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Functional changes in web design along the ontogeny of two orb-weavers

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Abstract. Orb webs evolved primarily to capture prey, though they also have other functions. Recently, it has been argued that the orb web does not work as a functional unit, but instead some sections or components have presumably been shaped by selection to increase capture success of large prey (relative to the spider size). Changes in these components (e.g., an increase capture area) presumably compromise the design and function of other components (e.g., density of adhesive threads). In this study, we explore the changes in the design of orb webs throughout the ontogeny of two orb-weaving spiders of the genus *Leucauge*: *L. mariana* (Taczanowski, 1881) and *L. argyra* (Walckenaer, 1841). Small nymphs of both species construct webs with a relatively larger capture area and higher density of adhesive spiral loops compared to webs of larger individuals. In addition, small nymphs of *L. argyra* construct webs with more radii. These features probably increase the probability of capturing large prey. Some web features show different trade-offs in the two species. For instance, the number of adhesive threads increases with capture area in webs of *L. mariana*, but decreases in *L. argyra*. The density of adhesive threads in webs of both species decreases as the area of the web increases, but decreases faster in *L. argyra*. Thus, small nymphs are capable of optimizing different structural components of the web to increase the probability of capturing large prey, but the trade-offs between web features vary between species.

Keywords: Web modularity, ontogenetic changes, *Leucauge argyra*, *Leucauge mariana*

Orb-web spiders are sit-and-wait predators whose prey capture success relies on the location and characteristics of the web. The capture success of orb-web spiders is directly related to at least three functions of the web: interception, stopping, and retention of prey (Denny 1976; Eberhard 1986, 1990; Lin et al. 1995; Craig 2003; Herberstein & Tso 2011). Interception of flying, jumping or falling prey depends on the spider's selection of the site to construct its web and on the web size, but stopping and retaining prey without the web breaking is related to the web design and the characteristics of the silk of different threads (Janetos 1986; Barrantes & Triana 2009; Blackledge et al. 2011).

Spiders can increase the probability of intercepting prey by increasing web size (Blackledge & Eliason 2007), but the probability of capturing large, especially profitable prey does not necessarily increase with web size for most species (Eberhard 2014). Combining some hypotheses that explain the function of changes in the density of radii (Zschokke 2002) and variation in the spacing of adhesive spiral turns (Heiling & Herberstein 1998) in different sections of the orb web, Eberhard (2014) proposed a "multitrap functional approach" to explain the function of the different sections of an orb web. This approach assumes that the probability of intercepting prey is correlated with web size, but the probability of stopping larger, especially profitable prey increases with radius density, and the probability of retaining this type of prey increases with the density of adhesive spiral threads.

Capturing large, profitable prey is uncommon for orb-web spiders, but their growth and reproduction rely heavily on such prey (Venner & Casas 2005). Thus, orb webs are likely designed for these rare, but profitable events, without abandoning the capture of small prey. Small prey presumably serve to sustain spiders until the next large catch (Venner & Casas 2005). Furthermore, energy requirement varies across spiders' sizes and it is known that small spider species (and presumably small young spiders, Mayntz et al. 2009) have a higher metabolic rate (Anderson 1970, 1996; Humphreys 1977). This sets a different trade-off for small spiders, which are expected to require a proportionally larger amount of energy than large spiders, but are likely to have fewer resources to allocate to web construction (e.g., body fat and proteins).

The multitrap functional approach allows for specific predictions of changes in web design according to the spiders' energy requirements. Thus, if small spiders have a higher metabolic rate and require a relatively larger amount of energy for successful development and growth than large spiders, more large, profitable prey (relative to the spider body size) are required (the rare, large prey hypothesis; Blackledge et al. 2011). Additionally, if webs of small spiders are targeting rare large prey, these webs are expected to be larger, to have a higher density of radii to stop and dissipate the kinetic energy of a moving prey, and to have higher density of adhesive threads (i.e., more closely spaced adhesive spiral loops along radii) to improve retention of large prey (Eberhard 1990; Blackledge et al. 2011; Sensenig et al. 2012; Eberhard 2014). Some of these conditions are thought to be mutually exclusive, e.g., increasing density of adhesive spiral threads could result in smaller orbs, potentially decreasing insect interception, because spiders have a finite amount of silk (Blackledge & Zevenbergen 2006; Blackledge & Eliason 2007).

There are at least three factors – spider size, the relative sizes of its silk glands, and food supply (which is expected to affect silk production) (Mayntz et al. 2009) – that might affect web size and density of threads (e.g., adhesive threads and radii) of orb webs. We examine here the correlative effect of spider size and body condition (measured as residuals from the regression of maximum cephalothorax width vs. maximum abdomen width, Jakob et al. 1996) on capture area, number of loops of adhesive threads, density of adhesive capture threads, and number of radii in two species of the genus *Leucauge*: *L. argyra* (Walckenaer, 1841) and *L. mariana* (Taczanowski, 1881) (Tetragnathidae). Specifically, we predict that (a) small

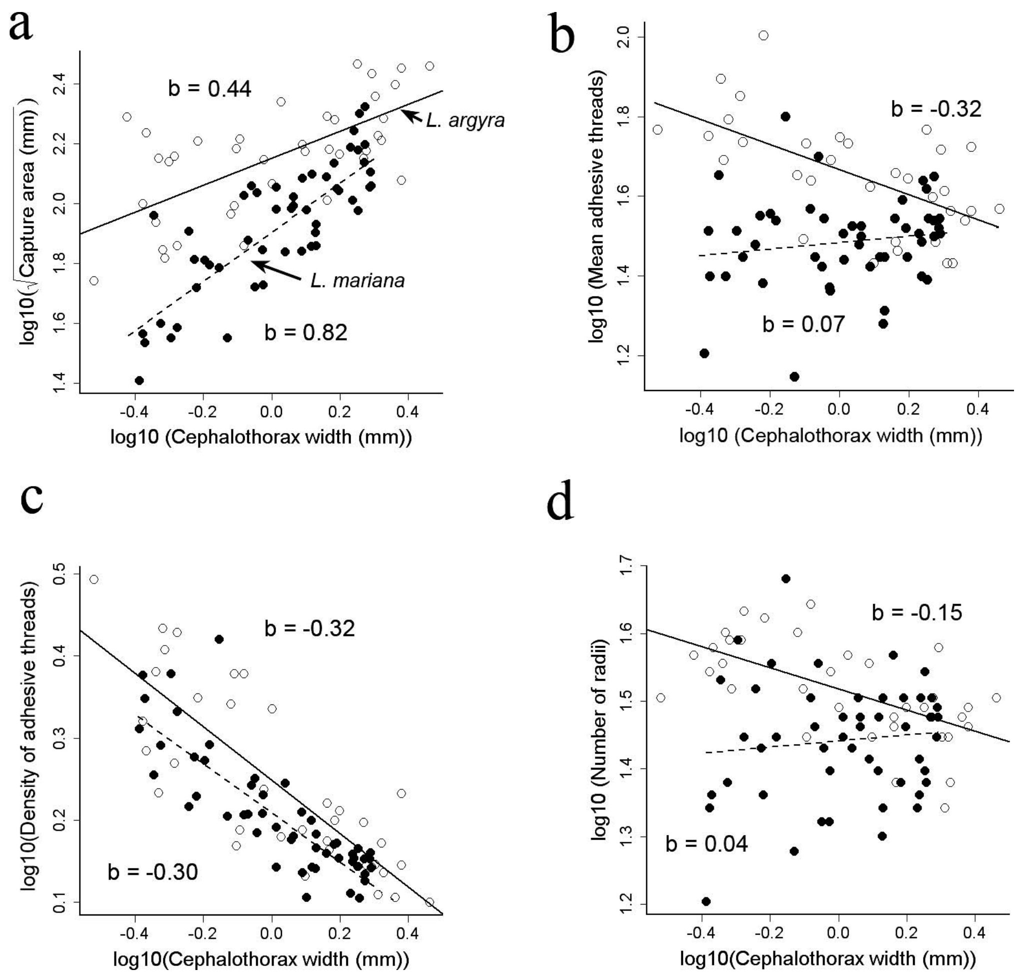

Figure 1.—Relationships between body size (cephalothorax width) and four response variables. (a) Capture area increases with size in both species. (b) The mean number of adhesive threads (sticky spiral loops) decreases with body size in *L. argyra* but not in *L. mariana*. (c) Density of adhesive threads (no. sticky spiral loops/ radii length along capture area) decreases with body size in both species. (d) Number of radii decreases with body size in *L. argyra* but not in *L. mariana*. The value of the slope, b, for each species is shown within each figure.

spiders should construct proportionally larger webs with higher density of adhesive capture threads and higher density of radii, to increase the probability of capturing large, profitable prey to meet their higher energy requirements; (b) spiders with poor body condition would construct larger webs independent of their body size, assuming that interception and prey capture increase with area of the orb web. The first prediction would be validated if small spiders construct proportionally larger and denser webs than large spiders (i.e., negative allometries log-log linear models), and the second prediction would be validated if large or small poorly fed spiders produce larger webs than well-fed spiders of the same size.

METHODS

Focal species.—Both *Leucauge* species construct their orb webs on early second growth vegetation, along forest edges between 0.20 to 1.70 m above ground (Eberhard & Huber 1998; Aisenberg & Barrantes 2011). Most webs vary from nearly horizontal to ca. 20° (GB, unpublished data) and webs of juveniles have a tangle above and below the orb (adults occasionally have also tangles; Triana et al. 2011); these tangles are denser in *L. argyra*. In Costa Rica, *L. argyra* occurs from sea level to approximately 500 m and *L. mariana* primarily from 700 to 1800 m.

General conditions.—We photographed webs and collected spiders: *L. argyra* at El Silencio, Quepos, Puntarenas province (09° 24′ N, 84° 01′ W, elevation 46 m above sea level.) in January 2013, and *L. mariana* on the campus of the University of Costa Rica (9° 54′ N, 84 °03′ W; elevation 1200 m), San José Province, Costa Rica, and Parque del Este, La Unión, Cartago, Costa Rica (9° 56′ N, 84° 00′ W; elevation 1400 m). We coated each web with talcum powder; placed a 1 cm long piece of graph paper on or just beside the web to serve as a scale prior to taking each picture; and then preserved the spider in 80% ethanol. All webs were photographed early in the morning (0700-1000) to include only the first of several webs these spiders typically construct each day. We found only five webs (3 of *L. mariana*, 2 of *L. argyra*) with a clear indication of spiders' prey capture (some spiral turns collapsed and the spider feeding on prey), and we had no control for the recent feeding history of spiders.

Table 1.—Number of estimated parameters [K], and results of Akaike information criterion [AIC], Δ_i(AIC) [AICi – min(AIC)], Akaike weights [w_i(AIC)] and Bayesian information Criterion [BIC] for the different models constructed for each response variable. ■ Indicates the optimal model for each response variable. Ceph = cephalothorax width.

Model rank	Explanatory variable	K	AIC	Δ_i(AIC)	w_i(AIC)	BIC
Leucauge argyra						
Response variable: Capture area						
	ceph * resid	4	-21.41	3.68	0.12	-13.93
	ceph + resid	3	-21.31	3.78	0.11	-15.20
	■ceph	2	-25.09	0	0.76	-20.42
Response variable: Mean no. spiral loops						
	ceph * resid	4	-35.46	5.15	0.07	-28.29
	ceph + resid	3	-35.40	5.21	0.06	-30.13
	■ceph	2	-40.61	0	0.87	-36.12
Response variable: No. radii						
	ceph * resid	4	-71.72	7.74	0.02	-64.71
	ceph + resid	3	-73.57	5.89	0.05	-67.83
	■ceph	2	-79.46	0	0.93	-75.07
Response variable: Density of adhesive spiral loops						
	ceph * resid	4	-20.00	3.32	0.14	-12.83
	ceph + resid	3	-19.25	4.07	0.10	-13.39
	■ceph	2	-23.32	0	0.76	-18.83
Leucauge mariana						
Response variable: Capture area						
	ceph * resid	4	-57.70	0	0.53	-48.35
	ceph + resid	3	-53.11	4.59	0.05	-45.54
	■ceph	2	-57.23	0.47	0.42	-51.50
Response variable: Mean no. spiral loops						
	ceph * resid	4	-60.52	0	0.56	-51.16
	ceph + resid	3	-56.58	3.94	0.08	-49.01
	■ceph	2	-59.69	0.83	0.37	-53.95
Response variable: No. radii						
	ceph * resid	4	-80.80	4.97	0.05	-71.65
	ceph + resid	3	-81.01	4.76	0.05	-73.61
	■ceph	2	-85.77	0	0.57	-80.15
Response variable: Density of adhesive spiral loops						
	ceph * resid	4	-79.42	3.65	0.12	-70.27
	ceph + resid	3	-79.09	3.98	0.10	-71.68
	■ceph	2	-83.07	0	0.77	-77.45
Both species						
Response variable: Capture area						
	spp * ceph * resid	8	-79.25	3.88	0.11	-57.70
	spp * ceph+ resid	5	-78.24	4.89	0.07	-63.66
	spp + ceph + resid	4	-70.48	12.65	0.00	-58.26
	■spp * ceph	4	-83.13	0	0.80	-70.92
	spp + ceph	3	-75.27	7.86	0.02	-65.46
	spp	2	-21.07	62.06	0.00	-13.67
	ceph	2	-38.53	44.6	0.00	-31.13
Response variable: Mean no. spiral loops						
	spp * ceph * resid	8	-97.98	4.13	0.10	-76.66
	spp * ceph+ resid	5	-97.75	4.36	0.09	-83.31
	spp + ceph + resid	4	-88.53	13.58	0.00	-76.43
	■spp * ceph	4	-102.11	0	0.79	-90.02
	spp + ceph	3	-93.02	9.09	0.01	-83.30
	spp	2	-92.29	9.82	0.01	-84.96
	ceph	2	-59.77	42.34	0.00	-52.44
Response variable: No. radii						
	spp * ceph * resid	8	-149.49	12.82	0.00	-128.52
	spp * ceph+ resid	5	-155.62	6.69	0.02	-141.40
	spp + ceph + resid	4	-152.96	9.35	0.00	81.48

Table 1.—Continued.

Model rank	Explanatory variable	K	AIC	Δ_i(AIC)	w_i(AIC)	BIC
	■spp * ceph	4	-161.54	0.77	0.36	-149.62
	spp + ceph	3	-158.81	3.50	0.09	-149.24
	spp	2	-162.31	0	0.53	-155.09
	ceph	2	-149.96	12.35	0.00	-142.74
Response variable: Density of adhesive spiral loops						
	spp * ceph * resid	8	-92.82	11.59	0.00	-71.73
	spp * ceph+ resid	5	-94.66	9.75	0.01	-80.37
	spp + ceph + resid	4	-99.29	5.12	0.06	-87.32
	spp * ceph	4	-99.76	4.65	0.08	-87.80
	■spp + ceph	3	-104.41	0	0.84	-94.78
	spp	2	-7.38	97.03	0.00	-0.13
	ceph	2	-87.11	17.3	0.00	-79.86
			Trade-off between variables			
Response variable: Capture area						
	spp * ceph * radii	8	-92.51	1.20	0.29	-71.53
	spp * radii + ceph	5	-91.68	2.03	0.19	-77.46
	■spp + ceph + radii	4	-93.71	0	0.52	-81.80
Response variable: Mean no. spiral loops						
	spp * ceph * capt	8	-122.91	7.97	0.02	70.45
	■spp * capt + ceph	5	-130.88	0	0.85	71.44
	spp * ceph + capt	5	-128.06	2.82	0.21	70.03
	spp + ceph + capt	4	-127.21	3.67	0.16	68.61
Response variable: Density of adhesive spiral loops						
	spp * ceph * capt	8	-124.53	8.34	0.01	71.27
	spp * ceph + capt	5	-125.24	7.63	0.02	68.62
	■spp * capt + ceph	5	-132.87	0	0.95	72.44
	spp + capt + ceph	4	-126.48	6.39	0.04	68.24

On each web photographed, we measured the capture area, the length of the longest radius along the capture area from the inner-most spiral turn (external edge of the free zone) to the outermost adhesive spiral turn, and along the radius opposite to the longest radius; we also measured the distance between sticky spiral threads along both of these radii, following Barrantes & Eberhard (2012). We used ImageJ (Rasband 2016) to measure all features on each web. Additionally, we calculated the density of adhesive spiral loops: the number of adhesive spiral loops/radius length along the capture area for the longest radii and those opposite the longest. For each spider, we measured the greatest cephalothorax and abdomen width using Dino-Eye Eyepiece digital color camera (Model AM423X) attached to the ocular of a Wild Model M3Z dissecting microscope (Wild Company, New York, USA). We used the residuals from the regression of maximum cephalothorax width vs. maximum abdomen width as a proxy of body condition (Jakob et al. 1996). We included a wide range of spider sizes that probably covered from the first stage out of the egg sac to adults (this based on sizes and some differences in coloration seen in spiderlings of these species); size of spiders correlates with spiders' developmental stages (Barrantes & Madrigal-Brenes 2008; Foelix 2011). We deposited voucher specimens in the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica.

Statistical analyses.—We used Generalized Least Squares Models (GLS; library nlme, using restricted maximum likelihood method-REML) to test the effect of spider size (i.e., cephalothorax width) and body condition on the square root of the capture area, mean number of adhesive spiral loops along the longest and the opposite radii, density of adhesive spiral threads, and number of radii. We ran the analyses first for each species alone, and then included both species to compare them. We also evaluated if species trade off differently for different web features. Specifically, we first tested the effect of number of radii and spider size on capture area and mean number and density of adhesive spiral loops, and then tested the effect of capture area and spider size on mean number and density of adhesive spiral threads between both species. In the first case, we selected number of radii as the predictor variable because spiders construct all radii first, prior to laying the adhesive threads, and in the second case, the capture area is defined by where the spider places the first turn of the adhesive thread, so that the number of turns of the adhesive spiral is likely a subsequent decision the spider makes after deciding where to place the first turn (Barrantes & Eberhard 2012). In cases when AIC values in models with interaction term (spp * predictor variable) were similar to the AIC of the optimal model (AIC differ by two or fewer units), we favored the first. This allowed us to compare the trade-offs of web features between both species. When the selected models included the interaction term, spider spp*cephalothorax, the interaction term tested whether body size (cephalothorax width) of both species scale similarly (not significant) or not (significant) for each of the response variables.

We performed a series of models for each response variable and selected the model that gives the most accurate description of the data based on AIC (Akaike Information Criterion) and AIC weights (Wagenmakers & Farrell 2004) (Table 1). We

Table 2.—Effect of spider size (cephalothorax width = ceph.) on five response variables: capture area (capt. a), mean number of sticky spiral loops, density (mean number of sticky spiral loops/mean radii length), and number of radii for *Leucauge argyra* (A), *L. mariana* (B), and between both species (C) based on Generalized Least Squares Models. It also includes the trade-offs between web features for both species (D). All numerical variables were $\log_{10}$ transformed.

A	*Leucauge argyra*			
Response variable: Capture area				
Effect	Coefficient	SE	T	P
intercept	2.16	0.02	90.28	<0.0001
ceph.	0.39	0.09	4.57	0.0001
Response variable: Mean no. spiral loops				
intercept	1.67	0.02	88.01	<0.0001
ceph.	-0.34	0.07	-4.88	<0.0001
Response variable: No. radii				
intercept	1.52	0.01	147.69	<0.0001
ceph.	-0.16	0.04	-4.44	0.0001
Response variable: Density				
intercept	-0.15	0.02	-6.21	<0.0001
ceph.	-0.75	0.09	-8.26	<0.0001
B	*Leucauge mariana*			
Response variable: Capture area				
intercept	1.91	0.02	111.80	<0.0001
ceph.	0.82	0.08	9.96	<0.0001
Response variable: Mean no. spiral loops				
intercept	1.48	0.02	88.49	<0.0001
ceph.	0.07	0.08	0.86	0.3909
Response variable: No. radii				
intercept	1.44	0.01	114.56	<0.0001
ceph.	0.04	0.06	0.74	0.4632
Response variable: Density				
intercept	-0.22	0.01	-17.26	<0.0001
ceph.	-0.75	0.06	-12.29	<0.0001
C	Both species			
Response variable: Capture area				
Effect	Coefficient	SE	T	P
intercept	2.16	0.02	99.02	<0.0001
L. mariana	-0.25	0.03	-8.60	<0.0001
ceph.	0.39	0.08	5.01	<0.0001
spp * ceph.	0.43	0.12	3.61	<0.0001
Response variable: Mean number of sticky spiral loops				
Effect	Coefficient	SE	T	P
Intercept	1.67	0.02	84.28	<0.0001
L. mariana	-0.20	0.03	-7.70	<0.0001
ceph.	-0.34	0.07	-4.67	<0.0001
spp * ceph.	0.41	0.11	3.84	<0.0001
Response variable: Number of radii				
Effect	Coefficient	SE	T	P
intercept	1.52	0.01	112.11	<0.0001
L. mariana	-0.08	0.02	-4.51	<0.0001
ceph.	-0.16	0.05	-3.37	0.0012
spp * ceph.	0.21	0.07	2.91	0.0047
Response variable: Density of adhesive spiral loops				
Effect	Coefficient	SE	T	P
intercept	-0.15	0.02	-7.84	<0.0001
L. mariana	-0.07	0.02	-2.74	0.0074
ceph.	-0.75	0.05	-14.21	<0.0001
D	Trade-off between variables			
Response variable: Capture area				
Effect	Coefficient	SE	T	P
intercept	1.24	0.48	2.58	0.0116
L. mariana	-0.32	0.56	-0.57	0.5667
ceph.	0.69	0.06	11.04	<0.0001
radii	0.59	0.31	1.86	0.0666
spp * radii	0.11	0.38	0.29	0.7697
Response variable: Mean number of adhesive threads				
Effect	Coefficient	SE	T	P
intercept	0.055	0.18	0.30	0.7632
L. mariana	-0.09	0.02	-4.40	<0.0001
ceph.	-0.06	0.04	-1.34	0.1831
radii	1.06	0.12	8.88	<0.0001
Response variable: Mean number of adhesive threads				
Effect	Coefficient	SE	T	P
intercept	0.95	0.23	3.98	0.0001
L. mariana	-0.73	0.23	-3.16	0.0022
ceph.	-0.48	0.07	-7.35	<0.0001
capt. a	0.33	0.11	3.03	0.0032
spp * capt. a	0.32	0.11	2.93	0.0044
Response variable: Density				
Effect	Coefficient	SE	T	P
intercept	1.38	0.23	5.97	<0.0001
L. mariana	-0.93	0.22	-4.15	<0.0001
ceph.	-0.44	0.06	-6.90	<0.0001
capt. a	-0.71	0.11	-6.66	<0.0001
spp * capt. a	0.36	0.11	3.41	0.0010

$\log_{10}$ transformed variables, and, in all cases, these transformed variables fit well the assumptions of normality of residuals and homogeneity of variances. In addition, we regressed body size against each of the response variables to obtain each species' slope to show graphically the effect of the interaction term. We used the R statistical language, version 3.0.1 (R Development Core Team 2014) for all analyses.

RESULTS

We analyzed four features of the orb web of *L. argyra* and *L. mariana* which are probably directly related to prey capture success: capture area, mean number of adhesive spiral loops, number of radii, and density of adhesive spiral loops.

Intra-specific analyses.—In *L. argyra*, small nymphs constructed webs with larger capture area, higher density of adhesive spiral loops, larger mean number of adhesive spiral loops, and more radii than larger individuals (slopes significantly lower than 1 in a log-log scale) (Table 2A, Fig. 1).

In *L. mariana*, small individuals constructed webs with proportionally larger capture area and higher density of adhesive spiral loops, but the size of spider did not have a significant effect on the mean number of adhesive spiral loops or the number of radii (Table 2B, Fig. 1). The selected models, based on AIC and other additional parameters, included only size (cephalothorax width) as the predictor variable (Table 1). In addition, in the excluded models, neither the body condition (Fig. 2) nor any interaction had a significant effect on the response variables.

Inter-specific analyses.—All four web features were significantly greater in webs of *L. argyra* than in webs of *L. mariana* (Table 2C). Small individuals of *L. argyra* constructed webs with greater capture area than did individuals of equal size of *L. mariana* (Fig. 1a; Table 2C). For both species, the capture area of the web increased with the spider size, but capture area increased at a greater rate in *L. mariana* (b = 0.82) than in *L.*

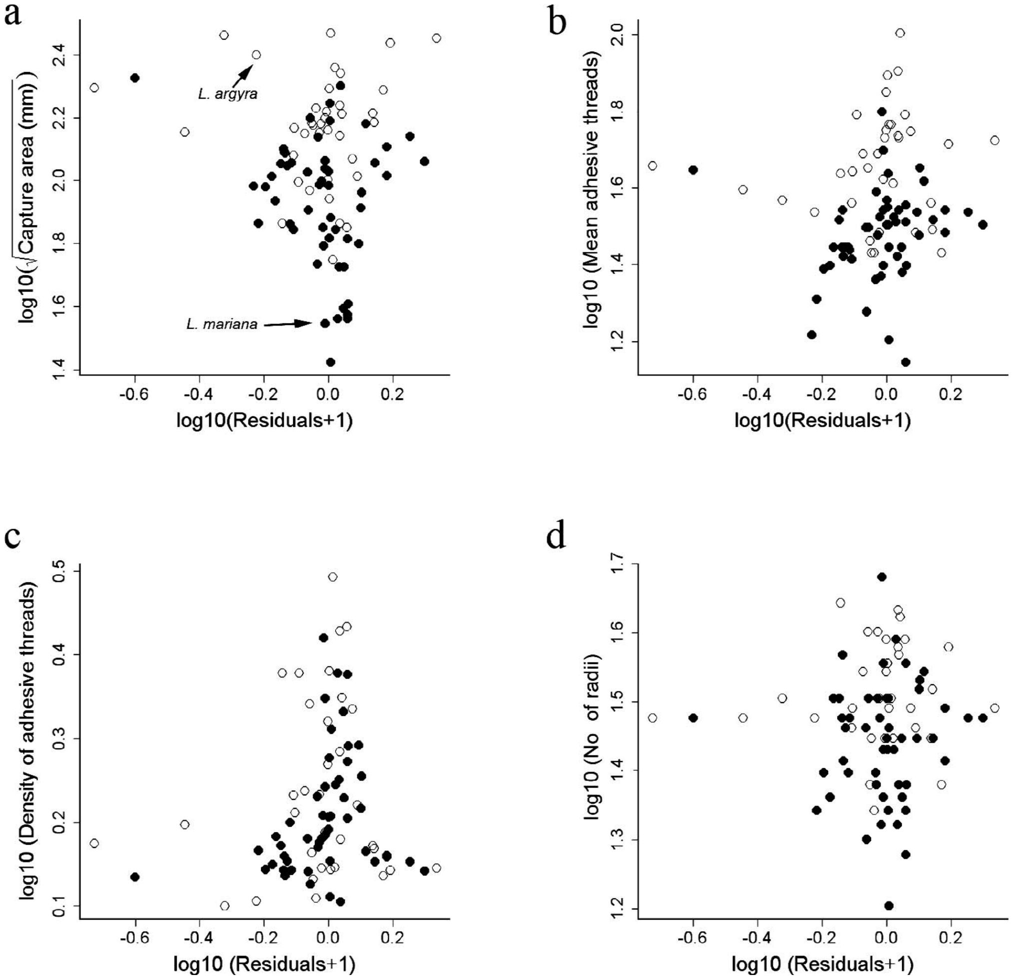

Figure 2.—Relationships between spider size and body condition (measured as residuals from the regression of maximum cephalothorax width vs. maximum abdomen width; Jakob et al. 1996) and four response variables for *L. argyra* and *L. mariana*. (a) Capture area. (b) Mean number of adhesive threads (sticky spiral loops). (c) Density of adhesive threads (no. sticky spiral loops/ radii length along capture area). (d) Number of radii. Residuals did not have a significant relationship with any of the response variables.

argyra (0.44), which resulted in a significant interaction between slopes of both species (Table 2C; Fig. 1a).

The number of adhesive spiral loops decreased drastically as the size of *L. argyra* spiders increased, but the size of the spider had little effect on the number of adhesive spiral loops in webs of *L. mariana* (Table 2C; Fig. 1b). Small *L. argyra* constructed webs with more adhesive spiral loops than large spiders, but the size of *L. mariana* spiders was not correlated with the number of adhesive spiral loops (Table 2C, Fig. 1b). The density of adhesive spiral loops decreased significantly with spider size in both species (Table 2C; Fig. 1c).

Small nymphs of *L. argyra* constructed webs with more radii than did small nymphs of *L. mariana* (Fig. 1d, Table 2C), however, the number of radii decreased rapidly with body size in *L. argyra*, but not in *L. mariana* (Fig. 1d). The body condition of spiders did not correlate with variation of any of the response variables.

Trade-offs between web features.—The trade-off between pairs of web features varied among features and between both species (Table 2D, Fig. 3). The number of adhesive threads increased with the number of radii in webs of both species (Table 2D, Fig. 3b), and increased with capture area in webs of *L. mariana*, but decreased in webs of *L. argyra* (Fig. 3c). Similarly, the capture area increased in webs of *L. mariana*, but decreased in webs of *L. argyra* with the number of radii (Fig. 3a). The density decreased with capture area in both species, but did so faster in *L. argyra* (Fig. 3d).

DISCUSSION

In general, our results support the hypothesis that the higher energy requirement of small spiders could influence those web features directly related with increasing capture of large prey, but the two species differed in several respects. The large number of radii in webs of small *L. argyra* is expected to increase the probability of stopping large prey as predicted for the "the radius density hypothesis" (Zschokke 2002; Eberhard 2014); more radii impacted by a prey will more effectively absorb the prey's momentum. The capture area was also greater for webs of *L. argyra* than for *L. mariana* at nearly all spider sizes (Fig. 1), but capture area increased faster relative to the spider size in *L. mariana* (Fig. 1). We do not have information that explains the differences in this relationship,

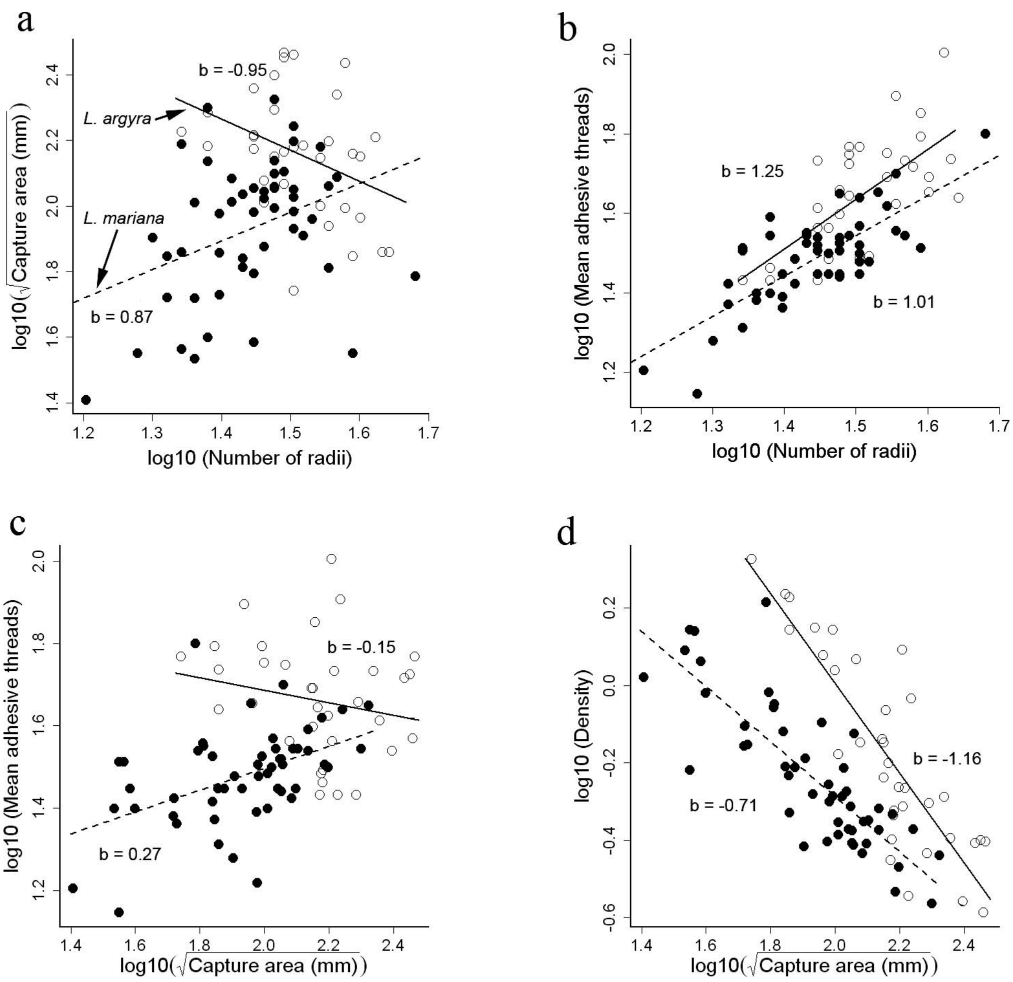

Figure 3.—Relationships between web features. (a) Capture area increases in *L. mariana* but decreases in *L. argyra* with the number of radii. (b) The mean number of adhesive threads increases with the number of radii in both species. (c) The mean number of adhesive threads increases in *L. mariana* but decreases in *L. argyra* as the capture area increases. (d) The density of adhesive threads decreases with the capture area in both species. The value of the slope, b, for each species is shown within each figure.

particularly considering that the ecology of both species is similar in several respects: their microhabitats have similar structure (e.g., early second growth), and their prey overlap at least at family level (Hodkinson 2005, GB unpubl. data). However, different stages in each species could still select particular insect sizes (based on their web design), for which data is unavailable.

There is a gradual change in the design of the web of both species in terms of capture area, density of adhesive threads, and number of radii (in *L. argyra*) as the spider grows. Radii are essential for stopping, particularly large prey. These are structural threads that effectively dissipate the kinetic energy of the flying, or falling prey. Consequently, the probability of capturing proportionally large prey increases in small spiders with the number of radii that a prey impact. A higher density of adhesive threads presumably increases prey retention and consequently the capture success, again in small spiders. This occurs because a higher number of adhesive threads adhere to the prey, retaining it long enough for the spider to deliver the attack (Eberhard 1986, 1990; Lin et al. 1995; Craig 2003; Blackledge et al. 2011; Herberstein & Tso 2011). Web features suggest that glands to produce adhesive threads (i.e., aggregate, ampullate, and flagelliform glands) may have different rates of silk production in small nymphs of both *Leucauge* species, which allow them to increase both area and density of adhesive threads. The change in density of adhesive spiral loops in webs of different size could also be influenced by other factors: the spider's morphology, metabolic rate, body condition, remaining amount of silk in glands, prey type and prey abundance (Eberhard 1988, 1990; Blackledge 2012), and wind condition. For instance, in webs of small nymphs, the higher density of radii could also maintain the thinner adhesive threads in place, preventing them from sagging and sticking together under windy conditions (Sensenig et al. 2010; Eberhard 2014). Another alternative explanation is that small nymphs add more threads to their webs to compensate for their proportionally thinner threads, as it occurs in small spider species (Sensenig et al. 2010).

Despite the general pattern found in webs of both spiders, some web features trade off differently between both species. Notably, the number of adhesive threads increases in *L. mariana*, but decreases in *L. argyra* as the capture area increases, and the density of adhesive threads decrease with capture area in both species, but faster in *L. argyra*. This suggests that there may be species specific trade-offs between web features to increase capture success of large prey, but until the trade-offs between web features of more species are known, this hypothesis will remain open.

The body condition did not correlate with variation of web features. For the body condition to affect web features, the spiders should be under poor feeding conditions for long periods of time (Sherman 1994; Heiling & Herberstein. 2000). However, it is unlikely that for generalist spiders like *Leucauge*, prey availability decreases so drastically in non-seasonal rain forests as to affect silk production and web features. At least for some orb web spiders, prey capture did not decrease during the driest periods in a relatively seasonal rain forests (Robinson & Robinson 1973).

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