

1 Orb-weaving spiders show a correlated syndrome of 2 morphology and web structure in the wild

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11

12 Abstract

13 Extended phenotypes are traits that exist outside the physical body of the organism. Despite
14 their potential role in the lives of both the organisms that express them and other organisms
15 that can be influenced by extended phenotypes, the consistency and covariance with
16 morphological and behaviour traits of extended phenotypes is rarely evaluated, especially in
17 wild organisms. We repeatedly measured an extended phenotype that directly influences an
18 organism's prey acquisition, the web structure, of wild orb-weaving spiders (*Micrathena*
19 *vigorsii*), which re-build their webs each day. We related web structure traits to behavioural
20 traits and body size (length). Both web diameter and web density were repeatably different
21 among individuals, while reaction to a predation threat was slightly so, but response to a
22 prey stimulus and web symmetry were not. There was a syndrome between morphology and
23 web structure traits, where larger spiders spun webs that were wider, had webs with
24 increased thread spacing, and the spider tended to react more slowly to a predation threat.

25 When a spider built a relatively larger web it was also relatively a less dense and less
26 symmetrical web. The repeatability of web construction and relationship with spider body
27 size we found may be common features of intra-population variation in web structure in
28 spiders. Individual variation along the morphology and web structure syndrome could
29 represent variation in individual foraging strategies, or age-based correlated changes. By
30 estimating the consistency and covariances of extended phenotypes we can begin to
31 evaluate what maintains their variation and how they might evolve.

32 **Key words:** extended phenotype, *Micrathena*, personality, syndrome, web structure

33

34 Introduction

35

36 Some phenotypes of organisms are “extended”, in that they exist beyond the physical body
37 of the organism (Dawkins 1978; Dawkins 1982). Examples include bird nests, beaver dams,
38 and spider webs. Extended phenotypes can relate to the survival, foraging, or mating
39 success of an individual, and those that use the environment the individual modifies
40 (including “ecosystem engineers”; Jones et al. 1994; Jones et al. 1997; Rosell et al. 2005;
41 Kooch and Jalilvand 2008; Jones et al. 2009; White and O'Donnell 2010; Ransom 2011;
42 Posthumus et al. 2015; Ringler et al. 2015; Fisher et al. 2019). When extended phenotypes
43 are repeatably expressed over the life of an organism, they have the potential to show
44 reversible plasticity, for example a bird may build a large nest one year and a small nest the
45 following year. Despite this plasticity, traits with the potential to be labile are often consistent
46 within an individual across time or in different environments, such that within a population
47 there can be considerable variation among-individuals in the mean trait they express (Bell et
48 al. 2009). Causes and consequences for this consistent among-individual variation has been
49 the source of great interest, especially within the last 20 years (Koolhaas et al. 1999; Dall et
50 al. 2004; Réale et al. 2007; Bell et al. 2009; Stamps and Groothuis 2010). However,
51 plasticity and consistency of extended phenotypes is not extensively documented (Venner et

52 al. 2000; Blamires 2010; Dirienzo and Montiglio 2016; Montiglio and DiRienzo 2016;
53 Blamires, Hasemore, et al. 2017; Blamires, Martens, et al. 2017). Furthermore, the
54 expression of extended phenotypes may covary with other repeatably expressed traits such
55 as behaviours, or more stable straits such as morphology, but again this is not often
56 documented (Dirienzo and Montiglio 2016; Montiglio and DiRienzo 2016). Yet, it is important
57 that we do so as extended phenotypes alter the environment an individual experiences,
58 possibly changing selection pressures both for itself and for other organisms that use the
59 same environment.

60 Evaluating the repeatability of extended phenotypes and their associations with other
61 aspects of behaviour and morphology has a variety of implications. First, as only a portion of
62 any among-individual variation will have a genetic basis, repeatability can set the upper limit
63 for heritability (Falconer 1981; Boake 1989; but see: Dohm 2002), and repeatability in
64 behaviour has various consequences for ecological and evolutionary processes (Dall et al.
65 2012; Sih et al. 2012; Wolf and Weissing 2012). Meanwhile, extended phenotypes being
66 correlated into “syndromes” with traits such as body size or boldness could help explain the
67 maintenance of variation in extended phenotypes within populations (Roff 1992; Sih, Bell,
68 Johnson, et al. 2004; Sih, Bell, and Johnson 2004). Further, trait associations can influence
69 how syndrome structure (i.e., the G-matrix) and its constituent traits evolve (Lande 1979;
70 Lande and Arnold 1983), which can sometimes impinge on adaptive evolution (Dochtermann
71 and Dingemanse 2013; Royauté et al. 2019). The repeatability of extended phenotypes and
72 their phenotypic integration with other traits is especially interesting because extended
73 phenotypes help to engineer the external environment surrounding an organism, and
74 therefore how selection acts on other traits. It is therefore necessary that we quantify the
75 repeatability of extended phenotypes and assess how they are correlated with other traits.

76 Here we quantify the degree of consistency of various aspects of an extended
77 phenotype and measure its covariance with body size and two behavioural traits. We studied
78 the orb-weaving spider *Micrathena vigorsi* (Araneae: Araneidae; Fig. 1a). While spider webs

79 were once thought to rigidly follow species specific patterns, more recent research has
80 identified both among- and within-individual variation in web structure, such as differences in
81 size, shape, the number of different kinds of threads/lines, and the number of mistakes made
82 in the web's construction (Sherman 1994; Heiling and Herberstein 2000; Venner et al. 2000;
83 Blamires 2010; Dirienzo and Montiglio 2016; Montiglio and DiRienzo 2016). See Heiling and
84 Herberstein (2000) for a review. Variation in web structure can influence what and how many
85 prey are caught (Uetz et al. 1978; Chacon and Eberhard 1980; Sensenig et al. 2010),
86 whether prey are retained (Blackledge and Zevenbergen 2006; Blamires, Martens, et al.
87 2017), how much protection the web provides from predators (Zevenbergen et al. 2008), and
88 may also reflect a spider's body condition (Blackledge and Zevenbergen 2007; Dirienzo and
89 Montiglio 2016 Jul), recent experience (Nakata and Ushimaru 1999; Venner et al. 2000),
90 and/or age (Anotaux et al. 2012; Anotaux et al. 2014). Spider web structure is therefore an
91 important phenotype for various components of a spider's fitness.

92 *Micrathena spp.* rebuild the orb of their web anew each day (Shelly 1984; Hodge
93 1987), and so allow one to easily measure the repeated expression of an extended
94 phenotype and determine if individuals consistently differ from each other over time. It also
95 allows us to see if there is day-to-day variation in web structure, if for example certain
96 environmental conditions consistently influence web structure for all individuals. Previous
97 studies on among-individual consistency in web structure have been conducted in captivity
98 (Dirienzo and Montiglio 2016; Montiglio and DiRienzo 2016; Dirienzo and Montiglio 2016 Jul;
99 DiRienzo and Dornhaus 2017; DiRienzo and Aonuma 2018), but our study took place in the
100 wild to assess the degree of consistency of behaviour and web structure, and how they
101 covary with each other and with spider body size, in a natural setting. Studies in
102 standardised laboratory settings are useful when we want to control for external factors, but
103 studies in free-living populations help us assess the degree of consistency and correlations
104 between traits that natural selection may be acting upon. Conducting studies in the wild also

105 avoids the potential confound that individual differences in phenotypes can be driven by
106 individual differences in response to laboratory conditions (Roche et al. 2016).

107 We estimated the phenotypic correlations between spider predation and anti-predator
108 behaviour, web structure traits, and body length. We then partitioned our estimated
109 covariances into the among-individual, among-date, and residual levels. We predicted that
110 larger spiders will build bigger and less dense webs (webs with fewer threads per area of the
111 web), as they will be targeting larger prey (Uetz et al. 1978; Chacon and Eberhard 1980;
112 Sensenig et al. 2010), and that larger spiders will more aggressively attack a prey stimulus
113 and will react less readily towards a predator stimulus (Rundle and Brönmark 2001; Mayer et
114 al. 2016). We also predicted that there will be a positive among-date covariance between
115 responses to predator and prey stimuli, as on hotter days spiders might be more responsive
116 in general to a range of different cues (Pruitt et al. 2011; Briffa et al. 2013). Finally, we
117 predicted a negative residual covariance between web diameter and both web density and
118 web symmetry, as on instances that a spider builds a relatively bigger web, it may also build
119 a less dense and less symmetrical web (Blamires 2010). We do not expect a relationship
120 here between web density and anti-predator behaviour (e.g. Blackledge and Zevenbergen
121 2007) as *M. vigorsii* do not use their web for defence. We investigated covariances among
122 six traits, all at the among-individual, among-date, and residual level (with some exceptions,
123 see below). This totals 45 covariances; we do not make predictions for each for the sake of
124 brevity.

125

126 **Methods**

127 **Data collection**

128 Our study took place between 16/6/ – 15/7 2019 near Tena in Ecuador (approx. lat long = -
129 1.044, -77.715), under the Ecuadorian Ministry of the Environment permit no. 014-2019-IC-
130 FLO-DNB/MA. We located individual *M. vigorsii* ($n = 55$) in a hedgerow along a transect at

131 the northern side of a road (route number: 436) between 9 and 121 cm above the ground
132 (mean = 59 cm). We assume all individuals in our study are adult females, as males of
133 *Micrathena* spp. are much smaller and stop building webs upon reaching maturity
134 (Chickering 1961; Shelly 1984; Hodge 1987). Once we found an individual, we marked its
135 location with a piece of flagging tape with the unique ID of the spider written on it. This
136 allowed us to return and phenotype the same individual on different days without disrupting
137 the individual's behaviour by capturing it and marking it directly. While *Micrathena* spp. do
138 rebuild their orb each day, the "frame" of the web remains in place, and so the position of the
139 web will vary minimally day-to-day. When two individuals were close together, we used their
140 size measurements and notes on individual characteristics such as colouration and exact
141 web location to identify them. We are therefore confident that we were able to repeatably
142 find and identify the same individuals. We only conducted testing between 14:00-17:00,
143 after web construction should have been completed, limiting the impact the time of day could
144 have on variation in behaviour and web structure.

145 The first time we found an individual, we measured its length (to the nearest 0.01
146 mm) using a pair of callipers (Traceable, Fisher Scientific, PA, USA) held up against the
147 spider in its web. In 10/55 of cases (18.2%; mostly at the start of the study before the
148 callipers were available) we did not measure the length of the individual. Following this, we
149 tested the individual for responsiveness towards a prey stimulus. To do this, we touched a
150 piece of wire attached to a modified vibrating device (8" Vibrating Jelly Dong, Top Cat Toys,
151 Chatsworth CA, USA) to the lowest point of the orb of the web. Assays like this are
152 commonly used to estimate foraging aggression in both solitary and social spiders
153 (Laskowski and Pruitt 2014; Dirienzo and Montiglio 2016; Lichtenstein et al. 2019). We timed
154 from the start of the vibrations until the spider touched the end of the vibrating wire. If the
155 spider did not respond within 180 seconds (55/210 tests that the spider did not flee before
156 the trial began) we set the spider's score at 180. Next, we waited for the spider to return to
157 the centre of the web and adopt a resting position (facing down towards the floor), before

158 testing it for a reaction to a predation threat. We tapped the abdomen of the spider lightly
159 with the extended lead of a mechanical pencil and recorded how many taps transpired until
160 the spider fled. If the spider did not react within 24 taps (26/210 tests the spider did not flee
161 before the trial began), we set the spider's score at 24. These tests gave us measures of two
162 behaviours: responsiveness to prey and reaction to a predator threat.

163 To quantify web structure, we counted the of number "radii" of the orb (strands
164 extending from the centre outwards), and the number of "spirals" (strands perpendicular to
165 the radii circling the centre) extending up, down, left and right from the centre of the web to
166 its perimeter (giving four separate counts; Fig. 1b; Sensenig et al. 2010). We then measured
167 the diameter of the web (to the nearest 1cm). We calculated web density as the number of
168 radii multiplied by the mean number of spirals, divided by the web area (assuming a circular
169 shape). Unfortunately, at the time of data collection we were not aware of Herberstein and
170 Tso's work, which indicates an ellipse is preferable is a circle for estimating web area
171 (Herberstein and Tso 2000, although assuming a circle still gives reasonable approximations
172 of true capture area; see also: Venner et al. 2001 for estimating the total capture thread
173 length). We calculated web symmetry as the variance among the four counts of the number
174 of spirals; for this measure lower values indicate a more symmetrical web (the correlation
175 between this value and the coefficient of variation in spiral counts was 0.936). We also
176 counted the number of lines attaching the web to the surrounding vegetation and measured
177 the centre of the web's height from the ground, but we do not analyse these data here.

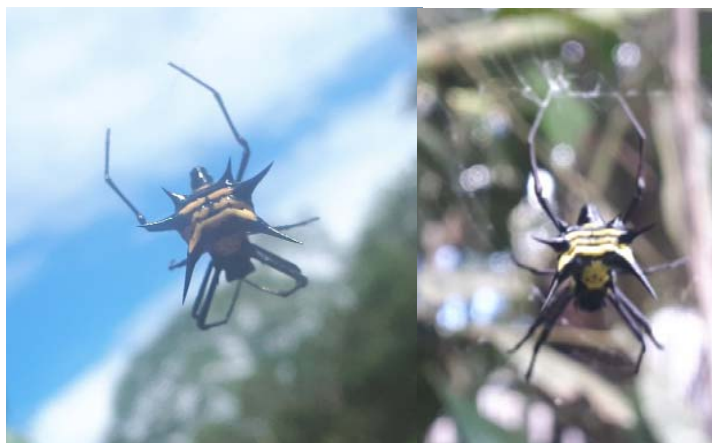
178 We returned to our transect regularly (but not quite daily), to locate and measure new
179 individuals and re-measure previously marked individuals. Not all individuals were located at
180 the same time and so were not measured on the same days. When re-measuring
181 individuals, we performed both behavioural tests and measures of the web described above,
182 but we did not re-measure their length, as we assumed it was relatively invariant at the time
183 scale we were working. Individuals' web structures and behaviours were measured on
184 average of 4.75 times (range 1-11, Fig. 1c). If we could not see an individual, we removed

185 the flagging type and recorded it as gone. If an individual was found but had spun no orb
186 that day, we did not measure its behaviour or its web structure, but also did not remove the
187 flagging tape, allowing us to return and identify the individual. If an individual fled as we
188 approached it, we measured its web structure and then left, returning later in the session to
189 attempt to measure its behaviour. If we could not measure its behaviour that day, we
190 recorded “NA” for both responsiveness to prey and reaction to a predation threat. If the
191 spider fled from its web during the test for responsiveness to prey, we scored its
192 responsiveness to prey as 180, and its reaction to a predation threat as 1. Our reasoning
193 here is that a spider fleeing a potential prey item was both unresponsive to the opportunity
194 and unwilling to face any potential predation risk. In five instances we re-tested such spiders
195 once they had returned to the centre of the web, and in all cases they either fled again, or
196 did not respond to the prey stimulus within 180 seconds, justifying our decision. We also
197 tested whether these modelling decisions influenced our results, see “Robustness to
198 modelling decisions”. In total we recorded 45 measures of length, 188 measures of
199 responsiveness to a prey stimulus (146 of which were directly observed rather than assigned
200 due to fleeing), 194 measures of reaction to a predation threat (146 of which were directly
201 observed rather than assigned due to fleeing), 200 diameters, and 197 measures of web
202 density and symmetry across 55 unique individuals (see Table 1 for means and variance of
203 each trait).

204

205

a.

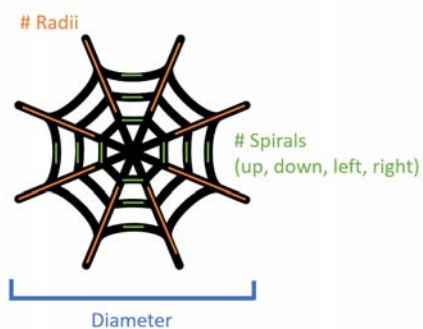


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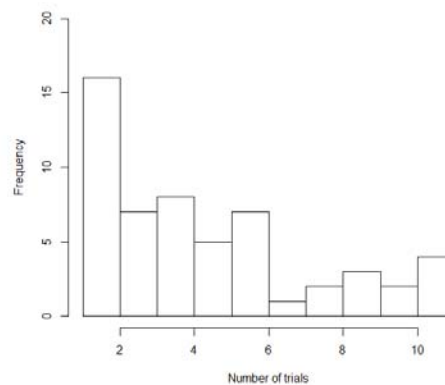


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b.



c.



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Figure 1. a. Pictures of *Micrathena vigorsii* (all DN Fisher). b. A diagram showing the

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different web characteristics used to calculate measures of web structure. c. Histogram of

210

the number of times individuals were tested for web structure.

211

212

213 **Table 1.** The means and variances of each of the six traits (to three significant figures). Note
214 that web symmetry was log-transformed prior to analysis, while this logged variable, body
215 length, web diameter and web evenness were mean centred and variance standardised prior
216 to being entered into the analysis.

Trait	Mean	Variance
Body length (mm)	13.5	5.22
Responsiveness to prey (seconds)	117	5300
Reaction to predator stimulus (taps)	7.54	66.9
Web diameter (cm)	19.4	16.1
Web density (threads/cm ²)	3.90	2.48
Web symmetry (variance)	32.1	1210

217

218 Data analysis

219 We first estimated the phenotypic correlations between each trait pair (Pearson's
220 correlations; Fig. 2). To partition these correlations to the among-individual, among-date, and
221 residual levels, we built a multivariate mixed model with each of the six traits as response
222 variables. Responsiveness to prey and reaction to predation used a Poisson error
223 distribution (log-link), while each web structure trait and body length used a Gaussian error
224 distribution. Web symmetry was log-transformed, and then this transformed variable, web
225 diameter, web density, and body length were mean centred and variance standardised
226 (Schielzeth 2010). We fitted the random effect of individual identity and estimated the
227 among-individual covariances among all six traits. We fitted the random effect of date and
228 estimated the among-date covariances among all traits except for length, which was only
229 measured on a single day per spider, and so we fixed the among-date variance to 0.0001.
230 We estimated the residual covariances between all traits, and also fixed the residual
231 variance for length to 0.0001, as it is only measured once per individual, following Houslay

232 and Wilson(2017). We estimated unique intercepts for each response variable. Spiders
233 might adjust their web structure or foraging behaviour over time as they gain information
234 about their foraging patch (Nakata and Ushimaru 1999). Therefore, we fitted trial number
235 (mean centred) as a fixed effect for each trait except length (which was only measured
236 once). The model was fitted in R (ver. 3.5.3; R Development Core Team 2016) with the
237 package “MCMCglmm” (Hadfield 2010). We used 550,000 iterations, a burn in of 50,000,
238 and a thinning interval of 100. Priors were set to be flat and relatively uninformative, with
239 70% of the phenotypic variance for the logged values of each trait placed on the residual
240 variance, 20% on the among-colony variance, and 10% on the among-date variance,
241 following Brommer (2017). We calculated adjusted repeatabilities (after accounting for trial
242 number) following Nakagawa and Schielzeth (2010).

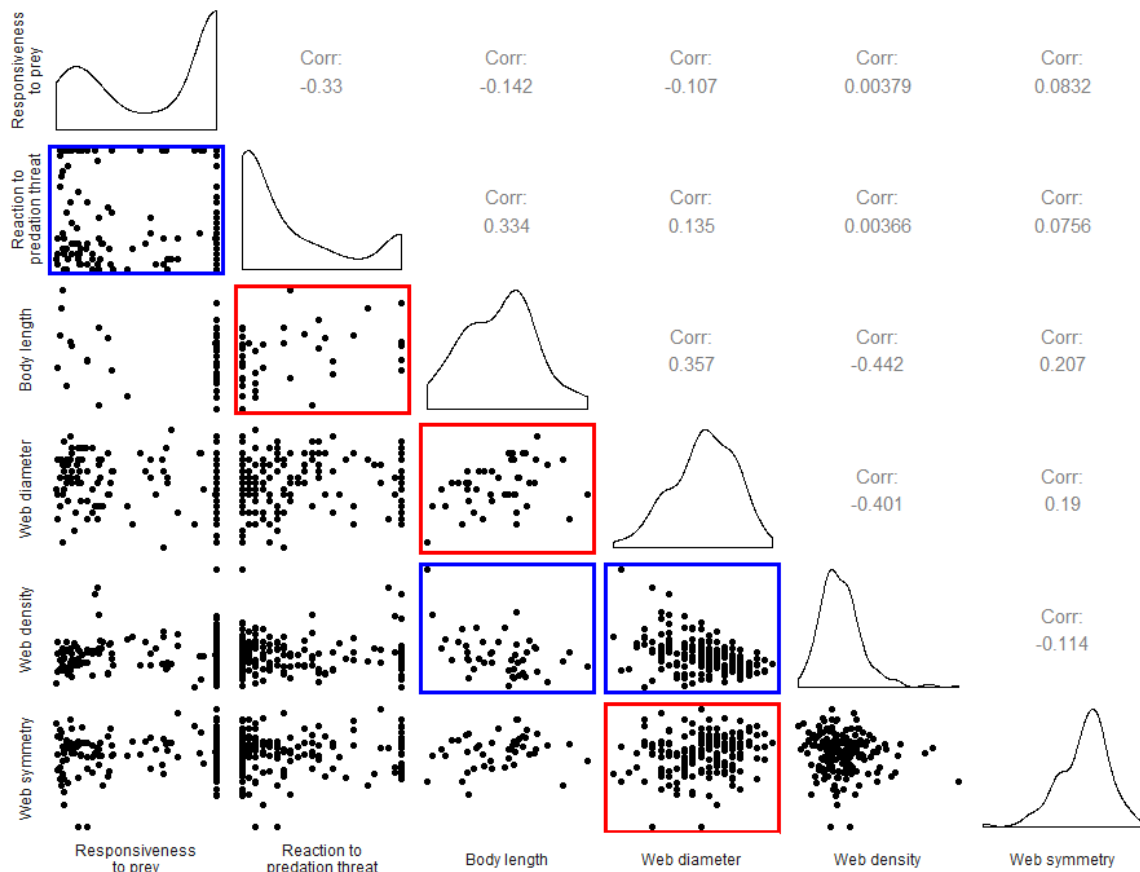
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244 Robustness to modelling decisions

245 We repeated the analysis with all behavioural scores that were assigned when an individual
246 fled rather than were directly observed set to “NA”. We also repeated this analysis with all
247 behavioural scores that were ceiling values (180 for responsiveness to prey, 24 for reaction
248 to a predation threat) set to “NA”. In each case our results did not change (full results of the
249 original model are given in Table S1, with these auxiliary results shown in Tables S2&3). We
250 therefore concluded that assigning behavioural scores to spiders that fled and giving
251 unresponsive spiders the maximum score for each behaviour had not biased our results. We
252 also repeated the original analysis without estimating any among-date covariances (as none
253 were different from zero; see Table S1 & Fig. S1). This too did not change our results (Table
254 S4), indicating that estimating the among-date covariances had not reduced our power and
255 prevented us from detecting any other among-individual or residual covariances. As such we
256 discuss the results as from the model where the among-date covariances were estimated.

257

258



259

260 **Figure 2.** Phenotypic relationships between each of our six traits (web symmetry has been
 261 log-transformed). Pearson's correlations are shown above the diagonal, pairwise plots below
 262 the diagonal, and histograms of each variable along the diagonal. Pairwise plots are
 263 bordered with red if the correlation was significant and positive, or bordered with blue if
 264 significant and negative.

265

266 Results

267

268 Repeatabilities

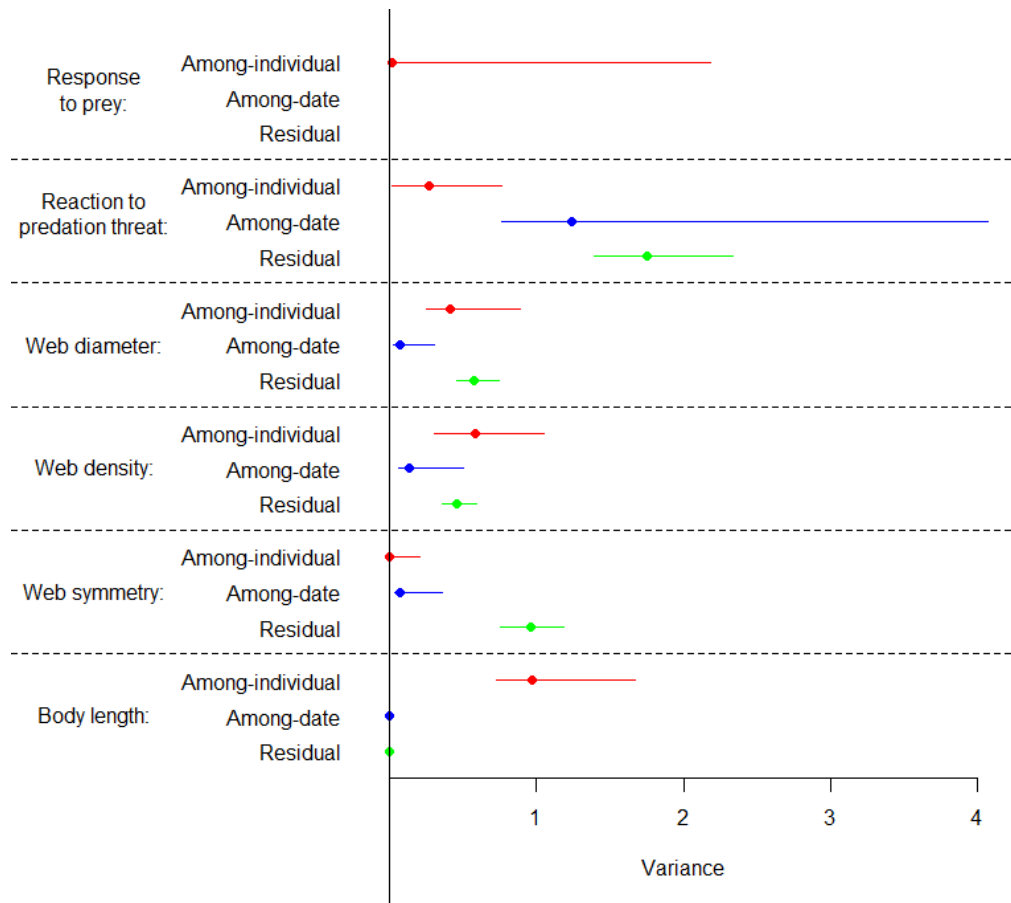
269 Web diameter was repeatable ($r = 0.427$, credible intervals [CIs] = 0.239 to 0.587), as was
270 web density ($r = 0.488$, CIs = 0.286 to 0.646). The response to the predator stimulus was
271 slightly repeatable ($r = 0.045$, CIs = < 0.001 to 0.159). Web symmetry was not repeatable (r
272 < 0.001 , CIs < 0.001 to 0.145), nor was response to the prey stimulus ($r < 0.001$, CIs < 0.001
273 to 0.012). Estimates for each of the among-individual, among-date, and residual variances
274 for each trait are shown in Fig. 3. Individuals tended to react more quickly to the predation
275 threat in later trials, although this effect marginally overlapped with zero (fixed effect of trial,
276 mode = -0.117, CIs = -0.252 to 0.011). Trial number did not influence any other trait.

277

278 Covariances

279 Body length, web diameter and web density were associated into a syndrome at the among-
280 individual level, such that longer spiders had wider and less dense webs (body length-web
281 diameter correlation = 0.404, CIs = 0.130 to 0.708; body length-web density correlation = -
282 0.608, CIs = -0.769 to -0.305, web diameter-web density correlation = -0.689, CIs = -0.865 to
283 -0.309). Reaction to the predation threat tended to be associated with these traits as well,
284 such spiders that reacted more slowly to the predation threat had longer bodies, and tended
285 to have wider webs and less dense webs, but the latter two of these correlations overlapped
286 with zero (reaction to predation-body length correlation = 0.620, CIs = 0.099 to 0.906;
287 reaction to predation-web diameter correlation = 0.554, CIs = -0.104 to 0.998; reaction to
288 predation-web density correlation = -0.744, CIs = -0.990 to 0.079). Plots of the estimated
289 among-individual relationships are shown in Fig. 4, with estimates for the among-individual
290 correlations shown in Fig. 5. Response to the prey stimulus and web symmetry were not
291 associated with the other traits among individuals (Figs. 4 & 5).

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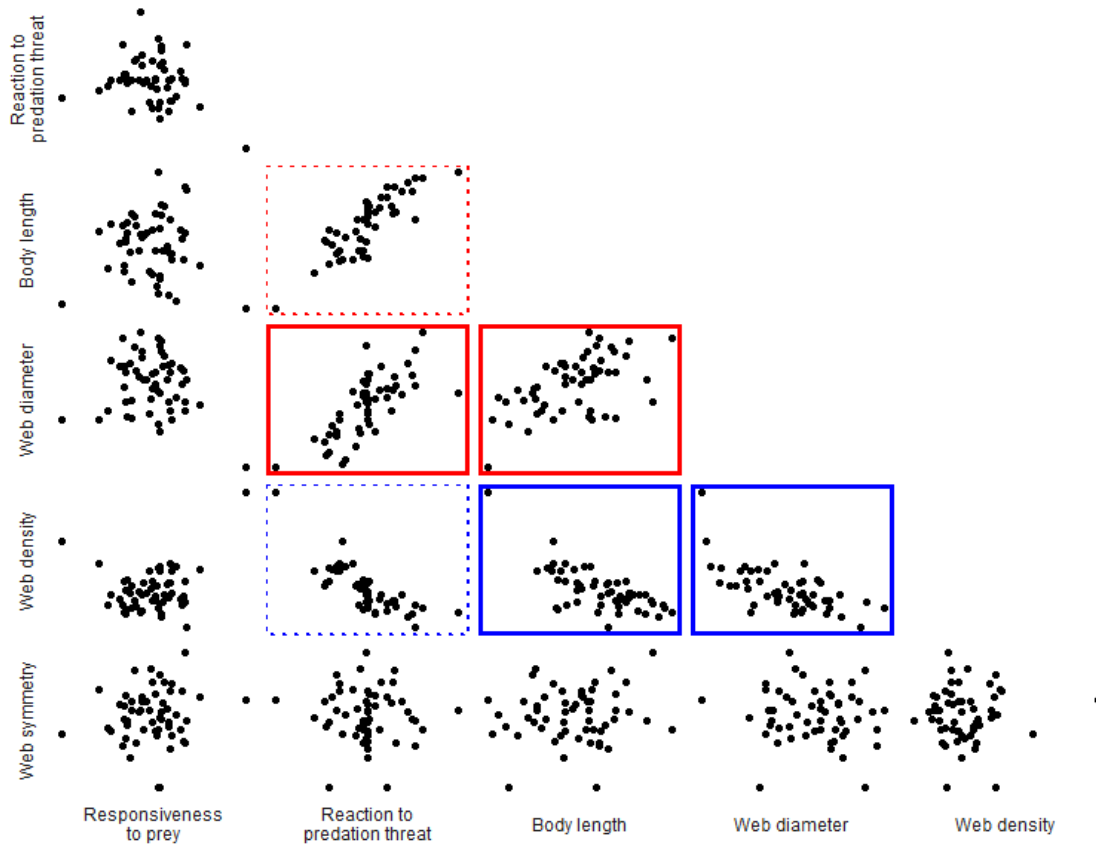
294 **Figure 3.** Variance in each trait partitioned to the among-individual (red), among-date (blue),
 295 or residual (green) levels. The among date variance for response to the prey stimulus was
 296 87, while the residual variance was 44, and so are not shown on this plot. Both the among-
 297 date and residual variance for length were suppressed to 0.0001.

298

299 At the residual level there were associations between web diameter, density and symmetry,
 300 such that when a spider built a relatively wider web it also built a relatively less symmetrical
 301 and less dense web (Fig. 6; web diameter-web density correlation = -0.303, CIs = -0.438 to -
 302 0.115; web diameter-web symmetry correlation = 0.245, CIs = 0.073 to 0.379; web density-
 303 web symmetry correlation = -0.277, CIs = -0.442 to -0.139). No other residual covariances
 304 were different from zero (Fig. 6). There was variation among days for responsiveness to

305 prey, reaction to predation, and somewhat so for web density (Fig. 3), but no among-date
306 covariances were different from zero (Fig. S1).

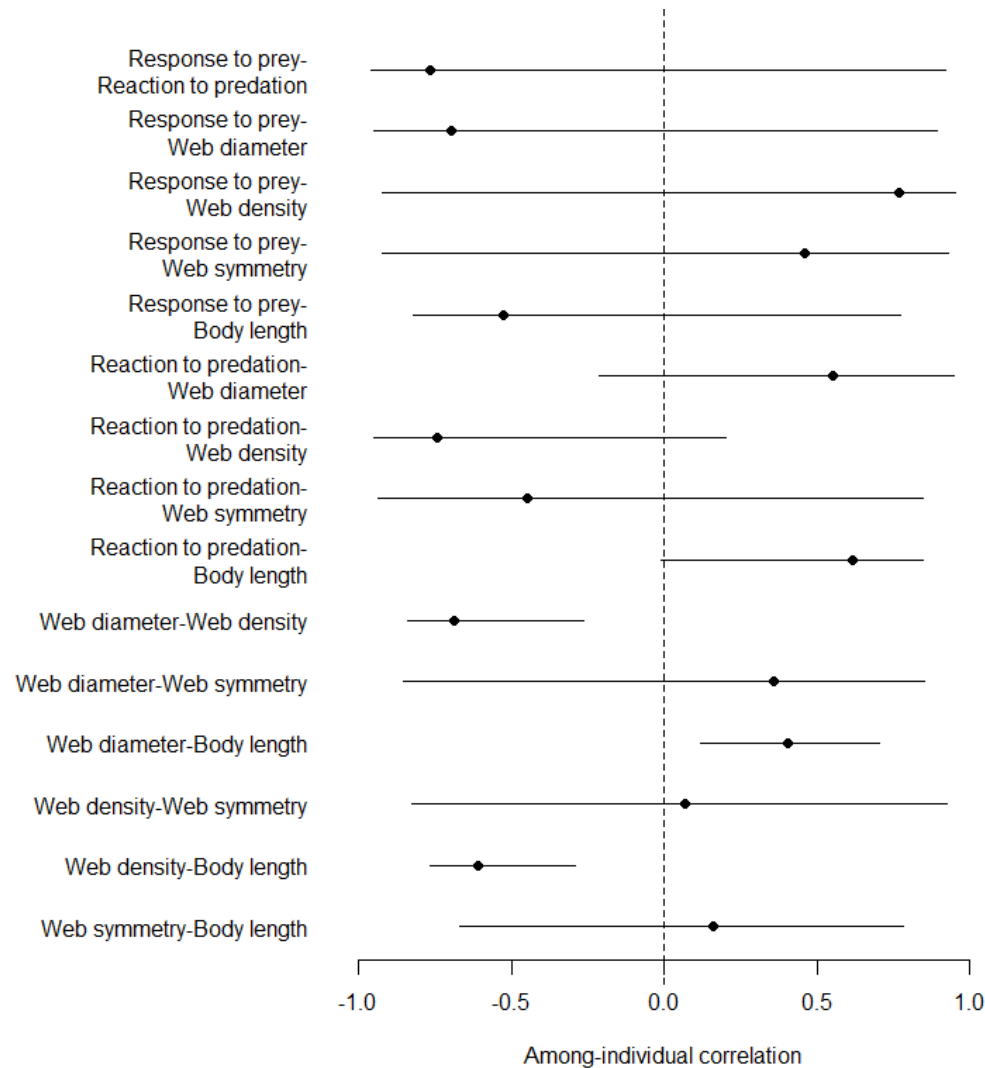
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309 **Figure 4.** Pairwise plots of the estimated among-individual relationships between the six
310 traits we studied, using best linear unbiased predictors extracted from the multivariate
311 model. Pairwise plots are bordered with red if the correlation was significant and positive, or
312 bordered with blue if significant and negative. The 95% credible intervals of the among-
313 individual correlations between reaction to predation and both web diameter and web density
314 overlapped zero, and so the borders are plotted with dashed lines.

315



316

317 **Figure 5.** Estimated modes and 95% credible intervals of the among-individual correlations.

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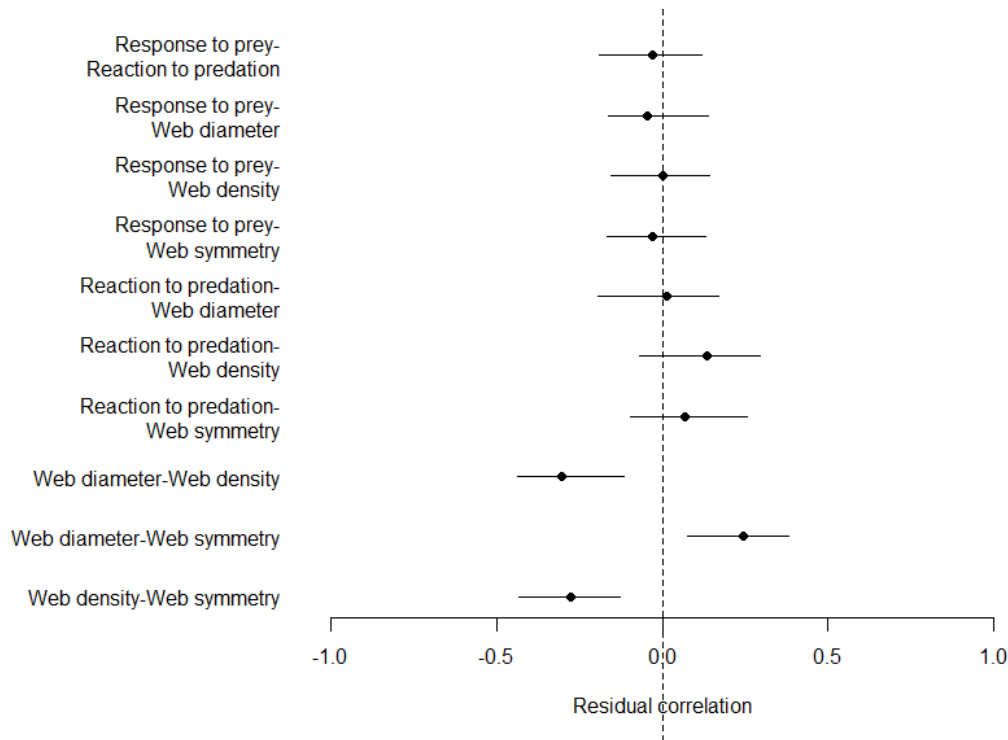
319 Discussion

320

321 Individuals may show consistent differences in aspects of their behaviour, but whether their
322 extended phenotypes are repeatable and covary with other behavioural traits is not well
323 studied. We found that individual *Micrathena vigorsii* have consistent differences in their web
324 diameters and web densities. These two web traits are correlated among-individuals into a
325 syndrome with body length, and possibly reaction to a predation stimulus, indicating they

326 might represent a single axis of variation. Responsiveness to a prey stimulus and web
327 symmetry were not repeatable among-individuals and so were not associated with any traits
328 among individuals.

329



330

331 **Figure 6.** Estimated modes and 95% credible intervals of the residual correlations. Note that
332 as the residual variance of body length was suppressed to 0.0001 it cannot covary at the
333 residual level with the other traits, and so is not plotted here.

334

335 Discovering a syndrome between web structure traits, morphology, and possibly behaviour
336 suggests they may function together as a single integrated whole (e.g. they are an
337 “evolutionary character”; Araya-Ajoy and Dingemanse 2014). This then raises questions as
338 to the syndrome’s functional role, and the processes maintaining variation in this syndrome
339 among-individuals (Sih, Bell, Johnson, et al. 2004; Sih, Bell, and Johnson 2004; Araya-Ajoy
340 and Dingemanse 2014). The relationship between body length and web diameter suggests a

341 simple biomechanical relationship between the size of spider (and perhaps the size of the
342 steps it takes) and the resulting web it spins. This may naturally cause a wider web to be
343 less dense, as a similar amount of silk is then spread over a larger area. However, if the
344 relationship between web diameter and density was purely due to silk limitation, we would
345 expect to see this trade-off at each level (among-date and residual) as well as at the among-
346 individual level. Yet, we did not. This hypothesis also does not explain why reaction to a
347 predation threat might be associated into the syndrome. Instead, variation in this size and
348 stubbornness syndrome may represent an active strategy by larger individuals to catch
349 larger and more nutritious, but possibly more dangerous, prey.

350 The density of a web may influence the type or size of prey it captures (Uetz et al.
351 1978; Chacon and Eberhard 1980; Blackledge and Zevenbergen 2006). Meanwhile, larger
352 and more stubborn spiders might be willing to tackle larger and more dangerous prey, which
353 smaller and more docile spiders would not risk (Mukherjee and Heithaus 2013; although
354 juveniles in some species may be forced to target sub-optimal, and possibly more
355 dangerous, prey; Elbroch et al. 2017). If body size and web size do relate to the type of prey
356 captured, variation in the syndrome we have detected here might instead represent variation
357 in individual foraging strategies (Bolnick et al. 2002; Ingram et al. 2018). In which case, we
358 might expect the types and sizes of the prey caught in individual *M. vigorsii* webs to show
359 consistent among-individual variation; a prediction that requires testing.

360 To predict how the syndrome might evolve, we need to know the degree to which it is
361 heritable, and whether it is under selection. Around 50% of among-individual variation in
362 behaviours may be based on additive genetic variance (Dochtermann et al. 2015), and
363 genetic correlations tend to have the same sign as underlying genetic correlations
364 (Dochtermann 2011) and so we could expect some of the (co)variation among-individuals in
365 web structure and body length to have a genetic basis. In terms of selection, for now we do
366 not have any estimates available for *M. vigorsii*. The different strategies may have equal
367 pay-offs, which would maintain variation even if the syndrome had a genetic basis (Mangel

368 and Stamps 2001; Stamps 2007). Alternatively, spiders may change their position in the
369 syndrome as they age, spinning wider and less dense webs (and possibly reacting less to
370 predation) as they grow. For example, in the orb-web spider *Zygiella x-notata*, webs have a
371 shorter total thread length, become less regular, and have more “anomalies” as individuals
372 age (Anotaux et al. 2012; Anotaux et al. 2014), and these changes increase prey handling
373 time (Anotaux et al. 2014). We could not detect this trend in our study, as it took place at a
374 time scale (one month, although each individual was tracked for considerably less time than
375 this) where we might not expect to see much measurable growth. Determining whether *M.*
376 *vigorsii* move through the size and stubbornness syndrome as they grow would require a
377 much longer study, and one probably performed in captivity to track individuals over their
378 entire lifetimes.

379 Some of the consistent variation in web structure we observed could be due to by
380 variation in microhabitat, as in our study individuals were only ever assayed in one
381 environment. Some variation in the amount of space a spider had to spin a web, the
382 available structural supports, or some microclimatic factor, could cause consistent
383 differences in web structure among-individuals (Zevenbergen et al. 2008; Blamires 2010;
384 Nakata 2012). However, DiRienzo and Montiglio (Dirienzo and Montiglio 2016; Montiglio and
385 DiRienzo 2016) also found consistent differences among-individuals in spider web structure,
386 but in a laboratory setting. Such a setting should hypothetically control for variation in
387 microhabitat, and so microhabitat variation could not be an explanation for consistent
388 differences in individual web structure in their study; raising the possibility that microhabitat
389 use may not fully explain our results either. Furthermore, a spider may select the
390 microhabitat that allows the spinning of a web of a certain structure (see also “niche
391 construction” Odling-Smee et al. 2003; Saltz and Nuzhdin 2014). Therefore, while web
392 structure and microhabitat could covary, this could still depend on the spider’s decision
393 making, and so would still be classed as a trait of the spider, not as one driven by the
394 environment.

395 Our results are generally in agreement with previous work. DiRienzo and Montiglio
396 (2016) found consistent differences among-individuals in web structure, and that black
397 widow spiders (*Latrodectus hesperus*) with longer femur–patellas build webs with more
398 gumfooted lines. We also found consistent differences among-individuals in web structure,
399 and a positive relationship between body size and web size. We therefore tentatively
400 suggest that these two elements could be general features of intra-population variation in
401 spider webs. More studies in other taxa with different extended phenotypes are required to
402 determine whether, within a population, larger individuals usually build bigger nests or larger
403 dams, and so on. DiRienzo and Montiglio (2016) also found that a higher number of
404 gumfooted lines is associated with increased foraging aggression. However, Montiglio and
405 DiRienzo (2016), also in *L. hesperus*, found a higher number of both gumfooted and
406 structural lines is associated with *decreased* foraging aggression, while boldness was not
407 associated with any web characteristics. Given that the relationship between behaviour and
408 web structure we detected overlapped with zero, and that responsiveness to a prey stimulus
409 was not associated with web structure, in aggregate it seems there is yet no clear pattern in
410 how web structure and behaviours are associated among-individuals.

411 The residual covariances between web diameter, web density, and web symmetry
412 indicates that when a spider builds a relatively larger web (relative to its own typical web
413 diameter) it also builds a relatively less symmetrical and less dense web. A spider may
414 struggle to apply its usual web spinning strategy at a greater spatial scale without making
415 mistakes, and so created a less symmetrical and less dense web when it tries to make a
416 larger web than usual. Alternatively, our measure of web symmetry could reflect the amount
417 of contact with prey the web experienced that day (webs are typically spun in the morning,
418 and all web measurements were taken in the afternoon). *M. vigorsii* do not leave prey
419 remains in their web (DN Fisher, pers obs.), but contact with prey, whether leading to a
420 successful capture or not, leads to the removal of spirals and radii. The removal of these
421 threads reduces density, as well as change the number of spirals along one axis but not

422 others, giving the impression of a less symmetrical web. A greater rate of contact with prey
423 would be expected with larger webs as they cover a greater area, but we would perhaps
424 expect this covariance to be present at the among-individual and among-date levels as well
425 as at the residual level. We therefore cannot identify what process might be driving the
426 residual covariances between web diameter, density, and symmetry at this time.

427 We note here that correlated measurement error can give residual covariances
428 between traits. We think this is unlikely to have occurred here, as web diameter and the
429 other measures of web structure were measured using different tools, and web density and
430 web symmetry were calculated once we had returned from the field. This reduces the
431 chance that we could make mistakes that simultaneously influenced all measurements.
432 Further, previous work has suggested that spiders spin webs suited for defence rather than
433 prey capture, and respond less to prey, following prey capture (Venner et al. 2000; Dirienzo
434 and Montiglio 2016 Jul). This would appear as a residual correlation between web diameter,
435 web density and responsiveness to prey in our analysis, but responsiveness to prey did not
436 covary with these traits at the residual (or any) level. This suggests *M. vigorsii* does not
437 simply reduce the investment in its web and its responsiveness to prey following a day
438 where it captured prey, though this would need to be confirmed experimentally.

439 There was a phenotypic correlation between responsiveness to prey and reaction to
440 predation (Fig. 2) that was not different from zero as an among-individual correlation (or
441 indeed at any other level; Figs. 4-6 & S1). This acts as a cautionary tale against assuming
442 any phenotypic correlations represent among-individual correlations (the “individual gambit”;
443 Brommer 2013). In general, we should be careful to identify at what level (within-individual,
444 among-individual, among-day) any hypothesised relationships between traits should exist,
445 and then construct statistical models that specifically estimate these terms, allowing us to
446 directly evaluate our hypotheses (Dingemanse and Dochtermann 2013; e.g. Moiron et al.
447 2016).

448

449 Conclusions

450 We found that *M. vigorsii* show consistent among-individual differences in aspects of web
451 structure, and that there is a syndrome between web structure and morphology such that
452 larger individuals spin wider and less dense webs. These may be general features of intra-
453 population (co)variation in morphology and extended phenotypes and could represent
454 among-individual variation in foraging strategies or aging-dependent changes in various
455 aspects of the phenotype. Reaction to a predator stimulus was very slightly repeatable and
456 this trait may be integrated into the among-individual syndrome with morphology and web
457 structure, but uncertainty was high. These results highlight how extended phenotypes can be
458 integrated into general suites of trait variation, and so selection likely acts upon these traits
459 in concert. We also found that when a spider builds a relatively wider web the web is also
460 relatively less dense and less symmetrical, suggesting spiders building relatively larger webs
461 make more mistakes than when building a web closer to the average size for that individual.
462 Responsiveness to a prey stimulus and web symmetry were not consistently different
463 among-individuals, and so are completely plastic or environmentally determined traits that
464 are not based on more stable individual characteristics. Extended phenotypes like the web
465 traits evaluated here represent a suite of biological traits that have perhaps been under-
466 studied in the past literature on individual variation, yet these traits represent important
467 biological variation that can play key roles in organisms' lives and in ecosystems more
468 broadly. Here we have demonstrated that, in a population of wild organisms, aspects of an
469 extended phenotype are integrated into a syndrome with morphological, and possibly
470 behavioural, traits. Therefore, our expectations for selection on and evolution of extended
471 phenotypes should consider how they integrate with other phenotypes under natural
472 conditions.

473

474 Author contributions

475 DNF and JNP designed the study. JY acquired the permits. DNF collected and analysed the
476 data and drafted the manuscript. All authors contributed to revisions of the manuscript and
477 approved the final version.

478

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485

486 Data accessibility

487 All data and R code used in the analysis will be made available upon publication.

488

489 References

- 490 Anotaux M, Marchal J, Châline N, Desquilbet L, Leborgne R, Gilbert C, Pasquet A. 2012.
491 Ageing alters spider orb-web construction. *Anim Behav.* 84(5):1113–1121.
492 doi:10.1016/j.anbehav.2012.08.017. [accessed 2019 Aug 13].
493 <https://linkinghub.elsevier.com/retrieve/pii/S0003347212003661>.
- 494 Anotaux M, Toscani C, Leborgne R, Châline N, Pasquet A. 2014. Aging and foraging
495 efficiency in an orb-web spider. *J Ethol.* 32(3):155–163. doi:10.1007/s10164-014-0404-6.
496 [accessed 2019 Aug 29]. <http://link.springer.com/10.1007/s10164-014-0404-6>.
- 497 Araya-Ajoy YG, Dingemans NJ. 2014. Characterizing behavioural “characters”: an
498 evolutionary framework. *Proc Biol Sci.* 281(1776):20132645. doi:10.1098/rspb.2013.2645.
499 [accessed 2014 Feb 4].
500 <http://rspb.royalsocietypublishing.org/content/281/1776/20132645.abstract>.
- 501 Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis.
502 *Anim Behav.* 77(4):771–783. doi:10.1016/j.anbehav.2008.12.022. [accessed 2013 Oct 17].
503 <http://linkinghub.elsevier.com/retrieve/pii/S0003347209000189>.
- 504 Blackledge TA, Zevenbergen JM. 2006. Mesh Width Influences Prey Retention in Spider Orb
505 Webs. *Ethology.* 112(12):1194–1201. doi:10.1111/j.1439-0310.2006.01277.x. [accessed

- 506 2019 Aug 20]. <http://doi.wiley.com/10.1111/j.1439-0310.2006.01277.x>.
- 507 Blackledge TA, Zevenbergen JM. 2007. Condition-dependent spider web architecture in the
508 western black widow, *Latrodectus hesperus*. *Anim Behav.* 73(5):855–864.
509 doi:10.1016/J.ANBEHAV.2006.10.014. [accessed 2019 Aug 20].
510 <https://www.sciencedirect.com/science/article/pii/S0003347207000528>.
- 511 Blamires SJ. 2010. Plasticity in extended phenotypes: Orb web architectural responses to
512 variations in prey parameters. *J Exp Biol.* 213(18):3207–3212. doi:10.1242/jeb.045583.
513 [accessed 2019 Aug 13]. <http://jeb.biologists.org/cgi/doi/10.1242/jeb.045583>.
- 514 Blamires SJ, Hasemore M, Martens PJ, Kasumovic MM. 2017. Diet-induced co-variation
515 between architectural and physicochemical plasticity in an extended phenotype. *J Exp Biol.*
516 220(5):876–884. doi:10.1242/jeb.150029. [accessed 2018 Feb 14].
517 <http://www.ncbi.nlm.nih.gov/pubmed/28011821>.
- 518 Blamires SJ, Martens PJ, Kasumovic MM. 2017. Fitness consequences of plasticity in an
519 extended phenotype. *J Exp Biol.* jeb.167288. doi:10.1242/jeb.167288. [accessed 2018 Feb
520 14]. <http://www.ncbi.nlm.nih.gov/pubmed/29361580>.
- 521 Boake CRB. 1989. Repeatability: Its role in evolutionary studies of mating behavior. *Evol*
522 *Ecol.* 3(2):173–182. doi:10.1007/BF02270919. [accessed 2019 Aug 26].
523 <http://link.springer.com/10.1007/BF02270919>.
- 524 Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R. 2002. Measuring individual-level
525 resource specialization. *Ecology.* 83(10):2936–2941. doi:10.1890/0012-
526 9658(2002)083[2936:MILRS]2.0.CO;2. [accessed 2019 Aug 27].
527 [https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/0012-
528 9658%282002%29083%5B2936%3AMILRS%5D2.0.CO%3B2](https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/0012-9658%282002%29083%5B2936%3AMILRS%5D2.0.CO%3B2).
- 529 Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel
530 analysis of plasticity, personality and predictability in hermit crabs. *Anim Behav.* 86(1):47–54.
531 doi:10.1016/j.anbehav.2013.04.009. [accessed 2014 Apr 3].
532 <http://www.scopus.com/inward/record.url?eid=2-s2.0-84880154762&partnerID=tZOtx3y1>.
- 533 Brommer JE. 2013. On between-individual and residual (co)variances in the study of animal
534 personality: are you willing to take the “individual gambit”? *Behav Ecol Sociobiol.*
535 67(6):1027–1032. doi:10.1007/s00265-013-1527-4. [accessed 2014 Oct 17].
536 <http://link.springer.com/10.1007/s00265-013-1527-4>.
- 537 Brommer JE. 2017. Multivariate Mixed Models in R- MCMCglmm examples. GitHub.
538 <https://github.com/JonBrommer/Multivariate-Mixed-Models-in-R/wiki/MCMCglmm-examples>.
- 539 Chacon P, Eberhard WG. 1980. Factors affecting numbers and kinds of prey caught in
540 artificial spider webs, with considerations of how orb webs trap prey. *Bull Br Arachnol Soc.*
541 5(1):29–38. [accessed 2019 Aug 26]. <http://britishspiders.org.uk/bulletin/050105.pdf>.
- 542 Chickering AM. 1961. The genus *Micrathena* (Araneae, Argiopidae) in Central America. *Bull*
543 *Mus Comp Zool.* 125(13):1–608. [accessed 2019 Aug 26].
544 <https://www.biodiversitylibrary.org/item/21158>.
- 545 Dall SRX, Bell AM, Bolnick DI, Ratnieks FLW. 2012. An evolutionary ecology of individual
546 differences. *Ecol Lett.* 15(10):1189–98. doi:10.1111/j.1461-0248.2012.01846.x. [accessed
547 2013 May 28]. <http://www.ncbi.nlm.nih.gov/pubmed/22897772>.
- 548 Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality:
549 consistent individual differences from an adaptive perspective. *Ecol Lett.* 7(8):734–739.
550 doi:10.1111/j.1461-0248.2004.00618.x. [accessed 2014 Jan 9].
551 <http://doi.wiley.com/10.1111/j.1461-0248.2004.00618.x>.

- 552 Dawkins R. 1978. Replicator selection and the extended phenotype. *Z Tierpsychol.*
553 47(1):61–76. doi:10.1111/j.1439-0310.1978.tb01823.x. [accessed 2018 Feb 12].
554 <http://doi.wiley.com/10.1111/j.1439-0310.1978.tb01823.x>.
- 555 Dawkins R. 1982. *The Extended Phenotype*. Oxford: Oxford University Press. [accessed
556 2018 Jan 8]. [https://web.natur.cuni.cz/filosof/markos/Publikace/Dawkins extended.pdf](https://web.natur.cuni.cz/filosof/markos/Publikace/Dawkins%20extended.pdf).
- 557 Dingemans NJ, Dochtermann NA. 2013. Quantifying individual variation in behaviour:
558 mixed-effect modelling approaches. *J Anim Ecol.* 82(1):39–54. doi:10.1111/1365-
559 2656.12013. [accessed 2013 May 21]. <http://www.ncbi.nlm.nih.gov/pubmed/23171297>.
- 560 DiRienzo N, Aonuma H. 2018. Plasticity in extended phenotype increases offspring defence
561 despite individual variation in web structure and behaviour. *Anim Behav.* 138:9–17.
562 doi:10.1016/j.ANBEHAV.2018.01.022. [accessed 2019 Sep 3].
563 <https://www.sciencedirect.com/science/article/pii/S0003347218300368>.
- 564 DiRienzo N, Dornhaus A. 2017. *Temnothorax rugatulus* ant colonies consistently vary in nest
565 structure across time and context. Marshall JAR, editor. *PLoS One.* 12(6):e0177598.
566 doi:10.1371/journal.pone.0177598. [accessed 2019 Sep 3].
567 <https://dx.plos.org/10.1371/journal.pone.0177598>.
- 568 Dirienzo N, Montiglio P-O. 2016. Linking consistent individual differences in web structure
569 and behavior in black widow spiders. *Behav Ecol.* 27(5):1424–1431.
570 doi:10.1093/beheco/arw048. [accessed 2019 Aug 13].
571 <https://academic.oup.com/beheco/article-lookup/doi/10.1093/beheco/arw048>.
- 572 Dirienzo N, Montiglio PO. 2016 Jul. The contribution of developmental experience vs.
573 condition to life history, trait variation and individual differences. Cotter S, editor. *J Anim*
574 *Ecol.* 85(4):915–926. doi:10.1111/1365-2656.12512. [accessed 2016 Aug 5].
575 <http://doi.wiley.com/10.1111/1365-2656.12512>.
- 576 Dochtermann NA. 2011. Testing Cheverud’s conjecture for behavioral correlations and
577 behavioral syndromes. *Evolution.* 65(6):1814–20. doi:10.1111/j.1558-5646.2011.01264.x.
578 [accessed 2015 Jan 29]. <http://www.ncbi.nlm.nih.gov/pubmed/21644966>.
- 579 Dochtermann NA, Dingemans NJ. 2013. Behavioral syndromes as evolutionary constraints.
580 *Behav Ecol.* 24(4):806–811. doi:10.1093/beheco/art002. [accessed 2015 Jan 27].
581 <http://beheco.oxfordjournals.org/content/early/2013/02/04/beheco.art002.full>.
- 582 Dochtermann NA, Schwab T, Sih A. 2015. The contribution of additive genetic variation to
583 personality variation: heritability of personality. *Proc Biol Sci.* 282(1798):20142201.
584 doi:10.1098/rspb.2014.2201. [accessed 2015 Jun 15].
585 <http://rspb.royalsocietypublishing.org/content/282/1798/20142201.short>.
- 586 Dohm MR. 2002. Repeatability estimates do not always set an upper limit to heritability.
587 *Funct Ecol.* 16(2):273–280. doi:10.1046/j.1365-2435.2002.00621.x. [accessed 2015 Jan 15].
588 <http://doi.wiley.com/10.1046/j.1365-2435.2002.00621.x>.
- 589 Elbroch LM, Feltner J, Quigley HB. 2017. Stage-dependent puma predation on dangerous
590 prey. *J Zool.* 302(3):164–170. doi:10.1111/jzo.12442. [accessed 2019 Aug 29].
591 <http://doi.wiley.com/10.1111/jzo.12442>.
- 592 Falconer D. 1981. *Introduction to Quantitative Genetics*. New York: The Ronald Press
593 Company. <https://archive.org/details/introductiontoq00falc>.
- 594 Fisher DN, Haines JA, Boutin S, Dantzer B, Lane JE, Coltman DW, McAdam AG. 2019.
595 Indirect effects on fitness between individuals that have never met via an extended
596 phenotype. Ostfeld R, editor. *Ecol Lett.* 22(4):697–706. doi:10.1111/ele.13230. [accessed
597 2019 Feb 11]. <http://doi.wiley.com/10.1111/ele.13230>.

- 598 Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: □:
599 The MCMCglmm R package. *J Stat Softw.* 33(2):1–22.
- 600 Heiling AM, Herberstein ME. 2000. Interpretations of orb-web variability: A review of past
601 and current ideas. *Ekol Bratislava.* 19(9993):97–106. [accessed 2019 Aug 29].
602 <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.487.9896&rep=rep1&type=pdf>.
- 603 Herberstein ME, Tso I-M. 2000. EVALUATION OF FORMULAE TO ESTIMATE THE
604 CAPTURE AREA AND MESH HEIGHT OF ORB WEBS (ARANEOIDEA, ARANEA). *J*
605 *Arachnol.* 28(2):180–184. doi:10.1636/0161-8202(2000)028[0180:eoftet]2.0.co;2. [accessed
606 2019 Aug 26]. [https://bioone.org/journals/The-Journal-of-Arachnology/volume-28/issue-2/0161-8202\(2000\)028\[0180:EOFTET\]2.0.CO;2/EVALUATION-OF-FORMULAE-TO-ESTIMATE-THE-CAPTURE-AREA-AND-MESH/10.1636/0161-8202\(2000\)028\[0180:EOFTET\]2.0.CO;2.full](https://bioone.org/journals/The-Journal-of-Arachnology/volume-28/issue-2/0161-8202(2000)028[0180:EOFTET]2.0.CO;2/EVALUATION-OF-FORMULAE-TO-ESTIMATE-THE-CAPTURE-AREA-AND-MESH/10.1636/0161-8202(2000)028[0180:EOFTET]2.0.CO;2.full).
- 610 Hodge BYMA. 1987. Macrohabitat selection by the orb-weaving spider, *Micrathena gracilis*.
611 *Psyche (Stuttg).* 94:347–361. [accessed 2019 Aug 26].
612 <http://downloads.hindawi.com/journals/psyche/1987/021317.pdf>.
- 613 Houslay TM, Wilson AJ. 2017. Avoiding the misuse of BLUP in behavioural ecology. *Behav*
614 *Ecol.* 12(Pt A):S9. doi:10.1093/beheco/arx023. [accessed 2017 Mar 2].
615 <https://academic.oup.com/beheco/article/3059669/Avoiding>.
- 616 Ingram T, Costa-Pereira R, Araújo MS. 2018. The dimensionality of individual niche
617 variation. *Ecology.* 99(3):536–549. doi:10.1002/ecy.2129. [accessed 2019 Aug 27].
618 <http://doi.wiley.com/10.1002/ecy.2129>.
- 619 Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. In:
620 *Ecosystem Management.* New York, NY: Springer New York. p. 130–147. [accessed 2018
621 Mar 19]. http://link.springer.com/10.1007/978-1-4612-4018-1_14.
- 622 Jones CG, Lawton JH, Shachak M. 1997. Positive and negative effects of organisms as
623 physical ecosystem engineers. *Ecology.* 78(7):1946–1957. doi:10.1890/0012-
624 9658(1997)078[1946:PANEOO]2.0.CO;2. [accessed 2018 Feb 12].
625 [http://onlinelibrary.wiley.com/doi/10.1890/0012-9658\(1997\)078\[1946:PANEOO\]2.0.CO;2/full](http://onlinelibrary.wiley.com/doi/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2/full).
- 626 Jones CG, Lawton JH, Shachak M. 2009. Organisms as Ecosystem Engineers. *Oikos.*
627 69(3):373–386. [accessed 2018 Feb 12]. https://link.springer.com/chapter/10.1007/978-1-4612-4018-1_14.
- 629 Kooch Y, Jalilvand H. 2008. Earthworms as ecosystem engineers and the most important
630 detritivores in forest soils. *Pakistan J Biol Sci PJBS.* 11(6):819–25. [accessed 2018 Mar 19].
631 <http://www.ncbi.nlm.nih.gov/pubmed/18814642>.
- 632 Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De
633 Jong IC, Ruis MA, Blokhuis HJ. 1999. Coping styles in animals: current status in behavior
634 and stress-physiology. *Neurosci Biobehav Rev.* 23(7):925–935. [accessed 2015 Mar 4].
635 <http://www.ncbi.nlm.nih.gov/pubmed/10580307>.
- 636 Lande R. 1979. Quantitative genetic analysis of multivariate evolution , applied to brain □:
637 body size allometry. *Evolution (N Y).* 33(1):402–416. doi:10.2307/2407630. [accessed 2016
638 Nov 17]. <http://www.jstor.org/stable/2407630?origin=crossref>.
- 639 Lande R, Arnold S. 1983. The measurement of selection on correlated characters. *Evolution*
640 *(N Y).* 37(6):1210–1226. doi:10.2307/2408842. [accessed 2016 Jun 27].
641 <http://www.jstor.org/stable/2408842?origin=crossref>.
- 642 Laskowski KL, Pruitt JN. 2014. Evidence of social niche construction: persistent and
643 repeated social interactions generate stronger personalities in a social spider. *Proc Biol Sci.*

- 644 281(1783):20133166. doi:10.1098/rspb.2013.3166. [accessed 2015 Mar 23].
645 <http://rspb.royalsocietypublishing.org/content/281/1783/20133166.abstract>.
- 646 Lichtenstein JLL, Fisher DN, McEwen BL, Nondorf DT, Calvache E, Schmitz C, Elässer J,
647 Pruitt JN. 2019. Collective aggressiveness limits colony persistence in high but not low
648 elevation sites in Amazonian social spiders. bioRxiv. doi:10.1101/610436.
649 www.biorxiv.org/content/10.1101/610436v1.
- 650 Mangel M, Stamps J. 2001. Trade-offs between growth and mortality and the maintenance
651 of individual variation in growth. *Evol Ecol*. 3(5):583–593. [accessed 2015 Mar 31].
652 <http://evolutionary-ecology.com/abstracts/v03/1315.html>.
- 653 Mayer M, Sine R, Brown GP. 2016. Bigger babies are bolder: effects of body size on
654 personality of hatchling snakes. *Behaviour*. 153(3). [accessed 2019 Aug 26].
655 https://brill.com/view/journals/beh/153/3/article-p313_4.xml.
- 656 Moiron M, Mathot KJ, Dingemanse NJ. 2016. A multi-level approach to quantify speed-
657 accuracy trade-offs in great tits (*Parus major*). *Behav Ecol*. 27(5):1539–1546.
658 doi:10.1093/beheco/arw077.
- 659 Montiglio P-O, DiRienzo N. 2016. There's no place like home: the contribution of direct and
660 extended phenotypes on the expression of spider aggressiveness. *Behav Ecol*.
661 27(6):arw094. doi:10.1093/beheco/arw094. [accessed 2016 Nov 22].
662 <https://academic.oup.com/beheco/article-lookup/doi/10.1093/beheco/arw094>.
- 663 Mukherjee S, Heithaus MR. 2013. Dangerous prey and daring predators: a review. *Biol Rev*.
664 88(3):550–563. doi:10.1111/brv.12014. [accessed 2019 Aug 29].
665 <http://doi.wiley.com/10.1111/brv.12014>.
- 666 Nakagawa S, Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a
667 practical guide for biologists. *Biol Rev*. 85(4):935–956. doi:10.1111/j.1469-
668 185X.2010.00141.x. [accessed 2013 May 22].
669 <http://www.ncbi.nlm.nih.gov/pubmed/20569253>.
- 670 Nakata K. 2012. Plasticity in an extended phenotype and reversed up-down asymmetry of
671 spider orb webs. *Anim Behav*. 83(3):821–826. doi:10.1016/J.ANBEHAV.2011.12.030.
672 [accessed 2018 Feb 14].
673 <https://www.sciencedirect.com/science/article/pii/S000334721200005X>.
- 674 Nakata K, Ushimaru A. 1999. Feeding experience affects web relocation and investment in
675 web threads in an orb-web spider, *Cyclosa argenteoalba*. *Anim Behav*. 57(6):1251–1255.
676 doi:10.1006/anbe.1999.1105. [accessed 2019 Aug 26].
677 <https://www.sciencedirect.com/science/article/pii/S0003347299911053>.
- 678 Odling-Smee FJ, Laland KN, Feldman MW. 2003. *Niche Construction: The Neglected
679 Process in Evolution*. Princeton: Princeton University Press. [accessed 2016 May 31].
680 <http://press.princeton.edu/titles/7691.html>.
- 681 Posthumus EE, Koprowski JL, Steidl RJ. 2015. Red squirrel middens influence abundance
682 but not diversity of other vertebrates. Mousseau TA, editor. *PLoS One*. 10(4):e0123633.
683 doi:10.1371/journal.pone.0123633. [accessed 2018 Dec 11].
684 <https://dx.plos.org/10.1371/journal.pone.0123633>.
- 685 Pruitt JN, Demes KW, Dittrich-Reed DR. 2011. Temperature Mediates Shifts in Individual
686 Aggressiveness, Activity Level, and Social Behavior in a Spider. *Ethology*. 117(4):318–325.
687 doi:10.1111/j.1439-0310.2011.01877.x. [accessed 2019 Apr 16].
688 <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1439-0310.2011.01877.x>.
- 689 R Development Core Team. 2016. R: A language and environment for statistical computing.

- 690 Team RDC, editor. *R Found Stat Comput.* 1(3.1.3):409. doi:10.1007/978-3-540-74686-7.
691 [accessed 2013 Sep 17]. <http://www.r-project.org>.
- 692 Ransom TS. 2011. Earthworms, as ecosystem engineers, influence multiple aspects of a
693 salamander's ecology. *Oecologia.* 165(3):745–754. doi:10.1007/s00442-010-1775-1.
694 [accessed 2018 Mar 19]. <http://link.springer.com/10.1007/s00442-010-1775-1>.
- 695 Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal
696 temperament within ecology and evolution. *Biol Rev.* 82(2):291–318. doi:10.1111/j.1469-
697 185X.2007.00010.x. [accessed 2013 May 21].
698 <http://www.ncbi.nlm.nih.gov/pubmed/17437562>.
- 699 Ringler M, Hödl W, Ringler E. 2015. Populations, pools, and peccaries: simulating the impact
700 of ecosystem engineers on rainforest frogs. *Behav Ecol.* 26(2):340–349.
701 doi:10.1093/beheco/aru243. [accessed 2015 Apr 30].
702 <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4374131&tool=pmcentrez&render>
703 [type=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4374131&tool=pmcentrez&render).
- 704 Roche D, Careau V, Binning S. 2016. Demystifying animal 'personality'(or not): why
705 individual variation matters to experimental biologists. *J Exp.* [accessed 2016 Nov 22].
706 <http://jeb.biologists.org/content/early/2016/11/15/jeb.146712.abstract>.
- 707 Roff DA. 1992. *The evolution of life histories*: theory and analysis. Chapman & Hall.
708 [accessed 2019 Aug 29]. <https://www.springer.com/gp/book/9780412023910>.
- 709 Rosell F, Bozsér O, Collen P, Parker H. 2005. Ecological impact of beavers *Castor fiber* and
710 *Castor canadensis* and their ability to modify ecosystems. *Mamm Rev.* 35(3–4):248–276.
711 doi:10.1111/j.1365-2907.2005.00067.x. [accessed 2018 Feb 12].
712 <http://doi.wiley.com/10.1111/j.1365-2907.2005.00067.x>.
- 713 Royauté R, Hedrick A, Dochtermann NA. 2019. Behavioral syndromes shape evolutionary
714 trajectories via conserved genetic architecture. *bioRxiv*.:619411. doi:10.1101/619411.
715 [accessed 2019 Sep 3]. <https://www.biorxiv.org/content/10.1101/619411v2>.
- 716 Rundle SD, Brönmark C. 2001. Inter- and intraspecific trait compensation of defence
717 mechanisms in freshwater snails. *Proc R Soc London Ser B Biol Sci.* 268(1475):1463–1468.
718 doi:10.1098/rspb.2001.1682. [accessed 2019 Aug 26].
719 <https://royalsocietypublishing.org/doi/10.1098/rspb.2001.1682>.
- 720 Saltz JB, Nuzhdin S V. 2014. Genetic variation in niche construction: implications for
721 development and evolutionary genetics. *Trends Ecol Evol.* 29(1):8–14.
722 doi:10.1016/J.TREE.2013.09.011. [accessed 2018 Feb 14].
723 <https://www.sciencedirect.com/science/article/pii/S0169534713002346>.
- 724 Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients.
725 *Methods Ecol Evol.* 1(2):103–113. doi:10.1111/j.2041-210X.2010.00012.x. [accessed 2014
726 Mar 21]. <http://doi.wiley.com/10.1111/j.2041-210X.2010.00012.x>.
- 727 Sensenig A, Agnarsson I, Blackledge TA. 2010. Behavioural and biomaterial coevolution in
728 spider orb webs. *J Evol Biol.* 23(9):1839–1856. doi:10.1111/j.1420-9101.2010.02048.x.
729 [accessed 2019 Aug 20]. <http://doi.wiley.com/10.1111/j.1420-9101.2010.02048.x>.
- 730 Shelly TE. 1984. Prey selection by the neotropical spider *Micrathena schreibersi* with notes
731 on web-site tenacity. *Proc Entomol Soc Washingt.* 86(3):493–502. [accessed 2019 Aug 26].
732 <https://www.biodiversitylibrary.org/item/55207>.
- 733 Sherman PM. 1994. The orb-web: an energetic and behavioural estimator of a spider's
734 dynamic foraging and reproductive strategies. *Anim Behav.* 48(1):19–34.
735 doi:10.1006/anbe.1994.1208. [accessed 2019 Aug 27].

- 736 <https://linkinghub.elsevier.com/retrieve/pii/S0003347284712085>.
- 737 Sih A, Bell AM, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary
738 overview. *Trends Ecol Evol.* 19(7):372–378. doi:10.1016/j.tree.2004.04.009. [accessed 2013
739 May 21]. <http://www.sciencedirect.com/science/article/pii/S0169534704001211>.
- 740 Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an intergrative
741 overview. *Q Rev Biol.* 79(3):241–277. [accessed 2013 Oct 14].
742 <http://www.ncbi.nlm.nih.gov/pubmed/15529965>.
- 743 Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural
744 syndromes. *Ecol Lett.* 15(3):278–89. doi:10.1111/j.1461-0248.2011.01731.x. [accessed
745 2014 Mar 20]. <http://www.ncbi.nlm.nih.gov/pubmed/22239107>.
- 746 Stamps J, Groothuis TGG. 2010. The development of animal personality: relevance,
747 concepts and perspectives. *Biol Rev.* 85(2):301–325. doi:10.1111/j.1469-
748 185X.2009.00103.x. [accessed 2019 Aug 26]. [http://doi.wiley.com/10.1111/j.1469-
749 185X.2009.00103.x](http://doi.wiley.com/10.1111/j.1469-185X.2009.00103.x).
- 750 Stamps JA. 2007. Growth-mortality tradeoffs and “personality traits” in animals. *Ecol Lett.*
751 10(5):355–363. doi:10.1111/j.1461-0248.2007.01034.x. [accessed 2014 Jan 24].
752 <http://www.ncbi.nlm.nih.gov/pubmed/17498134>.
- 753 Uetz G, Johnson A, Soc DS. 1978. Web placement, web structure, and prey capture in orb-
754 weaving spiders. *Bull Br Arachnol Soc.* [accessed 2019 Aug 26].
755 <http://britishspiders.org.uk/bulletin/040401.pdf>.
- 756 Venner S, Pasquet A, Leborgne R. 2000. Web-building behaviour in the orb-weaving spider
757 *Zygiella x-notata*: influence of experience. *Anim Behav.* 59(3):603–611.
758 doi:10.1006/ANBE.1999.1327. [accessed 2019 Aug 29].
759 <https://www.sciencedirect.com/science/article/pii/S0003347299913271>.
- 760 Venner S, Thevenard L, Pasquet A, Leborgne R. 2001. Estimation of the Web’s Capture
761 Thread Length in Orb-Weaving Spiders: Determining the Most Efficient Formula. *Ann*
762 *Entomol Soc Am.* 94(3):490–496. doi:10.1603/0013-8746(2001)094[0490:eotwsc]2.0.co;2.
763 [accessed 2019 Aug 29]. <https://academic.oup.com/aesa/article/94/3/490/11838>.
- 764 White J-SS, O’Donnell JL. 2010. Indirect effects of a key ecosystem engineer alter survival
765 and growth of foundation coral species. *Ecology.* 91(12):3538–3548. doi:10.1890/09-2322.1.
766 [accessed 2018 Apr 26]. <http://doi.wiley.com/10.1890/09-2322.1>.
- 767 Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution.
768 *Trends Ecol Evol.* 27(8):452–461. [accessed 2013 Nov 18].
769 <http://www.sciencedirect.com/science/article/pii/S0169534712001139>.
- 770 Zevenbergen JM, Schneider NK, Blackledge TA. 2008. Fine dining or fortress? Functional
771 shifts in spider web architecture by the western black widow *Latrodectus hesperus*. *Anim*
772 *Behav.* 76(3):823–829. doi:10.1016/J.ANBEHAV.2008.05.008. [accessed 2019 Aug 20].
773 <https://www.sciencedirect.com/science/article/pii/S0003347208002182>.
- 774