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29 examining the relationship between behaviour and interactions, we reveal the mechanisms
30 that underlie the emergence of adaptive group composition and collective behaviour.

31

32 **Keywords:** Collective behaviour, Stochastic Actor Oriented Models, Personality, Keystone
33 individual, Social network analysis, *Stegodyphus dumicola*

34

35 **Introduction**

36 Collective phenomena, where interactions among individuals produce emergent behaviours,
37 are ubiquitous in biology. Previous work on collective behaviour [1] typically assumes
38 homogeneity of agents' intrinsic characteristics and interaction rules. However,
39 heterogeneous interaction and consistent individual variation in behaviour over time, often
40 described as 'personality', are both increasingly recognized as pervasive and important for
41 emergent group function within animal societies [2-6]. Even limited behavioural
42 heterogeneity can be highly impactful. For example, just one 'keystone' individual, such as a
43 leader or a tutor, can affect the whole group [7, 8]. As such, the behavioural composition of
44 a group can be crucial to its success [9], and thus it is a key research challenge to explain
45 how such behavioural heterogeneity emerges.

46 The particular mechanism(s) by which keystone individuals' influence on other group
47 members is imparted can be direct, e.g., by leading a collective behaviour, or indirect, e.g.,
48 by catalysing particular behaviours of others in the group [10]. Keystone individuals can
49 induce long-term changes in others' behaviour [11], however, it is not known how these
50 behavioural changes occur. The impact on the behaviour of group members may be
51 mediated via social interactions, which can be studied using social networks [5, 12-14]. Such

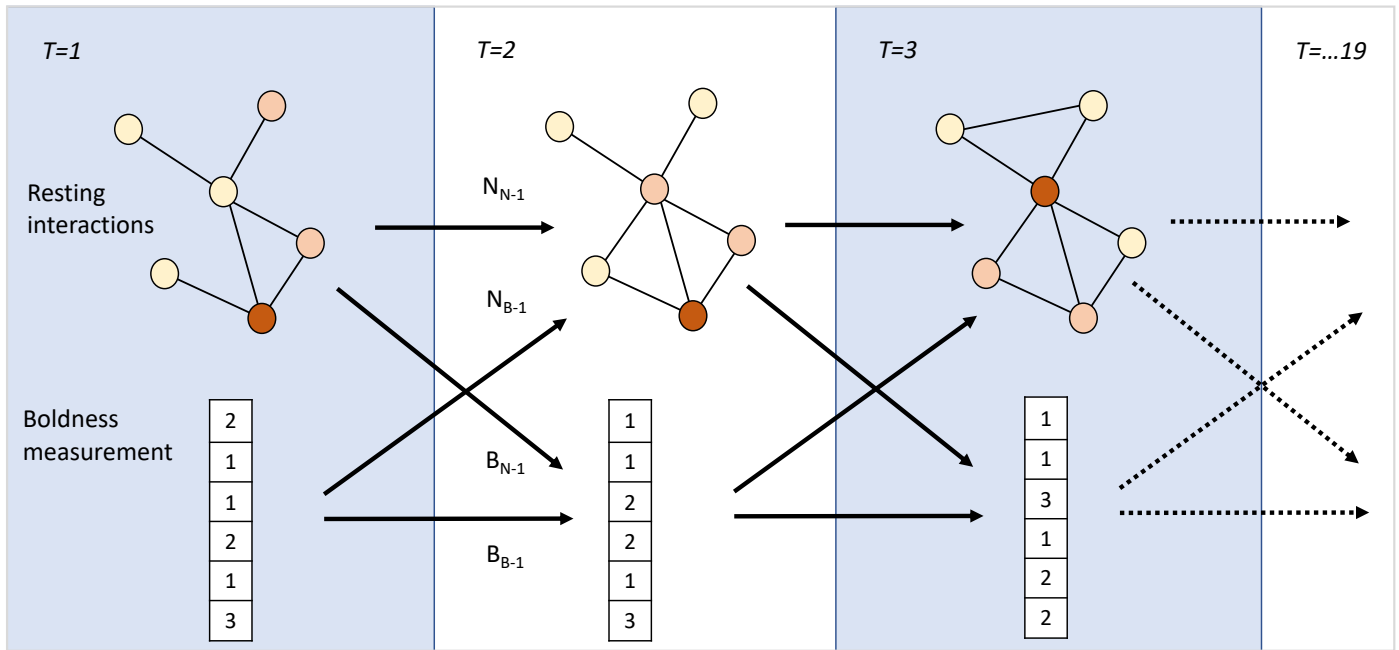
52 network representations of social interactions often reveal highly heterogeneous
53 interaction patterns that can influence collective outcomes [6, 15].

54 Behavioural plasticity is often overlooked in consideration of animal personality [16],
55 perhaps because of the seeming tension between behavioural consistency (the definition of
56 personality) and development [17]. Nevertheless, social interactions likely have a strong
57 influence on both short-term individual behaviour [18], and the development of group
58 members' behavioural traits [19]. This influence can be manifest over an individual's
59 lifetime: for example, in the long-tailed manakin, network position of juveniles predicts later
60 social status [20]. Generally however, the effect of social interactions on behavioural
61 plasticity has been comparatively understudied, probably in part because it is
62 methodologically challenging to estimate the relative influence of individual behavioural
63 traits on dynamic social interactions, and vice versa. Perhaps as a result, personality has
64 typically been assessed by observations across a short time period, often just a few days,
65 because it may not be stable in the longer-term [21, 22].

66 Explicit empirical work to identify joint changes in both interaction networks and
67 behaviour is therefore necessary to make further progress in attributing causal priority to
68 either internal processes that affect personality, or external forces such as social
69 interactions, in determining group behavioural compositions. Fortunately, a recently
70 developed simulation-based method of statistical inference, known as stochastic actor
71 oriented models (SAOMs) [23], now enables such studies of dynamic animal social networks
72 [24].

73 Stochastic actor oriented models (SAOMs) represent network dynamics of
74 longitudinal data, and can estimate the mutual effects of multiple micro-mechanisms that
75 may be operating simultaneously, such as personality and social influence. Importantly, the

76 SAOM framework allows one to study changing nodal variables alongside the network
77 dynamics: behavioural characteristics can be dependent variables, whereby the social
78 network influences the dynamics of behaviour, and the behaviour influences the dynamics
79 of the network. Thus, one can establish the relative influence of networks and behaviour as
80 they change over time (Figure 1). The actor-oriented aspect of SAOM refers to the changes
81 in network structure being modelled as stepwise choices by individuals, represented as
82 nodes in a network. The framework describes the agency of individuals deciding with whom
83 to form, maintain and dissolve social ties, as a function of their local social structure and
84 neighbours' behavioural traits [23, 25]. So far, there has been fairly limited use of SAOMs to
85 study animal systems (but see examples in: hyenas [26], vervet monkeys [27], rooks [28],
86 and *Drosophila* flies [29]).



87

Figure 1: Network-boldness co-dynamics in the SAOM framework. Each panel is one time point (observation), denoted as $T=1-19$. Node (spider) colors indicate boldness which is also listed for each individual in the table below each network. Spider social interactions, which are physical contacts between resting spiders, are represented, for each observation, by undirected, unweighted edges. Arrows between observations indicate possible mechanisms of causal influence: current boldness measurement may depend on the social position of individuals in the previous observation (B_{N-1}); network interactions may be shaped by the individuals' boldness in the previous observation (N_{B-1}); network structure in one observation may result from the social interactions in the previous observation (N_{N-1}), and boldness in one observation may result from the boldness in the previous observation (B_{B-1}). SAOM allows us to estimate all 4 effects. Figure adapted from [24].

88

89

90 *Stegodyphus dumicola* are social spiders that live in colonies of up to several
91 hundred individuals and exhibit cooperative behaviours such as prey capture and allo-
92 maternal care [30, 31]. The presence of just one very bold individual (keystone) in a group of
93 *S. dumicola* can substantially boost the prey capture success and mass gain of the whole
94 colony [32], with that individual's presence having long-term effects on other spiders'
95 boldness [11]. Boldness in this system is measured as the latency to resume movement after
96 experiencing an aversive stimulus [33, 34] and it is a repeatable behaviour, with a
97 repeatability of 0.63 measured when spiders are kept in isolation [35]. Boldness has been
98 shown to correlate with aggression [35], and thus provides insight into more general
99 behavioural tendencies. However, behavioural consistency seems to be contingent on a
100 stable social environment: boldness repeatability is much-reduced following social
101 disturbance [36] and such a disturbance reduces group performance [37]. This makes it
102 challenging to assess the mechanism of influence and longer-term identity of keystone
103 individuals. Furthermore, the identity of the boldest individual in the group does not
104 influence its impact on prey capture dynamics [38] – in this system, keystone refers to a
105 behavioural role rather than a specific individual [7].

106 Investigation into potential mechanisms of keystone influence on the group has
107 been conducted using computer simulations [39]. A priori, one can expect behavioural
108 variation among individuals in the same group to arise from either internal differences
109 (genetics and development) or external conditions (social context and ecological conditions)
110 [40]. Simulation investigation indicates that the effect of keystone individuals on social
111 organization could be mediated through either internal (behavioural persistence) or
112 external (social interaction) forces, as these models generate boldness distributions that
113 match the empirical distribution of *Stegodyphus* colonies found in the field [39]. Here, we

114 apply the SAOM framework to uncover the temporal dynamics of physical interaction
115 patterns and boldness in the social spider *S. dumicola*, and to determine if social
116 interactions affect boldness, and/or whether boldness affects who interacts with whom
117 (Figure 1).

118
119

120 **Methods**

121

122 *Animal collection and maintenance*

123 Colonies of adult *S. dumicola* were collected from roadside *Acacia* trees in the Northern
124 Cape of South Africa in March 2016. After transportation to the laboratory, they were fed
125 crickets weekly. Lab colonies contained only females – males are short-lived and rare (12%)
126 in natural colonies [41]. We created 24 groups of 10 adult female spiders each, from 3
127 source colonies. Groups were housed in large round containers (11cm diameter, 10cm
128 depth) with a vertical wire mesh (a 5x5cm sheet) to allow the spiders to build both a retreat
129 and a capture web. Experimental observations were made during June-August, 2016.

130

131 *Boldness*

132 Each spider's boldness was measured once a week using an established assay that recorded
133 the recovery of a spider from exposure to air puffs, which mimic the approach of an avian
134 predator [33]. After placing spiders individually in a plastic container (15x15cm) we waited
135 for 30sec until the spiders were acclimated and stopped moving around the arena, as in
136 recent studies [42-45]. We then administered two puffs of air to the anterior prosoma using
137 an infant nose-cleaning bulb. Spiders react to the air puffs by huddling, i.e. pulling their legs
138 under their body, and remaining motionless. Boldness was measured as the latency to

139 resume movement and move one body length. Because bolder individuals resume
140 movement faster, the latency to resume movement was subtracted from the maximum
141 duration of the procedure (600s) to create a metric that increases with boldness. We
142 designated as 'shy' those individuals with a latency to resume movement of 400-600s
143 (boldness of 0-200), while 'bold' individuals were those with a latency to resume movement
144 of 0-200s (boldness of 400-600). The abdomen of each spider was given a unique marking
145 with acrylic paint to track their behaviour over time.

146

147 *Group boldness composition*

148 We artificially created groups of 10 spiders with one of three boldness compositions: all
149 bold spiders, all shy spiders, and 9 shy individuals with one bold individual. Overall, these
150 groups contained more initially shy individuals than bold individuals because this represents
151 the spiders' natural boldness distribution (see figure 4 in Pinter-Wollman et al 2016 [39]).
152 Group composition converged after the first week (supplementary information and Figure
153 S1). To examine changes in groups' boldness compositions, we compared the boldness
154 distributions in week 1 to week 7.

155

156 *Social interactions*

157 We manually recorded the physical contacts among spiders three times a week (see below),
158 during the day, while spiders are inactive for long periods of time. Therefore, we refer to
159 these interactions as 'resting interactions' and define an interaction as a physical contact
160 between any body parts of two spiders, when the colony is not active. Colony activity is
161 minimal in the lab (initial web construction and collective predation when fed) and most of
162 the time spiders are resting. Therefore, observing their interactions every 2-3 days samples

163 most social interactions. We used the interactions to construct unweighted (binary),
164 undirected (symmetrical), networks for each spider group during each observation.

165 We calculated the skewness of each resting network's degree distribution (N=456),
166 to assess whether the spiders in each observed network tended to have a similar number of
167 interactions (skewness close to 0) or if degree was heterogeneous (skewness different from
168 0).

169

170 *Experimental procedure*

171 Each group was observed for 6.5 weeks. Boldness was measured once a week and resting
172 interactions, later translated into social networks, were observed three times a week with 2-
173 3 days separating each observation. We recorded the first set of resting interactions each
174 week immediately before measurement of boldness ('Day 1'). We recorded the second
175 resting network on Day 3, and the third resting network was recorded on Day 5. After
176 interactions were observed on Day 5, we fed each colony a single 4-week-old cricket, hence
177 all colonies had an equal opportunity to consume prey. This spacing of measures of
178 interactions allowed time for the spiders to recover from the disturbance caused by
179 measuring boldness on Day 1 (after observing the resting interaction). In week 7 we made a
180 final observation of boldness and the resting network. In total, there were 7 boldness
181 measures for each individual spider and 19 resting networks for each group.

182

183 *Stochastic actor oriented models*

184 To determine the relationship between boldness and social interactions using the SAOM
185 method, we first ensured that our data met the model assumptions. The SAOM method
186 requires an appropriate level of tie turnover between successive network observations (i.e.,

187 edges being created, maintained, or removed) measured using the Jaccard index of
188 similarity between successive observation waves [46]. Because several spider groups did not
189 have a Jaccard index greater than 0.2 when modelled individually, we aggregated groups by
190 source colony and group composition treatment, such that 24 groups became 8 (Table S1).
191 This aggregation allowed us to compare the different group composition treatments as
192 detailed in the supplementary material. We aggregated groups using structural zeros,
193 whereby two or more networks are included in one adjacency matrix, but the two sets of
194 nodes are not allowed to form edges between groups, only within them. This aggregation
195 achieved the appropriate level of tie turnover and allowed us to proceed with the SAOM
196 analysis. When nodes were removed because of spider death we specified structural zeros
197 for the relevant node in the time periods after its death, such that it can no longer
198 participate in network dynamics, and is not included in statistical estimation from that time
199 point.

200 Boldness was measured once per week, to minimize disruption to the spiders, and so
201 we interpolated the boldness measure to obtain boldness measures for all 3 sets of network
202 observations made each week. To calculate boldness at intermediate days (3 and 5), we
203 used a linear interpolation between the two known points on day 1 of that week and the
204 next week. The SAOM framework simulates network and behaviour changes through a
205 series of microsteps, i.e. the addition, maintenance or dissolution of a single network tie, or
206 a -1, 0, or +1 change in a spider's boldness covariate. The boldness range of 0-600 is too
207 wide for such microsteps, and therefore we translated it to a 1-3 scale, from 0-200, 200-400,
208 and 400-600. These groupings match the criteria we used for creating group compositions
209 of all shy and all-bold groups.

210 Although we created three group composition treatments, the behavioural
211 composition of the groups converged after the first week, and thus after the first week all
212 treatments had similar boldness compositions.

213 We used the SIENA framework (*Simulation Investigation for Empirical Network*
214 *Analysis*), to implement the SAOM analysis in the R package RSiena version 1.2.3 [46, 47],
215 with R version 3.3.3 [48]. To construct models we followed an iterative approach guided by
216 existing scientific insight and the hypotheses tested, as detailed in Fisher et al [24]. We
217 started with a simple set of core effects and then introduced further complexity to the
218 model. We were primarily interested in the effect of boldness on tie formation, and the
219 effect of social ties on boldness, and used effects that are specific to undirected
220 (symmetrical) ties.

221

222 *SAOM effects*

223 We included the following structural and behavioural effects in our SAOMs:

224 (1) **Network on boldness** – to measure the influence of network ties on boldness we
225 included the *average alter* effect (*avAlt*). This is the influence of the (averaged) behaviour of
226 alters (i.e. neighbouring spiders) upon interaction with a focal individual (i.e. the ‘actor’ in
227 SAOM). Here, a positive effect indicates that the formation of a social interaction tends to
228 increase boldness of the individual with lower boldness, while a negative effect indicates
229 that interactions tend to reduce boldness.

230 (2) **Boldness temporal dynamics** – to examine general tendencies in boldness over
231 time across all the spiders we included both a *linear shape* effect and a *quadratic shape*
232 effect. A zero value for the linear shape effect indicates drift toward the midpoint of the
233 range of the behavioural variable. A positive value indicates an increase, and a negative

234 value a decrease, in boldness over time. The quadratic shape effect indicates the presence
235 of feedback: positive values imply that an increase in boldness tends to be followed by
236 another boldness increase, as a self-reinforcing, 'addictive' behaviour [47]. A negative value
237 indicates a self-correcting negative feedback: boldness increases tend to be followed by
238 reductions in boldness and when boldness decreases, the push toward further decreases is
239 curtailed.

240 (3) **Boldness on interactions** – to measure the effect of boldness on the tendency to
241 form ties we included the *covariate effect*, *egoPlusAltX* (the covariate being boldness, in this
242 case). A positive covariate effect would indicate that bolder spiders are more likely to form
243 ties in general, while a negative effect would indicate that bolder spiders tend to be more
244 isolated.

245 The following effects depend on the network itself, separately from individual
246 behavioural co-variates.

247 (4) **Structural equivalence** – We examined two measures of structural equivalence:
248 (i) *Jaccard similarity effect (Jout)* – the extent to which two actors (connected or not) are
249 connected with the same third parties [49]. Thus, a positive Jout effect indicates that
250 individuals share a similar social environment. (ii) *Weighted structural equivalence effect*
251 (*from.w.ind*) – measures a preference to interact with individuals who have similar ties to
252 other individuals, weighted by the degrees (number of neighbours) of those others. A
253 positive *from.w.ind* suggests that structural equivalence is achieved by ties to third parties
254 with high degree.

255 (5) **Degree plus popularity (degPlus)** – a feedback effect for undirected networks,
256 representing (if positive) a tendency for nodes with high-degree (many neighbours) to

257 create and maintain relatively more ties than low-degree nodes. If negative, this indicates a
258 constraint on node degrees becoming too dispersed.

259 Network density and period-specific network and boldness effects were also
260 included. Network density (*density*), which is the ratio of observed ties to all possible ties,
261 takes the role of an intercept in a regression model, by controlling for the overall density
262 given all the other effects included in the models. Thus, while it is a necessary effect it is not
263 biologically informative. Finally, because we model the change in network tie formation and
264 boldness change over 19 observations, there are 18 period-specific rate constants for each
265 of these (inter-)dependent variables. Similar to network density, these constants are not of
266 focal interest [46].

267

268 To ensure that our data fit the SAOM we ran post-hoc statistical goodness-of-fit
269 (GOF) tests. We ensured that the simulated networks and behaviour variables in the SAOM
270 are sufficiently similar to empirical observations, across various relevant characteristics, and
271 that model convergence has been obtained (maximum convergence ratio < 0.25 , [46]). We
272 run 4 such GOF tests, on the Degree distribution, Geodesic distribution (the number of
273 nodes connected at a certain network distance), Triad census (the number of node triplets
274 with 1, 2, or 3 edges), and Behavior Distribution (the discrete behaviour dependent variable
275 ranged 1-3) (Table S2).

276 To assess the overall results of the SAOM analysis we conducted meta-analysis of the
277 8 SAOMs. When a common set of effects was identified that led to good model convergence
278 and adequate post-hoc goodness-of-fit tests across all 8 models, we performed a meta-
279 analysis of the model effects, to see if they are significantly different from zero. We did this
280 using the RSiena function *siena08*, which weights model effects according to their standard

281 error, into a final mean effect value with associated estimated 95% confidence interval. The
282 *siena08* function provides means, standard errors, and p values under a normality
283 assumption, and also under an alternative approach of modified iterated re-weighted least
284 squares (IWLS) developed by Snijders & Baerveldt for meta-analysis [50]. We present the
285 normality assumption results in the main text but both sets of results are presented in Table
286 S2, with the same overall results.

287

288 **Results**

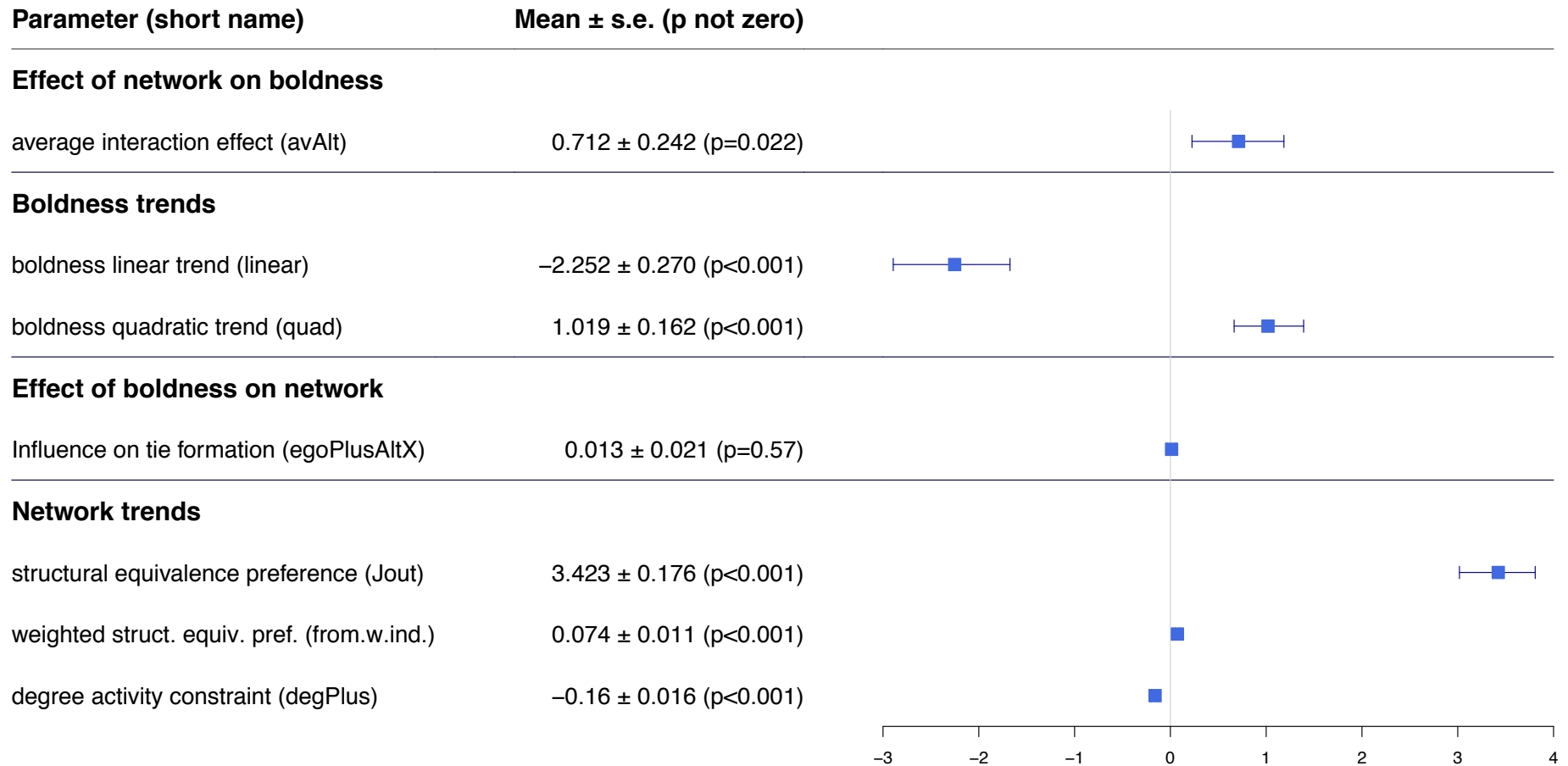
289 Interactions and time affected boldness, but boldness did not affect interactions. We found
290 several significant effects in our meta-analysis of the 8 SAOM models. When spiders
291 interacted with others that had a different boldness than themselves, the spider with the
292 lower boldness tended to increase its boldness in the next time step (significantly positive
293 *average alter* effect ($p=0.024$, Figure 2)). Boldness tended to decrease over time
294 (significantly negative *bold linear* effect ($p<0.001$, Figure 2)). However, once an individual's
295 boldness increased, there was a positive feedback pushing toward higher boldness (positive
296 *bold quadratic* effect ($p<0.001$, Figure 2)). Boldness distributions changed over the course of
297 7 weeks (Figure 3) such that by the end of the 7 weeks, boldness distributions resembled
298 those observed in the field and generated by models in which boldness tends to decrease
299 over time and increase when spiders interact [39].

300 Individuals' social interactions were not impacted by boldness but they were
301 influenced by the surrounding social environment. We did not detect a significant effect of
302 boldness on the tendency to form (or avoid) ties ($p=0.445$, Figure 2). At the same time,
303 spiders tended to interact with similar individuals as their nestmates: both *Jout* and
304 *from.w.ind* were positive effects ($p<0.001$ in both cases, Figure 2). Positive *from.w.ind*

305 further indicates that individuals with high-degree make a larger contribution to achieving
306 structural equivalence. Finally, we found a restriction on the dispersion of spider degrees
307 (negative *degPlus*, $p < 0.001$, Figure 2), likely because of physical limits on how many
308 individuals a spider can touch at once (i.e., a cap on higher degrees).

309 These observed trends were seen in all three behavioural composition treatments
310 (Figure 2, Table S2). For example, all the SAOMs, including the all-shy and all-bold
311 treatments, had a negative linear boldness trend. Furthermore, boldness compositions of
312 the three treatments converged within the first week (Figure S1). Thus, our findings reveal
313 that in a social context, boldness is more plastic than in isolation, and artificially
314 manipulating group boldness compositions is quickly rectified by endogenous group
315 processes.

316



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Figure 2: A forest plot showing meta-analysis results of the SAOMs' parameters. Social interactions between spiders exhibiting different boldness tend to increase the boldness of the shyer spider (*avAlt* effect). There is a general decrease in boldness over time (*linear*) but boldness increases are self-reinforcing (*quad*). There is no effect of boldness on the likelihood of forming (or avoiding) social ties (*egoPlusAltX*). Positive *Jout* and *from.w.ind* indicate a tendency for spiders to form ties with nestmates that interact with their neighbours: the positive *from.w.ind* effect suggests that individuals with high-degree centrality drive this trend. Negative *degPlus* implies a cap on the dispersion of spider degrees, likely because of physical restrictions on the maximum number of individuals a spider can touch.

324

325 The average degree distribution across all networks was unimodal (Figure S2), and the

326 skewness of the degree distributions of all networks was centred around zero (Figure S3).

327 This indicates that all spiders in a network tend to physically interact with a similar number

328 of nestmates when resting.

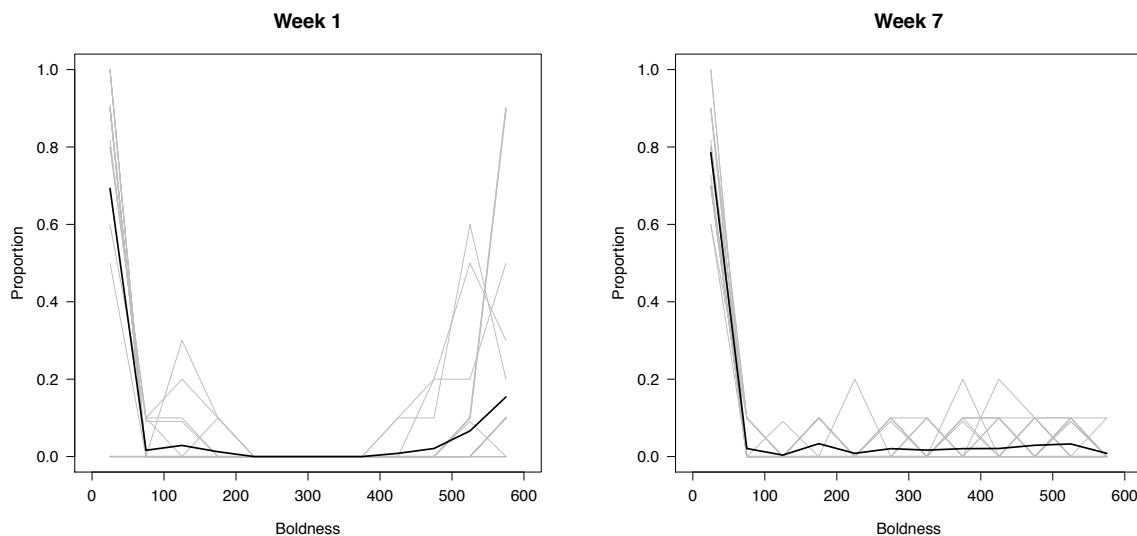


Figure 3: The empirical boldness distribution for each of the 24 groups (grey lines) and the average boldness distribution for all groups (black line), at (left) week 1 and (right) week 7.

329 Discussion

330 We found that social interactions promote changes in individual boldness in social spider

331 groups. While boldness is a highly repeatable trait for spiders kept in isolation [35], in a

332 social context we find that individuals' boldness is plastic. Specifically, social

333 interactions tend to increase boldness, such that a spider whose physical neighbours have

334 overall higher average boldness at one point in time, tends toward higher boldness values

335 itself. Here, where boldness has been analysed on a 1-3 scale, this finding is an aggregate

336 trend that encompasses any interactions in which one individual is bolder and the other

337 shy (i.e., 3-1, 3-2, and 2-1). The boldness-promoting effect of social interactions is

338 balanced against an overall decrease in boldness over time. Furthermore, spiders tend to

339 interact with the same individuals as their neighbours, especially those that are well
340 connected. This finding likely results from the spiders' preference to huddle together in the
341 nest retreat. This finding also suggests that an individual with high boldness (or even the
342 highest boldness, i.e., the keystone individual) could promote increases in boldness across
343 several individuals simultaneously, if more than one shy individual is socially connected to
344 that bold individual. Different spiders tend to interact with the same individuals, thus
345 boldness increases to a few central spiders may have widespread effects. We did not find
346 evidence that boldness influences the likelihood of forming social interactions. A question
347 for future research is how social interactions influence boldness. Perhaps spiders cue on
348 chemicals present on the body surface, like ants [51], or influence each other through small
349 movements. For example, if bold individuals are more agitated than others, their proximity
350 could affect their neighbours, directly or through web vibrations.

351 Our finding that bold spiders are no more or less likely to interact with other
352 individuals than their shy nestmates could be seen as contrary to expectations. For
353 example, social assortment according to behavioural type has been recognised in fish shoals
354 [52]. On the other hand, bolder spiders might be thought to prefer social isolation: bolder
355 three-spined stickleback fish have been observed to keep a greater distance from a partner,
356 while showing more leadership behaviour [53]. However, it is possible that boldness does
357 not correlate with sociability. Indeed, in a review of behavioural syndromes by Réale et al
358 [54] the shyness–boldness axis is distinguished from sociability. The natural distribution of
359 boldness in *Stegodyphus* groups is a few bolder individuals among a majority of shy
360 individuals [39], and hence with no behavioural assortment bold individuals are more likely
361 to interact with shy individuals by simple probability. Bolder individuals are more likely to
362 interact with the environment outside the nest during foraging, given increased

363 participation in prey capture in both the laboratory [32] and the field [55, 56], and thus may
364 be a source of disease vulnerability for other group members. Yet our findings here point
365 toward bold-shy interactions being an indispensable element in determining the
366 behavioural composition of the group, whereby boldness is 'passed on' by an as-yet
367 unidentified mechanism from bolder to shyer individuals. Bold-shy interactions thus
368 maintain a suitable group-level boldness distribution that promotes effective prey capture
369 [32, 57].

370 A general trend toward decreases in boldness over time, occurring separately from
371 the influence of the spiders' interaction network, is consistent with past findings. Recently
372 disturbed colonies of *S. dumicola* become shyer over time before recovering in boldness
373 [58]. However, the significantly positive quadratic shape effect on boldness that we
374 identified indicates that an increase in spider boldness generally tends to be self-reinforcing,
375 or 'addictive'. In this way, a spider with a low boldness rating, that transitions to a medium
376 rating, will be more likely to increase its boldness still further rather than reduce its
377 boldness. Thus, individuals with small initial increases in their boldness are more likely to
378 become a group's boldest group member in subsequent weeks. These boldest individuals
379 are known to be major determinants of the behaviour and success of the colony as a whole
380 [59]. Interestingly, despite different initial boldness compositions, by week 2 of the
381 experiment the average boldness of all groups was not different (see supplementary
382 material and Figure S1). This change, and the SAOM findings, indicate that social
383 interactions are apparently instrumental in changing artificially manipulated *S. dumicola*
384 boldness distributions to resemble those found in nature [39], which facilitate rapid prey
385 attack [32].

386 The results we present here corroborate the assumptions made in simulation work
387 on how the dynamics of boldness and social interactions result in skewed behavioural
388 distributions and can point to the model parameters that best fit the biological system [39].
389 The observed resting networks' degree distribution was unimodal (Figure S2), and the
390 skewness of the degree distributions of all networks was centred around zero (Figure S3),
391 similar to the uniform interaction rule in previous simulation work. These characteristics
392 indicate that all individuals are equally likely to interact with one another, regardless of their
393 boldness. Furthermore, our finding that boldness tends to decrease over time and that
394 boldness is acquired from bolder neighbours, points toward a scenario in the theoretical
395 model in which there is low persistence of boldness and high acquisition of boldness from
396 others. Indeed, the simulated boldness distributions for this parameter setting (low
397 persistence, high acquisition – LPHA) and a uniform interaction rule [39] qualitatively match
398 well with the empirical observations presented here (Figure 3).

399 One remaining open question, regarding influential keystone individuals in animal
400 collectives, is their replaceability: whether the specific individual or the role performed by
401 that individual is the most important [16]. Our results, indicating social plasticity of boldness
402 in accordance with [38], point to the existence of a keystone role rather than a keystone
403 individual [7]. With relatively low behavioural persistence, and high acquisition of behaviour
404 from others via social interactions, the boldest spiders in the group – the keystone(s) – are
405 highly influential but likely to change in identity over time. Indeed, in the case of *S.*
406 *dumicola*, while keystone individuals are important, they do not seem to be irreplaceable.
407 For example, iteratively removing and replacing shy individuals has a greater impact on the
408 colony's behaviour than replacing bold individuals [38].

409 One question arising from the boldness dynamics that we observed is what occurs
410 when there are no bolder individuals to impart their positive catalytic influence on the
411 boldness of other shyer individuals. In this case, one can see the importance of the
412 significant quadratic shape effect (the 'addictive' boldness increase effect), to magnify even
413 small boldness increases over time such that they become self-sustaining and do not require
414 constant social contact to support them. In a real-world system, small boldness differences
415 will always exist for such dynamics to work upon [39]. Such an inherent robustness of the
416 group-level skewed boldness phenotype, dependent on social dynamics alone, seems to
417 downplay the importance of internal, genetic or developmental differences for the
418 ontogenesis of keystones. Instead, it indicates that external factors, such as social and
419 ecological conditions, may be sufficient. In practice, boldness may be contingent on
420 physiological factors such as satiation, i.e. the time since last feeding, though evidence for
421 this idea are mixed [35, 60]. For periods longer than a few weeks, i.e. beyond the
422 observation range of the data examined here, life history stages relating to reproduction are
423 also likely to be important given the relatively short lives of female *Stegodyphus* of 1-2 years
424 [41].

425

426 **Conclusions**

427 Many animal groups are increasingly recognised to rely on heterogeneity in the behaviour
428 and social interactions of the group members for effective group function. However, the
429 relative importance of behaviour for shaping interactions, and interactions for shaping
430 behaviour, is poorly understood. We show that social interactions promote the increase of
431 boldness in social spiders, such that an optimal collective distribution in boldness is
432 attained. Boldness, however, does not make individuals more or less likely to physically

433 interact with others. Our findings are consistent with the uniform interactions, high
434 acquisition, low persistence model of keystone influence on groups of Pinter-Wollman et al
435 [39], and thus suggest that it is the keystone role, rather than the identity of the individual
436 acting it, that is important to such social groups [38]. Our findings have implications for the
437 understanding of personality in social groups, indicating a priority of an animal's social
438 environment for the development of personality. Future research should address in more
439 detail the specific mechanisms of how social interactions promote boldness, and the
440 dynamics of social networks and boldness in different ecological conditions in the field. This
441 should further elucidate the relative importance of internal vs. external factors for the
442 emergence of adaptive collective phenotypes.

443

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449

450

451 **Author contributions**

452 NPW and JNP designed the study, ERH analysed the data and wrote the first draft of the
453 manuscript, and BM, CF, BW, and NPW collected the data. All co-authors gave approval to
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455

456

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460

461 **Data accessibility**

462 The network and boldness data analysed in this paper is available on Dryad at...

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