

Does body size predict foraging effort? Patterns of material investment in spider orb webs

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Abstract

Body size affects almost all aspects of animals' resource use, and its scaling syntheses are well established in most biological fields. In contrast, how behavioral variation scales with body size is understudied. Understanding how body size influences behavior is important as behavior responds more readily to natural selection than many other traits, and foraging effort is a critical behavioral trait. Web spiders are good models for studying foraging effort because webs are physical records of behaviors. Variability in web architectures is well documented, but how spider size scales with foraging effort and web performance is virtually unknown. Here, we investigate behavioral allometry at three phylogenetic scales – broadly across orb-weaving spiders, among a recent radiation of species, and among individuals within species. Conducting a meta-analysis across a wide range of orb weavers, we investigate how foraging effort scales with body size by measuring effort as the volumes of the three silk gland secretions used for building orb webs. We show that volumes of web material scale negatively allometrically with body size, and suggest silk investment is an important limiting factor in evolution of web performance and body size. To assess whether such broad evolutionary trends exist at finer phylogenetic scales, we investigated how foraging effort scales with body size in a group of five closely related *Zygiella* s.l. species (Araneidae). We find that the general scaling pattern across orb weavers is only partially confirmed. Finally, we examine patterns among individuals within each of the *Zygiella* species. We find different patterns of silk use in relation to body size, and show that both web architecture and silk investment need to be quantified to estimate total foraging effort. In conclusion, we find support for the prediction that behavioral traits scale differently to body size at different phylogenetic scales and at the individual level.

Introduction

Body size affects practically all aspects of how animals use environmental resources. Body size scaling syntheses are well established in most biological fields, ranging from morphology, physiology and developmental biology, to life-history evolution, community ecology and biogeography (Dial, Greene & Irschick, 2008). However, the degree to which behavioral traits scale with body size is understudied, in part because behavioral phenotypes are derived from complex interactions between physiology and morphology, both of which are often easier to measure (Dial *et al.*, 2008). Understanding how body size influences behavior is important because behavior responds to natural selection more quickly

than other traits (West-Eberhard, 1989; Garland & Kelly, 2006). Foraging effort is a behavioral trait that plays a critical role in maximizing the fitness of animals (Lima & Dill, 1990; Ferrari, Sih & Chivers, 2009). Therefore, it is critical to understand how foraging effort might scale with body size. But foraging 'effort' per se can be hard to quantify. Orb web-building spiders are an exception because of their intimate dependence upon the web for prey capture. The architectures of orb webs represent physical records of the spiders' foraging behaviors (Blackledge, Kuntner & Agnarsson, 2011; Herberstein & Tso, 2011). More important, the total amount of silk used to construct an orb web is a direct measure of the material investment in foraging by the spider.

Webs vary greatly among spider groups and even within species (Eberhard, Agnarsson & Levi, 2008; Blackledge *et al.*, 2009). Changes in web architecture and silk mechanics critically influence web performance and thus the spiders' phenotypic performance (Blackledge *et al.*, 2011). However, while larger spider species use more silk, it is not entirely clear how silk amount scales with spider size, that is, whether different species produce proportionally similar amounts of silk in relation to body size. Furthermore, spiders change web architecture throughout their ontogeny (Eberhard, Barrantes & Madrigal-Brenes, 2008; Kuntner, Kralj-Fišer & Gregorič, 2010), and according to their size and feeding history (Blackledge *et al.*, 2011). They are also quite plastic within individual life stages. Orb spiders can increase or decrease the size of webs (Sherman, 1994; Venner, Pasquet & Leborgne, 2000; Blackledge & Zevenbergen, 2007), change the webs' symmetry (Herberstein & Heiling, 1999; Harmer, 2009; Kuntner, Gregorič & Li, 2010) and molecular composition of their silks (Tso, Wu & Hwang, 2005; Townley, Tillinghast & Neefus, 2006), 'decorate' their webs with additional silk structures (Blackledge, 1998; Li & Lee, 2004) and build protective barrier webs (Higgins, 1992; Uhl, 2008). However, only a single study investigated how spider size scales with foraging effort and web performance through ontogeny of a single orb-weaving spider species (Sensenig, Agnarsson & Blackledge, 2011). Even less is known of how variation in spider webs scales with body size. Craig (1987a) showed that larger orb web species use thicker threads, and Sensenig, Agnarsson & Blackledge (2010a) showed that larger species of orb web spiders evolved tougher silk concurrently with changes in silk structure and web architectures that maximize the stopping potentials of the orb webs.

Most studies investigating foraging effort in spiders used orb webs because of their straightforward architecture. Orb spiders also show a greater range of size variation compared with spiders spinning other types of webs such as cobwebs or aerial sheet webs. Perhaps more than any other type of web, orb webs function mainly as foraging devices, and the size and availability of prey are considered proximal cues inducing variability in orb webs (Vollrath & Selden, 2007; Blackledge, 2011). To provide initial insight into whether body size predicts material investment (as a measure of foraging effort) in orb web spiders, we examined the silk investment in orb webs in relation to body size in five closely related species of *Zygiella* sensu lato. We quantified the total volume of all three primary spinning gland secretions that spiders use for building orb webs: the major ampullate silk (MA silk), the flagelliform silk (Flag silk) and glue produced by aggregate glands. The radial threads of an orb web mainly consist of MA silk and function to stop the prey's flight, while the spiraling Flag silk coated with glue forms the sticky capture spiral that functions to retain prey (Figs 1 and 2; Sensenig *et al.*, 2012). Conducting a meta-analysis of 27 orb-weaving species, we first investigated how foraging effort scaled with body size across a wide range of orb weavers. To assess whether such interspecific trends were confirmed on a smaller phylogenetic scale, as well as between individuals within species, we investigated how foraging effort scaled with body size in a group of five closely

related *Zygiella* s.l. species. Our study addresses another important aspect of how to assess material investment in orb web spiders. Namely, most previous studies investigating foraging effort document only changes in web shape and architecture (e.g. Sherman, 1994; Vollrath & Samu, 1997; Venner *et al.*, 2000; Mayntz, Toft & Vollrath, 2009; Blamires, 2010). Relatively few studies examine how variability in orb web production is associated with the manipulation of single silk threads (e.g. diameter, tension etc.; Watanabe, 2000; Tso, Chiang & Blackledge, 2007; Liao, Chi & Tso, 2009; but see Blackledge & Zevenbergen, 2007; Boutry & Blackledge, 2008, 2009 for studies on cob web spiders). Furthermore, except for the single study of Sensenig *et al.* (2011), no study investigating foraging effort in orb web spiders explores both web architecture and silk thread use, although such information is critical for understanding spider foraging effort. For example, if individual spiders change web characteristics such as web size, the spacing between threads, or the total thread lengths, these changes do not necessarily correlate to foraging effort measured as amount of silk produced, as spiders can also control the diameter of silk threads and the amount of glue used (Blackledge, Cardullo & Hayashi, 2005; Boutry & Blackledge, 2008; Sensenig *et al.*, 2010b). Thus, in theory, a spider could produce a web twice the surface area using the same amount of silk, simply by producing longer and thinner threads. These two webs would consequently function very differently at intercepting and stopping flying insects. Because orb webs likely reflect a trade-off between high material costs of producing silk and catching efficiency (Zschokke *et al.*, 2006; Blackledge *et al.*, 2011), information about the interaction between web architecture and the investment in silk is critical for understanding the functional consequences of variation in webs. In addition to investigating the total material investment into foraging, we thus explored changes in several features of web architecture and silk investment in relation to body size.

Materials and methods

We collected novel data from five species of *Zygiella* s.l. (*Leviellus* + *Parazygiella* + *Stroemiellus* + *Zygiella*) and considered them in the context with previously published data from Sensenig *et al.* (2010a).

Field work and sample preparation

We sampled 18 webs of *Leviellus thorelli*, 10 webs of *Parazygiella montana*, 22 webs of *Stroemiellus stroemi*, 20 webs of *Zygiella keyserlingi* and 18 webs of *Zygiella x-notata* at six localities in Slovenia, from 7 September 2009 to 25 October 2009. In the field, we haphazardly selected webs of adult females, measured their horizontal and vertical diameters (Fig. 2a,b), and photographed them from a perpendicular angle to subsequently measure other web proportions and count threads (see 'Web measurements' for details). We then separately sampled the lower and upper halves of each web, where we sampled two radial threads and four outermost capture threads per each web part, summing up to four radial

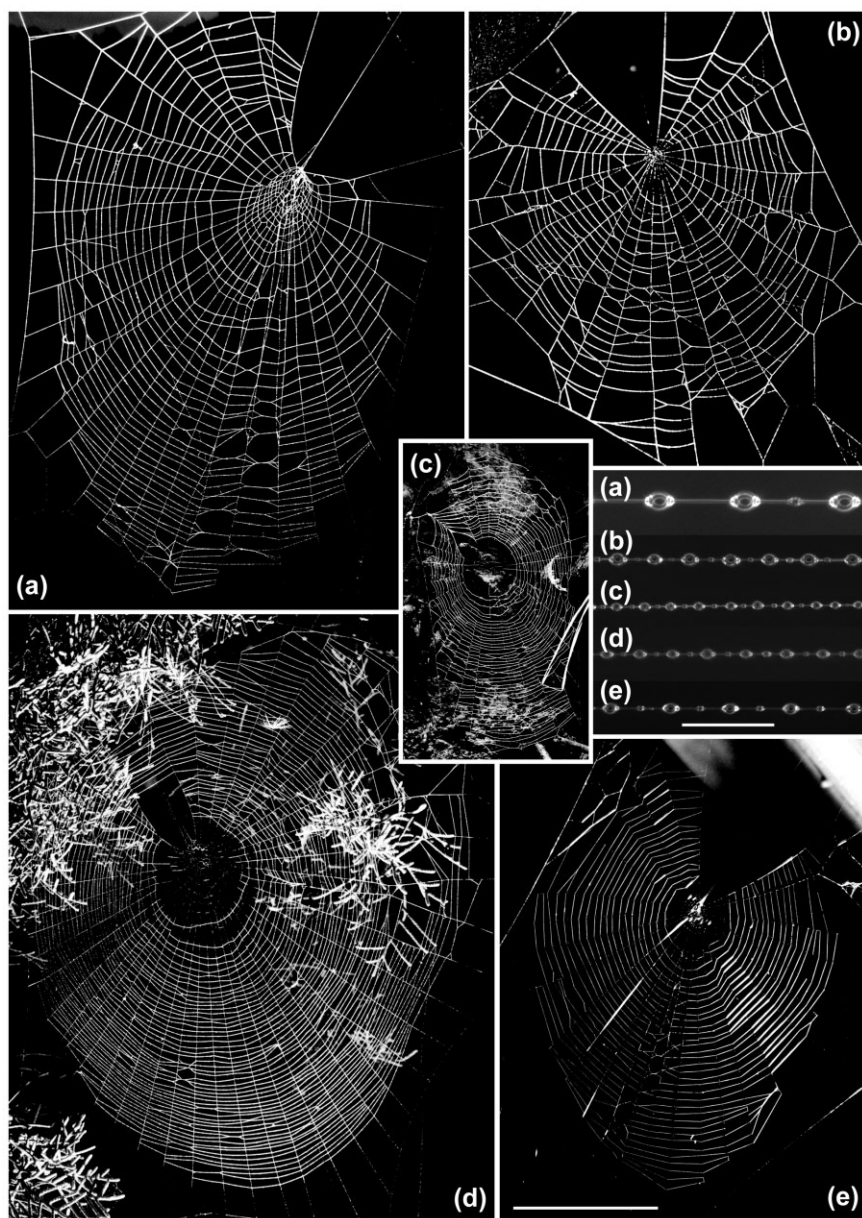


Figure 1 Orb webs and capture threads (inset, right) representing investigated species. (a–e) *L. thorelli*, *P. montana*, *S. stroemi*, *Z. keyserlingi* and *Z. x-notata*, respectively. Scale bars, 5 cm for webs and 150 μm for capture threads.

and eight capture threads per web (Fig. 2). We used microscope glass slides with stripes of raised support to preserve glue droplets. Also, note that ‘capture thread’ refers to the glue coated capture spiral between two adjacent radial threads.

We photographed all sampled capture threads using a Leica MZ16 stereomicroscope equipped with a Leica DFC 420C camera (Leica Microsystems, Wetzlar, Germany), at various magnifications such that at least 10 glue droplets were visible for each capture thread, in order to measure the number and size of glue droplets. We processed all samples at the same time in the same laboratory with a humidity of ~50% (capture threads ‘acclimatize’ to local humidity within

2–3 min), which resembled natural conditions and is comparable with other studies (Sensenig *et al.*, 2010a). In order to visualize the Flag strands constituting capture threads, we glued all samples to the microscope glass slides. We then photographed all radial and capture threads on two different locations, under 1000 \times magnification, to later estimate the diameters of MA and Flag strands constituting radial and capture threads, respectively (Blackledge *et al.*, 2005; see ‘Silk and glue quantification’ for details).

We measured carapace width as a measure of spider size. To infer whether body mass correlates with body size, we used abdomen volume as a measure of body mass (Jakob, Marshall & Uetz, 1996). We measured the width (AW), length (AL) and

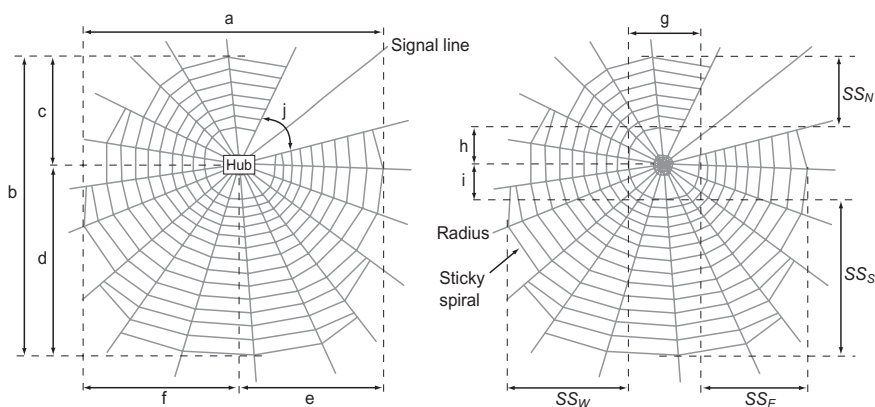


Figure 2 The architecture of a typical *Zygiella* s.l. web with measured parameters: a = web width; b = web height; c = hub to top; d = hub to bottom; e = hub to east side; f = hub to west side; g = free zone width; h = hub to capture thread above; i = hub to capture thread below; j = free-sector angle; SS_N , SS_S , SS_E , SS_W , number of capture threads north, south, east and west of hub, respectively.

height (AH) of each spider abdomen in order to calculate abdomen volume using the formula:

$$V_{abdomen} = \frac{4}{3} \cdot \pi \cdot \frac{AW \cdot AL \cdot AH}{2}$$

Web architecture quantification

From web photographs, we measured the distance from the hub to the outermost capture thread along all four axes (Fig. 2c–f), the horizontal and vertical diameters of the web hubs (Fig. 2g–i), counted radial threads (R_N ; Fig. 2), and counted capture threads on the four web axes (Fig. 2 SS_N , SS_E , SS_S , SS_W). Because webs of *Zygiella* s.l. mostly contain a capture thread free sector (Gregorič, Kostanjšek & Kuntner, 2010), we also measured its angle when present (Fig. 2j).

To quantify web architecture, we then calculated the following indices: Capture area (CA), that is, the area covered by capture threads, was calculated using the Ellipse–Hub formula (Blackledge & Gillespie, 2002) that we adjusted for free-sector webs:

$$CA = \frac{a}{2} \cdot \frac{b}{2} \cdot \pi - \frac{g}{2} \cdot \frac{(h+i)}{2} \cdot \pi - \pi \cdot c^2 \cdot \frac{j}{360}$$

The average mesh width (MW), that is, the average distance between adjacent capture threads, was calculated following Herberstein & Tso (2000):

$$MW = \frac{\frac{c-h}{SS_N-1} + \frac{d-i}{SS_S-1} + \frac{f-g}{SS_W-1} + \frac{e-g}{SS_E-1}}{4}$$

The total length of capture threads in the web was calculated using the ‘Capture thread length formula’ (CTL; Sherman, 1994; Sensenig *et al.*, 2010a) that we adjusted for free-sector webs:

$$CTL = \left(\pi - \frac{j_{(rad)}}{2} \right) \cdot \frac{SS_N + SS_E + SS_S + SS_W}{4} \cdot \left(\frac{a+b}{4} - \frac{g+h+i}{4} \right)$$

Silk and glue quantification

We estimated the cross-sectional areas of silks and sizes of glue droplets from photographs. Radial threads in *Zygiella* s.l. consist of four strands of major ampullate (MA) silk and four strands of minor ampullate silk. Because minor ampullate silk strands are much thinner than MA silk strands and thus add little to the total silk volume (Blackledge, Agnarsson & Kuntner, 2011), we measured only MA silk strands to calculate the total volume of invested radial silk. For each radial thread, we thus measured the diameter of all four MA silk strands on two parts of each radial thread. Capture threads consist of two strands of flagelliform (Flag) silk coated with glue. To calculate the total volume of invested Flag silk, we measured the diameter of both Flag silk strands on two parts of each capture thread. In order to maintain consistency with Sensenig *et al.* (2010a) we then calculated a ‘single strand equivalent’ diameter (SSE) that had the same total cross-sectional area as all of the strands composing an actual radial or capture thread. To calculate SSE for MA (d_{MA}) and Flag (d_{Flag}) silk threads, we used the average of all the measured diameters of strands in a thread in the following formulae:

$$d_{MA} = 4 \cdot r_{MAst}$$

$$d_{Flag} = 2 \cdot \sqrt{2} \cdot r_{Fst}$$

where r_{MAst} was the average measured radius of a single MA strand, and r_{Fst} was the average measured radius of a single Flag silk strand.

Following Sensenig *et al.* (2010a), we calculated the total volume of invested MA (V_{MA}) and Flag (V_{Flag}) silk using the formulae

$$V_{MA} = \frac{a+b}{4} \cdot R_N \cdot \pi \cdot \left(\frac{d_{MA}}{2} \right)^2$$

$$V_{Flag} = CTL \cdot \pi \cdot \left(\frac{d_{Flag}}{2} \right)^2$$

When orb web spiders build the capture thread, they coat the two Flag strands with glue excreted from aggregate glands. The glue coating then takes up atmospheric water and forms into glue droplets according to the diameter of the Flag thread and the glue coating volume, typically forming alternating larger and smaller droplets (Opell *et al.*, 2008; Blackledge *et al.*, 2011). To calculate the total volume of invested glue, we measured only larger glue droplets because the smaller ones represent a negligible amount of glue and their presence is variable (Opell *et al.*, 2008). We measured the average droplet distance (DD) among at least 10 glue droplets per capture thread, as well as the length and width of two haphazardly chosen glue droplets for every capture thread. Following Opell *et al.* (2008), we calculated the volume of a single glue droplet (SDV) using the formula

$$SDV = \frac{2 \cdot \pi \cdot \text{droplet width}^2 \cdot \text{droplet length}}{15}$$

Following Sensenig *et al.* (2011), we calculated the total volume of invested glue using the formula

$$V_G = SDV \cdot \frac{CTL}{DD}$$

Phylogenetic allometry among orb spiders

To investigate how the volumes of materials scale among orb-weaving spiders, we included data for 22 species (Supporting Information Appendix S2), published by Sensenig *et al.* (2010a), performed linear regression and then investigated the slopes of the regression lines (see ‘Allometry data analysis’ for details). To confirm that our allometry analysis corresponds to evolutionary correlation of spider size and foraging effort, we performed phylogenetically independent contrasts (PIC; Felsenstein, 1985) through the PDAP package (Midford, Garland & Maddison, 2002), implemented in Mesquite (Maddison & Maddison, 2013). We manually constructed the phylogeny used for PIC based on the phylogenies of Sensenig *et al.* (2010a) and Gregorič (unpubl. data).

Phylogenetic allometry in a recent radiation

To investigate how the volumes of materials scale among the five *Zygiella* s.l. species, we performed linear regression and then investigated the slopes of the regression lines (see ‘Allometry data analysis’ for details). We used medians as species values because the number of individuals measured for each species was not equal, and because the distribution of data was not always normal.

Individual allometry

We checked all data for normality using Kolmogorov–Smirnov tests. Because the distribution of data was not always normal, we used the Kruskal–Wallis test and Mann–

Whitney U -tests, including Bonferroni correction, to compare absolute silk and glue investment among the five *Zygiella* s.l. species. We did not normalize data for these tests in order to enable direct comparison of our results with other studies.

To investigate how the volumes of materials scale among individuals of the five *Zygiella* s.l. species, we performed linear regression and then investigated the slopes of the regression lines (see ‘Allometry data analysis’ for details). To investigate how spider size of individuals correlates with details in their web architecture and silk use, we normalized data by \log_{10} -transforming them, and then used Pearson’s correlation. All statistics were done in PASW 18 (Field, 2005).

Allometry data analysis

For all tests except PIC (Felsenstein, 1985), we \log_{10} -transformed all data to normalize them and give a linear relationship of compared quantities. Log-transforming both axes later enabled easier analysis of the slope of the linear functions fitting our data.

To test whether volumes of invested materials correlated with carapace width (spider size), we performed linear regression and then investigated the slopes of the regression lines. In a linear function where y is the log of silk volume and x is the log of carapace width

$$\log y = m \cdot \log x + \log b,$$

‘ m ’ conveys how silk investment changes with body size. Because we compared a linear measure of spider size (log carapace length) with a cubic measure of invested material (log silk volume), the isometric slope for such a log/log relationship equals three. Thus, if a linear function has a slope of $m = 3$, the investment of a material increases at an isometric rate with body size. If $m < 3$ or $m > 3$, the investment of a material allometrically increases at a slower (negatively allometrically) or faster (positively allometrically) rate, respectively. Instead of the logarithmic form, the relationship between two measured quantities could also be expressed in a non-logarithmic form, the form of a power law

$$y = b \cdot x^m$$

and in both cases m represents the scaling exponent.

To calculate if the slope of the linear function fitting our data significantly deviates from the isometric slope ($m = 3$), we used the formula

$$t = \left| \frac{(m-3)}{SE} \right|$$

where m is the slope of the linear function fitting our data. We used the calculated t to subsequently calculate the significance.

All statistics, except PIC, were done in PASW 18 (Field, 2005).

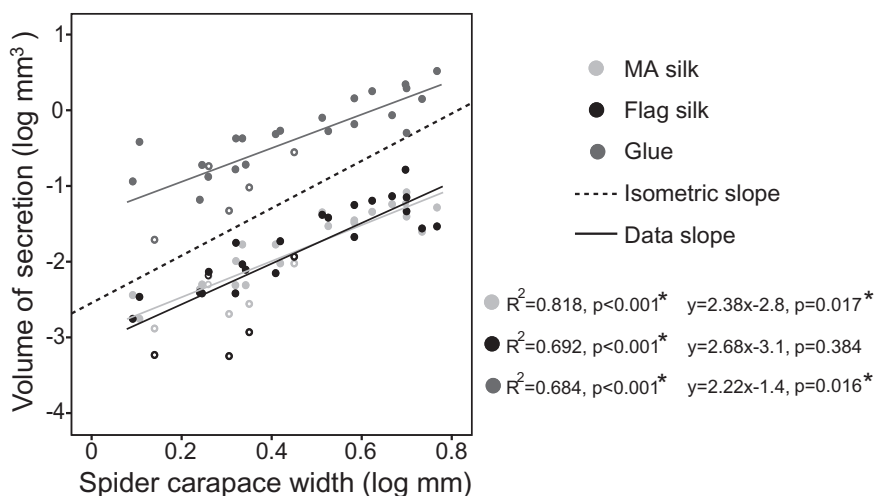


Figure 3 Correlations of major ampullate (radial threads) silk volume, flagelliform (capture silk threads) silk volume and glue with spider carapace width across 27 orb web spider species. In the linear function $y = m \cdot x + b$, 'm' represents its slope and 'x' represents the log of spider size. *P*-values next to linear functions represent the significance of whether the slope of linear function fitting our data differs significantly from the isometry slope $m = 3$ (dashed line). Significant correlations are marked using asterisk. Open circles denote the five *Zygiella* investigated here.

Results

Phylogenetic allometry among orb spiders

In the analysis combining the newly investigated *Zygiella* s.l. species with the 22 species investigated by Sensenig *et al.* (2010a), the investment of both silk types and glue increased slightly slower than carapace width (as a measure of spider size), respectively (Fig. 3). Although the correlations and the slopes of linear functions fitting these data were similar for all three materials, the linear function of the MA silk and glue volumes significantly differed from isometry, while this was not the case for Flag silk volume (Fig. 3). We additionally performed Felsenstein's independent contrasts (Felsenstein, 1985) and confirmed high evolutionary correlation of spider size and amount of invested web materials: MA silk ($P = 0.029$; $r = 0.847$), Flag silk ($P = 0.029$; $r = 0.689$) and glue ($P = 0.002$; $r = 0.784$) amounts all positively correlated with spider size.

Phylogenetic allometry in a recent radiation

The volumes of materials that the investigated *Zygiella* s.l. species use for building webs varied between species (Fig. 1; Supporting Information Appendix S1). *L. thorelli* used more MA and Flag silk than all other species, followed by *Z. keyserlingi* that used more MA and Flag silk than *P. montana*, *S. stroemi* and *Z. x-notata*. *L. thorelli* and *Z. keyserlingi* used more glue than other species. *P. montana* and *S. stroemi* used the least MA and Flag silk, and glue. While web architecture, for example, web size and symmetry, radial and capture thread counts, etc., characteristically vary between the five *Zygiella* s.l. species (Gregorič *et al.*, 2010), our results show that these species also used silk threads and glue droplets of significantly different sizes (Supporting Information Appendix S1).

While the investment of silks and glue increased slightly slower than spider size across the 22 orb-weaving species

(Fig. 3), none of the material volumes correlated with spider size across the five investigated *Zygiella* s.l. species. However, the slopes of linear functions fitting our data indicated an isometric or slightly negatively allometric relationship (Fig. 4d–e).

Individual allometry

The scaling patterns of carapace width with volumes of materials varied between *Zygiella* s.l. species (Fig. 4). The volumes of all materials scaled isometric to spider size in *L. thorelli* and *S. stroemi*: the amount of materials increased with the power of ~ 3 in relation to spider size in *L. thorelli*, and with the power ~ 5 – 7 in *S. stroemi* (Fig. 4a–c). On the other hand, no material volume correlated with spider size in *Z. keyserlingi*, *Z. x-notata* and *P. montana* (Fig. 4a–c). One *Z. keyserlingi* individual largely departed in size from others (Fig. 4a–c). To check if this individual influences our results, we excluded it in an extra analysis, Fig. 4, but this analysis did not change the overall correlation patterns (MA silk: $P = 0.456$, $R^2 = 0.033$; Flag silk: $P = 0.215$, $R^2 = 0.089$; glue: $P = 0.501$, $R^2 = 0.027$).

Larger individuals of the investigated *Zygiella* s.l. species altered their web architecture and silk use differently (Table 1). For example, larger individuals of both *L. thorelli* and *S. stroemi* used more of all three materials (Fig. 4), spread over larger capture areas (Table 1). However, larger individuals of *L. thorelli* produced thicker threads as well as fewer but substantially larger glue droplets, while larger individuals of *S. stroemi* produced threads of the same thickness and glue droplets of same size and number. Larger individuals of *Z. x-notata* produced larger glue droplets but fewer of them (Table 1), and thus the overall volume of invested glue was not correlated with spider size (Fig. 4). Carapace width in *Z. keyserlingi* and *P. montana* did not correlate with any of the investigated web parameters (Table 1).

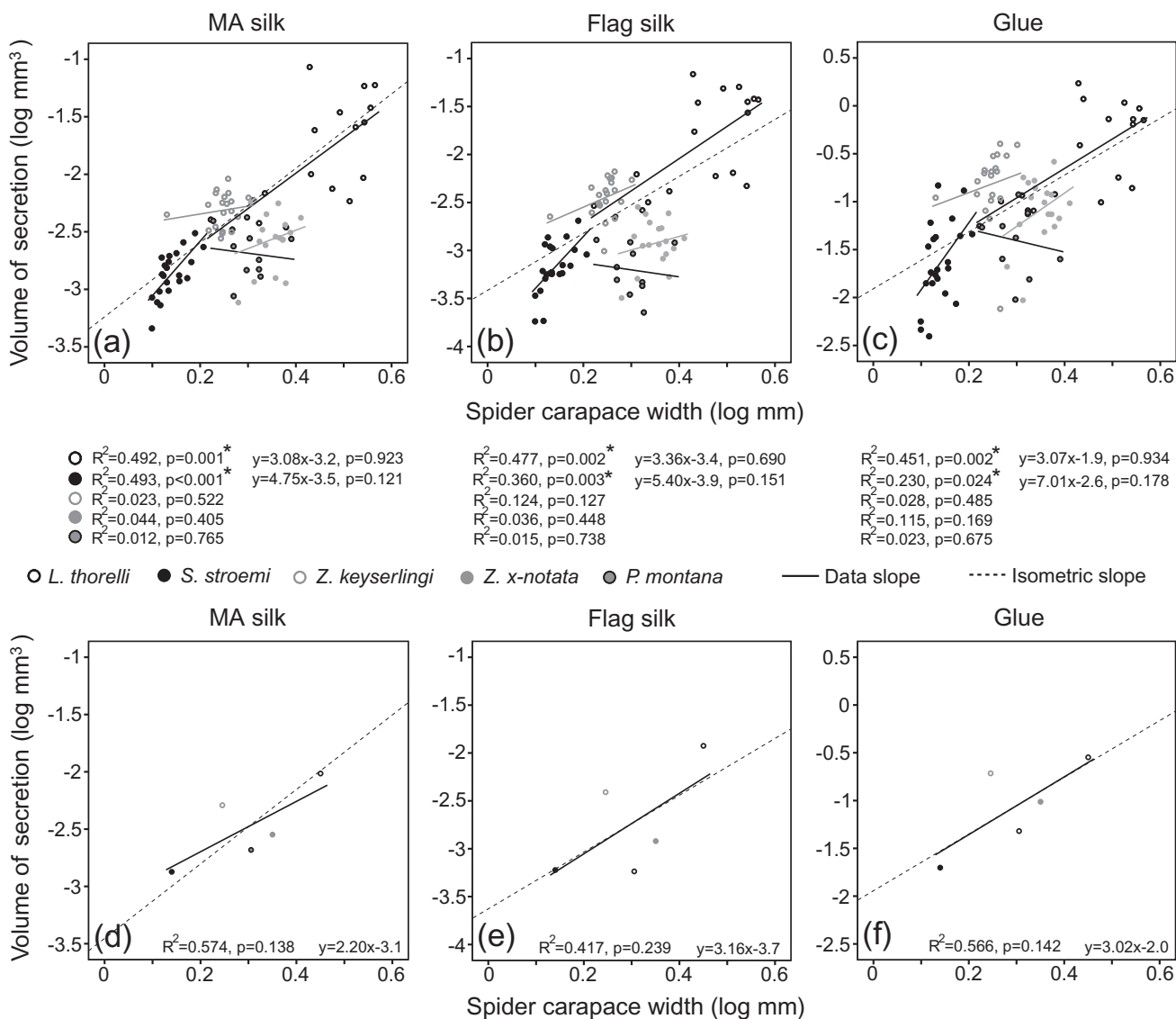


Figure 4 Correlations of major ampullate (radial threads) silk volume, flagelliform (capture silk threads) silk volume and glue with spider carapace width in the five investigated *Zygiella* s.l. species. In the linear function $y = m \cdot x + b$, 'm' represents its slope and 'x' represents the log of spider size. Asterisks mark significant correlations. The P-values next to linear functions fitting these significant correlations represent the significance of whether the slope of linear function fitting our data differs significantly from the isometry slope $m = 3$. No linear function is given for uncorrelated parameters.

Discussion

Foraging effort in orb-weaving spiders is expressed mainly as the amount of silk and glue used to build webs and critically influences web performance, and thus plays a key role in microhabitat adaptation of species and maximizing the fitness of individuals (Blackledge *et al.*, 2011; Harmer *et al.*, 2011). How web traits connected to web performance scale with body size is thus critical for understanding the body size and web evolution of orb web spiders. Few studies have investigated how foraging effort in spiders scales with body size, and no

single study has investigated how it scales across species. For example, in another orb weaver, *Neoscona arabesca*, body size through ontogeny scaled isometrically with MA and Flag silk investment and positively allometrically with glue investment. The material properties of MA silk remained constant while the webs became sparser and relatively smaller. These relationships then resulted in the web's stopping potential scaling isometrically with spider size while stickiness per area declined allometrically (Sensenig *et al.*, 2011). At the interspecific level, larger orb web species use more silk with improved material properties, resulting in webs with higher stopping potentials;

Table 1 Pearson's correlations of web variables and spider carapace width for the investigated *Zygiella* s.l. species

	<i>Leviellus thorelli</i> n = 18	<i>Parazygiella montana</i> n = 10	<i>Stroemiellus stroemi</i> n = 22	<i>Zygiella keyserlingi</i> n = 20	<i>Zygiella x-notata</i> n = 18
	Carapace width (log)	Carapace width (log)	Carapace width (log)	Carapace width (log)	Carapace width (log)
Body mass (log)	$P < 0.000$ $r = 0.968$	$P = 0.036$ $r = 0.555$	$P = 0.005$ $r = 0.579$	$P = 0.001$ $r = 0.679$	$P = 0.028$ $r = 0.518$
MA silk diam. (log)	$P = 0.001$ $r = 0.701$	$P = 0.442$ $r = -0.275$	$P = 0.695$ $r = 0.088$	$P = 0.331$ $r = 0.229$	$P = 0.745$ $r = 0.082$
Flag silk diam. (log)	$P = 0.001$ $r = 0.713$	$P = 0.580$ $r = -0.200$	$P = 0.237$ $r = 0.263$	$P = 0.193$ $r = 0.304$	$P = 0.356$ $r = -0.231$
No. of radial threads (log)	$P = 0.986$ $r = -0.005$	$P = 0.525$ $r = -0.228$	$P < 0.001$ $r = 0.683$	$P = 0.876$ $r = 0.037$	$P = 0.359$ $r = 0.230$
Capture silk length (log)	$P = 0.096$ $r = 0.404$	$P = 0.804$ $r = 0.073$	$P < 0.001$ $r = 0.542$	$P = 0.325$ $r = 0.232$	$P = 0.265$ $r = 0.278$
Glue droplet volume (log)	$P < 0.001$ $r = 0.786$	$P = 0.990$ $r = -0.005$	$P = 0.426$ $r = 0.179$	$P = 0.548$ $r = 0.143$	$P = 0.037$ $r = 0.495$
Glue droplets per mm (log)	$P < 0.001$ $r = -0.816$	$P = 0.776$ $r = -0.104$	$P = 0.966$ $r = -0.01$	$P = 0.678$ $r = -0.099$	$P = 0.009$ $r = -0.598$
Capture area (log)	$P = 0.023$ $r = 0.533$	$P = 0.279$ $r = 0.380$	$P = 0.003$ $r = 0.604$	$P = 0.396$ $r = 0.201$	$P = 0.283$ $r = 0.268$
Mesh width (log)	$P = 0.080$ $r = 0.423$	$P = 0.112$ $r = 0.534$	$P = 0.029$ $r = 0.465$	$P = 0.836$ $r = -0.049$	$P = 0.249$ $r = 0.287$

Significant results are bolded.

however, how these parameters scale with spider size is not entirely clear (Sensenig *et al.*, 2010a). By investigating silk and glue investment as well as web architecture in relation to spider size, we show that the material invested into orb webs increases slightly slower in proportion with body size across orb web spiders. Within the five *Zygiella* s.l. species investigated here, the invested materials vary significantly in whether and how they correlate with body size.

Phylogenetic allometry across orb spiders

Phylogenetic allometry of behavior is particularly understudied, and relationships of behavioral traits to body size are hypothesized to differ between clades and depend on the taxonomic level of the particular analysis (Dial *et al.*, 2008). We show that across 27 orb-weaving species of several families that range fivefold in size (Supporting Information Appendix S2), the amount of MA silk and glue that spiders use for building orb webs increased slightly slower than isometry in proportion with spider size, while Flag silk volume scaled isometrically (Fig. 3). Furthermore, a high ~70–80% of variation in these material amounts is explained by spider size alone (Fig. 3). As the amount of silks and glue is logically connected with the size of spinning glands, one would intuitively expect an isometric increase of spinning gland size with spider body size. However, web building is energetically costly and thus strongly influenced by the spiders' metabolic rate (Prestwich, 1977; Blackledge *et al.*, 2011). While higher material investment into webs should allow the building of better-performing webs, we find it likely that material investment is limited by metabolic rate of spiders. Metabolic rate scales with negative allometry across animals in general (West,

Brown & Enquist, 1997; Hulbert & Else, 2000), including spiders (Anderson, 1970, 1996). Similar to the metabolically costly web building in spiders, eye surface area and facet diameter scale negatively allometrically to body size in butterflies, bees, ants and other insects, and such negative allometry is associated with metabolic constraints (Zollikofer, Wehner & Fukushi, 1995; Merry *et al.*, 2006).

Although generalizations in allometry studies are difficult, most traits in animals seem to scale negatively with body size and any perfect isometry is regarded a special case (Bonduriansky & Day, 2003; Shingleton *et al.*, 2007). The few traits that exhibit positive allometry are mostly 'exaggerated or bizarre' and are usually shaped by sexual selection (Bonduriansky & Day, 2003; Bonduriansky, 2007). These general patterns correspond to material investment in orb web spiders increasing slightly slower in proportion with body size. However, larger spider species have generally evolved tougher silk, and the stopping potential per unit web area, the most important trait in stopping prey, thus increases positively allometrically with size, although the only study documenting this does not reveal the exact scaling exponent (Sensenig *et al.*, 2010a). These scaling patterns indicate that spiders in general might be constrained by the proportional amount of materials available to build webs, as larger webs seem to be challenged by disproportionately large kinetic energies from potential prey (Blackledge *et al.*, 2011). Evolving tougher silk and/or novel web architectures seems to compensate for that, as exemplified by the extremes in the largest orb web spider genus *Nephila* that builds very large and dense webs (Kuntner & Coddington, 2009; Sensenig *et al.*, 2010a), and by *Caerostris darwini* that uses the toughest known silk to construct the largest orb webs known (Agnarsson, Kuntner & Blackledge,

2010; Sensenig *et al.*, 2010a; Gregorič *et al.*, 2011). Nonetheless, the available silks and glue might present an important limiting factor in web performance and thus body size evolution of orb web spiders (Blackledge *et al.*, 2011).

Phylogenetic allometry in a recent radiation

The negatively allometric scaling of web materials with body size across orb web spiders is partially confirmed among the five investigated *Zygiella* s.l. species. Although the five data points of average material amounts are too few for a reliable statistical test, the slopes of linear functions fitting our data are close to isometric or negatively allometric (Fig. 4d,e). Furthermore, our preliminary molecular analysis reliably shows that *Zygiella* s.l. is a monophyletic group consisting of two clades, *Leviellus* + *Stroemiellus* and *Zygiella* + *Parazygiella* (Gregorič *et al.*, unpubl. data). Web investment scales differently within each of these two clades – our results hint at isometric scaling of materials and size in *Leviellus* + *Stroemiellus*, but not so in *Zygiella* + *Parazygiella*, although our sample size is too small to statistically test the prediction (Fig. 4d–f). Furthermore, our results indicate similar scaling patterns not only at the phylogenetic, but also at the individual level. Namely, among individuals of both *L. thorelli* and *S. stroemi*, the investment of all materials scales isometrically with body size, while material investment does not correlate with body size in *Z. keyserlingi*, *Z. x-notata* and *P. montana* (Fig 4a–c). This indicates that general scaling patterns across groups at a higher phylogenetic level might not always be reflected at the level of smaller monophyletic groups (Dial *et al.*, 2008). Such patterns thus further hint at a possibility that phylogenetic constraints explain, to some extent, behavioral variation even at the individual level.

Individual allometry

In addition to differences in how material investment in webs correlates with body size in *Zygiella* s.l., *L. thorelli* and *S. stroemi* also differ in details of how web architecture and silk use correlate to body size. Namely, these two species seem to have opposite patterns of material investment (Table 1). The capture area correlates positively with body size in both species, but in *L. thorelli*, the increase of total material volumes across the slightly larger web is due to using thicker threads and larger glue droplets, while in *S. stroemi*, the increase in material volumes is due to covering the substantially larger web using more radial and capture threads of same diameters and covered with glue droplets of same size and number. In other words, with increasing body size, webs of *L. thorelli* likely have higher stopping potentials and are thus capable of dissipating the kinetic energy of larger and/or faster flying prey, while webs of *S. stroemi* likely exhibit equal stopping potential per unit area but are capable of intercepting more prey (Craig, 1987b). However, these predictions cannot be further tested as the prey spectrum for most spider species, including the here investigated, is unknown.

Besides phylogenetic constraints, several other factors could explain the above mentioned patterns. First, the bodies

of growing spiders might change allometrically in a different way between species of different sizes, which might favor different web traits. Indeed, *L. thorelli* is significantly larger than *S. stroemi* and this might partially explain the differences in patterns of silk and glue use. However, as the other three species are of intermediate size, this hardly explains why there is no correlation of body size and foraging effort between individuals within them. Second, ecological factors might affect patterns of material investment. For example, orb webs are generally adapted to prey taxa that contribute the most caught biomass (Venner & Casas, 2005; Blackledge, 2011). Although most spiders are generalist predators (Birkhofer & Wolters, 2012; Pekar, Coddington & Blackledge, 2012), different spider species predominantly prey on certain invertebrate groups and/or certain sizes of prey (Nentwig, 1983, 1985; Pekar *et al.*, 2012). Thus, web properties that maximize foraging have likely been selected for, and thus might reflect adaptations to different prey taxa and their kinetic characteristics. Indeed, the here investigated species occupy different habitats in the same general area. *L. thorelli* and *P. montana* are widespread on human constructions, but occur on different elevations, *S. stroemi* builds arboricolous webs on trunks of certain trees, *Z. x-notata* occurs on human constructions and exposed vegetation in coastal regions, and *Z. keyserlingi* build its webs in coastal shrubs and bushes (Gregorič *et al.*, 2010).

Our results also highlight the importance of assessing foraging investment as the interplay between web architecture and silk. Namely, most previous studies investigating foraging effort document only changes in web shape and architecture, and often come to conflicting conclusions. For example, they show that hungry individuals of some species increase their foraging effort by building larger webs and/or using more threads, while sated individuals allocate their resources away from continuous foraging (e.g. Sherman, 1994; Venner *et al.*, 2000; Mayntz *et al.*, 2009), but several studies found no or even the opposite effect (Witt, Reed & Peakall, 1968; Vollrath & Samu, 1997; Nakata, 2007; Blamires, 2010). Our results show that different species might alter different parameters of webs, for example, changing thread diameters versus changing thread lengths, which both result in changed foraging effort. However, changed diameters would remain undetected if quantifying only web architecture, and the functional consequences of orb webs cannot be inferred correctly without such information.

There is another shortcoming that makes comparing and synthesizing all these findings difficult. While we consider our study an important step forward in understanding foraging effort in orb web spiders, none of the mentioned studies investigated the metabolic costs of web building *per se*. Thus, these studies are in fact underestimating total foraging investment and instead estimate foraging effort in terms of the invested materials. As the metabolic rate in spiders scales with negative allometry, corresponding to a general trend across animals (Anderson, 1970, 1996; West *et al.*, 1997; Hulbert & Else, 2000), this confirms the negatively allometrical scaling of body size and material volume among the 27 orb-weaving species and is unlikely to influence our results. Furthermore, Venner

et al. (2003) measured web architecture and metabolic costs during web building in relation to body mass and show that heavier individuals of *Z. x-notata* spent more energy in web building. As body size and body mass highly correlated among the individuals of all here investigated *Zygiella* s.l. species (Table 1), it is unlikely that potential differences in web building costs influenced our results.

Conclusions

We show here that the amount of material that orb-weaving spiders use for building webs scales negatively allometrically with body size across orb web spiders, and suggest that availability of silks and glue is an important limiting factor in the evolution of web performance and spider body size. We find support for the prediction that the allometry of behavioral traits across groups at a higher phylogenetic level is not always reflected at the level of smaller monophyletic groups or at the individual level. We also show that, according to their body size, individual spiders change their webs both in web architecture and silk investment, and one has to quantify both to better estimate foraging effort.

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References

- Agnarsson, I., Kuntner, M. & Blackledge, T.A. (2010). Bioprospecting finds the toughest biological material: extraordinary silk from a giant riverine orb spider. *PLoS ONE* **5**, e11234.
- Anderson, J.F. (1970). Metabolic rates of spiders. *Comp. Biochem. Physiol.* **33**, 51–72.
- Anderson, J.F. (1996). Metabolic rates of resting salticid and thomisid spiders. *J. Arachnol.* **24**, 129–134.
- Birkhofer, K. & Wolters, V. (2012). The global relationship between climate, net primary production and the diet of spiders. *Glob. Ecol. Biogeogr.* **21**, 100–108.
- Blackledge, T.A. (1998). Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). *J. Zool. (Lond.)* **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. & Gillespie, R.G. (2002). Estimation of capture areas of spider orb webs in relation to asymmetry. *J. Arachnol.* **30**, 70–77.
- Blackledge, T.A. & Zevenbergen, J.M. (2007). Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*. *Anim. Behav.* **73**, 855–864.
- Blackledge, T.A., Cardullo, R.A. & Hayashi, C.Y. (2005). Polarized light microscopy, variability in spider silk diameters, and the mechanical characterization of spider silk. *Invert. Biol.* **124**, 165–173.
- Blackledge, T.A., Scharff, N., Coddington, J.A., Szuts, T., Wenzel, J.W., Hayashi, C.Y. & Agnarsson, I. (2009). Reconstructing web evolution and spider diversification in the molecular era. *Proc. Natl. Acad. Sci. USA* **106**, 5229–5234.
- Blackledge, T.A., Kuntner, M. & Agnarsson, I. (2011). The form and function of spider orb webs: evolution from silk to ecosystems. In *Adv Ins Physiol, Vol 41: Spider physiology and behaviour – behaviour*: 175–262. Casas, J. (Ed.). Burlington: Academic Press.
- Blamires, S.J. (2010). Plasticity in extended phenotypes: orb web architectural responses to variations in prey parameters. *J. Exp. Biol.* **213**, 3207–3212.
- Bonduriansky, R. (2007). Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution* **61**, 838–849.
- Bonduriansky, R. & Day, T. (2003). The evolution of static allometry in sexually selected traits. *Evolution* **57**, 2450–2458.
- Boutry, C. & 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. A* **309A**, 542–552.
- Boutry, C. & Blackledge, T.A. (2009). Biomechanical variation of silk links spinning plasticity to spider web function. *Zoology* **112**, 451–460.
- Craig, C.L. (1987a). The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. *Am. Nat.* **129**, 47–68.
- Craig, C.L. (1987b). The ecological and evolutionary interdependence between web architecture and web silk spun by orb web weaving spiders. *Biol. J. Linn. Soc.* **30**, 135–162.
- Dial, K.P., Greene, E. & Irschick, D.J. (2008). Allometry of behavior. *Trends Ecol. Evol.* **23**, 394–401.
- Eberhard, W.G., Agnarsson, I. & Levi, H.W. (2008). Web forms and the phylogeny of theridiid spiders (Araneae: Theridiidae): chaos from order. *Syst. Biodivers.* **6**, 415–475.
- Eberhard, W.G., Barrantes, G. & Madrigal-Brenes, R. (2008). 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.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Ferrari, M.C.O., Sih, A. & Chivers, D.P. (2009). The paradox of risk allocation: a review and prospectus. *Anim. Behav.* **78**, 579–585.

- Field, A. (2005). *Discovering statistics using SPSS*: 816. London: Sage Publications.
- Garland, T. & Kelly, S.A. (2006). Phenotypic plasticity and experimental evolution. *J. Exp. Biol.* **209**, 2344–2361.
- Gregorič, M., Kostanjšek, R. & 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. & Kuntner, M. (2011). Darwin's bark spider: giant prey in giant orb webs (*Caerostris darwini*, Araneae: Araneidae)? *J. Arachnol.* **39**, 287–295.
- 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., Blackledge, T.A., Madin, J.S. & Herberstein, M.E. (2011). High-performance spider webs: integrating biomechanics, ecology and behaviour. *J. R. Soc. Interface* **8**, 457–471.
- Herberstein, M.E. & Heiling, A.M. (1999). Asymmetry in spider orb webs: a result of physical constraints? *Anim. Behav.* **58**, 1241–1246.
- Herberstein, M.E. & Tso, I.M. (2000). Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneidae, Araneae). *J. Arachnol.* **28**, 180–184.
- Herberstein, M.E. & Tso, I.M. (2011). Spider webs: evolution, diversity and plasticity. In *Spider behaviour: flexibility and versatility*: 57. Herberstein, M.E. (Ed.). Cambridge: Cambridge University Press.
- 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.
- Hulbert, A.J. & Else, P.L. (2000). Mechanisms underlying the cost of living in animals. *Annu. Rev. Physiol.* **62**, 207–235.
- Jakob, E.M., Marshall, S.D. & Uetz, G.W. (1996). Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61–67.
- Kuntner, M. & Coddington, J.A. (2009). Discovery of the largest orbweaving spider species: the evolution of gigantism in *Nephila*. *PLoS ONE* **4**, e7516.
- Kuntner, M., Gregorič, M. & Li, D.Q. (2010). Mass predicts web asymmetry in *Nephila* spiders. *Naturwissenschaften* **97**, 1097–1105.
- Kuntner, M., Kralj-Fišer, S. & Gregorič, M. (2010). Ladder webs in orb-web spiders: ontogenetic and evolutionary patterns in Nephilidae. *Biol. J. Linn. Soc.* **99**, 849–866.
- Li, D.Q. & Lee, W.S. (2004). Predator-induced plasticity in web-building behaviour. *Anim. Behav.* **67**, 309–318.
- Liao, C.P., Chi, K.J. & 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.
- Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation – a review and prospectus. *Can. J. Zool.* **68**, 619–640.
- Maddison, W.P. & Maddison, D.R. (2013). Mesquite: a modular system for evolutionary analysis. <http://mesquiteproject.org>
- Mayntz, D., Toft, S. & Vollrath, F. (2009). Nutrient balance affects foraging behaviour of a trap-building predator. *Biol. Lett.* **5**, 735–738.
- Merry, J.W., Morehouse, N.I., Yturralde, K. & Rutowski, R.L. (2006). The eyes of a patrolling butterfly: visual field and eye structure in the Orange Sulphur, *Colias eurytheme* (Lepidoptera, Pieridae). *J. Insect Physiol.* **52**, 240–248.
- Midford, P.E., Garland, T. & Maddison, W.P. (2002). PDAP:PDTree package for Mesquite, version 1.00.
- Nakata, K. (2007). Prey detection without successful capture affects spider's orb-web building behaviour. *Naturwissenschaften* **94**, 853–857.
- Nentwig, W. (1983). The non-filter function of orb webs in spiders. *Oecologia* **58**, 418–420.
- Nentwig, W. (1985). Prey analysis of 4 species of tropical orb-weaving spiders (Araneae, Araneidae) and a comparison with araneids of the temperate zone. *Oecologia* **66**, 580–594.
- Opell, B.D., Markley, B.J., Hannum, C.D. & 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.
- Pekar, S., Coddington, J.A. & Blackledge, T.A. (2012). Evolution of stenophagy in spiders (Araneae): evidence based on the comparative analysis of spider diets. *Evolution* **66**, 776–806.
- Prestwich, K.N. (1977). The energetics of web-building in spiders. *Comp. Biochem. Physiol. A* **57**, 321–326.
- Sensnig, A., Agnarsson, I. & Blackledge, T.A. (2010a). Behavioural and biomaterial coevolution in spider orb webs. *J. Evol. Biol.* **23**, 1839–1856.
- Sensnig, A., Agnarsson, I., Gondek, T.M. & Blackledge, T.A. (2010b). Webs in vitro and in vivo: spiders alter their orb-web spinning behavior in the laboratory. *J. Arachnol.* **38**, 183–191.
- Sensnig, A.T., Agnarsson, I. & Blackledge, T.A. (2011). Adult spiders use tougher silk: ontogenetic changes in web architecture and silk biomechanics in the orb-weaver spider. *J. Zool. (Lond.)* **285**, 28–38.
- Sensnig, A.T., Lorentz, K.A., Kelly, S.P. & Blackledge, T.A. (2012). Spider orb webs rely on radial threads to absorb prey kinetic energy. *J. R. Soc. Interface* **9**, 1880–1891.
- Sherman, P.M. (1994). The orb-web – an energetic and behavioral estimator of a spiders dynamic foraging and reproductive strategies. *Anim. Behav.* **48**, 19–34.
- Shingleton, A.W., Frankino, W.A., Flatt, T., Nijhout, H.F. & Emlen, D.J. (2007). Size and shape: the developmental regulation of static allometry in insects. *Bioessays* **29**, 536–548.
- Townley, M.A., Tillinghast, E.K. & 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.

- Tso, I.M., Wu, H.C. & 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., Chiang, S.Y. & Blackledge, T.A. (2007). Does the giant wood spider *Nephila pilipes* respond to prey variation by altering web or silk properties? *Ethology* **113**, 324–333.
- 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.
- Venner, S. & Casas, J. (2005). Spider webs designed for rare but life-saving catches. *Proc. Roy. Soc. Lond. Ser. B.* **272**, 1587–1592.
- Venner, S., Pasquet, A. & Leborgne, R. (2000). Web-building behaviour in the orb-weaving spider *Zygiella x-notata*: influence of experience. *Anim. Behav.* **59**, 603–611.
- Venner, S., Bel-Venner, M.C., Pasquet, A. & Leborgne, L. (2003). Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zygiella x-notata*. *Naturwissenschaften* **90**, 269–272.
- Vollrath, F. & Samu, F. (1997). The effect of starvation on web geometry in an orb-weaving spider. *Bull. Br. Arachnol. Soc.* **10**, 295–298.
- Vollrath, F. & Selden, P. (2007). The role of behavior in the evolution of spiders, silks, and webs. *Annu. Rev. Ecol. Evol. Syst.* **38**, 819–846.
- Watanabe, T. (2000). Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour. *Proc. Roy. Soc. Lond. Ser. B.* **267**, 565–569.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.
- West-Eberhard, M.J. (1989). Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20**, 249–278.
- Witt, P.N., Reed, C.F. & Peakall, D.B. (1968). *A spider's web: problems in regulatory biology*. New York: Springer Verlag.
- Zollikofer, C.P.E., Wehner, R. & Fukushi, T. (1995). Optical scaling in conspecific *Cataglyphis* ants. *J. Exp. Biol.* **198**, 1637–1646.
- Zschokke, S., Henaut, Y., Benjamin, S.P. & Garcia-Ballinas, J.A. (2006). Prey-capture strategies in sympatric web-building spiders. *Can. J. Zool.* **84**, 964–973.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. The volumes of invested silk and glue, and average web variables in the investigated *Zygiella* s.l. species: ME, median; IQR, interquartile range.

Appendix S2. Average invested volumes of MA silk, Flag silk and glue for species investigated by Sensenig *et al.* (2010a).