Optimal foraging, not biogenetic law, predicts spider orb web allometry

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SHORT COMMUNICATION

Optimal foraging, not biogenetic law, predicts spider orb web allometry

**Matjaž Gregorič · Heine C. Kiesbüy ·
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Abstract The biogenetic law posits that the ontogeny of an organism recapitulates the pattern of evolutionary changes. Morphological evidence has offered some support for, but also considerable evidence against, the hypothesis. However, biogenetic law in behavior remains underexplored. As physical manifestation of behavior, spider webs offer an interesting model for the study of ontogenetic behavioral changes. In orb-weaving spiders, web symmetry often gets distorted through ontogeny, and these changes have been interpreted to reflect the biogenetic law. Here, we test the biogenetic law hypothesis against the alternative, the optimal foraging hypothesis, by studying the allometry in *Leucauge venusta* orb webs. These webs range in inclination from vertical through tilted to horizontal; biogenetic law predicts that allometry relates to ontogenetic stage, whereas optimal foraging predicts that allometry relates to gravity. Specifically, pronounced asymmetry should only be seen in vertical webs under optimal foraging theory. We show that, through ontogeny, vertical webs in *L. venusta* become more asymmetrical in contrast to tilted and horizontal webs. Biogenetic law thus cannot explain *L. venusta* web allometry, but our results instead support optimization of foraging area in response to spider size.

Keywords Recapitulation theory · Ontogeny · Ontogenetic change · Asymmetry · Optimal foraging · *Leucauge venusta*

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Introduction

The biogenetic law, i.e. "ontogeny recapitulates phylogeny" as formulated by Haeckel in 1872 (Olsson et al. 2010), predicts that the ontogeny of an organism follows the pattern of preceding evolutionary changes in its lineage and was extensively debated throughout the past century (Nelson 1978; Olsson et al. 2010). Although morphological evidence refutes the biogenetic law as a truly general biological concept, several studies have observed some degree of parallelism between ontogeny and phylogeny (Gould 1992; Richardson and Keuck 2002). However, the ontogenetic changes in animal behavior are underexplored in this context, but have recently been suggested to potentially recapitulate phylogeny (Richardson and Keuck 2002; Eberhard et al. 2008; Nakata 2010).

Spider webs are a particularly convenient system to study ontogenetic changes in behavior. They represent a physical record of spiders' behaviors through all ontogenetic stages, enabling a measurement of the behavioral development through ontogeny (Benjamin and Zschokke 2004; Venner and Casas 2005; Vollrath and Selden 2007), and are furthermore easily quantified (Blackledge 2011). The architecture
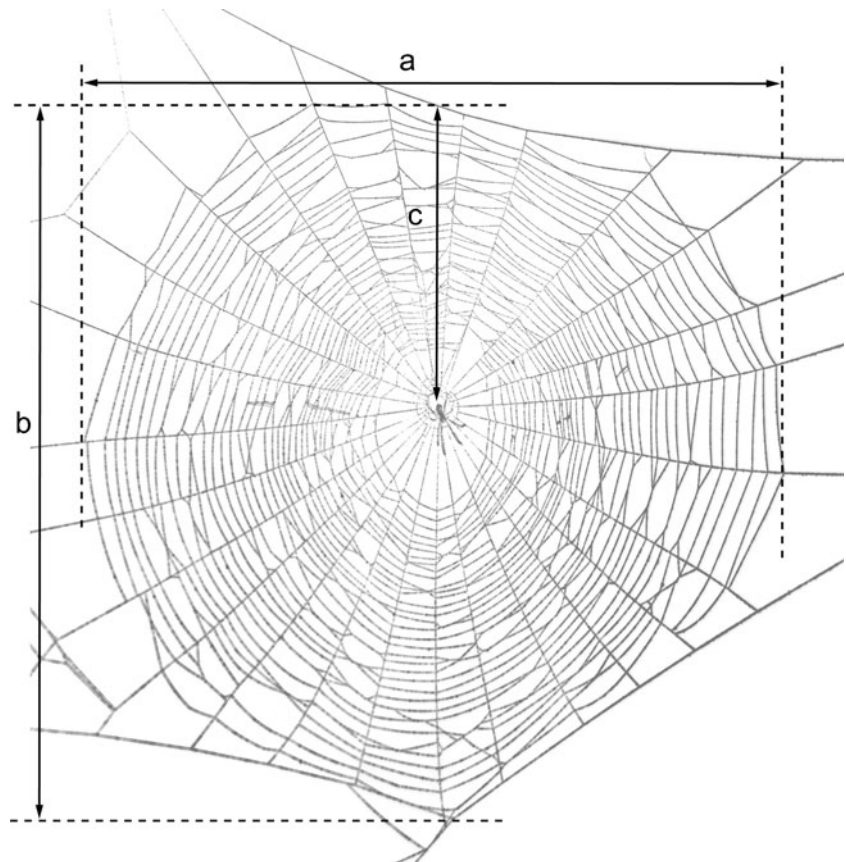
of spider webs changes through ontogeny in most of the families studied so far (Eberhard et al. 2008). The classical vertical wagon-wheel-shaped webs, or "orb webs," usually retain their general architecture through ontogeny. However, larger spiders build larger webs that tend to be more asymmetrical (Herberstein and Heiling 1999). Early instar orb-weaving spiders typically build symmetrical, circular orb webs with the web hub located close to the geometrical center, while adults mostly build vertically elongated webs with vertically displaced hubs (Eberhard 1990; Zschokke and Vollrath 1995). As the ancestral orb web was supposedly symmetric (Eberhard 1985; Eberhard et al. 2008; Hesselberg 2010), some studies consider such changes in web ontogeny to reflect the biogenetic law, summarizing data from 11 genera and 5 orb-weaving families (Eberhard et al. 2008; Hesselberg 2010). However, other studies have questioned such a general rule suggesting that other factors might affect web asymmetry (e.g., Heiling and Herberstein 1999; Kuntner et al. 2010a; Nakata 2010; Nakata and Zschokke 2010; Zschokke and Nakata 2010).

Nakata (2010) was the first to contrast the biogenetic law with the alternative hypothesis, which predicts that orb-weaving spiders as central place foragers maximize their prey catching by altering the symmetry of their webs as they grow. This hypothesis predicts that spiders displace the hubs of their webs somewhat above the webs' geometric center because of the difference in their upward and downward running speeds (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994). Due to gravity effects, running speed in different directions is logically affected by spider mass, and several studies show that spider size and mass correlate positively with hub displacement and/or web asymmetry (e.g., Herberstein and Heiling 1999; Bleher 2000; Kuntner et al. 2008, 2010a, b). Additionally, spiders typically face downwards while sitting at the hub, thus combining the effect of gravity and orientation to optimize prey catching (ap Rhisiart and Vollrath 1994; Zschokke and Nakata 2010).

We test these two alternative hypotheses by studying ontogenetic shifts in orb web allometry in the tetragnathid spider *Leucauge venusta*. This species builds orb webs that range from vertical to horizontal in inclination throughout all ontogenetic stages and is thus ideal to investigate the effect of the optimal foraging area versus the biogenetic law on spider orb web allometry. The optimal foraging hypothesis predicts that gravity does not have an impact on the symmetry of horizontal orb webs (ap Rhisiart and Vollrath 1994; Herberstein and Heiling 1999), but should affect the symmetry of vertical orb webs, shifting it towards asymmetry. On the other hand, the biogenetic law predicts that all webs should display a more or less equal web allometry, related to ontogeny (Eberhard et

Fig. 1 Web of *L. venusta* illustrating investigated parameters: **a** web width, **b** web height, **c** hub-to-top distance

al. 2008). A similar hypothesis predicts that experienced web-building spiders learn to build more efficient webs (Heiling and Herberstein 1999).

Methods

Contrary to most previous studies (e.g., Masters and Moffat 1983; ap Rhisiart and Vollrath 1994; Herberstein and Heiling 1999; Bleher 2000; Kuntner et al. 2008; Kuntner and Agnarsson 2009), we investigate instars through the entire ontogenetic range and also explore the effect of spider mass because it additionally affects vertical web asymmetry (Kuntner et al. 2010a). We used spider linear size and live mass to quantify ontogeny because they highly correlate with estimated ontogenetic stages, but explain ontogeny better (Kuntner et al. 2010a). As webs in captivity architecturally differ from webs in nature (Sensenig et al. 2010), we measured all webs in their natural setting.

We measured 98 webs of *L. venusta* on 28 October 2011 at El Verde, El Yunque State Forest, Luquillo (N18.32301, W65.81985) and on 20 November 2011 at Cambelache State Forest, Barceloneta (N18.45226, W66.59711), Puerto Rico. Webs were chosen haphazardly.

In the field, we dusted the webs with cornstarch to increase visual contrast and measured the following parameters (Fig. 1): a = web width (in centimeter), b = web height (in centimeter), c = top-to-hub distance (in centimeter), and inclination in arc degrees (0° to 90° with the extremes representing a perfectly horizontal and vertical web, respectively). In the laboratory, we weighed all spiders to the nearest 0.01 mg and measured the width of the carapace as a measure of spider linear size.

We calculated the two web asymmetry measures: first, hub displacement used as in Kuntner et al. (2008) and similar to the hub asymmetry index (Blackledge et al. 2011), defined with the formula $HD = \frac{b-c}{b}$; and second, the ladder index used as in Peters (1937) and Kuntner et al. (2008) and similar to the web asymmetry index (Blackledge et al. 2011) as a measure of web shape, delimited with the outermost sticky spiral and defined with the formula $LI = \frac{b}{a}$. We preferred hub displacement and ladder index to hub asymmetry and web asymmetry, respectively, because hub displacement and ladder index are linear and more readily visualized.

We grouped our web data into three inclination groups, horizontal (0–30°, N=39), tilted (31–60°, N=33), and vertical webs (61–90°, N=26). We tested all data for normality using the Kolmogorov–Smirnov test. Since only the data for carapace width were normally distributed, we log-transformed all other data. We then used Pearson's correlation to test if spider length and mass correlate with hub displacement and ladder index, and the analysis of variance to test if ladder index
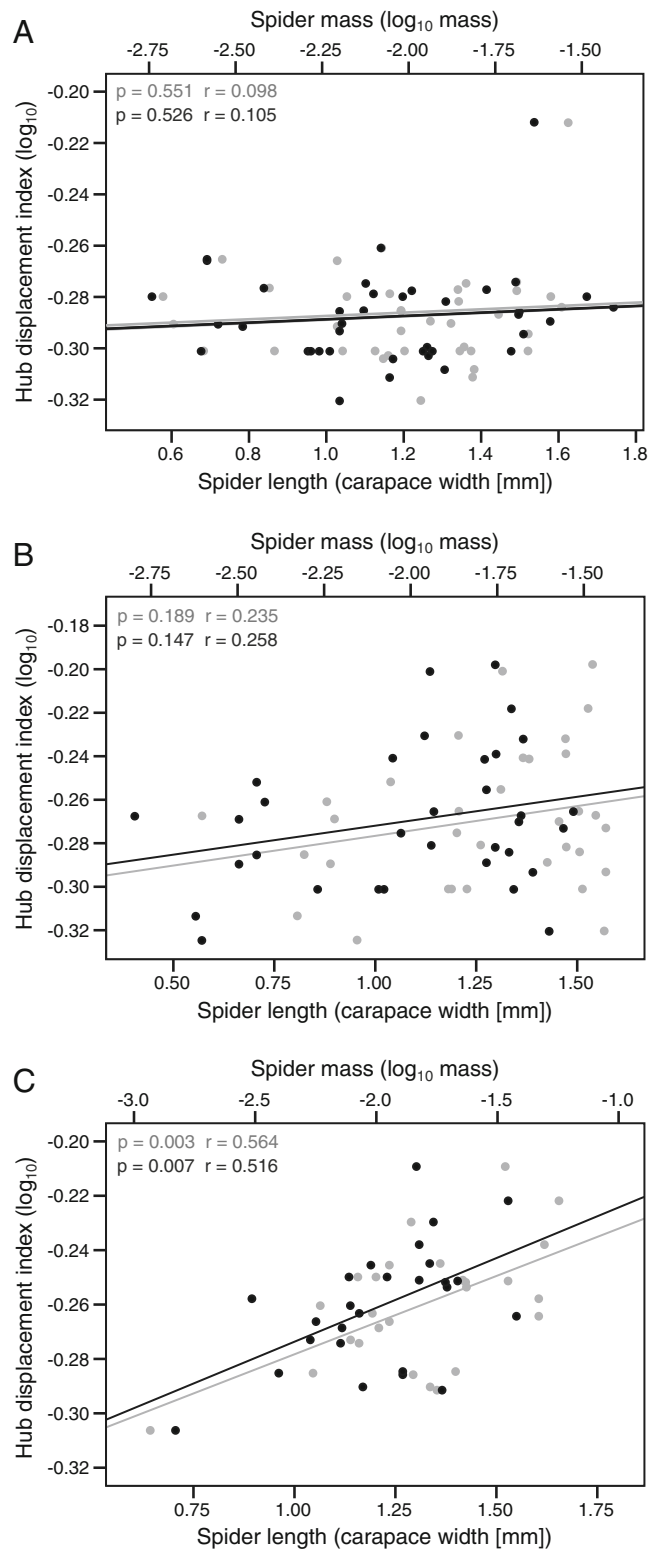

Fig. 2 Correlations between spider length and hub displacement (*gray circles*), and spider mass and hub displacement (*black circles*), in three inclination groups of *L. venusta* webs: the horizontal (**a**), tilted (**b**) and vertical (**c**) webs. The black and gray *p* values reflect the black and gray circles, respectively

differs between inclination groups. We performed all statistical tests in PASW 18 (Field 2005).

Results and discussion

Web inclination had a clear effect on web allometry (Fig. 2). In horizontal and tilted webs, hub displacement did not correlate with spider length and mass (Table 1, Fig. 2a and b). In vertical webs, however, hub displacement significantly correlated with spider length and mass (Table 1, Fig. 2c). The ladder index as a measure of web shape did not correlate with spider size (Table 1), nor did it differ between the three inclination groups ($F_{99,2}=1.343$, $p=0.266$).

The biogenetic law has been rejected in numerous studies (Gould 1992; Theissen and Saedler 1995; Richardson et al. 1997; Richardson and Keuck 2002), but there is some evidence for it in others, e.g., in bivalve muscles (Miyazaki and Mickevich 1982), paper wasps (Wenzel 1993), and among spiders, the webs of the family Theridiidae (Eberhard et al. 2008; Barrantes and Eberhard 2010). The present study investigates the ontogenetic changes in web architecture in the orb-weaving spider *L. venusta*. Our results show an increase in hub displacement through ontogeny in vertical webs, but not in horizontal or tilted webs, while web shape remains circular throughout the ontogeny of all spiders. Such ontogenetic change in orb web architecture is predicted by the optimal foraging hypothesis, but not by the biogenetic law.

That hubs become more displaced in vertical webs of larger spiders, but not in horizontal webs, indicates that web symmetry changes due to optimization of the spiders' foraging area, most likely because of the spiders' difference in upward and downward running speed (Herberstein and Heiling 1999; Kuntner et al. 2010a). That webs remain circular throughout ontogeny further indicates that increased differences in running speed affect web symmetry, as that

difference can only explain the increased hub displacement. Changes in web shape are usually a result of limited web space (Kuntner et al. 2010b; Harmer and Herberstein 2009) or prey adaptation (Eberhard 1975). As *L. venusta* build webs in unlimited aerial space, and because circular webs are better prey-catching devices than asymmetrically shaped webs (Harmer et al. 2012), web shape was not expected to change through ontogeny. While spiders also change web architecture in relation to prey and habitat (Herberstein and Tso 2011), our results are likely not affected by such factors as the webs we measured were located within a small area.

Orb webs are spiders' extended phenotypes employed in all ontogenetic stages and thus directly influence their fitness (Eberhard 1990; Herberstein and Tso 2011). Web architecture that maximizes foraging success throughout the spiders' lives is likely to be selected for. This is supported by other studies, e.g., different species of *Cyclosa* enlarge different parts of their webs in relation to which side the spiders are facing (Nakata and Zschokke 2010), *Telaprocera* spiders build highly vertically elongated webs when in horizontally limited space and the more efficient circular webs when in unlimited space (Harmer and Herberstein 2009), and heavier individuals of several species build more asymmetrical webs (Herberstein and Heiling 1999; Kuntner et al. 2010a). Additionally, experienced spiders also learn which parts of the web are most successful in catching prey (Heiling and Herberstein 1999). Furthermore, Coslovsky and Zschokke (2009) investigated the building costs in different parts of an orb web. Contrary to predictions, they found that building of the lower half of the web is costlier than the building of the upper half. Enlarging the lower half of the web by displacing the hub upwards thus indicates that an optimal foraging area is under even stronger selection pressure with building cost as an opposing force.

Although web allometry in *L. venusta* cannot be explained by invoking the biogenetic law, the ultimate test of whether ontogeny recapitulates the evolutionary steps of *Leucauge*

Table 1 Paerson's correlations of spider length/mass and two asymmetry indices (hub displacement, ladder index) in three inclination groups of *L. venusta* webs

Correlation	P	r	N
Spider length and hub displacement (horizontal webs)	0.551	0.098	39
Spider mass and hub displacement (horizontal webs)	0.526	0.105	39
Spider length and ladder index (horizontal webs)	0.674	−0.07	39
Spider mass and ladder index (horizontal webs)	0.557	−0.097	39
Spider length and hub displacement (tilted webs)	0.189	0.235	33
Spider mass and hub displacement (tilted webs)	0.147	0.258	33
Spider length and ladder index (tilted webs)	0.942	−0.013	33
Spider mass and ladder index (tilted webs)	0.953	−0.011	33
Spider length and hub displacement (vertical webs)	0.003	0.564	26
Spider mass and hub displacement (vertical webs)	0.007	0.516	26
Spider length and ladder index (vertical webs)	0.933	0.017	26
Spider mass and ladder index (vertical webs)	0.788	−0.055	26

spiders would have to include phylogenetic data. Currently, however, a *Leucauge* phylogeny is not available, and thus, the evolution of *Leucauge* webs is unknown. Additionally, some authors argue that the ancestral orb web was probably symmetric and circular (Eberhard et al. 2008; Hesselberg 2010), but until solid evidence exists for such assumption, the ancestral orb web remains of limited use in tests of the biogenetic law. Furthermore, since the spider group Orbiculariae comprises approximately 12,000 species (Coddington 1986; Griswold et al. 1998; Garb et al. 2006; Blackledge et al. 2009), a reconstructed ancestral web architecture of such a diverse group would provide only a limited power in the context of testing the biogenetic law. Evolutionary tests thus will require ancestral reconstruction of the orb web at the nodes under study, rather than the common ancestor of Orbiculariae.

In conclusion, the ontogeny of *L. venusta* webs does not reflect the biogenetic law but is consistent with the foraging optimization. The extent to which our findings in *L. venusta* can be generalized to other orb web spiders is difficult to estimate. However, because the web is primarily a foraging structure, we predict that future studies of ontogenetic changes in orb webs will support foraging optimization, especially when considering phylogenetic patterns of investigated spider groups. Ontogenetic changes in non-foraging behavior and what factors influence them require further study and are also likely influenced by many factors under selection.

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