

Repeatability but no short-term plasticity in the web architecture of *Latrodectus hesperus* western black widow spiders (Araneae: Theridiidae)

Cory H. Thompson  | Rafael L. Rodríguez  | Clinton Sergi

Behavioral & Molecular Ecology Group,
Department of Biological Sciences,
University of Wisconsin-Milwaukee,
Milwaukee, WI, USA

Correspondence

Cory H. Thompson, University of Wisconsin-Milwaukee, Biological Sciences, 3209 N. Maryland Ave., Milwaukee, WI 53201-0413, USA.

Email: thomp635@uwm.edu

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Abstract

A spider's web is an extended phenotype and a direct product of behavior. Variation in web architecture may be the result of individual differences in genotype, environment, or experience. We analyzed variation in the web architecture of western black widow spiders, *Latrodectus hesperus*, by testing two hypotheses: (a) intrinsic individual differences and (b) plasticity according to experience of the site of prey capture. We used treatments manipulating the site of prey capture experienced by the spiders: sheet only, gum-footed lines only, and alternating patterns between sheet and gum-footed lines equally. We found considerable consistent individual variation (repeatability of $r = .56$) in one web component (gum-footed lines) and negligible plasticity in either component. We discuss our results in terms of the potential for the design of these web components to respond to selection, and of potential additional causes of variation in extended phenotypes.

KEYWORDS

experience-mediated plasticity, *Latrodectus*, plasticity, repeatability, web architecture

1 | INTRODUCTION

Extended phenotypes—constructions like termite cities, caddisfly houses, and beaver dams—are often the product of animal behavior (Dawkins, 1982). Consequently, the adjustability of behavior (Zuk, Bastiaans, Langkilde, & Swanger, 2014) may allow animals to make extended phenotypes adaptively plastic, according to the conditions in which they are built (Blamires, 2010; Blamires, Martens, & Kasumovic, 2018; Craig, 2003; DiRienzo & Aonuma, 2018; Head, Fox, & Barber, 2017). However, extended phenotypes are also relatively stable and long-lasting, in comparison with the behavior that produced them (Schaedelin & Taborsky, 2009). These two features make extended phenotypes convenient, easily described, yet powerful sources of insight into the factors that shape animal decision making (Blamires et al., 2018; Turner, 2000).

Spider webs are prime examples of extended phenotypes that are produced by innate behavioral programs, and yet sensitive to

the spider's environment and foraging experience (Nakata, 2012). Certain orb-web spiders, for example, adjust the architecture of their web and/or their investment in its silk in response to feeding frequency and nutrient requirements (Blamires, 2010; Blamires et al., 2018). Other species of orb-weaver alter web structure and silk allocation in response to the type or location of prey capture (Blamires, Chao, Liao, & Tso, 2011; Nakata, 2012). Yet other species alter web architecture to optimize prey capture when the physical structure of the environment varies (Diniz, Vasconcellos-Neto, & Stefani, 2017). Examples of plasticity in webs are not limited to two-dimensional orbs. There is also evidence of plasticity in silk investment overall and in specific components of the three-dimensional webs of black widow spiders based upon satiety and the presence of neighboring conspecific and heterospecific spiders (Blackledge & Zevenbergen, 2007; Salomon, 2007; Zevenbergen, Schneider, & Blackledge, 2008).

Here, we ask whether western black widow spiders (*Latrodectus hesperus* Chamberlin & Ivie 1935) alter the design of their web according to their experience of the site of prey capture. As with

many other theridiids, *L. hesperus* constructs a three-dimensional cobweb consisting of a sheet from which a forest of gum-footed lines extends vertically to a substrate (Benjamin & Zschokke, 2003) (Figure 1a). The gum-footed lines have a bead of glue at the bottom that sticks to prey that contact it as they walk by, while the sheet—a dense tangle of web—serves as the web's primary protective element (Blackledge, Swindeman, & Hayashi, 2005). Nevertheless, a substantial minority (e.g., approx. 10% biomass in Salomon, 2011) of the prey consumed by *L. hesperus* are flying insects that are probably snared by the sheet rather than the gum-footed lines (C. Sergi pers. obs.), prompting the question of whether experience of prey capture by either component influences the spiders' web architecture decisions.

We analyzed variation in *L. hesperus* web design by testing two non-exclusive hypotheses. First, the plasticity hypothesis posits that *L. hesperus* modify their investment in web components according to their experience with prey capture at different sites on their webs. This hypothesis predicts that, when *L. hesperus* consistently capture prey on a given web component, they will allocate more resources to that component. We tested this hypothesis with an experiment that manipulated the spider's experience of the site of prey capture over 4 weeks.

The second hypothesis allows for the possibility that the spiders adjust the architecture of their webs over longer intervals than encompassed by our experiment, as well as for additional components of variation, such as individual differences in genotype. There is evidence of such consistent individual variation in gum-footed lines and overall web size (DiRienzo & Montiglio, 2016). If the magnitude of these potential causes of variation is large, then consistent individual differences in investment in the web components (i.e., repeatability; Bell, Hankison, & Laskowski, 2009) should have a larger effect than the experience treatments.

We also tested for a trade-off in silk investment in the different web components, as a potential cause of individual variation in web architecture.

2 | METHODS

We collected 60 adult female *L. hesperus* in Medford, Oregon in June of 2017, and immediately shipped them to the University of Wisconsin-Milwaukee. We housed each spider at the laboratory in a 473-ml plastic deli cup. To standardize satiety levels in the spiders, we fed each spider one cricket (1 cm-long *Acheta domesticus*) per week over 2 weeks, then waited four days before beginning the experiment.

To start the experiment, we moved each spider into a cardboard frame (l × w × h: 27.6 × 15.9 × 8.9 cm). The frames contained a hollow triangular cardboard retreat (5 × 5 × 5 cm) at the top central region of one of the two walls. The frames had no lateral walls so that the spider's web could be viewed without obstruction. We kept the frames in clear, plastic "shoe-box" containers (30 × 15.25 × 10 cm). We applied petroleum jelly lightly and evenly to the lateral walls of each plastic enclosure so that when constructing their web within the cardboard frames, each spider would be unable to attach silk to the plastic walls. Thus, each cardboard frame could easily be removed from its plastic enclosure for the purpose of feeding and photographing each web without damaging it.

We gave each spider 1 week to construct a web in these frames before beginning the experiment. We then randomly assigned each spider to one of three treatments that differed in the site of prey capture, as follows. We gave prey (*A. domesticus*) to the spiders either: (a) only on the sheet of the web, holding the cricket with a forceps in contact with the center of the sheet until the spider initiated its capture behavior (flicking silk at the cricket); (b) only to a gum-footed line, holding the cricket with a forceps at the base of the gum-footed line that was attached closest to the center of the sheet until the spider initiated its capture behavior; or (c) alternating between sheet and gum-footed line; for each spider assigned to this treatment, we alternated whether the first feeding was on the sheet or gum-footed line component. We gave each spider one cricket each week over 4 weeks. We aimed to reach a sample size of $n = 20$ for each treatment.

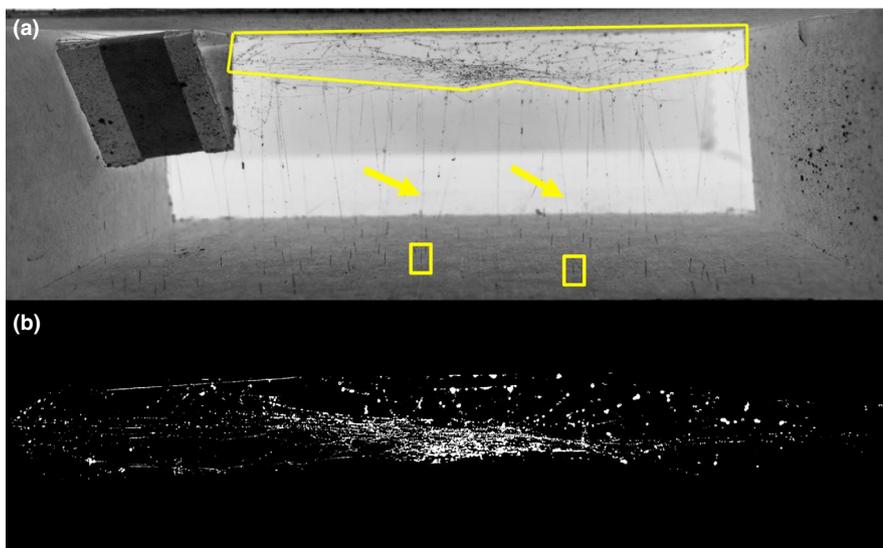


FIGURE 1 Components of the web of *Latrodectus hesperus* spiders. (a) Reverse-gray scale image of a typical web constructed in one of the cardboard frames used in our experiment. The cross-sectional area of the sheet of this web is outlined at the top of the image. The gum-footed lines (examples shown with arrows) are easily identified by the sticky glue near their attachment to the substrate (examples shown with rectangles). (b) The sheet of this web, after being processed in IMAGEJ to calculate its area (see Methods)

After 4 weeks of these treatments, we photographed each spider's web so that we could count the number of gum-footed lines and estimate the cross-sectional area of the sheet (see below). To take a picture of the webs, we coaxed the spiders from their retreat by gently vibrating the sheet with a forceps, then removed them from their web, and lightly dusted each web with flour. We then placed the dusted webs within a shadow-box lined with matt-black poster board. Using an Apple iPhone 7, we took two images of each web, one focused on the side profile of the sheet, and the other focused on the side profile of the gum-footed lines.

We then destroyed each web, removing all debris from the frames, and replaced each spider in its frame. We allowed the spiders 1 week to construct its second web. Although shorter than the interval we allowed the spiders for constructing their first web (4 weeks), this interval allowed enough time for the spider to build a full web, while allowing us to test for changes in web design not confounded by further feeding experience (as could happen with longer intervals requiring further feeding).

We then photographed the second web the spiders built as above. Thus, we took two images for each spider: one of its first web at the end of the 4 week treatment period, and one of its second web 1 week after destruction of its first web.

We imported each image into IMAGEJ (National Institute of Health). From these pictures, we counted each individual gum-footed line visually (Figure 1a). To estimate the cross-sectional area of the sheet web, we first set the scale of each image by using the set scale function in IMAGEJ to measure a cardboard reference with known dimensions that we included in each image. We then selected only the part of the image that included the sheet and copied the selected sheet to a new image with a black background. We then used the threshold function in IMAGEJ to select only the pixels within the sheet that corresponded to the web silk, and the measure function to calculate the area of those pixels (Figure 1b). This method provides a reliable measure of the total amount of silk on the sheet component of the web (Blackledge & Zevenbergen, 2007).

Three of the 60 initial spiders did not accept a cricket during the treatment phase, reducing our sample size, and we excluded another two spiders because the image of their web was overexposed. Thus, our final sample size was $n = 55$ spiders for first webs and $n = 56$ spiders for second webs.

2.1 | Statistical analysis

An effect of experience of prey capture site could manifest itself gradually, over the 4 weeks over which we implemented the treatments, and/or abruptly, upon construction of the second web at the end of the treatment phase (see above). We therefore tested for differences in web architecture at two stages: with the spiders' first webs at the end of the treatment period, and with the spiders' second webs.

To test for an effect of the treatments on the spiders' first webs, we used a linear model with cross-sectional sheet area or the number

of gum-footed lines (fit separately) as the dependent variable, and experience treatment as the explanatory variable.

To test for an effect of the treatments on the spiders' second webs, we used a linear model with cross-sectional sheet area or the number of gum-footed lines (fit separately) as the dependent variable. The model with cross-sectional sheet area as the dependent variable had the following explanatory variables: experience treatment, the cross-sectional sheet area of the first web (as a preliminary test for repeatability), and the number of gum-footed lines of the second web (to test for a trade-off with the sheet component). The model with the number of gum-footed lines as the dependent variable had the following explanatory variables: experience treatment, the number of gum-footed lines of the first web (as a preliminary test for repeatability), and the cross-sectional sheet area of the second web (to test for a trade-off with sheet area).

To formally estimate the repeatability of the architecture of the web components, we used linear mixed models with both values for cross-sectional sheet area or for the number of gum-footed lines (fit separately) as the dependent variable, and the following explanatory variables: spider ID (fit as a random term with the Restricted Maximum Likelihood [REML] Method), experience treatment, and web ID (first or second, to test for differences between these webs in the size of each component). The percentage variance component for spider ID provided the repeatability estimate (Nakagawa & Schielzeth, 2010). Rather than tests of significance, the REML method we used calculates 95% confidence intervals, and repeatability is detected when the interval does not overlap zero. This analysis yields a repeatability estimate that is analogous to calculating the Pearson product-moment correlation between the values for first and second webs for each of the web components for each spider, but that also allows controlling for additional factors (i.e., treatment, overall mean differences between the first and second webs).

Finally, we compared the range of variation and the coefficient of variation (CV) in both web components between first and second webs.

We conducted all analyses with JMP v. 7.0.1 (SAS Institute).

3 | RESULTS

The first webs built by the spiders did not differ significantly between treatments of experience of prey capture site, in either cross-sectional sheet area ($F_{2,52} = 2.87, p = .07$) or in number of gum-footed lines ($F_{2,52} = 0.92, p = .40$; x-axes in Figure 2).

For the second webs built by the spiders, there were significant differences in cross-sectional sheet area between treatments (Table 1). These differences were small, however (y-axis in Figure 2a), barely below the threshold for significance (Table 1), and mainly notable between the mixed treatment (least square $\bar{x} \pm SE$ sheet area = 236 ± 21 mm²) and the sheet and gum-footed line treatments (170 ± 21 , and 172 ± 21 mm²). There were no significant differences in the number of gum-footed lines between treatments (Table 2; y-axis in Figure 2b).

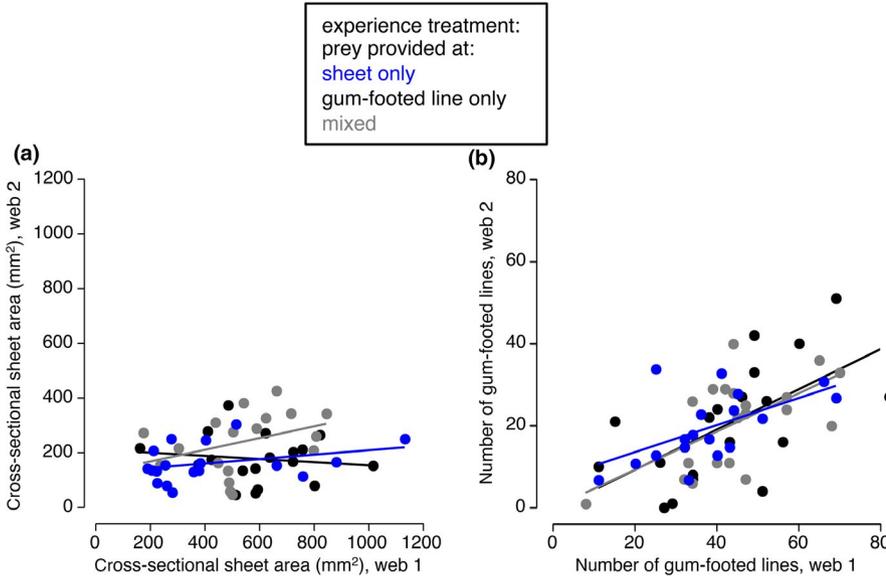


FIGURE 2 Test for plasticity and repeatability in the architecture of *Latrodectus hesperus* webs. (a) Cross-sectional area of the sheet component for the first and second webs built by the spiders. (b) Gum-footed line component for the first and second webs built by the spiders. Colors and inset box indicate the treatments of experience of the site of prey capture. (If you are viewing this in gray scale, the treatments are as follows: dark gray: sheet only; black: gum-footed line only; light gray: mixed)

TABLE 1 Variation in the cross-sectional area of the sheet component of *Latrodectus hesperus* webs, according to experience of the site of prey capture, prior investment in the sheet, and current investment in the gum-footed line component

Term	df	F	p
Experience treatment	2, 49	3.25	.047
Current gum-footed lines (2nd web)	1, 49	3.16	.08
Prior cross-sectional sheet area (1st web)	1, 49	1.44	.24

Note: Significant term highlighted in bold.

The components of the spiders' webs differed in their repeatability. We detected no repeatability for the area of the cross-sectional sheet web: the 95% CI for the term for spider ID overlapped zero, and its percentage variance component was small, corresponding to $r = .10$ (Table 3). Inspection of Figure 2a shows little relationship between the cross-sectional area of the sheet for the first and second webs the spiders built. As expected from the longer construction interval we afforded to the first webs than the second webs (4 vs. 1 week, see Methods), first webs had overall larger cross-sectional sheet areas than second webs (Table 3, Figure 2a).

By contrast, there was large-effect size repeatability for the number of gum-footed lines: the 95% CI for the term for spider ID did not overlap zero, and its percentage variance component was large, corresponding to $r = .56$ (Table 4). Figure 2b shows the relationship between the number of gum-footed lines for the first and second webs the spiders built. As above, first webs also had overall more gum-footed lines than second webs (Table 4, Figure 2b).

Although the range of variation was greater for first than for second webs (Figure 2), coefficients of variation were greater for second webs: CVs for first and second web gum-footed lines were 36% and 56%, respectively; CVs for first and second web cross-sectional sheets areas were 46% and 49%, respectively.

TABLE 2 Variation in the gum-footed line component of *Latrodectus hesperus* webs according to experience of the site of prey capture, prior investment in gum-footed lines, and current investment in the sheet

Term	df	F	p
Experience treatment	2, 51	0.51	.61
Current cross-sectional sheet area (2nd web)	1, 51	3.41	.07
Prior gum-footed lines (1st web)	1, 51	27.9	<.0001

Note: Significant term highlighted in bold.

TABLE 3 Repeatability of the cross-sectional area of the sheet component of *Latrodectus hesperus* webs

Random term			
	95% CI	% var. comp.	
Spider ID	-5,152.7 to 11,315.6	10.4	
Fixed terms			
	df	F	p
Experience treatment	2, 52.42	2.89	.065
Web ID (first, second)	1, 54.15	107.5	<.0001

Note: We show the 95% confidence interval (CI) and percentage variance component for the random term (spider ID), and F-ratio tests for the fixed effects. Significant term highlighted in bold.

Finally, we found no evidence of trade-offs between the web components: In the analysis of variation in the sheet component of the web (Table 1), the term for the current gum-footed line component was only marginally significant; and, in the analysis of variation in the gum-footed line component (Table 2), the term for the current sheet component was also only marginally significant. Further, in most of the treatments, the relationship (if any) between these

TABLE 4 Repeatability of the gum-footed line component of *Latrodectus hesperus* webs

Random term			
	95% CI	% var. comp.	
Spider ID	48.6–163.4	56.5	
Fixed terms			
	df	F	p
Experience treatment	2, 54	0.51	.60
Web ID (first, second)	1, 56	163.9	<.0001

Note: We show the 95% confidence interval (CI) and percentage variance component for the random term (spider ID), and *F*-ratio tests for the fixed effects. Significant term (and random term whose 95% CI did not overlap zero) highlighted in bold.

components would be positive rather than negative (Figure 3). Because of the apparent differences in slope between these relationships, we ran additional linear models that included an interaction between treatment and the corresponding web component (e.g., treatment × current gum-footed line component for the analysis of variation in the sheet component). Those interaction terms were not significant ($F \leq 1.19$, $p \geq .31$).

4 | DISCUSSION

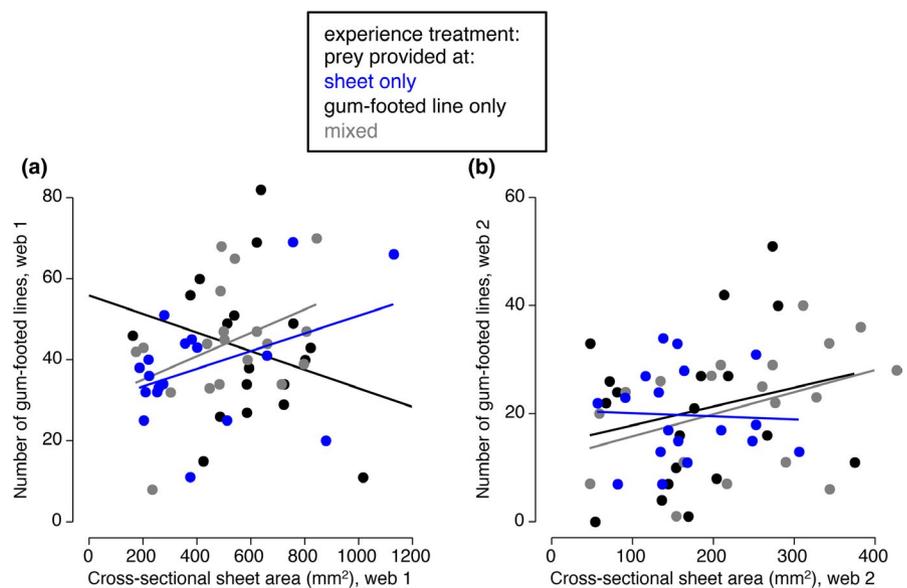
We tested for plasticity and repeatability in the web architecture of *L. hesperus* spiders. Manipulating the site on the web where spiders captured prey revealed some plasticity in allocation to the sheet or gum-footed line components: The spiders did not modify their webs gradually over the weeks during which we implemented the treatments; in their second webs, they did build larger sheets in the mixed treatment; this difference was small, and barely reached the significance cutoff, and we considered unlikely to have biological

importance. We also found no trade-off between web components (which may reflect the plentiful conditions in the laboratory, as we fed each spider weekly). We did find, however, substantial consistent individual variation (high-effect size repeatability) in the number of gum-footed lines per web, but not in the cross-sectional area of the sheet web, in agreement with a prior study (DiRienzo & Montiglio, 2016).

This combination of results suggests a number of potential interpretations. First, black widow spiders may vary web architecture according to their experience of the site of prey capture on their web at larger time scales than involved in our experiment (i.e., over longer intervals than 4 weeks). Alternatively, web plasticity in these spiders may follow cues other than experience of the site of prey capture. For example, the spiders might respond to differences in prey features; for example, the type of vibrations they make on the web or their behavior as they struggle to break free (Escalante, 2015) (and see also DiRienzo & Aonuma, 2018; Zevenbergen et al., 2008). Another possibility is that the spiders may vary web architecture when prey are less plentiful, or that they vary an aspect of web design that we did not measure (e.g., the planar extent of the sheet, which was fixed in our experiment by the size of the frames we gave them). Further, individual differences in web architecture may be due in part to variation in genotype or in the individual's unique features; for example, body condition, (although we expect this factor to be relatively unimportant in our data, as we standardized the life stage and satiation of the spiders we tested). It will be interesting to explore the contribution of such factors to variation in spider webs and other extended phenotypes.

We found repeatability in one component of *L. hesperus* webs (gum-footed lines) but not the other (sheet). This was not because the sheet component was any less variable than the gum-footed line component, as their CVs were comparable. Thus, it was the consistency of individual variation that was greater for gum-footed lines. This may be because the size of the sheet reflects how much spiders walk around the experimental boxes, as spiders leave a dragline

FIGURE 3 Test for a trade-off between the web components in *Latrodectus hesperus*. (a) First webs built by the spiders. (b) Second webs built by the spiders. Individual spiders varied in the sheet (*x*-axes) and gum-footed lines (*y*-axes) they produced, but the amount of silk allocated to each component was uncorrelated (Tables 1 and 2). Colors and inset box indicate the treatments of experience of the site of prey capture. (If you are viewing this in gray scale, the treatments are as follows: dark gray: sheet only; black: gum-footed line only; light gray: mixed)



behind as they move about, and spiders that move about more might produce larger sheets (Krafft & Cookson, 2012). If individual differences in overall movement were not consistent across the two webs, it might explain low repeatability in the sheet. If movement is similarly variable in nature, our results suggest that investment in gum-footed lines may be more likely to respond to selection, either on fixed forms or in their plasticity, than in the sheet (Bell et al., 2009).

Our results suggest that black widow spiders have evolved a web architecture that is optimized for a single foraging strategy (with the gum-footed lines), and that they have not been selected to alter web architecture in response to capturing prey in different areas of the web (at least when they experience differences in prey capture location at short time scales). Black widows capture at least some prey on the web sheet (Salomon, 2011; C. Sergi pers. obs.), but these capture events are perhaps not sufficiently common or consistent for spiders to evolve web architecture plasticity in response to short-term differences in prey capture location.

We conclude that plasticity in an extended phenotype can be context dependent. Although we detected no plasticity in black widow web architecture in response to their experience of the site of prey capture, other studies have found these spiders to modify their webs in response to other factors (short-term physiological or environmental changes) (Blackledge & Zevenbergen, 2007; DiRienzo & Aonuma, 2018; Zevenbergen et al., 2008). Further, orb-web spiders do vary web architecture according to their experience of the site of prey capture (Heiling & Herberstein, 1999; Nakata, 2012). It will be interesting to explore the kinds patterns of variation in environmental conditions that select for plasticity or canalization in different components of animal extended phenotypes.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

ORCID

Cory H. Thompson  <https://orcid.org/0000-0002-6556-8495>
Rafael L. Rodríguez  <https://orcid.org/0000-0003-0262-0839>

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