

1 Collective behaviour is not robust to disturbance, yet parent and offspring 2 colonies resemble each other in social spiders

3

4 David N. Fisher^{*1}, James L.L. Lichtenstein², Raul Costa-Pereira¹, Justin Yeager³, and Jonathan N.
5 Pruitt^{1,2}

6 * Corresponding author: davidnfisher@hotmail.com

7 1. Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main St
8 West, Hamilton, Ontario, L8S 4K1, Canada

9 2. Department of Ecology, Evolution & Marine Biology, University of California - Santa Barbara,
10 Santa Barbara, CA USA 93106

11 3. Biodiversidad Medio Ambiente y Salud (BIOMAS), Direccion General de Investigacion,
12 Universidad de las Américas, Quito, Ecuador

13

14 Abstract

15 Groups of animals possess phenotypes such as collective behaviour, which may determine the fitness
16 of group members. However, the stability and robustness to perturbations of collective phenotypes in
17 natural conditions is not established. Furthermore, whether group phenotypes are transmitted from
18 parent to offspring groups is required for understanding how selection on group phenotypes
19 contributes to evolution, but parent-offspring resemblance at the group level is rarely estimated. We
20 evaluated robustness to perturbation and parent-offspring resemblance of collective foraging
21 aggressiveness in colonies of the social spider *Anelosimus eximius*. Among-colony differences in
22 foraging aggressiveness were consistent over time but changed if the colony was perturbed through
23 the removal of individuals, or via their removal and subsequent return. Offspring and parent colony
24 behaviour were correlated, but only once the offspring colony had settled after being translocated.

25 The parent-offspring resemblance was not driven by a shared elevation but could be due to other
26 environmental factors. Laboratory collective behaviour was not correlated with behaviour in the
27 field. Colony aggression seems sensitive to initial conditions and easily perturbed between
28 behavioural states. Despite this sensitivity, offspring colonies have collective behaviour that
29 resembles that of their parent colony, provided they are given enough time to settle into the
30 environment.

31 **Key words:** Anelosimus, collective behaviour, heritability, behavioural state, perturbation

32

33 [Introduction](#)

34 Many organisms form groups (Ward and Webster 2016). These aggregations can help individuals
35 avoid predation, acquire resources, find mates, and so on (Bilde et al. 2007; Frank 2007; Dobson et
36 al. 2012; Almberg et al. 2015; Groenewoud et al. 2016). For many of these purposes, groups use
37 collective behaviour, where individuals act in a co-ordinated or synchronised manner (Sumpter
38 2006). Collective behaviours cannot always be understood in terms of a simple sum of the actions of
39 individuals and so groups can possess phenotypes that simply do not exist at the individual level
40 (Parrish and Edelstein-Keshet 1999; Modlmeier et al. 2014; Farine et al. 2017). Group phenotypes
41 are therefore a tier of biological organisation that require direct study, both in terms of how they
42 relate to selection and evolution at the individual level, as well as in and of themselves (Couzin
43 2009).

44 Individual traits can range from being highly consistent within an individual to highly
45 variable (Bell et al. 2009). An individual might retain its behaviour in spite of a disturbance, or it
46 might find its behaviour changed as a result of a disturbance (Tuomainen and Candolin 2010; Sih et
47 al. 2011). The same could be true of group phenotypes; the collective behaviour of groups may resist
48 disturbances, or it may be altered by them (Flack et al. 2005, 2006; Smith et al. 2013; Kubitzka et al.

49 2015; Formica et al. 2016). For instance, collective behaviours might be “self-organised”, where
50 individuals re-create the same group behaviour after disturbances by following the same set of
51 interaction patterns that created the initial group behaviour (Bonabeau et al. 1997; Fisher and Pruitt
52 2019; Fisher et al. 2019). In contrast, groups might change their behaviour following disturbances, if
53 they are shunted into different “states” following a disturbance (Flack et al. 2005, 2006; Doering et
54 al. 2018; Pruitt et al. 2018), or engage in non-linear interactions that give divergent trajectories, and
55 so different group phenotypes, from a similar set of starting conditions (May and Oster 1976; Cole
56 1994; Fisher et al. 2018; Honegger and de Bivort 2018). However, the robustness of group
57 phenotypes to disturbances is not well documented (Flack et al. 2005, 2006; Smith et al. 2013;
58 Kubitzka et al. 2015; but see: Formica et al. 2016).

59 If group phenotypes are resistant to disturbances and stable over time, then they can influence
60 the survival and reproductive success of individuals within those groups (Wray et al. 2011; Keiser
61 and Pruitt 2014; Pruitt and Goodnight 2014; Pruitt et al. 2017, 2019). Stability in group phenotypes
62 is important because it determines the degree to which they can be subject to natural selection (in a
63 population of groups, if all group phenotypes vary widely these phenotypes cannot be associated
64 with relative fitness). One of the most extreme forms of group disturbance is group fission, whereby
65 a subset of group members disperse or bud off to form a smaller, “daughter” group (Vollrath 1982;
66 Aviles 1986). The collective behaviour of these daughter groups can be similar to that of their parent
67 group and so exhibit a crude kind of collective or group-level heritability (Bienefeld and Pirchner
68 1990; Pruitt et al. 2017, 2019). However, unlike individual-level traits (Houle 1992), the heritability
69 of group-level traits is not widely documented. This therefore makes it hard to judge how, if at all,
70 group-level selection can contribute to evolution and adaptation (Wilson 1997b,a; Gardner and
71 Grafen 2009; Queller and Strassmann 2009).

72 We therefore had two questions surrounding collective behaviour. First, is collective
73 behaviour robust to disturbance? Second, is collective behaviour transmitted from parent group to

74 offspring group in staged fission events? If both of these are true, then we might expect group
75 phenotypes such as collective behaviours to play a more important role in evolution than is currently
76 thought. We investigated these questions in a Neo-tropical social spider, *Anelosimus eximius*
77 (Araneae: Theridiidae). *Anelosimus eximius* is classified as “non-territorial permanent social” (Avilés
78 1997), where individuals (sometimes numbering into the 10,000s; Avilés 1997) from overlapping
79 generations live together in the same web structure and cooperate in web-building, prey capture, and
80 alloparental care (Vollrath 1986; Ebert 1988; Avilés and Tufiño 1998; Avilés and Harwood 2012;
81 Avilés and Guevara 2017; Pruitt and Avilés 2017). This allows them to feed on larger prey than
82 would be expected of a spider of their body size and to endure environments where related species
83 with lower levels of sociality cannot (Guevara and Avilés 2015; Avilés and Guevara 2017;
84 Fernandez-Fournier et al. 2018). Once prey make contact with the web, social spiders collectively
85 rush to immobilise it. How quickly the colony responds to a potential prey item can be an important
86 determinant of colony success and so this is the collective behaviour that we focus on here (hereafter
87 “foraging aggressiveness”; Lichtenstein et al. 2019).

88

89 [Methods](#)

90 [Data collection](#)

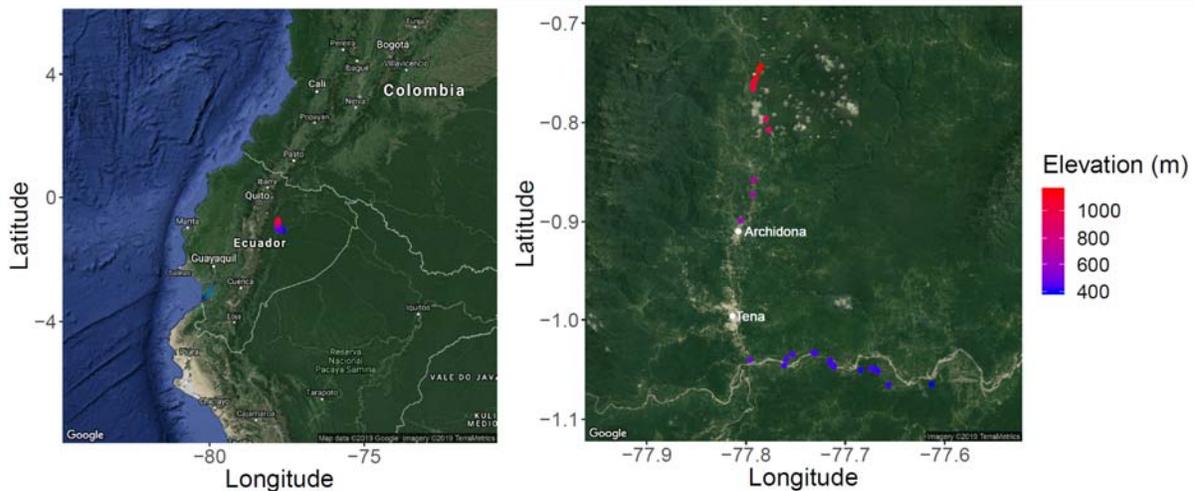
91 Our study took place in June and July 2019, near Tena, Ecuador (Fig. 1), under the Ecuadorian
92 Ministry of the Environment permit no. 014-2019-IC-FLO-DNB/MA. We located colonies of *A.*
93 *eximius* on roadsides, where they are relatively conspicuous on hedgerows, fences, and in trees. Their
94 webs are composed of a “basket” at the base, with a sheet and tangle capture web above (Yip et al.
95 2008). Once we found colonies, we marked their location and recorded GPS coordinates to allow us
96 to re-locate them. We then recorded their elevation and measured the height, width and depth of the
97 basket. We found 45 colonies that were suitable for our study, being within reach of an observer and

98 located within a morning's drive of our laboratory. We tested these 45 colonies' foraging
99 aggressiveness three times over six days (every other day). Our test for foraging aggressiveness was
100 the colony's speed to attack a vibrating stimulus (following: Lichtenstein et al. 2019). We stimulated
101 colonies to attack by touching a piece of wire fixed to a modified handheld vibratory device (8"
102 Vibrating Jelly Dong, Top Cat Toys, Chatsworth CA, USA) to a small piece of leaf placed in the
103 web. The leaf was always placed on the edge of the basket of the web, and we waited at least 60
104 seconds from the placement of the leaf before introducing the vibrations. The vibrations running
105 through the leaf simulate a prey item caught in the web; assays similar to this are often used to
106 estimate foraging aggressiveness in social (e.g. Laskowski and Pruitt 2014; Lichtenstein et al. 2019)
107 and solitary (Dirienzo and Montiglio 2016; Montiglio and DiRienzo 2016) spiders. We timed the
108 number of seconds from the start of the vibrations until a spider touched the leaf. If the colony did
109 not respond within 10 minutes the score was set at 600 (2.3% of all trials). This test is repeatable
110 among-colonies over four days ($r = 0.26$) and, at high altitudes, influences colony survival over a 11
111 month period (Lichtenstein et al. 2019), indicating it captures relatively stable aspects of colony
112 collective behaviour.

113 After these three baseline collective aggressiveness tests, we assigned each colony randomly
114 to one of three treatments. Fifteen colonies were "removal", 15 "procedural control" and 15
115 "control". For the removal and procedural control colonies, we returned three days after the 3rd
116 behavioural test and removed a subset of spiders from each colony, placed them in sealed plastic
117 boxes (190 x 190 x 90 mm) with sticks to support web building, and transported them back to our
118 laboratory. Individuals were collected either by gently shaking the web and catching spiders that
119 dropped or scooping a small bit of webbing into a large plastic box. We counted the number of
120 individuals that were large ($>2\text{mm}$ in body length), medium sized ($<2\text{mm}$ & $>1\text{mm}$ in body length)
121 or small ($<1\text{mm}$ in body length), with size being estimated by eye. We endeavoured not to destroy

122 any vegetation the web was built on, in order to preserve the web's structure. Control colonies were
123 left undisturbed.

124



125

126 **Figure 1.** Maps showing the location of each of the *Anelosimus eximius* colonies in the study,
127 with the elevation of the colony indicated by the colour (red = high elevation, blue = low
128 elevation). In the right map the towns of Tena and Archidona are indicated with white points.

129

130 Each subset of spiders that we collected was left undisturbed to acclimatise to captivity in their box
131 for two days. Boxes had four airholes to provide oxygen, and spiders were provided a moist piece of
132 paper on the 4th day of their captivity for hydration; they were not fed. We then tested the foraging
133 aggressiveness of each of the 30 captive colonies three times over six days (every other day; the 1st
134 laboratory test beginning five days after the last pre-disturbance test). We modified the assay slightly
135 to account for the new setting: we reduced the power of the vibrations to avoid over-amplification in
136 the small box, and the wire was touched directly to the web rather than to a small leaf. These
137 laboratory assays were used to assess the resemblance of parent and daughter colonies in a common
138 garden environment. Although we might expect behaviour in the laboratory to differ substantially

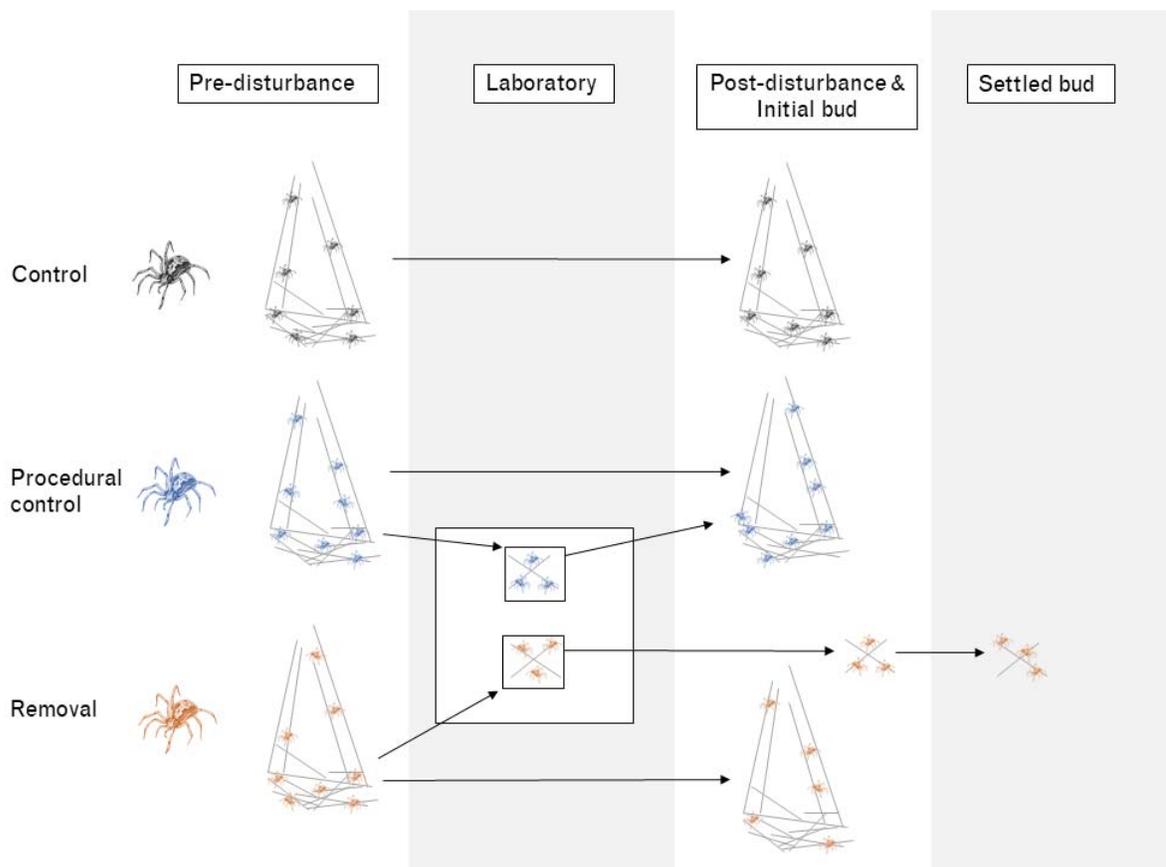
139 from that in the field, due to the lack of all natural cues (but see: Boon et al. 2008; Herborn et al.
140 2010; Fisher et al. 2015; Yuen et al. 2016), we might still expect the ranking of colonies in terms of
141 their foraging aggression to be similar in both the laboratory and in the field. In this case a positive
142 correlation would be expected.

143 Following their 3rd test (on the same day), the spiders from procedural control colonies were
144 placed directly back into their source (parental) colony. The colonies in this treatment group
145 therefore lost no spiders but experienced the physical disturbance of the sampling event. Spiders
146 from the removal treatment were placed in vegetation similar to what the parent colony had built its
147 web on, but 5-10m away from the parent colony. This was designed to mimic the fission of a colony
148 and the foundation of a new colony by a subset of individuals (sociotomy), which occurs naturally in
149 *A. eximius* as colonies grow in size (Vollrath 1982; Venticinque et al. 1993; Avilés 1997). These
150 “bud colonies” were used to assess the heritability of colony behaviours when in the same
151 environment as their parent colony. At this point we discovered that eight of the parent colonies had
152 been destroyed by workers clearing roadsides. Two of these colonies were in the procedural control
153 group, but we could not return the previously removed spiders to a now destroyed colony, so we
154 placed these spiders into vegetation 5-10m away as bud colonies.

155 Two days after returning them to the wild, we tested the collective aggressiveness of each
156 surviving parent colony (n = 37) and each bud colony three times over six days (every other day)
157 using the same method as before. In three instances the bud colony was completely abandoned,
158 leaving 14 bud colonies (including the additional two colonies that were originally part of the
159 procedural control group) to assay for foraging aggressiveness. To evaluate the robustness of *A.*
160 *eximius* colonies to disturbance, we tested for a correlation between parent colonies’ pre- and post-
161 disturbance behaviours. We evaluated transmission of aggressiveness from parent to daughter group
162 by testing for a correlation between the pre-disturbance behaviour of parent colonies and the
163 behaviour of bud colonies in a common garden setting (the laboratory) and a natural setting (the bud

164 colony behaviours). During the three tests of the bud colony foraging aggressiveness, we observed
165 the bud colonies frequently changing position and orientation in the vegetation. We thought it was
166 likely that there was an initial “settling” phase after returning the bud colonies to the wild from
167 captivity. Therefore, starting eight days after their 3rd test, we tested each bud colony another three
168 times over six days (every other day). This procedure was meant to capture bud colony behaviour
169 following a settlement period (“settled bud behaviour”, the initial three tests hereafter being referred
170 to as “initial bud behaviour”). A schematic outlining the sampling regime for the study is shown in
171 Fig. 2.

172



173

174 **Figure 2.** A schematic demonstrating our study design. In the pre-disturbance phase 45 colonies
175 were tested three times over six days for foraging aggressiveness. For two thirds of these colonies (in

176 the “removal” and “procedural control” groups) spiders were then removed to the laboratory, where
177 they were tested three times over six days for foraging aggressiveness. Following this, spiders in the
178 procedural control groups were returned to their original colony, while spiders in the removal groups
179 were placed near the original colony as “bud colonies”. We then tested all original colonies and all
180 bud colonies three times over six days. Following this we tested each bud colony another three times
181 over six days to measure “settled” behaviour.

182

183 Data analysis

184 To assess the stability of colony behaviour over time in face of the disturbance, we initially estimated
185 the phenotypic correlation (Pearson’s correlations in all cases) between the log of pre-disturbance
186 foraging aggressiveness and the log of post-disturbance foraging aggressiveness, with a colony’s first
187 measure pre-disturbance paired with its first measured post-disturbance, and so on. However, this
188 does not estimate the among-colony correlation between pre- and post-disturbance behaviours,
189 instead it conflates among-colony, among-date and residual variation (analogous to the “individual
190 gambit”; Brommer 2013; Dingemanse and Dochtermann 2013). To directly estimate the among-
191 colony correlation between pre- and post-disturbance foraging aggressiveness, we built multivariate
192 models in MCMCglmm (Hadfield 2010) with the logs of pre-disturbance foraging aggressiveness
193 and post-disturbance foraging aggressiveness as response variables. We entered “NA” for the post-
194 disturbance trials for colonies that had been destroyed. This allowed us to include their scores for the
195 pre-disturbance trials in the model, which should improve the estimate of the among-colony variance
196 in pre-disturbance foraging aggressiveness. We estimated the among-colony variances and
197 covariance between pre- and post-disturbance foraging aggressiveness, the among-date variances for
198 these traits (but no covariance as the two behaviours were never tested on the same day) and the
199 residual variances for each behaviour (but no covariance as the two behaviours were never measured

200 at the same time). We included the log of colony basket volume (height*depth*width), mean centred
201 and scaled to a variance of one, and the trial number (1-3), mean centred, as fixed effects for each
202 behaviour. This was done in case colony foraging aggressiveness covaried with size (Yip et al. 2008;
203 Pruitt et al. 2011) and in case the colonies changed their behaviour over time.

204 To test if the disturbed colonies changed their behaviour more than the control colonies, we
205 estimated the raw phenotypic correlations for each of the three treatment groups. We then we fitted
206 the multivariate model described above to each of the three treatment groups separately and
207 compared the magnitude and distributions of the among-colony correlations. If the control group had
208 a stronger correlation between pre- and post-disturbance foraging aggressiveness than the removal or
209 the procedural control groups, we could conclude that the disturbance disrupted colony collective
210 behaviour.

211 To assess the resemblance of collective behaviour between parent and offspring colonies, we
212 first estimated the phenotypic correlations between log-transformed pre-disturbance foraging
213 aggressiveness, log-transformed laboratory foraging aggressiveness, and log-transformed bud colony
214 foraging aggressiveness, associating the first pre-disturbance trial, the first laboratory trial, and the
215 first bud trial and so on. However, phenotypic correlations such as this (including those based on
216 only a single measure of parents and offspring, e.g. Pruitt et al. 2017, or those based on averages of
217 parent and offspring colony traits, e.g. Pruitt et al., 2019) conflate among- and within-colony
218 covariance, when only the former is relevant for assessing whether more aggressive parent colonies
219 have more aggressive daughter colonies (Brommer 2013; Dingemanse and Dochtermann 2013; see
220 also Niemela and Dingemanse 2018 for a discussion of the issues with using a single measure of
221 behaviour to estimate covariances). To estimate the among-colony correlation, we built multivariate
222 models in MCMCglmm, with the logs of pre-disturbance foraging aggressiveness, laboratory
223 foraging aggressiveness, and bud foraging aggressiveness as response variables. We estimated the
224 among-colony variances and covariance between these three traits. This is analogous to a parent-

225 offspring regression, which overestimates heritability compared to estimates from an “animal model”
226 (Kruuk 2004). We did not have a colony level pedigree, nor could we calculate the relatedness
227 among colonies by some other means. Therefore, the parent-offspring covariance we estimate here
228 should be taken as an upper limit for the true colony level heritability.

229 We also estimated among-date variance for each behaviour (but no covariance as the
230 behaviours were never tested on the same day) and the residual variance for each behaviour (but no
231 covariance as the behaviours were never measured at the same time). We included the log of colony
232 volume as a fixed effect for pre-disturbance behaviour, and the number of adults removed from the
233 colony and so tested in both the laboratory and as a bud colony (summing large and medium spiders,
234 so any greater than 1mm in body length) as fixed effects for laboratory and bud behaviour. This was
235 done in case colony size impacted foraging aggressiveness. These fixed effects were scaled to a
236 mean of zero and a variance of one. We also include trial number (1-3) as a fixed effect, mean
237 centred, in case the colonies changed their behaviour over time.

238 We estimated the raw phenotypic correlations once with the 1st-3rd tests on the bud colonies
239 (initial bud behaviour) and once with the 4th-6th tests (settled bud behaviour). We also re-fitted the
240 multivariate model using the 4th-6th tests instead of the 1st-3rd tests. If collective behaviour was
241 inherited from parent colony to offspring colony, we expected a positive among-colony correlation
242 between the pre-disturbance and bud behaviours. If behaviour in the laboratory reflects behaviour in
243 the field, then there would also be a positive among-colony correlation between the pre-disturbance
244 and laboratory foraging aggressiveness. Further, if the 4th-6th tests on the bud colonies reflects settled
245 behaviour, we expected the among-colony correlation between pre-disturbance foraging
246 aggressiveness and the settled bud foraging aggressiveness to be stronger than the correlation
247 between pre-disturbance foraging aggressiveness and the initial bud foraging aggressiveness.

248 For all multivariate models we used a Gaussian error structure for each response variable,
249 550,000 iterations, a burn in of 50,000, and a thinning interval of 100. Priors were set to be flat and
250 relatively uninformative, with 70% of the phenotypic variance for the logged values of each trait
251 placed on the residual variance, 20% on the among-colony variance, and 10% on the among-date
252 variance (following: Brommer 2017).

253

254 Results

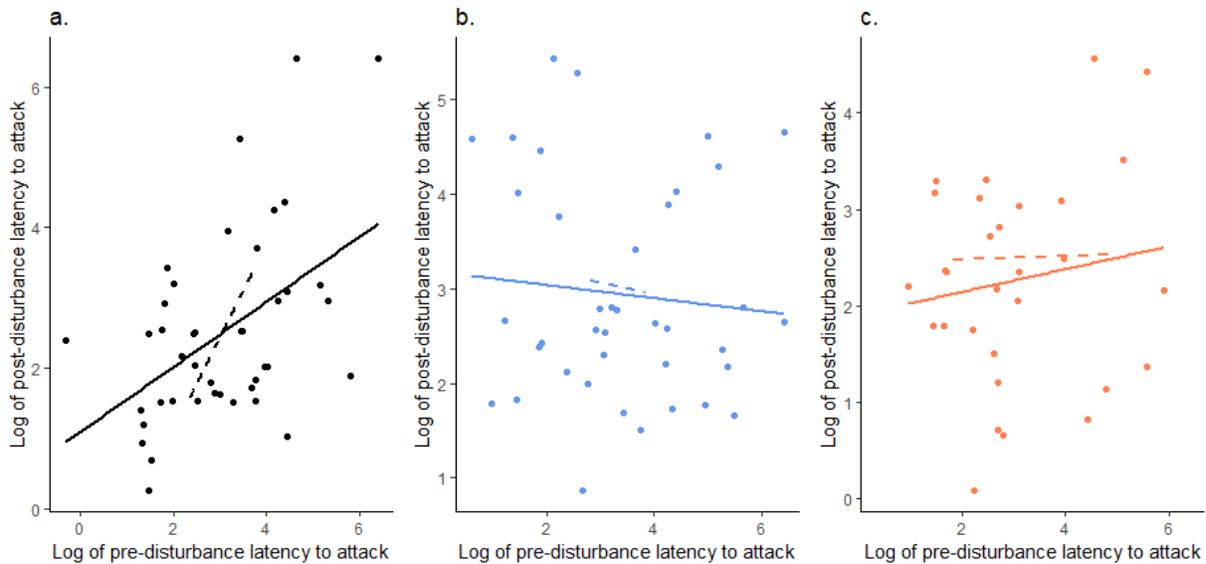
255 Robustness to disturbance

256 Across all treatments, pre-disturbance foraging aggressiveness showed consistent differences among
257 colonies, (repeatability (r) of logged values = 0.152, credible intervals (CIs) = -0.060 to 0.348). Post-
258 disturbance foraging aggressiveness was also consistently different among-colonies (r = 0.376, CIs =
259 0.158 to 0.555). We therefore conclude that each colony is in a relatively stable behavioural “state”
260 of a particular level of foraging aggressiveness during the six days we measured them. The
261 phenotypic correlation between pre- and post-disturbance foraging aggressiveness was significant
262 and positive (r = 0.217, t = 2.321, df = 109, p = 0.022). At the among-colony level, pre-disturbance
263 foraging aggressiveness positively covaried with post-disturbance foraging aggressiveness, although
264 the 95% CIs of the among-colony covariance overlapped zero (covariance mode = 0.167, CIs = -
265 0.103 to 0.598, correlation mode = 0.547, CIs = -0.124 to 0.850). Full model results are provided in
266 the supplementary materials (Table S1). These findings suggest that colony collective behaviour is
267 stable over time.

268 The phenotypic correlation between pre- and post-disturbance foraging aggressiveness in the
269 control group was quite strong and positive (Fig. 3a, r = 0.482, t = 3.483, df = 40, p = 0.001), absent
270 in the procedural control group (Fig. 3b, r = -0.093, t = -0.567, df = 37, p = 0.574), and weakly
271 positive but non-significant in the removal group (Fig. 3c, r = 0.151, t = 0.809, df = 28, p = 0.425).

272 At the among-colony level, for the control group, there was a positive correlation between pre- and
273 post-disturbance foraging aggressiveness (Fig. 3a, covariance mode = 0.245, CIs = -0.240 to 1.080,
274 correlation mode = 0.701, CIs = -0.177 to 0.953), no correlation at all in the procedural control
275 group (Fig. 3b, covariance mode = -0.001, CIs = -0.621 to 0.464, correlation mode = 0.051, CIs = -
276 0.773 to 0.726), and a weak positive correlation in the removal group (Fig. 3c, covariance mode =
277 0.094, CIs = -0.547 to 1.086, correlation mode = 0.637, CIs = -0.595 to 0.925). Note that the CIs of
278 all of these correlations overlap zero and hence each other. See Tables S2-4 in the supplementary
279 materials for full model results. Among-colony correlations therefore largely matched the phenotypic
280 correlations (Fig. 3a-c). These results collectively convey that perturbing colonies by removing
281 individuals disrupted colony collective behaviour, especially if the individuals were subsequently
282 returned.

283



284

285 **Figure 3.** The relationship between the logs of pre- and post-disturbance foraging aggressiveness
286 in the three treatment groups (a. control, b. procedural control, c. removal). Solid lines show the
287 phenotypic correlations, while dashed lines showed the estimated among-colony correlations from
288 the multivariate model.

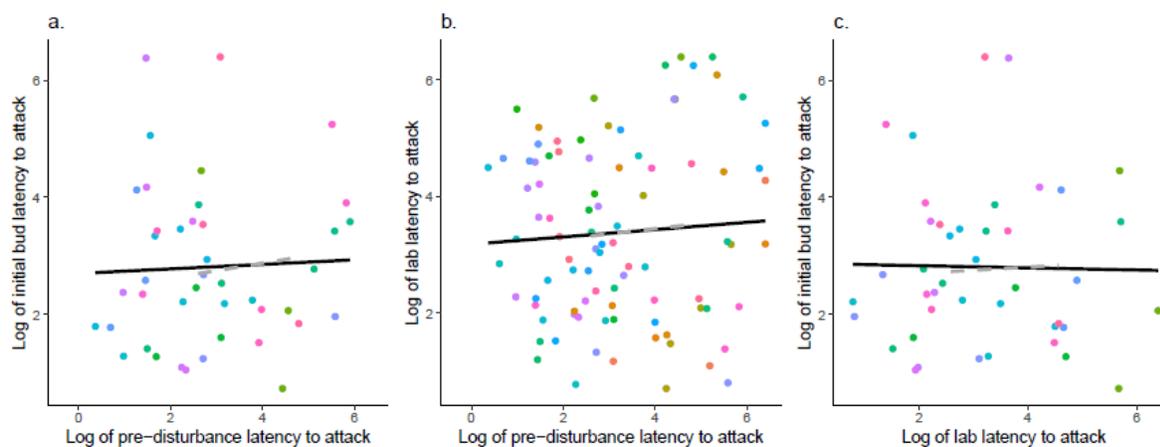
289

290 Transmission of collective behaviour

291 Colonies showed consistent differences in foraging aggressiveness in the laboratory ($r = 0.282$, CIs =
292 0.080 to 0.472). Bud colonies showed a small amount consistent differences in in the initial three
293 measures of foraging aggressiveness ($r = 0.082$, CIs = 0.024 to 0.332). There was no phenotypic
294 correlation between pre-disturbance foraging aggressiveness and initial bud foraging aggressiveness
295 (Fig. 4a, $r = 0.043$, $t = 0.272$, $df = 40$, $p = 0.787$) or laboratory foraging aggressiveness (Fig. 4b, $r =$
296 0.065, $t = 0.610$, $df = 88$, $p = 0.543$). Laboratory and initial bud behaviour were also not correlated
297 (Fig. 4c, $r = -0.019$, $t = -0.120$, $df = 40$, $p = 0.905$). Correlations were also absent at the among-
298 colony level (pre-disturbance & initial bud foraging aggressiveness: Fig. 4a, covariance mode =
299 0.042, CIs = -0.314 to 0.502, correlation mode = 0.143, CIs = -0.553 to 0.814; pre-disturbance &
300 laboratory foraging aggressiveness: Fig. 4b, covariance mode = 0.004, CIs = -0.342 to 0.431,
301 correlation mode = 0.133, CIs = -0.504 to 0.651; laboratory & initial bud foraging aggressiveness:
302 Fig. 4c, covariance mode = 0.008, CIs = -0.462 to 0.560, correlation mode = 0.386, CIs = -0.631 to
303 0.779). Full model results are given in the supplementary materials (Table S5).

304 Settled bud behaviour showed consistent differences among-colonies in foraging
305 aggressiveness ($r = 0.161$, CIs = 0.044 to 0.464). There was a phenotypic correlation between
306 settled bud behaviour and foraging aggressiveness (Fig. 5a, $r = 0.464$, $t = 3.317$, $df = 40$, $p =$
307 0.002), but not between settled bud behaviour and laboratory foraging aggressiveness (Fig. 5b, $r =$
308 -0.117, $t = -0.743$, $df = 40$, $p = 0.462$). At the among-colony level, settled bud foraging
309 aggressiveness was positively correlated with pre-disturbance foraging aggressiveness, although
310 the CIs overlapped zero (Fig. 5a, covariance mode = 0.136, CIs = -0.214 to 0.696, correlation
311 mode = 0.576, CIs = -0.269 to 0.896). Laboratory foraging aggressiveness was not correlated with
312 settled bud foraging aggressiveness (Fig. 5b, covariance mode = 0.005, CIs = -0.534 to 0.549,

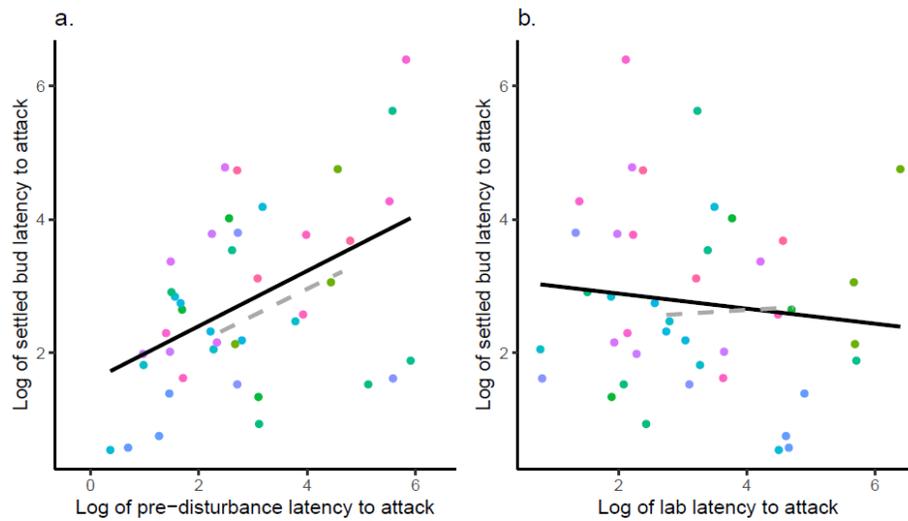
313 correlation mode = 0.133, CIs = -0.675 to 0.736). Full model results are given in the
314 supplementary materials (Table S6). Therefore, as for the robustness to disturbance, phenotypic
315 correlations matched the among-colony correlations. These results suggest that parent and
316 offspring colony collective behaviours can resemble each other, but only once the offspring colony
317 had settled into an environment close to that of the parental colony's.
318



319
320 **Figure 4.** The relationship between a. pre-disturbance foraging aggressiveness and lab foraging
321 aggressiveness, b. pre-disturbance foraging aggressiveness and initial bud foraging aggressiveness,
322 and c. lab foraging aggressiveness and initial bud foraging aggressiveness. Point colours indicate
323 different colonies. Solid black lines show the phenotypic correlations, while the dashed grey lines
324 show the estimated among-colony correlations from the multivariate model.

325
326 The volume of the colony's basket, number of adults, and trial number did not influence foraging
327 aggressiveness in any of the models. There was some variation among days in foraging aggression,
328 see Tables S1-6 for estimates.

329



330

331 **Figure 5.** The relationship between a. pre-disturbance foraging aggressiveness and settled bud
332 foraging aggressiveness, and b. lab foraging aggressiveness and settled bud foraging
333 aggressiveness. Point colours indicate different colonies. Solid black lines show the phenotypic
334 correlations, while the dashed grey lines show the estimated among-colony correlations.

335

336 Discussion

337 Organisms in groups can possess collective behaviours, which can be subject to selection. How
338 robust these collective behaviours are to disturbance, and whether they are transmitted from parent
339 groups to offspring groups, is however not well known. Here we show that the foraging
340 aggressiveness of *A. eximius* colonies is consistent over a period of several weeks and presumably
341 longer, given that at high elevations foraging aggressiveness can influence colony survival over
342 many months (Lichtenstein et al. 2019). Yet, colony behaviour is not robust to perturbation,
343 especially if individuals are removed from the colony and then returned. We further found that bud
344 colonies had collective behaviour that resembled that of their parent colony, but this was only

345 apparent once the bud colony had spent over a week settling after the translocation and was not
346 apparent when comparing laboratory measures of the bud colony with the parent colony.

347 First, we note here that, while the all patterns we detected in the study were qualitatively
348 same at the among-colony level as at the phenotypic level, the 95% credible intervals of all among-
349 colony correlations overlapped zero. From inspection of the correlation coefficients (see also Figs. 3-
350 5), we can see the among-colony correlations are often stronger than the phenotypic correlations.
351 Therefore, the overlap with zero is likely due to high uncertainty, probably due to our study using
352 fewer than 50 colonies, and fewer than 20 colonies in each treatment group, rather than a small effect
353 size. We therefore take the liberty of discussing among-colony correlations that are of the same
354 strength or stronger than an equivalent and statistically significant phenotypic correlation. We do this
355 because we consider these results to represent meaningful biological trends rather than statistical
356 error.

357

358 Collective behaviour is vulnerable to disturbance

359 There were consistent differences among colonies in both pre- and post-disturbance behaviour, but
360 no covariance between pre- and post-disturbance behaviours in the procedural control and removal
361 treatment groups. This suggests that foraging aggressiveness represents a semi-stable state that a
362 colony is in, but that the colony is shifted to a different state by perturbations, as colonies did not
363 retain the same level of foraging aggressiveness when individuals were removed or when the colony
364 was disturbed by the removal and then return of individuals. Discussing populations or ecosystems
365 as “systems” that can exist in different states has a long history in ecology (May 1974; Solé and
366 Goodwin 2000). Referring to social groups in this way is less common, but interest in the utility of
367 this viewpoint is growing (Flack et al. 2005, 2006; Doering et al. 2018; Pruitt et al. 2018). Social
368 systems have previously been shown to be vulnerable to shifts from calm to antagonistic states due to

369 the removal of key individuals (Flack et al. 2005, 2006) or due to gradual heating (Doering et al.
370 2018). Here we have found that the removal of individuals combined with a physical disturbance to
371 the colony causes the colony to shift from one state of foraging aggression to another, although we
372 did not observe a general increase in aggression due to the perturbations. In fact, mean foraging
373 aggressiveness was equal in the control and removal treatment groups, and lower (longer latencies)
374 in the procedural control group. We concluded this based on comparing the intercepts for post-
375 disturbance foraging aggressiveness between the models for each treatment (although note that the
376 95% credible intervals overlapped in all cases, see Tables S2-4). Instead, we have observed that a
377 colony adopts a different, yet still repeatable, behaviour to what it displayed before the disturbance.

378 As spider colonies did not return to their original foraging aggressiveness after the
379 disturbance, consistent differences in behaviour among-colonies probably do not rely on some
380 underlying stable trait of the colony (as is suggested for “pace of life syndrome” hypotheses for
381 consistent among-individual differences in behaviour; (Réale et al. 2010)). Instead, consistent
382 differences among colonies may depend on social interactions that generate positive feedback loops
383 that cause colonies to diverge in behaviour (e.g. Luttbeg and Sih 2010). Such multiplicative
384 interactions can give systems that are highly sensitive to initial conditions, and hence give variable
385 trajectories and final states (Boyce 1992; Hastings et al. 1993; Cole 1994). Therefore, following the
386 perturbation, *A. eximius* colonies may engage in interactions that, despite being deterministic and so
387 giving rise to consistent behaviour, nevertheless follow divergent trajectories and so do not give the
388 same behavioural trait as the colony previously possessed (Fisher et al. 2018). Interactions between
389 individual *A. eximius* within the colony that catalyse increased aggression could give this dynamic,
390 while interactions between the whole colony and its environment might also generate sufficient
391 feedback. Currently, our understanding of the development of *A. eximius* colony collective behaviour
392 is insufficient to allow us to judge the likely relative contributions of these two possibilities.
393 However, social network analysis on the distance related social spider *Stegodypus dumicola* hint that

394 positive feedback within colonies can cause the accentuation of individual differences within groups
395 (Hunt et al. 2018), raising the possibility something similar could happen in *A. eximius*.

396 Removing individuals and then adding them back to the colony (as occurred in the procedural
397 control group) completely removed any relationship between pre- and post-disturbance foraging
398 aggressiveness. This suggests that removing individuals for a time and then returning them
399 destabilises collective behaviour much more than simply removing them. The returning spiders may
400 not have been recognised by their old colony-mates, and a period of antagonism may have disrupted
401 colony behaviour. Social (and subsocial) spiders are thought to discriminate between kin and non-kin
402 (Evans 1999; Bilde and Lubin 2001; Beavis et al. 2007; Schneider and Bilde 2008; Grinsted et al.
403 2011). However, *A. eximius* is known to accept intruders from the different colonies as well as from
404 the same colony (Pasquet et al. 1997), suggesting there would have been limited antagonism towards
405 the returning spiders. Instead, Pasquet *et al.* (1997) observed that the presence of an intruder
406 increases the nearest neighbour distance within a colony. This change could then influence collective
407 foraging aggressiveness. For now, we propose that the especially destabilised foraging behaviour of
408 these colonies stems from their effectively experiencing two social disturbance as opposed to just
409 one: having both lost a subset of group members and regained them, regardless of the familiarity of
410 these group members.

411

412 Parent and offspring colony collective behaviours resemble each other, but only once
413 settled into the same environment

414 Parent colony behaviour (pre-disturbance) only covaried with bud colony behaviour once the bud
415 colony had settled. This suggests that a group phenotype can be transmitted from parent to offspring
416 colonies, like individual behaviours often are. However, this was only apparent over a week after the
417 bud colony was been returned to the wild, suggesting there is an initial settling period before the bud

418 colony regains the collective behaviour its parent colony showed. Further, parent colony foraging
419 aggressiveness did not covary with laboratory foraging aggressiveness. Behaviour in the laboratory
420 could therefore represent a different trait to behaviour in the wild, perhaps owing to colonies'
421 residing in completely different environments. In short, it could be that that bud colonies were
422 permitted to reassume a shared environment that drives the correlation between parent colony and
423 bud colony (Kruuk and Hadfield 2007). If this is so, then foraging aggressiveness might itself not be
424 transmitted between parent and offspring groups.

425 To evaluate the possible influence of a shared environment, we need to identify an
426 environmental variable that could drive such a parent-offspring resemblance (Kruuk and Hadfield
427 2007). Foraging aggressiveness in *A. eximius* decreases at higher elevations (Lichtenstein et al.
428 2019), and our study included colonies from 398m to 1146m above sea level (Fig.1). We tested
429 whether it was elevation that drove the parent-offspring correlation by re-fitting the model for pre-
430 disturbance and settled bud foraging aggressiveness (the model also contained laboratory foraging
431 aggressiveness as a third response, but it is not important here) with the elevation of the colony
432 (mean centred and scaled to a variance of one) as a fixed effect. In this model, pre-disturbance
433 foraging aggression was lower (latencies tended to be longer) at higher elevations, although the
434 credible intervals for the effect overlapped zero (fixed effect mode = 0.392, CIs = -0.059 to 0.836),
435 but settled bud foraging aggressiveness did not change with elevation (fixed effect mode = 0.034,
436 CIs = -1.001 to 1.261). In this model the relationship between pre-disturbance and settled bud
437 foraging aggressiveness was roughly the same as in the model without elevation (covariance mode =
438 0.119, CIs = -0.212 to 0.715, correlation mode = 0.583, CIs = -0.283 to 0.892). This therefore
439 suggests that sharing the same elevation was not driving the similarity between parent and offspring
440 colonies. However, it is possible that other environmental variables are driving the resemblance.

441 An alternative explanation for the parent-offspring colony resemblance is that different
442 colonies use different but repeatable behaviour rules to assemble colony behaviour. Therefore, once

443 offspring colonies had settled, they were able to recreate the collective behaviour of the parent
444 colony. While such a dynamic suggests a colony's collective behaviour would resist a perturbation, it
445 may take some time for the original collective behaviour to re-establish. Notably, extra time which
446 was granted to the offspring colonies because of their conspicuous readjustments in the foliage, but
447 not to the parent colonies post-disturbance. If we had tracked the parent colonies post-disturbance for
448 a longer period of time, we may have seen their foraging aggressiveness return to its pre-disturbance
449 level.

450 The outcome of selection on collective behaviour are quite different if collective behaviour is
451 determined by an environmental variable (other than elevation) versus a directly transmitted quality
452 of the parent colony. Relatedness within *A. eximius* colonies is typically very high (average $r = 0.92$
453 across four populations in Suriname, although r was estimated as 0.18 based on two nearby colonies
454 at a site in Panama; (Smith and Hagen 1996)), and so selection at the colony level could be expected
455 to give adaptation at the colony-level (Gardner and Grafen 2009; Queller and Strassmann 2009). If
456 collective behaviour is determined by the environment, then selection will most likely favour
457 colonies that best match their behaviour to the environment. In this case, changes to populations'
458 behaviour across generations is more likely to reflect changes in habitat availabilities or selection
459 acting on some aspect of colonies' habitat preferences or dispersal abilities. In contrast, if foraging
460 aggressiveness is genuinely directly passed from parent colony to offspring colony, and given at high
461 elevations we can observe selection against high foraging aggression (Lichtenstein et al. 2019), then
462 we might expect mean aggression at high elevations to decrease across generations by selection
463 acting directly on colony behaviour.

464

465 Conclusions

466 In summary, we found that the foraging aggressiveness of *A. eximius* colonies is relatively stable
467 over time but can be disrupted by perturbations. Returning individuals to their source colony disrupts
468 a colony's collective foraging even more than simply removing individuals from a colony. Offspring
469 colonies have collective behaviour that resembles that of their parent colony, and this does not
470 appear to be driven by a shared elevation. Instead, other forces like shared microhabitat preferences
471 or the direct transmission of colony interaction rules, genetically determined behaviours, or plastic
472 states (e.g., hunger levels, aggression levels) may drive resemblance of parent and offspring colonies.
473 Appreciating that groups possess behavioural states, and that these states may be influenced by
474 external perturbations yet still be passed from parent group to offspring group, should help us
475 understand the role of group phenotypes in ecological and evolutionary processes.

476

477 [Author contributions](#)

478 DNF, JLLL and JNP designed the study. JY acquired the permits. DNF, JLLL & RCP collected the
479 data. DNF analysed the data and drafted the manuscript. All authors contributed to revisions of the
480 manuscript and approved the final version.

481

482 [Acknowledgements](#)

483 We thank J. B. Barnett, H. M. Anderson and B. L. McEwen for being excellent colleagues in the
484 field. We also thank T. D. Swanson and the staff of the Andes and Amazon Field School at Iyarina
485 for making our stay as comfortable and enjoyable as possible. Funding was provided by a Canada
486 150 Research Chair award to JNP. We have no conflicts of interest.

487

488 [Data accessibility](#)

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

490

491 [References](#)

492 Almberg, E. S., P. C. Cross, A. P. Dobson, D. W. Smith, M. C. Metz, D. R. Stahler, and P. J.

493 Hudson. 2015. Social living mitigates the costs of a chronic illness in a cooperative carnivore.

494 *Ecol. Lett.* 18:660–667.

495 Avilés, L. 1986. Sex-Ratio Bias and Possible Group Selection in the Social Spider *Anelosimus*

496 *eximius*. *Am. Nat.* 128:1–12.

497 Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp.

498 476–498 in J. C. Choe and B. J. Crespi, eds. *The Evolution of Social Behavior in Insects and*

499 *Arachnids*. Cambridge University Press, Cambridge.

500 Avilés, L., and J. Guevara. 2017. Sociality in Spiders. Pp. 188–223 in D. R. Rubenstein and P.

501 Abbot, eds. *Comparative Social Evolution*. Cambridge University Press, Cambridge.

502 Avilés, L., and G. Harwood. 2012. A Quantitative Index of Sociality and Its Application to Group-

503 Living Spiders and Other Social Organisms. *Ethology* 118:1219–1229. Wiley/Blackwell

504 (10.1111).

505 Avilés, L., and P. Tufiño. 1998. Colony Size and Individual Fitness in the Social Spider *Anelosimus*

506 *eximius*. *Am. Nat.* 152:403–418. The University of Chicago PressThe American Society of

507 Naturalists.

508 Beavis, A. S., D. M. Rowell, and T. Evans. 2007. Cannibalism and kin recognition in *Delena*

509 *cancerides* (Araneae: Sparassidae), a social huntsman spider. *J. Zool.* 271:233–237. John Wiley

510 & Sons, Ltd (10.1111).

511 Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-

512 analysis. *Anim. Behav.* 77:771–783. Elsevier Ltd.

- 513 Bienefeld, K., and F. Pirchner. 1990. Heritabilities for several colony traits in the honeybee (*Apis*
514 *mellifera carnica*). *Apidologie* 21:175–183. EDP Sciences.
- 515 Bilde, T., K. S. Coates, K. Birkhofer, T. Bird, A. A. Maklakov, Y. Lubin, and L. Avilés. 2007.
516 Survival benefits select for group living in a social spider despite reproductive costs. *J. Evol.*
517 *Biol.* 20:2412–2426.
- 518 Bilde, T., and Y. Lubin. 2001. Kin recognition and cannibalism in a subsocial spider. *J. Evol. Biol.*
519 14:959–966.
- 520 Bonabeau, E., G. Theraulaz, J.-L. Deneubourg, S. Aron, and S. Camazine. 1997. Self-organization in
521 social insects. *Trends Ecol. Evol.* 12:188–193. Elsevier Current Trends.
- 522 Boon, A. K., D. Réale, and S. Boutin. 2008. Personality, habitat use, and their consequences for
523 survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* 117:1321–1328.
- 524 Boyce, M. S. 1992. Population Viability Analysis. *Annu. Rev. Ecol. Syst.* 23:481–506.
- 525 Brommer, J. E. 2017. Multivariate Mixed Models in R- MCMCglmm examples.
- 526 Brommer, J. E. 2013. On between-individual and residual (co)variances in the study of animal
527 personality: are you willing to take the “individual gambit”? *Behav. Ecol. Sociobiol.* 67:1027–
528 1032.
- 529 Cole, B. J. 1994. Chaos and Behaviour: The Perspective of Nonlinear Dynamics. Pp. 423–444 *in* L.
530 A. Real, ed. *Behavioral Mechanisms in Evolutionary Ecology*. University of Chicago Press.
- 531 Couzin, I. D. 2009. Collective cognition in animal groups. *Trends Cogn. Sci.* 13:36–43. Elsevier
532 Current Trends.
- 533 Dingemanse, N. J., and N. a Dochtermann. 2013. Quantifying individual variation in behaviour:
534 mixed-effect modelling approaches. *J. Anim. Ecol.* 82:39–54.

- 535 Dirienzo, N., and P.-O. Montiglio. 2016. Linking consistent individual differences in web structure
536 and behavior in black widow spiders. *Behav. Ecol.* 27:1424–1431. Narnia.
- 537 Dobson, F. S., V. A. Viblanc, C. M. Arnaud, and J. O. Murie. 2012. Kin selection in Columbian
538 ground squirrels: Direct and indirect fitness benefits. *Mol. Ecol.* 21:524–531. Blackwell
539 Publishing Ltd.
- 540 Doering, G. N., I. Scharf, H. V. Moeller, and J. N. Pruitt. 2018. Social tipping points in animal
541 societies in response to heat stress. *Nat. Ecol. Evol.* 2:1298–1305. Nature Publishing Group.
- 542 Ebert, D. 1988. Behavioral asymmetry in relation to body weight and hunger in the tropical social
543 spider *Anelosimus eximius* (Araneae, Theridiidae). *J. Arachnol.*
- 544 Evans, T. A. 1999. Kin recognition in a social spider. *Proc. R. Soc. London. Ser. B Biol. Sci.*
545 266:287–292. The Royal Society .
- 546 Farine, D. R., A. Strandburg-Peshkin, I. D. Couzin, T. Y. Berger-Wolf, and M. C. Crofoot. 2017.
547 Individual variation in local interaction rules can explain emergent patterns of spatial
548 organization in wild baboons. *Proc. R. Soc. B Biol. Sci.* 284.
- 549 Fernandez-Fournier, P., J. Guevara, C. Hoffman, and L. Avilés. 2018. Trait overdispersion and the
550 role of sociality in the assembly of social spider communities across the Americas. *Proc. Natl.*
551 *Acad. Sci. U. S. A.* 115:6010–6015. National Academy of Sciences.
- 552 Fisher, D. N., M. Brachmann, and J. B. Burant. 2018. Complex dynamics and the development of
553 behavioural individuality. *Anim. Behav.* 138:e1–e6.
- 554 Fisher, D. N., A. James, R. Rodriguez-Munoz, and T. Tregenza. 2015. Behaviour in captivity
555 predicts some aspects of natural behaviour, but not others, in a wild cricket population. *Proc.*
556 *Biol. Sci.* 282:20150708.
- 557 Fisher, D. N., and J. N. Pruitt. 2019. Insights from the study of complex systems for the ecology and

- 558 evolution of animal populations. *Curr. Zool.*, doi: 10.1093/cz/zoz016.
- 559 Fisher, K., M. West, A. M. Lomeli, S. H. Woodard, and J. Purcell. 2019. Are societies resilient?
560 Challenges faced by social insects in a changing world. Springer International Publishing.
- 561 Flack, J. C., M. Girvan, F. B. M. de Waal, and D. C. Krakauer. 2006. Policing stabilizes construction
562 of social niches in primates. *Nature* 439:426–9.
- 563 Flack, J. C., D. C. Krakauer, and F. B. M. de Waal. 2005. Robustness mechanisms in primate
564 societies: a perturbation study. *Proc. R. Soc. B Biol. Sci.* 272:1091–1099.
- 565 Formica, V., C. Wood, P. Cook, and E. Brodie. 2016. Consistency of animal social networks after
566 disturbance. *Behav. Ecol.* 28:85–93. Oxford University Press.
- 567 Frank, S. A. 2007. All of life is social. *Curr. Biol.* 17:R648–R650.
- 568 Gardner, A., and A. Grafen. 2009. Capturing the superorganism: A formal theory of group
569 adaptation. John Wiley & Sons, Ltd (10.1111).
- 570 Grinsted, L., T. Bilde, and P. d’Ettorre. 2011. Cuticular hydrocarbons as potential kin recognition
571 cues in a subsocial spider. *Behav. Ecol.* 22:1187–1194. Narnia.
- 572 Groenewoud, F., J. G. Frommen, D. Josi, H. Tanaka, A. Jungwirth, and M. Taborsky. 2016.
573 Predation risk drives social complexity in cooperative breeders. *Proc. Natl. Acad. Sci. U. S. A.*
574 113:4104–9. National Academy of Sciences.
- 575 Guevara, J., and L. Avilés. 2015. Ecological predictors of spider sociality in the Americas. *Glob.*
576 *Ecol. Biogeogr.* 24:1181–1191. Wiley/Blackwell (10.1111).
- 577 Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: The
578 MCMCglmm R package. *J. Stat. Softw.* 33:1–22.
- 579 Hastings, A., C. L. Hom, S. Ellner, P. Turchin, and H. C. J. Godfray. 1993. Chaos in Ecology: Is

- 580 Mother Nature a Strange Attractor? *Annu. Rev. Ecol. Syst.* 24:1–33.
- 581 Herborn, K. A., R. Macleod, W. T. S. Miles, A. N. B. Schofield, L. Alexander, and K. E. Arnold.
582 2010. Personality in captivity reflects personality in the wild. *Anim. Behav.* 79:835–843.
583 Elsevier Ltd.
- 584 Honegger, K., and B. de Bivort. 2018. Stochasticity, individuality and behavior. *Curr. Biol.* 28:R8–
585 R12. Cell Press.
- 586 Houle, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics* 130:195–204.
- 587 Hunt, E. R., B. Mi, C. Fernandez, B. M. Wong, J. N. Pruitt, and N. Pinter-Wollman. 2018. Social
588 interactions shape individual and collective personality in social spiders. *Proc. R. Soc. B Biol.*
589 *Sci.* 285.
- 590 Keiser, C. N., and J. N. Pruitt. 2014. Personality composition is more important than group size in
591 determining collective foraging behaviour in the wild. *Proc. Biol. Sci.* 281:20141424.
- 592 Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the “animal
593 model.” *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 359:873–90. The Royal Society.
- 594 Kruuk, L. E. B., and J. D. Hadfield. 2007. How to separate genetic and environmental causes of
595 similarity between relatives. *J. Evol. Biol.* 20:1890–1903. Blackwell Publishing Ltd.
- 596 Kubitzka, R. J., J. Suhonen, and T. Vuorisalo. 2015. Effects of experimental perturbation of group
597 structure on hierarchy formation and behaviour in House Sparrows. *Ornis Fenn.* 92:157–171.
- 598 Laskowski, K. L., and J. N. Pruitt. 2014. Evidence of social niche construction: persistent and
599 repeated social interactions generate stronger personalities in a social spider. *Proc. Biol. Sci.*
600 281:20133166.
- 601 Lichtenstein, J. L. L., D. N. Fisher, B. L. McEwen, D. T. Nondorf, E. Calvache, C. Schmitz, J.

- 602 Elässer, and J. N. Pruitt. 2019. Collective aggressiveness limits colony persistence in high but
603 not low elevation sites in Amazonian social spiders. bioRxiv, doi: 10.1101/610436.
- 604 Luttbeg, B., and A. Sih. 2010. Risk, resources and state-dependent adaptive behavioural syndromes.
605 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365:3977–3990.
- 606 May, R. M. 1974. Biological Populations With Nonoverlapping Generations - Stable Points, Stable
607 Cycles, And Chaos. *Science* (80-.). 186:645–647.
- 608 May, R. M., and G. F. Oster. 1976. Bifurcations and Dynamic Complexity in Simple Ecological
609 Models. *Am. Nat.* 110:573–599.
- 610 Modlmeier, A. P., C. N. Keiser, J. V. Watters, A. Sih, and J. N. Pruitt. 2014. The keystone individual
611 concept: an ecological and evolutionary overview. *Anim. Behav.* 89:53–62.
- 612 Montiglio, P.-O., and N. DiRienzo. 2016. There’s no place like home: the contribution of direct and
613 extended phenotypes on the expression of spider aggressiveness. *Behav. Ecol.* 27:arw094.
- 614 Niemela, P. T., and N. J. Dingemans. 2018. On the usage of single measurements in behavioural
615 ecology research on individual differences. *Anim. Behav.* 145:99–105.
- 616 Parrish, J. K., and L. Edelstein-Keshet. 1999. Complexity, pattern, and evolutionary trade-offs in
617 animal aggregation. *Science* 284:99–101. American Association for the Advancement of
618 Science.
- 619 Pasquet, A., M. Trabalon, A. G. Bagnères, and R. Leborgne. 1997. Does group closure exist in the
620 social spider *Anelosimus eximius*? Behavioural and chemical approach. *Insectes Soc.* 44:159–
621 169. Birkhäuser Verlag.
- 622 Pruitt, J. N., and L. Avilés. 2017. Social spiders: mildly successful social animals with much
623 untapped research potential. *Anim. Behav.* Academic Press.

- 624 Pruitt, J. N., A. Berdahl, C. Riehl, N. Pinter-Wollman, H. V Moeller, E. G. Pringle, L. M. Aplin, E. J.
625 H. Robinson, J. Grilli, P. Yeh, V. M. Savage, M. H. Price, J. Garland, I. C. Gilby, M. C.
626 Crofoot, G. N. Doering, and E. A. Hobson. 2018. Social tipping points in animal societies.
627 *Proceedings. Biol. Sci.* 285:20181282. The Royal Society.
- 628 Pruitt, J. N., and C. J. Goodnight. 2014. Site-specific group selection drives locally adapted group
629 compositions. *Nature* 514:359–362. Nature Research.
- 630 Pruitt, J. N., C. J. Goodnight, and S. E. Riechert. 2017. Intense group selection selects for ideal group
631 compositions, but selection within groups maintains them. *Anim. Behav.* 124:15–24. Academic
632 Press.
- 633 Pruitt, J. N., G. Iturralde, L. Avilés, and S. E. Riechert. 2011. Amazonian social spiders share similar
634 within-colony behavioural variation and behavioural syndromes. *Anim. Behav.* 82:1449–1455.
635 Academic Press.
- 636 Pruitt, J. N., B. L. McEwen, S. T. Cassidy, G. M. Najm, and N. Pinter-Wollman. 2019. Experimental
637 evidence of frequency-dependent selection on group behaviour. *Nat. Ecol. Evol.* 3:702–707.
638 Nature Publishing Group.
- 639 Queller, D. C., and J. E. Strassmann. 2009. Beyond society: The evolution of organismality. *Philos.*
640 *Trans. R. Soc. B Biol. Sci.* 364:3143–3155. The Royal Society.
- 641 Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P.-O. Montiglio. 2010.
642 Personality and the emergence of the pace-of-life syndrome concept at the population level.
643 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365:4051–4063.
- 644 Schneider, J. M., and T. Bilde. 2008. Benefits of cooperation with genetic kin in a subsocial spider.
645 *Proc. Natl. Acad. Sci. U. S. A.* 105:10843–6. National Academy of Sciences.
- 646 Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-

- 647 induced rapid environmental change. *Evol. Appl.* 4:367–387. Blackwell Publishing Ltd.
- 648 Smith, C. E., B. J. Hurley, C. N. Toms, A. D. Mackey, M. Solangi, and S. A. Kuczaj. 2013.
- 649 Hurricane impacts on the foraging patterns of bottlenose dolphins *Tursiops truncatus* in
- 650 Mississippi sound. *Mar. Ecol. Prog. Ser.* 487:231–244.
- 651 Smith, D. R., and R. H. Hagen. 1996. Population structure and interdemic selection in the
- 652 cooperative spider *Anelosimus eximius*. *J. Evol. Biol.* 9:589–608. John Wiley & Sons, Ltd
- 653 (10.1111).
- 654 Solé, R. V., and B. Goodwin. 2000. *Signs of Life: How Complexity Pervades Biology*. 1st ed. Basic
- 655 Books, New York.
- 656 Sumpter, D. J. T. 2006. The principles of collective animal behaviour. *Philos. Trans. R. Soc. Lond.*
- 657 *B. Biol. Sci.* 361:5–22.
- 658 Tuomainen, U., and U. Candolin. 2010. Behavioural responses to human-induced environmental
- 659 change. *Biol. Rev.* 86:640–657. Wiley/Blackwell (10.1111).
- 660 Venticinque, E. M., H. G. Fowler, and C. A. Silva. 1993. Modes and Frequencies of Colonization
- 661 and its Relation to Extinctions, Habitat and Seasonality in the Social Spider *Anelosimus*
- 662 *Eximius* in the Amazon (Araneidae: Theridiidae). *Psyche* (New York) 100:35–41.
- 663 Vollrath, F. 1982. Colony Foundation in a Social Spider. *Z. Tierpsychol.* 60:313–324. John Wiley &
- 664 Sons, Ltd (10.1111).
- 665 Vollrath, F. 1986. Eusociality and extraordinary sex ratios in the spider *Anelosimus eximius*
- 666 (Araneae: Theridiidae). *Behav. Ecol. Sociobiol.* 18:283–287. Springer-Verlag.
- 667 Ward, A., and M. Webster. 2016. *Sociality: The Behaviour of Group-Living Animals*. Springer.
- 668 Wilson, D. S. 1997a. Altruism and organism: Disentangling the themes of multilevel selection

669 theory. P. *in* American Naturalist.

670 Wilson, D. S. 1997b. Introduction: multilevel selection theory comes of age. *Am. Nat.* 150

671 Suppl:S1–S21. The University of Chicago Press.

672 Wray, M. K., H. R. Mattila, and T. D. Seeley. 2011. Collective personalities in honeybee colonies

673 are linked to colony fitness. *Anim. Behav.* 81:559–568.

674 Yip, E. C., K. S. Powers, and L. Avilés. 2008. Cooperative capture of large prey solves scaling

675 challenge faced by spider societies. *Proc. Natl. Acad. Sci.*

676 Yuen, C. H., N. Pillay, M. Heinrichs, I. Schoepf, and C. Schradin. 2016. Personality traits are

677 consistent when measured in the field and in the laboratory in African striped mice (*Rhabdomys*

678 *pumilio*). *Behav. Ecol. Sociobiol.* 70:1235–1246. Springer Berlin Heidelberg.

679