involve silk (Robinson, 1982; Robinson and Robinson, 1980). For instance, males bind their mates with silk in *Nephila pilipes* (Kuntner et al., 2009), *Herennia papuana* (Robinson and Robinson, 1980) and *C. darwini* (Gregorič, personal observation). Mate binding silks are poorly understood, but may provide chemical or physical stimulation to females.

Much of the inter-specific variation in web architecture and silk biomechanics among orb web spiders is likely due to natural selection on how webs function in prey capture (see Section 2). For instance, orb web-weaving *Tetragnatha* in Hawaii show strong patterns of divergence in web architectures among sympatric species (Blackledge et al., 2003a), but convergence among unrelated species on different islands (Blackledge and Gillespie, 2004). The recent emphasis on how similar pressures from divergent natural selection can lead to ecological speciation (Dieckmann and Doebeli, 1999; Rundle and Nosil, 2005; Schluter, 1998, 2001; Via, 2001) suggests the hypothesis that at least some speciation in spiders might be mediated in part by orb webs themselves, as the ways in which orb web architectures and silks adapt to prey capture also change the 'arena' in which males and females court.

7.3 MOLECULAR ECOLOGY OF SILK PRODUCTION

Perhaps the most exciting frontier for spider web biology is the potential to integrate new understanding of the genetic and physiological control of silk production with web function. This is already beginning to occur at a

macroevolutionary level for hypotheses about the origin of novel silk proteins (Ayoub and Hayashi, 2008; Craig, 2003; Garb et al., 2006). However, the complexity of factors determining the phenotypes of silk threads often makes it difficult to link changes in the material properties of silks to specific physiological mechanisms. Moreover, what happens at the individual level? For instance, how do plasticity in silk production and web architecture (see Section 4) interact in determining web function and ultimately spider fitness?

7.4 BIOMIMICRY

Most research on spider silk is motivated not by understanding biology, but rather by the biomimetic potential for development of the 'next generation' of fibres for use by the military, industry, and medicine (Altman et al., 2003; Hinman et al., 2000). The unfortunate disjunction between silk researchers in the lab and arachnologists studying webs in the field hampers both endeavours (Harmer et al., 2010). Silk genes are enormously diverse and complex (Garb et al., 2010; Gatesy et al., 2001), as is the physical spinning of the liquid feedstock into solid fibres (Vollrath and Knight, 2001; Vollrath et al., 2001). Comparative biology provides a vital tool to sift through that complexity and ultimately identify which details of silk production are essential and, therefore the desired focus of biomimetics, and which are labile and perhaps the result of natural selection and adaptation to particular specializations (e.g. Garb et al., 2010; Gatesy et al., 2001). Unfortunately, both silk genes and silk spinning are currently largely investigated in only a tiny number of ecologically and phylogenetically similar species. A biology-driven approach also promises to yield new discoveries such as the incredible dragline silk produced by Darwin's bark spider, *C. darwini*, which ranks as the toughest biomaterial known (Agnarsson et al., 2010). This example is particularly noteworthy as the discovery of the silk was itself driven by the unusual natural history of the spider (Kuntner and Agnarsson, 2010). The prospects are not limited simply to development of new fibres, but also include learning how to build robust, but light-weight structures that mimic webs (Alam et al., 2007), new types of adhesives (Sahni et al., 2011), and even novel sensory structures (e.g. Barth, 2002; Casas and Dangles, 2010).

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References

- Agnarsson, I. (2002). Sharing a web—on the relation of sociality and kleptoparasitism in theridiid spiders (Theridiidae, Araneae). *J. Arachnol.* **30**, 181–188.
- Agnarsson, I. (2003a). The phylogenetic placement and circumscription of the genus *Synotaxus* (Araneae: Synotaxidae), a new species from Guyana, and notes on theridioid phylogeny. *Invertebr. Syst.* **17**, 719–734.
- Agnarsson, I. (2003b). Spider webs as habitat patches—the distribution of kleptoparasites (*Argyrodes*, Theridiidae) among host webs (*Nephila*, Tetragnathidae). *J. Arachnol.* **31**, 344–349.
- Agnarsson, I. (2004). Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zool. J. Linn. Soc.* **141**, 447–626.
- Agnarsson, I. (2006). A revision of the New World *eximius* lineage of *Anelosimus* (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars. *Zool. J. Linn. Soc.* **146**, 453–593.
- Agnarsson, I. (2011). Habitat patch size and isolation as predictors of occupancy and number of argyrodine spider kleptoparasites in *Nephila* webs. *Naturwissenschaften* **98**, 163–167.
- Agnarsson, I. and Blackledge, T. A. (2009). Can a spider web be too sticky? Tensile mechanics constrains the evolution of capture spiral stickiness in orb weaving spiders. *J. Zool. (London)* **278**, 134–140.
- Agnarsson, I., Avilés, L., Coddington, J. A. and Maddison, W. P. (2006). Sociality in theridiid spiders: repeated origins of an evolutionary dead end. *Evolution* **60**, 2342–2351.
- Agnarsson, I., Kuntner, M. and Blackledge, T. A. (2010). Bioprospecting finds the toughest biological material: extraordinary silk from a giant riverine orb spider. *PLoS One* e11234, doi:10.1371/journal.pone.0011234.
- Alam, M. S. and Jenkins, C. H. (2005). Damage tolerance in naturally compliant structures. *Int. J. Damage Mech.* **14**, 365–384.
- Alam, M. S., Wahab, M. A. and Jenkins, C. H. (2007). Mechanics in naturally compliant structures. *Mech. Mater.* **39**, 145–160.
- Altman, G. H., Diaz, F., Jakuba, C., Calabro, T., Horan, R. L., Chen, J. S., Lu, H., Richmond, J. and Kaplan, D. L. (2003). Silk-based biomaterials. *Biomaterials* **24**, 401–416.
- Álvarez-Padilla, F., Dimitrov, D., Giribet, G. and Hormiga, G. (2009). Phylogenetic relationships of the spider family Tetragnathidae (Araneae, Araneoidea) based on morphological and DNA sequence data. *Cladistics* **25**, 109–146.
- Anderson, J. F. (1970). Metabolic rates of spiders. *Comp. Biochem. Physiol.* **33**, 51–72.
- Anderson, J. F. (1974). Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). *Ecology* **55**, 576–585.
- ap Rhisiart, A. and Vollrath, F. (1994). Design features of the orb web of the spider, *Araneus diadematus*. *Behav. Ecol.* **5**, 280–287.
- Argintean, S., Chen, J., Kim, M. and Moore, A. M. F. (2006). Resilient silk captures prey in black widow cobwebs. *Appl. Phys. Mater. Sci. Process.* **82**, 235–241.
- Arnedo, M. A., Coddington, J., Agnarsson, I. and Gillespie, R. G. (2004). From a comb to a tree: phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes. *Mol. Phylogenet. Evol.* **31**, 225–245.
- Arnedo, M. A., Hormiga, G. and Scharff, N. (2009). Higher-level phylogenetics of linyphiid spiders (Araneae, Linyphiidae) based on morphological and molecular evidence. *Cladistics* **25**, 231–262.

- Askarieh, G., Hedhammar, M., Nordling, K., Saenz, A., Casals, C., Rising, A., Johansson, J. and Knight, S. D. (2010). Self-assembly of spider silk proteins is controlled by a pH-sensitive relay. *Nature* **465**, 236–238.
- Augsten, K., Muhlig, P. and Herrmann, C. (2000). Glycoproteins and skin-core structure in *Nephila clavipes* spider silk observed by light and electron microscopy. *Scanning* **22**, 12–15.
- Aviles, L. (1997). Causes and consequences of cooperation and permanent-sociality in spiders. In: *The Evolution of Social Insects and Arachnids* (eds Choe, J. C. and Crespi, B. J.), pp. 476–498. Cambridge University Press, Cambridge.
- Ayoub, N. A. and Hayashi, C. Y. (2008). Multiple recombining loci encode MaSp1, the primary constituent of dragline silk, in widow spiders (*Latrodectus*: Theridiidae). *Mol. Biol. Evol.* **25**, 277–286.
- Ayoub, N. A., Garb, J. E., Tinghitella, R. M., Collin, M. A. and Hayashi, C. Y. (2007). Blueprint for a high-performance biomaterial: full-length spider dragline silk genes. *PLoS One* **2**, e514, doi:10.1371/journal.pone.0000514.
- Baba, Y. (2003). Testing for the effect of detritus stabilimenta on foraging success in *Cyclosa octotuberculata* (Araneae: Araneidae). *Acta Arachnol.* **52**, 1–3.
- Baba, Y. and Miyashita, T. (2006). Does individual internal state affect the presence of a barrier web in *Argiope bruennichi* (Araneae: Araneidae)? *J. Ethol.* **24**, 75–78.
- Barghout, J. Y. J., Thiel, B. L. and Viney, C. (1999). Spider (*Araneus diadematus*) cocoon silk: a case of non-periodic lattice crystals with a twist? *Int. J. Biol. Macromol.* **24**, 211–217.
- Barth, F. G. (1997). Vibratory communication in spiders: adaptation and compromise at many levels. In: *EXS (Basel); Orientation and Communication in Arthropods* (ed Lehrer, M. E.), pp. 247–272. Birkhaeuser Verlag, New York.
- Barth, F. G. (2002). *A Spider's World: Sense and Behavior*. Springer-Verlag, Berlin.
- Becker, N., Oroudjev, E., Mutz, S., Cleveland, J. P., Hansma, P. K., Hayashi, C. Y., Makarov, D. E. and Hansma, H. G. (2003). Molecular nanosprings in spider capture-silk threads. *Nat. Mater.* **2**, 278–283.
- Bell, F. I., McEwen, I. J. and Viney, C. (2002). Fibre science—supercontraction stress in wet spider dragline. *Nature* **416**, 37.
- Bell, J. R., Bohan, D. A., Shaw, E. M. and Weyman, G. S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bull. Entomol. Res.* **95**, 69–114.
- Benjamin, S. P. and Zschokke, S. (2002). Untangling the tangle-web: web construction behavior of the comb-footed spider *Steatoda triangulosa* and comments on phylogenetic implications (Araneae: Theridiidae). *J. Insect Behav.* **15**, 791–809.
- Benjamin, S. P. and Zschokke, S. (2003). Webs of theridiid spiders: construction, structure and evolution. *Biol. J. Linnean Soc.* **78**, 293–305.
- Benjamin, S. P. and Zschokke, S. (2004). Homology, behaviour and spider webs: web construction behaviour of *Linyphia hortensis* and *L. triangularis* (Araneae: Linyphiidae) and its evolutionary significance. *J. Evol. Biol.* **17**, 120–130.
- Benjamin, S. P., Duggelin, M. and Zschokke, S. (2002). Fine structure of sheet-webs of *Linyphia triangularis* (Clerck) and *Microlinyphia pusilla* (Sundevall), with remarks on the presence of viscid silk. *Acta Zool.* **83**, 49–59.
- Bilde, T. and Lubin, Y. (2011). Group living in spiders: cooperative breeding and coloniality. In: *Spider Behaviour: Flexibility and Versatility* (ed Herberstein, M. E.), pp. 276–307. Cambridge University Press, New York.
- Bittencourt, D., Dittmar, K., Lewis, R. V. and Rech, E. L. (2010). A MaSp2-like gene found in the Amazon mygalomorph spider *Avicularia juruensis*. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **155**, 419–426.

- Blackledge, T. A. (1998a). Signal conflict in spider webs driven by predators and prey. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 1991–1996.
- Blackledge, T. A. (1998b). Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). *J. Zool.* **246**, 21–27.
- Blackledge, T. A. (2011). Prey capture in orb weaving spiders: Are we using the best metric? *J. Arachnol.* **39**, 205–210.
- Blackledge, T. A. and Eliason, C. M. (2007). Functionally independent components of prey capture are architecturally constrained in spider orb webs. *Biol. Lett.* **3**, 456–458.
- Blackledge, T. A. and Gillespie, R. G. (2002). Estimation of capture areas of spider webs in relation to web asymmetry. *J. Arachnol.* **30**, 70–77.
- Blackledge, T. A. and Gillespie, R. G. (2004). Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. *Proc. Natl. Acad. Sci. USA* **101**, 16228–16233.
- Blackledge, T. A. and Hayashi, C. Y. (2006a). Silken toolkits: biomechanics of silk fibers spun by the orb web spider *Argiope argentata*. *J. Exp. Biol.* **209**, 2452–2461.
- Blackledge, T. A. and Hayashi, C. Y. (2006b). Unraveling the mechanical properties of composite silk threads spun by cribellate orb-weaving spiders. *J. Exp. Biol.* **209**, 3131–3140.
- Blackledge, T. A. and Wenzel, J. W. (1999). Do stabilimenta in orb webs attract prey or defend spiders? *Behav. Ecol.* **10**, 372–376.
- Blackledge, T. A. and Wenzel, J. W. (2000). The evolution of cryptic spider silk: a behavioral test. *Behav. Ecol.* **11**, 142–145.
- Blackledge, T. A. and Wenzel, J. W. (2001). Silk mediated defense by an orb web spider against predatory mud-dauber wasps. *Behaviour* **138**, 155–171.
- Blackledge, T. A. and Zevenbergen, J. M. (2006). Mesh width influences prey retention in spider orb webs. *Ethology* **112**, 1194–1201.
- Blackledge, T. A. and Zevenbergen, J. M. (2007). Condition dependent spider web architecture in the western black widow *Latrodectus hesperus*. *Anim. Behav.* **73**, 855–864.
- Blackledge, T. A., Binford, G. J. and Gillespie, R. G. (2003a). Resource use within a community of Hawaiian spiders (Araneae: Tetragnathidae). *Ann. Zool. Fenn.* **40**, 293–303.
- Blackledge, T. A., Coddington, J. A. and Gillespie, R. G. (2003b). Are three-dimensional spider webs defensive adaptations? *Ecol. Lett.* **6**, 13–18.
- Blackledge, T. A., Cardullo, R. A. and Hayashi, C. Y. (2005a). Polarized light microscopy, variability in spider silk diameters, and the mechanical characterization of spider silk. *Invertebr. Biol.* **124**, 165–173.
- Blackledge, T. A., Summers, A. P. and Hayashi, C. Y. (2005b). Gumfooted lines in black widow cobwebs and the mechanical properties of spider capture silk. *Zoology* **108**, 41–46.
- Blackledge, T. A., Boutry, C., Wong, S. C., Baji, A., Dhinojwala, A., Sahni, V. and Agnarsson, I. (2009a). How super is supercontraction? Persistent versus cyclic response to humidity in spider dragline silk. *J. Exp. Biol.* **212**, 1981–1989.
- Blackledge, T. A., Coddington, J. A. and Agnarsson, I. (2009b). Fecundity increase supports adaptive radiation hypothesis in spider web evolution. *Commun. Integr. Biol.* **2**, 459–463.
- Blackledge, T. A., Scharff, N., Coddington, J. A., Szüts, T., Wenzel, J. W., Hayashi, C. Y. and Agnarsson, I. (2009c). Reconstructing web evolution and spider diversification in the molecular era. *Proc. Natl. Acad. Sci. USA* **106**, 5229–5234.
- Blamires, S. J. (2010). Plasticity in extended phenotypes: orb web architectural responses to variations in prey parameters. *J. Exp. Biol.* **213**, 3207–3212.

- Blamires, S. J., Thompson, M. B. and Hochuli, D. F. (2007). Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? *Austral Ecol.* **32**, 551–563.
- Blamires, S. J., Hochuli, D. F. and Thompson, M. B. (2008). Why cross the web: decoration spectral properties and prey capture in an orb spider (*Argiope keyserlingi*) web. *Biol. J. Linnean Soc.* **94**, 221–229.
- Blamires, S. J., Hochuli, D. F. and Thompson, M. B. (2009). Prey protein influences growth and decoration building in the orb web spider *Argiope keyserlingi*. *Ecol. Entomol.* **34**, 545–550.
- Blamires, S. J., Chao, I. C. and Tso, I. M. (2010a). Prey type, vibrations and handling interactively influence spider silk expression. *J. Exp. Biol.* **213**, 3906–3910.
- Blamires, S. J., Lee, Y. H., Chang, C. M., Lin, I. T., Chen, J. A., Lin, T. Y. and Tso, I. M. (2010b). Multiple structures interactively influence prey capture efficiency in spider orb webs. *Anim. Behav.* **80**, 947–953.
- Blasingame, E., Tuton-Blasingame, T., Larkin, L., Falick, A. M., Zhao, L., Fong, J., Vaidyanathan, V., Visperas, A., Geurts, P., Hu, X. Y., La Mattina, C. and Vierra, C. (2009). Pyriform spidroin 1, a novel member of the silk gene family that anchors dragline silk fibers in attachment discs of the black widow spider, *Latrodectus hesperus*. *J. Biol. Chem.* **284**, 29097–29108.
- Bond, J. E. and Opell, B. D. (1998). Testing adaptive radiation and key innovation hypotheses in spiders. *Evolution* **52**, 403–414.
- Bonthrone, K. M., Vollrath, F., Hunter, B. K. and Sanders, J. K. M. (1992). The elasticity of spiders webs is due to water-induced mobility at a molecular-level. *Proc. R. Soc. Lond. B Biol. Sci.* **248**, 141–144.
- Boutry, C. and Blackledge, T. A. (2008). The common house spider alters the material and mechanical properties of cobweb silk in response to different prey. *J. Exp. Zool.* **309A**, 542–552.
- Boutry, C. and Blackledge, T. A. (2009). Biomechanical variation of silk links spinning plasticity to spider web function. *Zoology* **112**, 451–460.
- Boutry, C. and Blackledge, T. A. (2010). Evolution of supercontraction in spider silk: structure-function relationship from tarantulas to orb-weavers. *J. Exp. Biol.* **213**, 3505–3514.
- Breed, A. L., Levine, V. D., Peakall, D. B. and Witt, P. N. (1964). The fate of the intact orb web of the spider *Araneus diadematus*. *Behaviour* **23**, 43–60.
- Bristowe, W. S. (1939). *The Comity of Spiders*. The Ray Society, London.
- Brooks, A. E., Brothers, T. J., Creager, M. S. and Lewis, R. V. (2007). A novel methodology to explore the viscoelasticity of spider major ampullate silk. *J. Appl. Biomater. Biomech.* **5**, 158–165.
- Brown, K. M. (1981). Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia* **50**, 380–385.
- Bruce, M. J. (2006). Silk decorations: controversy and consensus. *J. Zool.* **269**, 89–97.
- Bruce, M. J. and Herberstein, M. E. (2006). The influence of predator cues on orb-web spider foraging behaviour. *Ethol. Ecol. Evol.* **18**, 91–98.
- Bruce, M. J., Herberstein, M. E. and Elgar, M. A. (2001). Signalling conflict between prey and predator attraction. *J. Evol. Biol.* **14**, 786–794.
- Bruce, M. J., Heiling, A. M. and Herberstein, M. E. (2004). Web decorations and foraging success in ‘*Araneus*’ *eburnus* (Araneae: Araneidae). *Ann. Zool. Fenn.* **41**, 563–575.
- Bush, A. A., Yu, D. W. and Herberstein, M. E. (2008). Function of bright coloration in the wasp spider *Argiope bruennichi* (Araneae: Araneidae). *Proc. R. Soc. B.* **275**, 1337–1342.

- Caraco, T. and Gillespie, R. G. (1986). Risk-sensitivity: foraging mode in an ambush predator. *Ecology (Tempe)* **67**, 1180–1185.
- Carrel, J. E., Burgess, H. K. and Shoemaker, D. M. (2000). A test of pollen feeding by a linyphiid spider. *J. Arachnol.* **28**, 243–244.
- Cartan, C. K. and Miyashita, T. (2000). Extraordinary web and silk properties of *Cyrtarachne* (Araneae, Araneidae): a possible link between orb-webs and bolas. *Biol. J. Linnean Soc.* **71**, 219–235.
- Casas, J. and Dangles, O. (2010). Physical ecology of fluid flow sensing in arthropods. *Annu. Rev. Entomol.* **55**, 505–520.
- Casem, M. L., Collin, M. A., Ayoub, N. A. and Hayashi, C. Y. (2010). Silk gene transcripts in the developing tubuliform glands of the Western black widow, *Latrodectus hesperus*. *J. Arachnol.* **38**, 99–103.
- Chacón, P. and Eberhard, W. G. (1980). Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. *Bull. Br. Arachnol. Soc.* **5**, 29–38.
- Cheng, R. C., Yang, E. C., Lin, C. P., Herberstein, M. E. and Tso, I. M. (2010). Insect form vision as one potential shaping force of spider web decoration design. *J. Exp. Biol.* **213**, 759–768.
- Chittka, L., Shmida, A., Troje, N. and Menzel, R. (1994). Ultraviolet as a component of flower reflections, and the colour perception of hymenoptera. *Vision Res.* **34**, 1489–1508.
- Chmiel, K., Herberstein, M. E. and Elgar, M. A. (2000). Web damage and feeding experience influence web site tenacity in the orb-web spider *Argiope keyserlingi* Karsch. *Anim. Behav.* **60**, 821–826.
- Choresch, O., Bayarmagnai, B. and Lewis, R. V. (2009). Spider web glue: two proteins expressed from opposite strands of the same DNA sequence. *Biomacromolecules* **10**, 2852–2856.
- Cloudsley-Thompson, J. L. (1995). A review of the anti-predator devices of spiders. *Bull. Br. Arachnol. Soc.* **10**, 81–96.
- Coddington, J. (1982). Monophyletic origin of orb webs. *Am. Zool.* **22**, 886.
- Coddington, J. (1986a). The monophyletic origin of the orb web. In: *Spiders: Webs, Behavior and Evolution* (ed Shear, W. A.), pp. 319–363. Stanford University Press, Stanford.
- Coddington, J. A. (1986b). The genera of the spider family Theridiosomatidae. *Smithson. Contr. Zool.* 1–96.
- Coddington, J. A. (1986c). Orb webs in "non-orb weaving" ogre-faced spiders (Araneae: Dinopidae): a question of genealogy. *Cladistics* **2**, 53–67.
- Coddington, J. A. (1989). Spinneret silk spigot morphology: evidence for the monophyly of orb-weaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. *J. Arachnol.* **17**, 71–96.
- Coddington, J. A. and Levi, H. W. (1991). Systematics and evolution of spiders (Araneae). *Annu. Rev. Ecol. Syst.* **22**, 565–592.
- Coddington, J. and Sobrevila, C. (1987). Web manipulation and two stereotyped attack behaviors in the ogre-faced spider *Deinopis spinosus* Marx (Araneae, Deinopidae). *J. Arachnol.* **15**, 213–225.
- Coddington, J. and Valerio, C. E. (1980). Observations of the web and behavior of *Wendilgarda spiders* (Araneae: Theridiosomatidae). *Psyche (Cambridge)* **87**, 93–106.
- Coddington, J. A., Hormiga, G. and Scharff, N. (1997). Giant female or dwarf male spiders? *Nature* **385**, 687–688.
- Coddington, J. A., Ubick, D., Paquin, P., Cushing, P. E. and Roth, V. (2005). Symphytognathidae. Spiders of North America: An Identification Manual, pp. 226–227. American Arachnological Society.

- Colgin, M. A. and Lewis, R. V. (1998). Spider minor ampullate silk proteins contain new repetitive sequences and highly conserved non-silk-like "spacer regions". *Protein Sci.* **7**, 667–672.
- Corcobado, G., Rodriguez-Girones, M. A., De Mas, E. and Moya-Larano, J. (2010). Introducing the refined gravity hypothesis of extreme sexual size dimorphism. *BMC Evol. Biol.* **10**, 236.
- Cox, J. A. and NeSmith, C. C. (2007). Acadian flycatcher caught in the web of a golden silk orb-weaver. *Florida Field Nat.* **35**, 46–48.
- Craig, C. L. (1986). Orb-web visibility—the influence of insect flight behavior and visual physiology on the evolution of web designs within the Araneioidea. *Anim. Behav.* **34**, 54–68.
- Craig, C. L. (1987a). The ecological and evolutionary interdependence between web architecture and web silk spun by orb web weaving spiders. *Biol. J. Linnean Soc.* **30**, 135–162.
- Craig, C. L. (1987b). The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. *Am. Nat.* **129**, 47–68.
- Craig, C. L. (1988). Insect perception of spider orb webs in three light habitats. *Funct. Ecol.* **2**, 277–282.
- Craig, C. L. (1995). Webs of deceit. *Nat. Hist.* **104**, 33–35.
- Craig, C. L. (1997). Evolution of arthropod silks. *Annu. Rev. Entomol.* **42**, 231–267.
- Craig, C. L. (2003). *Spider Webs and Silk: Tracing Evolution from Molecules to Genes to Phenotypes*. Oxford University Press, New York.
- Craig, C. L. and Bernard, G. D. (1990). Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* **71**, 616–623.
- Craig, C. L. and Ebert, K. (1994). Color and pattern in predator-prey interactions—the bright body colors and patterns of a tropical orb-spinning spider attract flower-seeking prey. *Funct. Ecol.* **8**, 616–620.
- Craig, C. L., Bernard, G. D. and Coddington, J. A. (1994). Evolutionary shifts in the spectral properties of spider silks. *Evolution* **48**, 287–296.
- Craig, C. L., Weber, R. S. and Bernard, G. D. (1996). Evolution of predator-prey systems: spider foraging plasticity in response to the visual ecology of prey. *Am. Nat.* **147**, 205–229.
- Craig, C. L., Riekel, C., Herberstein, M. E., Weber, R. S., Kaplan, D. and Pierce, N. E. (2000). Evidence for diet effects on the composition of silk proteins produced by spiders. *Mol. Biol. Evol.* **17**, 1904–1913.
- Craig, C. L., Wolf, S. G., Davis, J. L. D., Hauber, M. E. and Maas, J. L. (2001). Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. *Evolution* **55**, 986–993.
- Cunniff, P. M., Fossey, S. A., Auerbach, M. A. and Song, J. W. (1994). Mechanical properties of major ampullate gland silk fibers extracted from *Nephila clavipes* spiders. In: *Silk Polymers* (eds Kaplan, D., Adams, W. W., Farmer, B. and Viney, C.), pp. 234–251. American Chemical Society, Washington, DC.
- Denny, M. (1976). Physical properties of spider's silks and their role in design of orb-webs. *J. Exp. Biol.* **65**, 483–506.
- Dicko, C., Knight, D., Kenney, J. M. and Vollrath, F. (2004). Secondary structures and conformational changes in flagelliform, cylindrical, major, and minor ampullate silk proteins. Temperature and concentration effects. *Biomacromolecules* **5**, 2105–2115.
- Dieckmann, U. and Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature* **400**, 354–357.
- Eberhard, W. G. (1972). Web of *Uloborus diversus* (Araneae-Uloboridae). *J. Zool. (London)* **66**, 417–465.

- Eberhard, W. G. (1973). Stabilimenta on webs of *Uloborus diversus* (Araneae-Uloboridae) and other spiders. *J. Zool.* **171**, 367–384.
- Eberhard, W. G. (1975). Inverted ladder orb web of *Scoloderus* sp. and intermediate orb of *Eustala* sp. Araneae—Araneidae. *J. Nat. Hist.* **9**, 93–106.
- Eberhard, W. G. (1976). Physical properties of sticky spirals and their connections—sliding connections in orb webs. *J. Nat. Hist.* **10**, 481–488.
- Eberhard, W. G. (1977). Rectangular orb webs of *Synotaxus* (Araneae-Theridiidae). *J. Nat. Hist.* **11**, 501–507.
- Eberhard, W. G. (1980). The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneidae). *Psyche (Cambridge)* **87**, 143–170.
- Eberhard, W. G. (1982). Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* **36**, 1067–1095.
- Eberhard, W. G. (1986). Effects of orb-web geometry on prey interception and retention. In: *Spiders, Webs, Behavior and Evolution* (ed Shear, W. A.), pp. 70–100. Stanford University Press, Stanford.
- Eberhard, W. G. (1987). Construction behavior of non-orb weaving cribellate spiders and the evolutionary origin of orb webs. *Bull. Br. Arachnol. Soc.* **7**, 175–178.
- Eberhard, W. G. (1988). Behavioral flexibility in orb web construction—effects of supplies in different silk glands and spider size and weight. *J. Arachnol.* **16**, 295–302.
- Eberhard, W. G. (1989). Niche expansion in the spider *Wendilgarda galapagensis* (Araneae, Theridiosomatidae) on Cocos Island. *Rev. Biol. Trop.* **37**, 163–168.
- Eberhard, W. G. (1990a). Early stages of orb construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* (Araneae, Uloboridae and Tetragnathidae), and their phylogenetic implications. *J. Arachnol.* **18**, 205–234.
- Eberhard, W. G. (1990b). Function and phylogeny of spider webs. *Annu. Rev. Ecol. Syst.* **21**, 341–372.
- Eberhard, W. G. (1995). The web and building behavior of *Synotaxus ecuadorensis* (Araneae, Synotaxidae). *J. Arachnol.* **23**, 25–30.
- Eberhard, W. G. (2000a). Breaking the mold: behavioral variation and evolutionary innovation in *Wendilgarda* spiders (Araneae Theridiosomatidae). *Ethol. Ecol. Evol.* **12**, 223–235.
- Eberhard, W. G. (2000b). Spider manipulation by a wasp larva. *Nature* **406**, 255–256.
- Eberhard, W. G. (2001a). Trolling for water striders: active searching for prey and the evolution of reduced webs in the spider *Wendilgarda* sp (Araneae, Theridiosomatidae). *J. Nat. Hist.* **35**, 229–251.
- Eberhard, W. G. (2001b). Under the influence: webs and building behavior of *Plesiometa argyra* (Araneae, Tetragnathidae) when parasitized by *Hymenoepimecis argyraphaga* (Hymenoptera, Ichneumonidae). *J. Arachnol.* **29**, 354–366.
- Eberhard, W. G. (2003). Substitution of silk stabilimenta for egg sacs by *Allocyclosa bifurca* (Araneae: Araneidae) suggests that silk stabilimenta function as camouflage devices. *Behaviour* **140**, 847–868.
- Eberhard, W. G. (2007a). Miniaturized orb-weaving spiders: behavioural precision is not limited by small size. *Proc. R. Soc. B.* **274**, 2203–2209.
- Eberhard, W. G. (2007b). Stabilimenta of *Philoponella vicina* (Araneae: Uloboridae) and *Gasteracantha cancriformis* (Araneae: Araneidae): evidence against a prey attractant function. *Biotropica* **39**, 216–220.
- Eberhard, W. G. (2008). *Araneus expletus* (Araneae, Araneidae): another stabilimentum that does not function to attract prey. *J. Arachnol.* **36**, 191–194.
- Eberhard, W. G. (2010a). Possible functional significance of spigot placement on the spinnerets of spiders. *J. Arachnol.* **38**, 407–414.
- Eberhard, W. G. (2010b). Recovery of spiders from the effects of parasitic wasps: implications for fine-tuned mechanisms of manipulation. *Anim. Behav.* **79**, 375–383.

- Eberhard, W. G., Agnarsson, I. and Levi, H. W. (2008a). Web forms and phylogeny of theridiid spiders (Araneae: Theridiidae). *Syst. Biodivers.* **6**, 415–475.
- Eberhard, W. G., Barrantes, G. and Madrigal-Brenes, R. (2008b). Vestiges of an orb-weaving ancestor? The "biogenetic law" and ontogenetic changes in the webs and building behavior of the black widow spider *Latrodectus geometricus* (Araneae Theridiidae). *Ethol. Ecol. Evol.* **20**, 211–244.
- Edmonds, D. T. and Vollrath, F. (1992). The contribution of atmospheric water-vapor to the formation and efficiency of a spider's capture web. *Proc. R. Soc. Lond. B Biol. Sci.* **248**, 145–148.
- Edmunds, J. (1986). The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in West Africa, with a discussion of the function of stabilimenta. In: *Proceedings of the Ninth International Congress of Arachnology, Panama 1983* (eds Eberhard, W. G., Lubin, Y. D. and Robinson, B. C.), pp. 61–72. Smithsonian Institution Press, Washington, DC.
- Edmunds, J. and Edmunds, M. (1986). The defensive mechanisms of orb weavers (Araneae, Araneidae) in Ghana West Africa. In: *Proceedings of the Ninth International Congress of Arachnology, Panama 1983* (eds Eberhard, W. G., Lubin, Y. D. and Robinson, B. C.), pp. 73–89. Smithsonian Institution Press, Washington, DC.
- Edwards, W., Whytlaw, P. A., Congdon, B. C. and Gaskett, C. (2009). Is optimal foraging a realistic expectation in orb-web spiders? *Ecol. Entomol.* **34**, 527–534.
- Eisner, T. and Nowicki, S. (1983). Spider web protection through visual advertisement—role of the stabilimentum. *Science* **219**, 185–187.
- Eisner, T., Ettersha, G. and Alsop, R. (1964). Adhesiveness of spider silk. *Science* **146**, 1058–1061.
- Elgar, M. A. (1993). Inter-specific associations involving spiders: kleptoparasitism, mimicry and mutualism. *Mem. Queensl.* **33**, 411–430.
- Elgar, M. A. (1994). Experimental evidence of a mutualistic association between two web-building spiders. *J. Anim. Ecol.* **63**, 880–886.
- Elgar, M. A., Allan, R. A. and Evans, T. A. (1996). Foraging strategies in orb-spinning spiders: ambient light and silk decorations in *Argiope aetherea* Walckenaer (Araneae: Araneoidea). *Aust. J. Ecol.* **21**, 464–467.
- Elices, M., Pérez-Rigueiro, J., Plaza, G. and Guinea, G. V. (2004). Recovery in spider silk fibers. *J. Appl. Polym. Sci.* **92**, 3537–3541.
- Elices, M., Plaza, G. R., Arnedo, M. A., Pérez-Rigueiro, J., Torres, F. G. and Guinea, G. V. (2009). Mechanical behavior of silk during the evolution of orb-web spinning spiders. *Biomacromolecules* **10**, 1904–1910.
- Endler, J. A. (1993a). The color of light in forests and its implications. *Ecol. Monogr.* **63**, 1–27.
- Endler, J. A. (1993b). Some general comments on the evolution and design of animal communication systems. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **340**, 215–225.
- Ewer, R. F. (1972). The devices in the web of the West-African spider *Argiope flavipalpis*. *J. Nat. Hist.* **6**, 159–167.
- Foelix, R. F. (2011). *Biology of Spiders*. 3rd ed. Oxford University Press, Oxford.
- Ford, M. J. (1977). Energy costs of the predation strategy of the web-spinning spider *Lepthyphantes zimmermanni* Berktau (Linyphiidae). *Oecologia (Berlin)* **28**, 341–349.
- Forster, L. M. and Forster, R. R. (1985). A derivative of the orb web and its evolutionary significance. *N. Z. J. Zool.* **12**, 455–465.
- Frische, S., Maunsbach, A. B. and Vollrath, F. (1998). Elongate cavities and skin-core structure in *Nephila* spider silk observed by electron microscopy. *J. Microsc.-Oxf.* **189**, 64–70.

- Gaines, W. A. and Marcotte, W. R. (2008). Identification and characterization of multiple Spidroin 1 genes encoding major ampullate silk proteins in *Nephila clavipes*. *Insect Mol. Biol.* **17**, 465–474.
- Gaines, W. A., Sehorn, M. G. and Marcotte, W. R. (2010). Spidroin n-terminal domain promotes a pH-dependent association of silk proteins during self-assembly. *J. Biol. Chem.* **285**, 40745–40753.
- Garb, J. E. and Hayashi, C. Y. (2005). Modular evolution of egg case silk genes across orb-weaving spider superfamilies. *Proc. Natl. Acad. Sci. USA* **102**, 11379–11384.
- Garb, J. E., DiMauro, T., Vo, V. and Hayashi, C. Y. (2006). Silk genes support the single origin of orb webs. *Science* **312**, 1762.
- Garb, J. E., Ayoub, N. A. and Hayashi, C. Y. (2010). Untangling spider silk evolution with spidroin terminal domains. *BMC Evol. Biol.* **10**.
- Garrido, M. A., Elices, M., Viney, C. and Pérez-Rigueiro, J. (2002a). Active control of spider silk strength: comparison of drag line spun on vertical and horizontal surfaces. *Polymer* **43**, 1537–1540.
- Garrido, M. A., Elices, M., Viney, C. and Pérez-Rigueiro, J. (2002b). The variability and interdependence of spider drag line tensile properties. *Polymer* **43**, 4495–4502.
- Gatesy, J., Hayashi, C., Motriuk, D., Woods, J. and Lewis, R. (2001). Extreme diversity, conservation, and convergence of spider silk fibroin sequences. *Science* **291**, 2603–2605.
- Gawryszewski, F. M. and Motta, P. C. (2008). The silk tuft web decorations of the orb-weaver *Gasteracantha cancriformis*: testing the prey attraction and the web advertisement hypotheses. *Behaviour* **145**, 277–295.
- Gemenio, C., Yeagan, K. V. and Haynes, K. F. (2000). Aggressive chemical mimicry by the bolas spider *Mastophora hutchinsoni*: identification and quantification of a major prey's sex pheromone components in the spider's volatile emissions. *J. Chem. Ecol.* **26**, 1235–1243.
- Gertsch, W. J. (1949). *American spiders*. D. Van Nostrand Co., Princeton.
- Getty, R. M. and Coyle, F. A. (1996). Observations on prey capture and anti-predator behaviors of ogre-faced spiders (Deinopis) in southern Costa Rica (Araneae, Deinopidae). *J. Arachnol.* **24**, 93–100.
- Geurts, P., Zhao, L., Hsia, Y., Gnesa, E., Tang, S., Jeffery, F., La Mattina, C., Franz, A., Larkin, L. and Vierra, C. (2010). Synthetic spider silk fibers spun from pyriform spidroin 2, a glue silk protein discovered in orb-weaving spider attachment discs. *Biomacromolecules* **11**, 3495–3503.
- Gheysens, T., Beladjal, L., Gellynck, K., Van Nimmen, E., Van Langenhove, L. and Mertens, J. (2005). Egg sac structure of *Zygiella x-notata* (Arachnida, Araneidae). *J. Arachnol.* **33**, 549–557.
- Gillespie, R. G. (1991). Predation through impalement of prey: the foraging behavior of *Doryonychus raptor* (Araneae, Tetragnathidae). *Psyche (Cambridge)* **98**, 337–350.
- Gillespie, R. G. (2004). Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359.
- Gillespie, R. G., Croom, H. B. and Palumbi, S. R. (1994). Multiple origins of a spider radiation in Hawaii. *Proc. Natl. Acad. Sci. USA* **91**, 2290–2294.
- Goldsmith, T. H. (1961). The color vision of insects. In: *Light and Life* (eds McElroy, W. D. and Glass, B.), pp. 771–794. John Hopkins Press.
- Gonzaga, M. O. and Sobczak, J. F. (2007). Parasitoid-induced mortality of *Araneus omnicolor* (Araneae, Araneidae) by *Hymenoepimecis* sp. (Hymenoptera, Ichneumonidae) in southeastern Brazil. *Naturwissenschaften* **94**, 223–227.
- Gonzaga, M. O. and Vasconcellos-Neto, J. (2005). Testing the functions of detritus stabilimenta in webs of *Cyclosa fililineata* and *Cyclosa morretes* (Araneae: Araneidae): do they attract prey or reduce the risk of predation? *Ethology* **111**, 479–491.

- Gonzaga, M. O., Sobczak, J. F., Penteado-Dias, A. M. and Eberhard, W. G. (2010). Modification of *Nephila clavipes* (Araneae Nephilidae) webs induced by the parasitoids *Hymenoepimecis bicolor* and *H. robertsae* (Hymenoptera Ichneumonidae). *Ethol. Ecol. Evol.* **22**, 151–165.
- Gorb, S. N., Niederegger, S., Hayashi, C. Y., Summers, A. P., Voetsch, W. and Walther, P. (2006). Silk-like secretion from tarantula feet. *Nature* **443**, 407.
- Gorb, S. N., Niederegger, S., Hayashi, C. Y., Summers, A. P., Votsch, W. and Walther, P. (2009). Silk production from tarantula feet questioned reply. *Nature* **461**, E9–E10.
- Gosline, J. M., Guerette, P. A., Ortlepp, C. S. and Savage, K. N. (1999). The mechanical design of spider silks: from fibroin sequence to mechanical function. *J. Exp. Biol.* **202**, 3295–3303.
- Graham, D. L. (1997). Spider webs and windows as potentially important sources of hummingbird mortality. *J. Field Ornithol.* **68**, 98–101.
- Gregorič, M., Kostanjšek, R. and Kuntner, M. (2010). Orb web features as taxonomic characters in *Zygiella* s.l. (Araneae: Araneidae). *J. Arachnol.* **38**, 319–327.
- Gregorič, M., Agnarsson, I., Blackledge, T. A. and Kuntner, M. (2011). Darwin's bark spider: Giant prey in giant orb webs (*Caerostris darwini*, Araneae: Araneidae)? *J. Arachnol.* **39**, 294–302.
- Griswold, C. E., Coddington, J. A., Hormiga, G. and Scharff, N. (1998). Phylogeny of the orb-web building spiders (Araneae, Orbicularia: Deinopoidea, Araneoidea). *Zool. J. Linn. Soc.* **123**, 1–99.
- Grostal, P. and Walter, D. E. (1997). Kleptoparasites or commensals? Effects of *Argyrodos antipodianus* (Araneae: Theridiidae) on *Nephila plumipes* (Araneae: Tetragnathidae). *Oecologia* **111**, 570–574.
- Grubb, D. T. and Jelinski, L. W. (1997). Fiber morphology of spider silk: the effects of tensile deformation. *Macromolecules* **30**, 2860–2867.
- Guehrs, K. H., Schlott, B., Grosse, F. and Weisshart, K. (2008). Environmental conditions impinge on dragline silk protein composition. *Insect Mol. Biol.* **17**, 553–564.
- Guerette, P. A., Ginzinger, D. G., Weber, B. H. F. and Gosline, J. M. (1996). Silk properties determined by gland-specific expression of a spider fibroin gene family. *Science* **272**, 112–115.
- Guinea, G. V., Elices, M., Pérez-Rigueiro, J. and Plaza, G. (2003). Self-tightening of spider silk fibers induced by moisture. *Polymer* **44**, 5785–5788.
- Guinea, G. V., Elices, M., Pérez-Rigueiro, J. and Plaza, G. R. (2005). Stretching of supercontracted fibers: a link between spinning and the variability of spider silk. *J. Exp. Biol.* **208**, 25–30.
- Guinea, G. V., Pérez-Rigueiro, J., Plaza, G. R. and Elices, M. (2006). Volume constancy during stretching of spider silk. *Biomacromolecules* **7**, 2173–2177.
- Hagn, F., Eisoldt, L., Hardy, J. G., Vendrely, C., Coles, M., Scheibel, T. and Kessler, H. (2010). A conserved spider silk domain acts as a molecular switch that controls fibre assembly. *Nature* **465**, 239–244.
- Hajer, J., Maly, J., Hruba, L. and Rehakova, D. (2009). Egg sac silk of *Theridiosoma gemmosum* (Araneae: Theridiosomatidae). *J. Morphol.* **270**, 1269–1283.
- Harmer, A. M. T. (2009). Elongated orb-webs of Australian ladder-web spiders (Araneidae: *Telaprocera*) and the significance of orb-web elongation. *J. Ethol.* **27**, 453–460.
- Harmer, A. M. T. and Framenau, V. W. (2008). *Telaprocera* (Araneae: Araneidae), a new genus of Australian orb-web spiders with highly elongated webs. *Zootaxa* **1956**, 59–80.
- Harmer, A. M. T. and Herberstein, M. E. (2009). Taking it to extremes: what drives extreme web elongation in Australian ladder web spiders (Araneidae: *Telaprocera maudae*)? *Anim. Behav.* **78**, 499–504.

- Harmer, A. M. T., Blackledge, T. A., Madin, J. S. and Herberstein, M. E. (2010). High-performance spider webs: integrating biomechanics, ecology and behaviour. *J. R. Soc. Interface* **8**, 457–471.
- Hauber, M. E. (1998). Web decorations and alternative foraging tactics of the spider *Argiope appensa*. *Ethol. Ecol. Evol.* **10**, 47–54.
- Hausdorf, B. (1999). Molecular phylogeny of araneomorph spiders. *J. Evol. Biol.* **12**, 980–985.
- Hawthorn, A. C. and Opell, B. D. (2002). Evolution of adhesive mechanisms in cribellar spider prey capture thread: evidence for van der Waals and hygroscopic forces. *Biol. J. Linnean Soc.* **77**, 1–8.
- Hawthorn, A. C. and Opell, B. D. (2003). van der Waals and hygroscopic forces of adhesion generated by spider capture threads. *J. Exp. Biol.* **206**, 3905–3911.
- Hayashi, C. Y. and Lewis, R. V. (1998). Evidence from flagelliform silk cDNA for the structural basis of elasticity and modular nature of spider silks. *J. Mol. Biol.* **275**, 773–784.
- Hayashi, C. Y. and Lewis, R. V. (2000). Molecular architecture and evolution of a modular spider silk protein gene. *Science* **287**, 1477–1479.
- Hayashi, C. Y. and Lewis, R. V. (2001). Spider flagelliform silk: lessons in protein design, gene structure, and molecular evolution. *Bioessays* **23**, 750–756.
- Hayashi, C. Y., Shipley, N. H. and Lewis, R. V. (1999). Hypotheses that correlate the sequence, structure, and mechanical properties of spider silk proteins. *Int. J. Biol. Macromol.* **24**, 271–275.
- Hayashi, C. Y., Blackledge, T. A. and Lewis, R. V. (2004). Molecular and mechanical characterization of aciniform silk: uniformity of iterated sequence modules in a novel member of the spider silk fibroin gene family. *Mol. Biol. Evol.* **21**, 1950–1959.
- Haynes, K. F., Gemenio, C., Yeargan, K. V., Millar, J. G. and Johnson, K. M. (2002). Aggressive chemical mimicry of moth pheromones by a bolas spider: how does this specialist predator attract more than one species of prey? *Chemoecology* **12**, 99–105.
- Head, G. (1995). Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (Class Araneae). *Evolution* **49**, 776–781.
- Heiling, A. M. (1999). Why do nocturnal orb-web spiders (Araneidae) search for light? *Behav. Ecol. Sociobiol.* **46**, 43–49.
- Henaut, Y. and Machkour-M'Rabet, S. (2010). Interspecific aggregation around the web of the orb spider *Nephila clavipes*: consequences for the web architecture of *Leucauge venusta*. *Ethol. Ecol. Evol.* **22**, 203–209.
- Henaut, Y., Machkour-M'Rabet, S., Winterton, P. and Calme, S. (2010). Insect attraction by webs of *Nephila clavipes* (Araneae: Nephilidae). *J. Arachnol.* **38**, 135–138.
- Henry, T. J. (1999). The spider-commensal plant bug genus *Ranzovius* (Heteroptera: Miridae: Phylinae) revisited: three new species and a revised key, with the description of a new sister genus and a phylogenetic analysis. *Acta Soc. Zool. Bohem.* **63**, 93–115.
- Herberstein, M. E. (2000). Foraging behaviour in orb-web spiders (Araneidae): do web decorations increase prey capture success in *Argiope keyserlingi* Karsch, 1878? *Aust. J. Zool.* **48**, 217–223.
- Herberstein, M. E. (2011). *Spider Behaviour: Flexibility and Versatility*. Cambridge University Press, New York.
- Herberstein, M. E. and Fleisch, A. F. (2003). Effect of abiotic factors on the foraging strategy of the orb-web spider *Argiope keyserlingi* (Araneae: Araneidae). *Austral Ecol.* **28**, 622–628.
- Herberstein, M. E. and Tso, I. M. (2000). Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneoidea, Araneae). *J. Arachnol.* **28**, 180–184.
- Herberstein, M. E. and Tso, I. M. (2011). Spider webs: evolution, diversity and plasticity. In: *Spider Behavior: Flexibility and Versatility* (ed Herberstein, M. E.), pp. 57–98. Cambridge University Press, New York.

- Herberstein, M. E., Craig, C. L., Coddington, J. A. and Elgar, M. A. (2000a). The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biol. Rev. (Cambridge)* **75**, 649–669.
- Herberstein, M. E., Craig, C. L. and Elgar, M. A. (2000b). Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evol. Ecol. Res.* **2**, 69–80.
- Herberstein, M. E., Gaskett, A. C., Glencross, D., Hart, S., Jaensch, S. and Elgar, M. A. (2000c). Does the presence of potential prey affect web design in *Argiope keyserlingi* (Araneae, Araneidae)? *J. Arachnol.* **28**, 346–350.
- Hesselberg, T. and Vollrath, F. (2004). The effects of neurotoxins on web-geometry and web-building behaviour in *Araneus diadematus* Cl. *Physiol. Behav.* **82**, 519–529.
- Hieber, C. S. (1984). Orb-web orientation and modification by the spiders *Araneus diadematus* and *Araneus gemmoides* (Araneae, Araneidae) in response to wind and light. *Zeitschrift Für Tierpsychologie/J. Comp. Ethol.* **65**, 250–260.
- Higgins, L. (1990). Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes*. *J. Insect Behav.* **3**, 773–783.
- Higgins, L. (1992). Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae, Tetragnathidae). *J. Insect Behav.* **5**, 635–655.
- Higgins, L. (2002). Female gigantism in a New Guinea population of the spider *Nephila maculata*. *Oikos* **99**, 377–385.
- Higgins, L. (2006). Quantitative shifts in orb-web investment during development in *Nephila clavipes* (Araneae, Nephilidae). *J. Arachnol.* **34**, 374–386.
- Higgins, L. E. and Buskirk, R. E. (1992). A trap-building predator exhibits different tactics for different aspects of foraging behavior. *Anim. Behav.* **44**, 485–499.
- Higgins, L. and Rankin, M. A. (1999). Nutritional requirements for web synthesis in the tetragnathid spider *Nephila clavipes*. *Physiol. Entomol.* **24**, 263–270.
- Higgins, L. E., Townley, M. A., Tillinghast, E. K. and Rankin, M. A. (2001). Variation in the chemical composition of orb webs built by the spider *Nephila clavipes* (Araneae, Tetragnathidae). *J. Arachnol.* **29**, 82–94.
- Hingston, R. W. G. (1927). Protective devices in spiders' snares, with a description of seven new species of orb-weaving spiders. *Proc. Zool. Soc. Lond.* **28**, 259–293.
- Hinman, M. B. and Lewis, R. V. (1992). Isolation of a clone encoding a second dragline silk fibroin—*Nephila clavipes* dragline silk is a two protein fiber. *J. Biol. Chem.* **267**, 19320–19324.
- Hinman, M. B., Jones, J. A. and Lewis, R. V. (2000). Synthetic spider silk: a modular fiber. *Trends Biotechnol.* **18**, 374–379.
- Hormiga, G. (1994). A revision and cladistic analysis of the spider family Pimoidae (Araneioidea: Araneae). *Smithson. Contr. Zool.* **549**, 1–104.
- Hormiga, G., Eberhard, W. G. and Coddington, J. A. (1995). Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). *Aust. J. Zool.* **43**, 313–364.
- Hormiga, G., Scharff, N. and Coddington, J. A. (2000). The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Syst. Biol.* **49**, 435–462.
- Horton, C. C. (1980). A defensive function for the stabilimenta of two orb-weaving spiders (Araneae, Araneidae). *Psyche (Cambridge)* **87**, 13–20.
- Hu, X. Y., Kohler, K., Falick, A. M., Moore, A. M. F., Jones, P. R., Sparkman, O. D. and Vierra, C. (2005a). Egg case protein-1—a new class of silk proteins with fibroin-like properties from the spider *Latrodectus hesperus*. *J. Biol. Chem.* **280**, 21220–21230.
- Hu, X. Y., Lawrence, B., Kohler, K., Falick, A. M., Moore, A. M. F., McMullen, E., Jones, P. R. and Vierra, C. (2005b). Araneoid egg case silk: a fibroin with novel

- ensemble repeat units from the black widow spider, *Latrodectus hesperus*. *Biochemistry* **44**, 10020–10027.
- Hu, X. Y., Yuan, J., Wang, X. D., Vasanthavada, K., Falick, A. M., Jones, P. R., La Mattina, C. and Vierra, C. A. (2007). Analysis of aqueous glue coating proteins on the silk fibers of the cob weaver, *Latrodectus hesperus*. *Biochemistry* **46**, 3294–3303.
- Humphreys, W. F. (1992). Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae: Argiopinae). *Bull. Br. Arachnol. Soc.* **9**, 47–52.
- Jackson, R. R. and Whitehouse, M. E. A. (1986). The biology of New Zealand and Queensland [Australia] pirate spiders (Araneae, Mimetidae): aggressive mimicry, araneophagy and prey specialization. *J. Zool. A* **210**, 279–303.
- Janetos, A. C. (1986). Web-site selection: are we asking the right questions? In: *Spiders, Webs, Behavior, and Evolution* (ed Shear, W. A.), pp. 9–22. Stanford University Press, Stanford.
- Japyassu, H. F. and Ades, C. (1998). From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). *Behaviour* **135**, 931–956.
- Japyassu, H. F. and Viera, C. (2002). Predatory plasticity in *Nephilengys cruentata* (Araneae: Tetragnathidae): relevance for phylogeny reconstruction. *Behaviour* **139**, 529–544.
- Jin, H. J. and Kaplan, D. L. (2003). Mechanism of silk processing in insects and spiders. *Nature* **424**, 1057–1061.
- Jorger, K. M. and Eberhard, W. G. (2006). Web construction and modification by *Achaearanea tessellata* (Araneae, Theridiidae). *J. Arachnol.* **34**, 511–523.
- Kaston, B. J. (1964). The evolution of spider webs. *Am. Zool.* **4**, 191–207.
- Kawamoto, T. H. and Japyassu, H. F. (2008). Tenacity and silk investment of two orb weavers: considerations about diversification of the Araneoidea. *J. Arachnol.* **36**, 418–424.
- Kelly, S. P., Sensenig, A., Lorentz, K. A. and Blackledge, T. A. (2011). Damping capacity is evolutionarily conserved in the radial silk of orb weaving spiders. *Zoology* **114**, 233–238.
- Kerr, A. M. (1993). Low frequency of stabilimenta in orb webs of *Argiope appensa* (Araneae: Araneidae) from Guam: an indirect effect of an introduced avian predator? *Pac. Sci.* **47**, 328–337.
- Keten, S. and Buehler, M. J. (2008). Geometric confinement governs the rupture strength of H-bond assemblies at a critical length scale. *Nano Lett.* **8**, 743–748.
- Keten, S., Xu, Z. P., Ihle, B. and Buehler, M. J. (2010). Nanoconfinement controls stiffness, strength and mechanical toughness of beta-sheet crystals in silk. *Nat. Mater.* **9**, 359–367.
- Kevan, P., Giufa, M. and Chittka, L. (1996). Why are there so many and so few white flowers? *Trends Plant Sci.* **1**, 280–284.
- Kiltie, R. A. (1996). Whorled, wiled webs. *Trends Ecol. Evol.* **11**, 232–233.
- Knight, D. P. and Vollrath, F. (1999). Liquid crystals and flow elongation in a spider's silk production line. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 519–523.
- Knight, D. P., Knight, M. M. and Vollrath, F. (2000). Beta transition and stress-induced phase separation in the spinning of spider dragline silk. *Int. J. Biol. Macromol.* **27**, 205–210.
- Knoflach, B. (1998). Mating in *Theridion varians* Hahn and related species (Araneae: Theridiidae). *J. Nat. Hist.* **32**, 545–604.
- Knoflach, B. (2004). Diversity in the copulatory behaviour of comb-footed spiders (Araneae, Theridiidae). *Denisia* **12**, 161–256.
- Ko, F. K. and Jovicic, J. (2004). Modeling of mechanical properties and structural design of spider web. *Biomacromolecules* **5**, 780–785.

- Köhler, T. and Vollrath, F. (1995). Thread biomechanics in the two orb-weaving spiders *Araneus diadematus* (Araneae, Araneidae) and *Uloborus walckenaerius* (Araneae, Uloboridae). *J. Exp. Zool.* **271**, 1–17.
- Krink, T. and Vollrath, F. (2000). Optimal area use in orb webs of the spider *Araneus diadematus*. *Naturwissenschaften* **87**, 90–93.
- Kümmerlen, J., vanBeek, J. D., Vollrath, F. and Meier, B. H. (1996). Local structure in spider dragline silk investigated by two-dimensional spin-diffusion nuclear magnetic resonance. *Macromolecules* **29**, 2920–2928.
- Kuntner, M. (2005). A revision of *Herennia* (Araneae: Nephilidae: Nephilinae), the Australasian ‘coin spiders’. *Invertebr. Syst.* **19**, 391–436.
- Kuntner, M. (2006). Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). *Zool. Scr.* **35**, 19–62.
- Kuntner, M. (2007). A monograph of *Nephilengys*, the pantropical ‘hermit spiders’ (Araneae, Nephilidae, Nephilinae). *Syst. Entomol.* **32**, 95–135.
- Kuntner, M. and Agnarsson, I. (2009). Phylogeny accurately predicts behaviour in Indian Ocean *Clitaetra* spiders (Araneae: Nephilidae). *Invertebr. Syst.* **23**, 193–204.
- Kuntner, M. and Agnarsson, I. (2010). Web gigantism in Darwin’s bark spider, a new species from Madagascar (Araneidae: *Caerostris*). *J. Arachnol.* **38**, 346–356.
- Kuntner, M. and Coddington, J. A. (2009). Discovery of the largest orbweaving spider species: the evolution of gigantism in *Nephila*. *PLoS One* **4**, e7516. doi:10.1371/journal.pone.0007516.
- Kuntner, M., Coddington, J. A. and Hormiga, G. (2008a). Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. *Cladistics* **24**, 147–217.
- Kuntner, M., Haddad, C. R., Aljančić, G. and Blejec, A. (2008b). Ecology and web allometry of *Clitaetra irenae*, an arboricolous African orb-weaving spider (Araneae, Araneoidea, Nephilidae). *J. Arachnol.* **36**, 583–594.
- Kuntner, M., Kralj-Fišer, S., Schneider, J. M. and Li, D. (2009). Mate plugging via genital mutilation in nephilid spiders: an evolutionary hypothesis. *J. Zool.* **277**, 257–266.
- Kuntner, M., Gregorič, M. and Li, D. (2010a). Mass predicts web asymmetry in *Nephila* spiders. *Naturwissenschaften* **97**, 1097–1105.
- Kuntner, M., Kralj-Fišer, S. and Gregorič, M. (2010b). Ladder webs in orb-web spiders: ontogenetic and evolutionary patterns in Nephilidae. *Biol. J. Linnean Soc.* **99**, 849–866.
- Landolf, M. A. and Barth, F. G. (1996). Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **179**, 493–508.
- Lefevre, T., Boudreault, S., Cloutier, C. and Pezolet, M. (2008). Conformational and orientational transformation of silk proteins in the major ampullate gland of *Nephila clavipes* spiders. *Biomacromolecules* **9**, 2399–2407.
- Levi, H. W. (1993). The neotropical orb-weaving spiders of the genera *Wixia*, *Pozonia*, and *Ocrepeira* (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* **153**, 47–141.
- Levi, H. W. (1997). The American orb weavers of the genera *Mecynogea*, *Manogea*, *Kapogea*, and *Cyrtophora* (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* **155**, 215–255.
- Li, D. and Lee, W. S. (2004). Predator-induced plasticity in web-building behaviour. *Anim. Behav.* **67**, 309–318.
- Li, S. F. Y., McGhie, A. J. and Tang, S. L. (1994). New internal structure of spider dragline silk revealed by atomic-force microscopy. *Biophys. J.* **66**, 1209–1212.

- Li, D., Lim, M. L. M., Seah, W. K. and Tay, S. L. (2004). Prey attraction as a possible function of discoid stabilimenta of juvenile orb-spinning spiders. *Anim. Behav.* **68**, 629–635.
- Liao, C. P., Chi, K. J. and Tso, I. M. (2009). The effects of wind on trap structural and material properties of a sit-and-wait predator. *Behav. Ecol.* **20**, 1194–1203.
- Lin, L. H., Edmonds, D. T. and Vollrath, F. (1995). Structural engineering of an orb-spider's web. *Nature (London)* **373**, 146–148.
- Linskens, H. F., Ciampolini, F. and Cresti, M. (1993). Spider webs as pollen traps. *Proc. K. Ned. Akad. Wet. Biol. Chem. Geol. Phys. Med. Sci.* **96**, 415–425.
- Liu, Y., Shao, Z. Z. and Vollrath, F. (2008a). Elasticity of spider silks. *Biomacromolecules* **9**, 1782–1786.
- Liu, Y., Spönnner, A., Porter, D. and Vollrath, F. (2008b). Proline and processing of spider silks. *Biomacromolecules* **9**, 116–121.
- Lopardo, L. and Hormiga, G. (2008). Phylogenetic placement of the Tasmanian spider *Acrobleps hygrophilus* (Araneae, Anapidae) with comments on the evolution of the capture web in Araneioidea. *Cladistics* **24**, 1–33.
- Lubin, Y. D. (1973). Web structure and function: the non-adhesive orb web of *Cyrtophora moluccensis* (Doleschall) (Araneae: Araneidae). *Form. Funct.* **6**, 337–358.
- Lubin, Y. D. (1975). Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae, Araneidae) on Daphne and Santa Cruz islands, Galapagos. *J. Arachnol.* **2**, 119–126.
- Lubin, Y. D. (1986). Web building and prey capture in the Uloboridae. In: *Spiders: Webs, Behavior, and Evolution* (ed Shear, W. A.), pp. 132–171. Stanford University Press, Stanford.
- Lubin, Y. D., Eberhard, W. G. and Montgomery, G. G. (1978). Webs of *Miagrammopes* (Araneae: Uloboridae) in the neotropics. *Psyche (Cambridge)* **85**, 1–23.
- Ludy, C. and Lang, A. (2006). Bt maize pollen exposure and impact on the garden spider, *Araneus diadematus*. *Entomol. Exp. Appl.* **118**, 145–156.
- Madriral-Brenes, R. and Barrantes, G. (2009). Construction and function of the web of *Tidarren sisypheoides* (Araneae: Theridiidae). *J. Arachnol.* **37**, 306–311.
- Madsen, B., Shao, Z. Z. and Vollrath, F. (1999). Variability in the mechanical properties of spider silks on three levels: interspecific, intraspecific and intraindividual. *Int. J. Biol. Macromol.* **24**, 301–306.
- Marples, B. J. (1967). The spinnerets and epiandrous glands of spiders. *J. Linn. Soc. Lond.* **46**, 209–222.
- Marples, B. J. (1969). Observations on decorated webs. *Bull. Br. Arachnol. Soc.* **1**, 13–18.
- Marson, J. E. (1947a). Some observations on the ecological variation and development of the cruciate zigzag camouflage device of *Argiope pulchella* (Thor). *Proc. Zool. Soc. Lond.* **117**, 219–227.
- Marson, J. E. (1947b). Some observations on the variations in the camouflage devices used by *Cyclosa insulana* (Costa), an asiatic spider, in its web. *Proc. Zool. Soc. Lond.* **117**, 598–605.
- Masters, W. M. (1984). Vibrations in the orbwebs of *Nuctenea sclopetaria* (Araneidae): 1. Transmission through the web. *Behav. Ecol. Sociobiol.* **15**, 207–216.
- Masters, W. M. and Moffat, A. J. M. (1983). A functional explanation of top-bottom asymmetry in vertical orb webs. *Anim. Behav.* **31**, 1043–1046.
- Matsumoto, R. (2009). "Veils" against predators: modified web structure of a host spider induced by an ichneumonid parasitoid, *Brachyzapus nikkoensis* (Uchida) (Hymenoptera). *J. Insect Behav.* **22**, 39–48.
- Mayntz, D. and Toft, S. (2000). Effect of nutrient balance on tolerance to low quality prey in a wolf spider (Araneae: Lycosidae). *Ekol. Bratisl.* **19**, 153–158.

- Mayntz, D. and Toft, S. (2001). Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia* **127**, 207–213.
- Mayntz, D., Toft, S. and Vollrath, F. (2009). Nutrient balance affects foraging behaviour of a trap-building predator. *Biol. Lett.* **5**, 735–738.
- McCrate, A. T. and Uetz, G. W. (2010). Kleptoparasites: a twofold cost of group living for the colonial spider, *Metepeira incrassata* (Araneae, Araneidae). *Behav. Ecol. Sociobiol.* **64**, 389–399.
- McKeown, K. C. (1952). *Australian Spiders*. Angus and Robertson, Sydney.
- McNett, B. J. and Rypstra, A. L. (1997). Effects of prey supplementation on survival and web site tenacity of *Argiope trifasciata* (Araneae, Araneidae): a field experiment. *J. Arachnol.* **25**, 352–360.
- Menzel, R. and Shmida, A. (1993). The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a case study. *Isr. J. Plant Sci.* **45**, 141–156.
- Miller, J. A. (2007). Review of erigonine spider genera in the neotropics (Araneae: Linyphiidae, Erigoninae). *Zool. J. Linn. Soc.* **149**, 1–263.
- Miller, J. A., Carmichael, A., Ramirez, M. J., Spagna, J. C., Haddad, C. R., Rezac, M., Johannesen, J., Kral, J., Wang, X. P. and Griswold, C. E. (2010). Phylogeny of entelegyne spiders: affinities of the family Penestomidae (NEW RANK), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). *Mol. Phylogenet. Evol.* **55**, 786–804.
- Miyashita, T. (1997). Factors affecting the difference in foraging success in three co-existing *Cyclosa* spiders. *J. Zool.* **242**, 137–149.
- Miyashita, T., Maezono, Y. and Shimazaki, A. (2004). Silk feeding as an alternative foraging tactic in a kleptoparasitic spider under seasonally changing environments. *J. Zool.* **262**, 225–229.
- Moya-Laraño, J., Halaj, J. and Wise, D. H. (2002). Climbing to reach females: Romeo should be small. *Evolution* **56**, 420–425.
- Naftilan, S. A. (1999). Transmission of vibrations in funnel and sheet spider webs. *Int. J. Biol. Macromol.* **24**, 289–293.
- Nakata, K. (2007). Prey detection without successful capture affects spider's orb-web building behaviour. *Naturwissenschaften* **94**, 853–857.
- Nakata, K. (2009). To be or not to be conspicuous: the effects of prey availability and predator risk on spider's web decoration building. *Anim. Behav.* **78**, 1255–1260.
- Nakata, K. (2010a). Attention focusing in a sit-and-wait forager: a spider controls its prey-detection ability in different web sectors by adjusting thread tension. *Proc. R. Soc. B.* **277**, 29–33.
- Nakata, K. (2010b). Does ontogenetic change in orb web asymmetry reflect biogenetic law? *Naturwissenschaften* **97**, 1029–1032.
- Nakata, K. and Ushimaru, A. (1999). Feeding experience affects web relocation and investment in web threads in an orb-web spider, *Cyclosa argenteoalba*. *Anim. Behav.* **57**, 1251–1255.
- Nakata, K. and Zschokke, S. (2010). Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speed in *Cyclosa*. *Proc. R. Soc. B.* **277**, 3019–3025.
- Neet, C. R. (1990). Function and structural variability of the stabilimenta of *Cyclosa insulana* (Costa) (Araneae, Araneidae). *Bull. Br. Arachnol. Soc.* **8**, 161–164.
- Nentwig, W. (1982). Why do certain insects escape from a spider's web? *Oecologia (Berlin)* **53**, 412–417.
- Nentwig, W. (1983). The non-filter function of orb webs in spiders. *Oecologia* **58**, 418–420.

- Nentwig, W. (1985). Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). *Behav. Ecol. Sociobiol.* **17**, 79–85.
- Nentwig, W. and Rogg, H. (1988). The cross stabilimentum of *Argiope argentata* (Araneae: Araneidae): nonfunctional or a nonspecific stress reaction? *Zool. Anz.* **221**, 248–266.
- Nielsen, E. (1932). *The Biology of Spiders*, 2 Vols. Levin & Munksgaard, Copenhagen.
- Opell, B. D. (1982). Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae, Uloboridae). *J. Arachnol.* **10**, 185–191.
- Opell, B. D. (1994a). The ability of spider cribellar prey capture thread to hold insects with different surface features. *Funct. Ecol.* **8**, 145–150.
- Opell, B. D. (1994b). Factors governing the stickiness of cribellar prey capture threads in the spider family Uloboridae. *J. Morphol.* **221**, 111–119.
- Opell, B. D. (1994c). Increased stickiness of prey capture threads accompanying web reduction in the spider family Uloboridae. *Funct. Ecol.* **8**, 85–90.
- Opell, B. D. (1996). Functional similarities of spider webs with diverse architectures. *Am. Nat.* **148**, 630–648.
- Opell, B. D. (1997a). A comparison of capture thread and architectural features of deinopoid and araneoid orb-webs. *J. Arachnol.* **25**, 295–306.
- Opell, B. D. (1997b). The material cost and stickiness of capture threads and the evolution of orb-weaving spiders. *Biol. J. Linnean Soc.* **62**, 443–458.
- Opell, B. D. (1998). Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk. *Funct. Ecol.* **12**, 613–624.
- Opell, B. D. (1999). Redesigning spider webs: stickiness, capture area and the evolution of modern orb-webs. *Evol. Ecol. Res.* **1**, 503–516.
- Opell, B. D. (2002). How spider anatomy and thread configuration shape the stickiness of cribellar prey capture threads. *J. Arachnol.* **30**, 10–19.
- Opell, B. D. and Bond, J. E. (2001). Changes in the mechanical properties of capture threads and the evolution of modern orb-weaving spiders. *Evol. Ecol. Res.* **3**, 567–581.
- Opell, B. D. and Eberhard, W. (1984). Resting postures of orb-weaving uloborid spiders (Araneae, Uloboridae). *J. Arachnol.* **11**, 396.
- Opell, B. D. and Hendricks, M. L. (2007). Adhesive recruitment by the viscous capture threads of araneoid orb-weaving spiders. *J. Exp. Biol.* **210**, 553–560.
- Opell, B. D. and Hendricks, M. L. (2009). The adhesive delivery system of viscous capture threads spun by orb-weaving spiders. *J. Exp. Biol.* **212**, 3026–3034.
- Opell, B. D. and Hendricks, M. L. (2010). The role of granules within viscous capture threads of orb-weaving spiders. *J. Exp. Biol.* **213**, 339–346.
- Opell, B. D. and Schwend, H. S. (2007). The effect of insect surface features on the adhesion of viscous capture threads spun by orb-weaving spiders. *J. Exp. Biol.* **210**, 2352–2360.
- Opell, B. D. and Schwend, H. S. (2008). Persistent stickiness of viscous capture threads produced by araneoid orb-weaving spiders. *J. Exper. Zool.* **309A**, 11–16.
- Opell, B. D. and Schwend, H. S. (2009). Adhesive efficiency of spider prey capture threads. *Zoology* **112**, 16–26.
- Opell, B. D., Sandidge, J. S. and Bond, J. E. (2000). Exploring functional associations between spider cribella and calamistra. *J. Arachnol.* **28**, 43–48.
- Opell, B. D., Bond, J. E. and Warner, D. A. (2006). The effects of capture spiral composition and orb-web orientation on prey interception. *Zoology* **109**, 339–345.
- Opell, B. D., Markley, B. J., Hannum, C. D. and Hendricks, M. L. (2008). The contribution of axial fiber extensibility to the adhesion of viscous capture threads spun by orb-weaving spiders. *J. Exp. Biol.* **211**, 2243–2251.

- Opell, B. D., Tran, A. M. and Karinschak, S. E. (2011). Adhesive compatibility of cribellar and viscous prey capture threads and its implications for the evolution of orb-weaving spiders. *J. Exper. Zool.* **315**, 376–384.
- Ortlepp, C. S. and Gosline, J. M. (2004). Consequences of forced silking. *Biomacromolecules* **5**, 727–731.
- Ortlepp, C. and Gosline, J. M. (2008). The scaling of safety factor in spider draglines. *J. Exp. Biol.* **211**, 2832–2840.
- Osaki, S. (1996). Spider silk as mechanical lifeline. *Nature* **384**, 419.
- Pasquet, A., Ridwan, A. and Leborgne, R. (1994). Presence of potential prey affects web building in an orb-weaving spider *Zygiella x-notata*. *Anim. Behav.* **47**, 477–480.
- Peakall, D. B. (1971). Conservation of web proteins in the spider *Araneus diadematus*. *J. Exp. Zool.* **176**, 257–264.
- Peakall, D. B. and Witt, P. N. (1976). Energy budget of an orb web-building spider. *Comp. Biochem. Physiol.* **54**, 187–190.
- Perez-Miles, F., Panzera, A., Ortiz-Villatoro, D. and Perdomo, C. (2009). Silk production from tarantula feet questioned. *Nature* **461**, E9.
- Pérez-Rigueiro, J., Elices, M., Plaza, G., Real, J. I. and Guinea, G. V. (2005). The effect of spinning forces on spider silk properties. *J. Exp. Biol.* **208**, 2633–2639.
- Perry, D. J., Bittencourt, D., Siltberg-Liberles, J., Rech, E. L. and Lewis, R. V. (2010). Piriform spider silk sequences reveal unique repetitive elements. *Biomacromolecules* **11**, 3000–3006.
- Peters, H. (1937). Studien am Netz der Kreuzspinne (*Aranea diadema*). 1. Die Grundstruktur des Netzes und Beziehungen zum Bauplan des Spinnenkörpers. *Morphol. Ökol. Tiere* **33**, 128–150.
- Peters, H. M. (1990). On the structural and glandular origin of the bridging lines used by spiders for moving to distant places. *Acta Zool. Fennica* **190**, 309–314.
- Peters, H. M. (1993). Functional organization of the spinning apparatus of *Cyrtophora citricola* with regard to the evolution of the web (Araneae, Araneidae). *Zoomorphology* **113**, 153–163.
- Peters, H. M. (1995). Ultrastructure of orb spiders' gluey capture threads. *Naturwissenschaften* **82**, 380–382.
- Peterson, J. A., Romero, S. A. and Harwood, J. D. (2010). Pollen interception by linyphiid spiders in a corn agroecosystem: implications for dietary diversification and risk-assessment. *Arthr. Plant Inter.* **4**, 207–217.
- Piel, W. H. and Nutt, K. J. (1997). *Kaira* is a likely sister group to *Metepeira*, and *Zygiella* is an araneid (Araneae, Araneidae): evidence from mitochondrial DNA. *J. Arachnol.* **25**, 262–268.
- Platnick, N. I. (2011). The World Spider Catalog, Version 11.5. Online at <http://research.amnh.org/iz/spiders/catalog> (American Museum of Natural History).
- Prenter, J., Elwood, R. W. and Montgomery, W. I. (1999). Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution* **53**, 1987–1994.
- Prestwich, K. N. (1977). The energetics of web-building in spiders. *Comp. Biochem. Physiol.* **57A**, 321–326.
- Prokop, P. and Gryglakova, D. (2005). Factors affecting the foraging success of the wasp-like spider *Argiope bruennichi* (Araneae): role of web design. *Biologia* **60**, 165–169.
- Putthananat, S., Tapadia, P., Zarkoob, S., Miller, L. D., Eby, R. K. and Adams, W. W. (2004). The color of dragline silk produced in captivity by the spider *Nephila clavipes*. *Polymer* **45**, 1933–1937.
- Rao, D. (2009). Experimental evidence for the amelioration of shadow competition in an orb-web spider through the 'ricochet' effect. *Ethology* **115**, 691–697.

- Rayor, L. S. (1997). Attack strategies of predatory wasps (Hymenoptera: Pompilidae; Sphecidae) on colonial orb web-building spiders (Araneidae: *Metepeira incrassata*). *J. Kans. Entomol. Soc.* **69**, 67–75.
- Reed, C. F., Witt, P. N., Scarboro, M. B. and Peakall, D. B. (1970). Experience and the orb web. *Dev. Psychobiol.* **3**, 251–265.
- Richardson, M. L. and Hanks, L. M. (2009). Partitioning of niches among four species of orb-weaving spiders in a grassland habitat. *Environ. Entomol.* **38**, 651–656.
- Riechert, S. E. and Lockley, T. (1984). Spiders as biological-control agents. *Annu. Rev. Entomol.* **29**, 299–320.
- Riechert, S. E. and Luczak, J. (1982). Spider foraging: behavioral responses to prey. In: *Spider Communication: Mechanisms and Ecological Significance* (ed Rovner, J. S.), pp. 353–385. Princeton University Press, Princeton.
- Rind, F. C., Birkett, C. L., Duncan, B. J. A. and Ranken, A. J. (2011). Tarantulas cling to smooth vertical surfaces by secreting silk from their feet. *J. Exp. Biol.* **214**, 1874–1879.
- Risch, P. (1977). Quantitative analysis of orb web patterns in four species of spiders. *Behav. Genet.* **7**, 199–238.
- Rising, A., Hjalm, G., Engstrom, W. and Johansson, J. (2006). N-terminal nonrepetitive domain common to dragline, flagelliform, and cylindrical spider silk proteins. *Biomacromolecules* **7**, 3120–3124.
- Rittschof, C. C. and Ruggles, K. V. (2010). The complexity of site quality: multiple factors affect web tenure in an orb-web spider. *Anim. Behav.* **79**, 1147–1155.
- Robinson, M. H. (1969). Predatory behavior of *Argiope argentata* (Fabricius). *Am. Zool.* **9**, 161–173.
- Robinson, M. H. (1982). Courtship and mating-behavior in spiders. *Annu. Rev. Entomol.* **27**, 1–20.
- Robinson, M. H. and Lubin, Y. D. (1979). Specialists and generalists: the ecology and behavior of some web-building spider from Papua New Guinea. I. *Herennia ornaticissima*, *Argiope ocyaloides*, and *Arachnura melanura* (Araneae: Araneidae). *Pac. Insects* **21**, 97–132.
- Robinson, M. H. and Mirick, H. (1971). The predatory behavior of the golden-web spider *Nephila clavipes* (Aranea: Araneidae). *Psyche (Cambridge)* **78**, 123–139.
- Robinson, M. H. and Robinson, B. (1970). Stabilimentum of the orb web spider, *Argiope argentata*—an improbable defence against predators. *Can. Entomol.* **102**, 641–655.
- Robinson, M. H. and Robinson, B. (1972). Structure, possible function and origin of a remarkable ladder-web built by a New Guinea orb-web spider (Araneae- Araneidae). *J. Nat. Hist.* **6**, 687–694.
- Robinson, M. H. and Robinson, B. C. (1973a). Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithson. Contr. Zool.* **149**, 1–76.
- Robinson, M. H. and Robinson, B. C. (1973b). The stabilimenta of *Nephila clavipes* and the origins of stabilimentum-building in araneids. *Psyche (Cambridge)* **80**, 277–288.
- Robinson, B. C. and Robinson, M. H. (1974). Biology of some *Argiope* species from New Guinea—predatory behavior and stabilimentum construction (Araneae-Araneidae). *Zool. J. Linn. Soc.* **54**, 145–159.
- Robinson, M. H. and Robinson, B. (1975). Evolution beyond the orb web—web of the araneid spider *Pasilobus* sp., Its structure, operation and construction. *Zool. J. Linn. Soc.* **56**, 301–314.
- Robinson, M. H. and Robinson, B. C. (1980). Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pac. Insects Monogr.* **36**, 1–218.

- Robinson, M. H. and Valerio, C. E. (1977). Attacks on large or heavily defended prey by tropical salticid spiders. *Psyche (Cambridge)* **84**, 1–10.
- Rodríguez-Girones, M. A., Corcobado, G. and Moya-Laraño, J. (2010). Silk elasticity as a potential constraint on spider body size. *J. Theor. Biol.* **266**, 430–435.
- Ross, L. (1950). Northern Yellowthroat, *Geothlypis trichas*, caught in spider web. *Auk* **67**, 521–522.
- Rousseau, M. E., Lefevre, T. and Pezolet, M. (2009). Conformation and orientation of proteins in various types of silk fibers produced by *Nephila clavipes* Spiders. *Biomacromolecules* **10**, 2945–2953.
- Rundle, H. D. and Nosil, P. (2005). Ecological speciation. *Ecol. Lett.* **8**, 336–352.
- Rypstra, A. L. (1981). The effect of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes*. *Oikos* **37**, 179–182.
- Rypstra, A. L. (1982). Building a better insect trap—an experimental investigation of prey capture in a variety of spider webs. *Oecologia* **52**, 31–36.
- Sahni, V., Blackledge, T. A. and Dhinojwala, A. (2010). Viscoelastic solids explain spider web stickiness. *Nat. Commun.* **1**, 19, doi:10.1038/ncomms1019.
- Sahni, V., Blackledge, T. A. and Dhinojwala, A. (2011). A review on spider silk adhesion. *J. Adhesion* **87**, 595–614.
- Samu, F. and Vollrath, F. (1992). Spider orb web as bioassay for pesticide side-effects. *Entomol. Exp. Appl.* **62**, 117–124.
- Samu, F., Matthews, G. A., Lake, D. and Vollrath, F. (1992). Spider webs are efficient collectors of agrochemical spray. *Pestic. Sci.* **36**, 47–51.
- Sandoval, C. P. (1994). Plasticity in web design in the spider *Parawixia bistriata*—a response to variable prey type. *Funct. Ecol.* **8**, 701–707.
- Savage, K. N. and Gosline, J. M. (2008). The role of proline in the elastic mechanism of hydrated spider silks. *J. Exp. Biol.* **211**, 1948–1957.
- Savage, K. N., Guerette, P. A. and Gosline, J. M. (2004). Supercontraction stress in spider webs. *Biomacromolecules* **5**, 675–679.
- Scharff, N. and Coddington, J. A. (1997). A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zool. J. Linn. Soc.* **120**, 355–434.
- Scheffer, S. J., Uetz, G. W. and Stratton, G. E. (1996). Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). *Behav. Ecol. Sociobiol.* **38**, 17–23.
- Schlinger, E. I. (1987). The biology of Acroceridae. In: *Ecophysiology of Spiders* (ed Nentwig, W.), pp. 319–327. Springer-Verlag, New York.
- Schluter, D. (1998). Ecological causes of speciation. In: *Endless Forms: Species and Speciation* (eds Howard, D. J. and Berlocher, S. H.), pp. 114–129. Oxford University Press, Inc, New York.
- Schluter, D. (2001). Ecology and the origin of species. *Trends Ecol. Evol.* **16**, 372–380.
- Schneider, J. M. and Vollrath, F. (1998). The effect of prey type on the geometry of the capture web of *Araneus diadematus*. *Naturwissenschaften* **85**, 391–394.
- Schoener, T. W. and Spiller, D. A. (1992). Stabilimenta characteristics of the spider *Argiope argentata* on small islands—support of the predator defense hypothesis. *Behav. Ecol. Sociobiol.* **31**, 309–318.
- Schütt, K. (2000). The limits of the Araneoidea (Arachnida: Araneae). *Aust. J. Zool.* **48**, 135–153.
- Seah, W. K. and Li, D. (2001). Stabilimenta attract unwelcome predators to orb-webs. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 1553–1558.
- Seah, W. K. and Li, D. (2002). Stabilimentum variations in *Argiope versicolor* (Araneae: Araneidae) from Singapore. *J. Zool.* **258**, 531–540.
- Sensenig, A., Agnarsson, I. and Blackledge, T. A. (2010). Behavioural and biomaterial coevolution in spider orb webs. *J. Evol. Biol.* **23**, 1839–1856.

- Sensenig, A., Lorentz, K. A., Kelly, S. P. and Blackledge, T. A. (2011). Spider orb webs rely on radial threads to absorb prey energy. *J. Exp. Biol.* **114**, 233–238.
- Sherman, P. M. (1994). The orb web—an energetic and behavioral estimator of a spider's dynamic foraging and reproductive strategies. *Anim. Behav.* **48**, 19–34.
- Shinkai, A. and Shinkai, E. (1997). The web structure and the predatory behavior of *Wendilgarda* sp. (Araneae: Theridiosomatidae). *Acta Arachnol.* **46**, 53–60.
- Simon, E. (1864). *Histoire naturelle des araignées* (Aranéides). Librairie Encyclopédique de Roret, Paris.
- Smallwood, P. D. (1993). Web-site tenure in the Long-Jawed spider—is it risk-sensitive foraging, or conspecific interactions. *Ecology* **74**, 1826–1835.
- Smith, R. B. and Mommsen, T. P. (1984). Pollen feeding in an orb-weaving spider. *Science* **226**, 1330–1332.
- Spagna, J. C. and Gillespie, R. G. (2008). More data, fewer shifts: Molecular insights into the evolution of the spinning apparatus in non-orb-weaving spiders. *Mol. Phylogenet. Evol.* **46**, 347–368.
- Sponner, A., Unger, E., Grosse, F. and Weisshart, K. (2004). Conserved C-termini of spidroins are secreted by the major ampullate glands and retained in the silk thread. *Biomacromolecules* **5**, 840–845.
- Sponner, A., Schlott, B., Vollrath, F., Unger, E., Grosse, F. and Weisshart, K. (2005). Characterization of the protein components of *Nephila clavipes* dragline silk. *Biochemistry* **44**, 4727–4736.
- Sponner, A., Vater, W., Monajembashi, S., Unger, E., Grosse, F. and Weisshart, K. (2007). Composition and hierarchical organisation of a spider silk. *PLoS One* **2**, E998, doi:10.1371/journal.pone.0000998.
- Starks, P. T. (2002). The adaptive significance of stabilimenta in orb-webs: a hierarchical approach. *Ann. Zool. Fennici* **39**, 307–315.
- Stowe, M. K. (1978). Observation of two nocturnal orbweavers that build specialized webs: *Scoloderus cordatus* and *Wixia ectypa* (Araneae: Araneidae). *J. Arachnol.* **6**, 141–146.
- Stowe, M. K. (1986). Prey specialization in the Araneidae. In: *Spiders, Webs, Behavior, and Evolution* (ed Shear, W. A.), pp. 101–131. Stanford University Press, Stanford.
- Stowe, M. K., Tumlinson, J. H. and Heath, R. R. (1987). Chemical mimicry: bolas spiders emit components of moth prey species sex pheromones. *Science* **236**, 964–967.
- Suter, R. B. (1978). *Cyclosa turbinata* (Araneae, Araneidae)—prey discrimination via web-borne vibrations. *Behav. Ecol. Sociobiol.* **3**, 283–296.
- Suter, R. B. (1991). Ballooning in spiders—results of wind tunnel experiments. *Ethol. Ecol. Evol.* **3**, 13–25.
- Swanson, B. O., Blackledge, T. A., Beltrán, J. and Hayashi, C. Y. (2006a). Variation in the material properties of spider dragline silk across species. *Appl. Phys. A Mater. Sci. Process.* **82**, 213–218.
- Swanson, B. O., Blackledge, T. A., Summers, A. P. and Hayashi, C. Y. (2006b). Spider dragline silk: correlated and mosaic evolution in high performance biological materials. *Evolution* **60**, 2539–2551.
- Swanson, B. O., Blackledge, T. A. and Hayashi, C. Y. (2007). Spider capture silk: performance implications of variation in an exceptional biomaterial. *J. Exp. Zool. A Ecol. Genet. Physiol.* **307A**, 654–666.
- Tan, E. J., Seah, S. W. H., Yap, L.-M. Y. L., Goh, P. M., Gan, W., Liu, F. and Li, D. (2010). Why do orb-weaving spiders (*Cyclosa ginnaga*) decorate their webs with silk spirals and plant detritus? *Anim. Behav.* **79**, 179–186.
- Tanaka, K. (1989). Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. *Oecologia (Berlin)* **81**, 459–464.

- Thery, M. and Casas, J. (2009). The multiple disguises of spiders: web colour and decorations, body colour and movement. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 471–480.
- Timm, R. M. and Losilla, M. (2007). Orb-weaving spider, *Argiope savignyi* (Araneidae), predation on the proboscis bat *Rhynchonycteris naso* (Emballonuridae). *Caribbean J. Sci.* **43**, 282–284.
- Tolbert, W. W. (1974). Aerial dispersal behavior of two orb weaving spiders. *Psyche (Cambridge)* **84**, 13–27.
- Tolbert, W. W. (1975). Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *Psyche (Cambridge)* **82**, 29–52.
- Townley, M. A. and Tillinghast, E. K. (1988). Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component, gabamide. *J. Arachnol.* **16**, 303–319.
- Townley, M. A., Tillinghast, E. K. and Cherim, N. A. (1993). Molt-related changes in ampullate silk gland morphology and usage in the araneid spider *Araneus cavaticus*. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **340**, 25–38.
- Townley, M. A., Tillinghast, E. K. and Neefus, C. D. (2006). Changes in composition of spider orb web sticky droplets with starvation and web removal, and synthesis of sticky droplet compounds. *J. Exp. Biol.* **209**, 1463–1486.
- Traw, M. B. (1995). A revision of the neotropical orb-weaving spider genus *Scoloderus* (Araneae: Araneidae). *Psyche (Cambridge)* **102**, 49–72.
- Tseng, L. and Tso, I. M. (2009). A risky defence by a spider using conspicuous decoys resembling itself in appearance. *Anim. Behav.* **78**, 425–431.
- Tso, I. M. (1999). Behavioral response of *Argiope trifasciata* to recent foraging gain: a manipulative study. *Am. Midl. Nat.* **141**, 238–246.
- Tso, I. M. (2004). The effect of food and silk reserve manipulation on decoration-building of *Argiope aetheroides*. *Behaviour* **141**, 603–616.
- Tso, I. M., Wu, H. C. and Hwang, I. R. (2005). Giant wood spider *Nephila pilipes* alters silk protein in response to prey variation. *J. Exp. Biol.* **208**, 1053–1061.
- Tso, I. M., Huang, J. P. and Liao, C. P. (2007a). Nocturnal hunting of a brightly coloured sit-and-wait predator. *Anim. Behav.* **74**, 787–793.
- Tso, I. M., Jiang, S. Y. and Blackledge, T. A. (2007b). Does the giant wood spider *Nephila pilipes* respond to prey variation by altering web or silk properties? *Ethology* **113**, 324–333.
- Tsychenko, V. P. (1986). New confirmation of the convergent origin of orb webs in cribellate and cribellate spiders. *Dokl. Akad. Nauk SSSR* **287**, 1270–1273.
- Turnbull, A. L. (1973). Ecology of the true spiders (Araneomorphae). *Annu. Rev. Entomol.* **18**, 305–348.
- Uetz, G. W. (1989). The "ricochet effect" and prey capture in colonial spiders. *Oecologia* **81**, 154–159.
- Uetz, G. W. and Hartsock, S. P. (1987). Prey selection in an orb-weaving spider: *Micrathena gracilis* (Araneae: Araneidae). *Psyche* **94**, 103–116.
- Uhl, G. (2008). Size dependent occurrence of different types of web decorations and a barrier web in the tropical spider *Argiope argentata* (Fabricius 1775) (Araneae Araneidae). *Trop. Zool.* **21**, 97–108.
- Uma, D. B. and Weiss, M. R. (2010). Chemical mediation of prey recognition by spider-hunting wasps. *Ethology* **116**, 85–95.
- Van Nimmen, E., Gellynck, K., Gheysens, T., Van Langenhove, L. and Mertens, J. (2005). Modeling of the stress-strain behavior of egg sac silk of the spider *Araneus diadematus*. *J. Arachnol.* **33**, 629–639.

- Van Nimmen, E., Gellynck, K., Van Langenhove, L. and Mertens, J. (2006). The tensile properties of cocoon silk of the spider *Araneus diadematus*. *Text. Res. J.* **76**, 619–628.
- Vanderhoff, E. N., Byers, C. J. and Hanna, C. J. (2008). Do the color and pattern of *Micrathena gracilis* (Araneae: Araneidae) attract prey? Examination of the prey attraction hypothesis and crypsis. *J. Insect Behav.* **21**, 469–475.
- Vasanthavada, K., Hu, X., Falick, A. M., La Mattina, C., Moore, A. M. F., Jones, P. R., Yee, R., Reza, R., Tuton, T. and Vierra, C. (2007). Aciniform spidroin, a constituent of egg case sacs and wrapping silk fibers from the black widow spider *Latrodectus hesperus*. *J. Biol. Chem.* **282**, 35088–35097.
- Venner, S. and Casas, J. (2005). Spider webs designed for rare but life-saving catches. *Proc. R. Soc. B.* **272**, 1587–1592.
- Venner, S., Pasquet, A. and Leborgne, R. (2000). Web-building behaviour in the orb-weaving spider *Zygiella x-notata*: influence of experience. *Anim. Behav.* **59**, 603–611.
- Venner, S., Thevenard, L., Pasquet, A. and Leborgne, R. (2001). Estimation of the web's capture thread length in orb-weaving spiders: determining the most efficient formula. *Ann. Entomol. Soc. Am.* **94**, 490–496.
- Venner, S., Bel-Venner, M. C., Pasquet, A. and Leborgne, R. (2003). Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zygiella x-notata*. *Naturwissenschaften* **90**, 269–272.
- Venner, S., Chades, I., Bel-Venner, M. C., Pasquet, A., Charpillet, F. and Leborgne, R. (2006). Dynamic optimization over infinite-time horizon: web-building strategy in an orb-weaving spider as a case study. *J. Theor. Biol.* **241**, 725–733.
- Via, S. (2001). Sympatric speciation in animals: the ugly duckling grows up. *Trends Ecol. Evol.* **16**, 381–390.
- Vogelei, A. and Greissl, R. (1989). Survival strategies of the crab spider *Thomisus onustus* Walckenaer 1806 (Chelicerata, Arachnida, Thomisidae). *Oecologia* **80**, 513–515.
- Vollrath, F. (1984). Kleptobiotic interactions in invertebrates. In: *Producers and Scroungers: Strategies of Exploitation and Parasitism* (ed Barnes, C. J.), pp. 61–94. Chapman & Hall, New York.
- Vollrath, F. (1985). Web spider's dilemma—a risky move or site dependent growth. *Oecologia* **68**, 69–72.
- Vollrath, F. (1998). Dwarf males. *Trends Ecol. Evol.* **13**, 159–163.
- Vollrath, F. and Edmonds, D. T. (1989). Modulation of the mechanical properties of spider silk by coating with water. *Nature* **340**, 305–307.
- Vollrath, F. and Knight, D. P. (1999). Structure and function of the silk production pathway in the spider *Nephila edulis*. *Int. J. Biol. Macromol.* **24**, 243–249.
- Vollrath, F. and Knight, D. P. (2001). Liquid crystalline spinning of spider silk. *Nature* **410**, 541–548.
- Vollrath, F. and Köhler, T. (1996). Mechanics of silk produced by loaded spiders. *Proc. R. Soc. Lond. B Biol. Sci.* **263**, 387–391.
- Vollrath, F. and Parker, G. A. (1992). Sexual dimorphism and distorted sex-ratios in spiders. *Nature* **360**, 156–159.
- Vollrath, F. and Samu, F. (1997). The effect of starvation on web geometry in an orb-weaving spider. *Bull. Br. Arachnol. Soc.* **10**, 295–298.
- Vollrath, F. and Selden, P. (2007). The role of behavior in the evolution of spiders, silks, and webs. *Annu. Rev. Ecol. Evol. Syst.* **38**, 819–846.
- Vollrath, F. and Tillinghast, E. K. (1991). Glycoprotein glue beneath a spider web's aqueous coat. *Naturwissenschaften* **78**, 557–559.
- Vollrath, F., Fairbrother, W. J., Williams, R. J. P., Tillinghast, E. K., Bernstein, D. T., Gallagher, K. S. and Townley, M. A. (1990). Compounds in the droplets of the orb spider's viscid spiral. *Nature* **345**, 526–528.

- Vollrath, F., Downes, M. and Krachkov, S. (1997). Design variability in web geometry of an orb-weaving spider. *Physiol. Behav.* **62**, 735–743.
- Vollrath, F., Knight, D. P. and Hu, X. W. (1998). Silk production in a spider involves acid bath treatment. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 817–820.
- Vollrath, F., Madsen, B. and Shao, Z. Z. (2001). The effect of spinning conditions on the mechanics of a spider's dragline silk. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 2339–2346.
- Walter, A., Elgar, M. A., Bliss, P. and Moritz, R. F. A. (2008). Molting interferes with web decorating behavior in *Argiope keyserlingi* (Araneae, Araneidae). *J. Arachnol.* **36**, 538–544.
- Walter, A., Bliss, P., Elgar, M. A. and Moritz, R. F. A. (2009). *Argiope bruennichi* shows a drinking-like behaviour in web hub decorations (Araneae, Araneidae). *J. Ethol.* **27**, 25–29.
- Watanabe, T. (1999). Prey attraction as a possible function of the silk decoration of the uloborid spider *Octonoba sybotides*. *Behav. Ecol.* **10**, 607–611.
- Watanabe, T. (2000). Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 565–569.
- Watanabe, T. (2001). Effects of web design on the prey capture efficiency of the uloborid spider *Octonoba sybotides* under abundant and limited prey conditions. *Zool. Sci.* **18**, 585–590.
- Wehner, R. (1981). Spatial vision in arthropods. In: *Handbook of Sensory Physiology VII (6c)* (ed Autrum, H.), pp. 287–615. Springer-Verlag, New York.
- Weng, J. L. and Barrantes, G. (2007). Natural history and larval behavior of the parasitoid *Zatypota petronae* (Hymenoptera: Ichneumonidae). *J. Hymenopt. Res.* **16**, 326–335.
- Wherry, T. and Elwood, R. W. (2009). Relocation, reproduction and remaining alive in the orb-web spider. *J. Zool.* **279**, 57–63.
- Whitehouse, M. (2011). Kleptoparasitic spiders of the subfamily Argyrocinidae: a special case of behavioral plasticity. In: *Spider Behaviour: Flexibility and Versatility* (ed Herberstein, M. E.), pp. 348–387. Cambridge University Press, New York.
- Whitehouse, M., Agnarsson, I., Miyashita, T., Smith, D., Cangialosi, K., Masumoto, T., Li, D. Q. and Henaut, Y. (2002). *Argyrodes*: phylogeny, sociality and interspecific interactions—a report on the *Argyrodes* symposium, Badplaas 2001. *J. Arachnol.* **30**, 238–245.
- Wise, D. H. (1993). *Spiders in ecological webs*. Cambridge University Press, New York.
- Witt, P. N., Reed, C. F. and Peakall, D. B. (1968). *A Spider's Web*. Springer Verlag, Berlin.
- Work, R. W. (1981). A comparative study of the supercontraction of major ampullate silk fibers of orb web-building spiders (Araneae). *J. Arachnol.* **9**, 299–308.
- Wunderlich, J. (2004). Fossil spiders in amber and copal. Conclusions, revisions, new taxa and family diagnoses of fossil and extant taxa. *Beiträge Araneol.* **3A-B**, 1–1908.
- Xu, M. and Lewis, R. V. (1990). Structure of a protein superfiber—spider dragline silk. *Proc. Natl. Acad. Sci. USA* **87**, 7120–7124.
- Yeagan, K. V. (1994). Biology of bolas spiders. *Annu. Rev. Entomol.* **39**, 81–99.
- Zax, D. B., Armanios, D. E., Horak, S., Malowniak, C. and Yang, Z. T. (2004). Variation of mechanical properties with amino acid content in the silk of *Nephila clavipes*. *Biomacromolecules* **5**, 732–738.
- Zevenbergen, J. M., Schneider, N. K. and Blackledge, T. A. (2008). Fine dining or fortress? Functional shifts in spider web architecture by the western black widow *Latrodectus hesperus*. *Anim. Behav.* **76**, 823–829.
- Zheng, Y. M., Bai, H., Huang, Z. B., Tian, X. L., Nie, F. Q., Zhao, Y., Zhai, J. and Jiang, L. (2010). Directional water collection on wetted spider silk. *Nature* **463**, 640–643.

- Zschokke, S. (1999). Nomenclature of the orb-web. *J. Arachnol.* **27**, 542–546.
- Zschokke, S. (2002). Ultraviolet reflectance of spiders and their webs. *J. Arachnol.* **30**, 246–254.
- Zschokke, S. and Vollrath, F. (1995a). Unfreezing the behaviour of two orb spiders. *Physiol. Behav.* **58**, 1167–1173.
- Zschokke, S. and Vollrath, F. (1995b). Web construction patterns in a range of orb-weaving spiders (Araneae). *Eur. J. Entomol.* **92**, 523–541.
- Zschokke, S., Henaut, Y., Benjamin, S. P. and Garcia-Ballinas, J. A. (2006). Prey-capture strategies in sympatric web-building spiders. *Can. J. Zool./Rev. Can. Zool.* **84**, 964–973.