1   **Resting networks and personality predict attack speed in social spiders**

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14   **Significance statement**

15   Certain animals in a group, such as leaders, may have a more important role than other

16   group members in determining their collective behavior. Often these individuals are defined

17   by their behavioral attributes, for example, being bolder than others. We show that in social

18   spiders both the behavioral traits of the influential individual, and its interactions with other

19   group members, shape its role in affecting how quickly the group collectively attacks prey.

20

21   **Abstract**

22   Groups of social predators capture large prey items collectively, and their social interaction

23   patterns may impact how quickly they can respond to time-sensitive predation

24   opportunities. We investigated whether various organizational levels of resting interactions

25   (individual, sub-group, group), observed at different intervals leading up to a collective prey

26   attack, impacted the predation speed of colonies of the social spider *Stegodyphus dumicola*.

27   We found that in adult spiders overall group connectivity (average degree) increased group

28   attack speed. However, this effect was detected only immediately before the predation

29   event; connectivity two and four days before prey capture had little impact on the collective

30   dynamics. Significantly, lower social proximity of the group's boldest individual to other

31   group members (closeness centrality) immediately prior and two days before prey capture

32   was associated with faster attack speeds. These results suggest that for adult spiders, the

33   long-lasting effects of the boldest individual on the group's attack dynamics are mediated by

34   its role in the social network, and not only by its boldness. This suggests that behavioural

35   traits and social network relationships should be considered together when defining

36   keystone individuals in some contexts. By contrast, for subadult spiders, while the group

37   maximum boldness was negatively correlated with latency to attack, no significant resting

38   network predictors of latency to attack were found. Thus, separate behavioural mechanisms

39   might play distinctive roles in determining collective outcomes at different developmental

40   stages, timescales, and levels of social organization.

41

42   **Introduction**

43   Group living can benefit group members through access to mates, protection from

44   predators, and increased foraging opportunities (Krause and Ruxton 2002). A variety of

45   animals engage in cooperative hunting to capture prey that is larger than what they could

46   capture alone. Examples of cooperative hunting can be seen in chimpanzees (Boesch 2002),

47   lions (Stander 1992), wild dogs (Creel and Creel 1995), hawks (Bednarz 1988), killer whales

48   (Pitman and Durban 2012) and invertebrates such as ants (Witte et al. 2010), and social

49   spiders (Whitehouse and Lubin 1999). During collective prey capture, individuals often

50   coordinate their behaviour through social interactions, to maximize their capture success

51   (Stander 1992; Boesch 2002; Pitman and Durban 2012). A shorter latency to attack can

52   reduce the time and effort needed to capture prey, and increases the probability of success,

53   thus conferring important fitness benefits to all group members (Pasquet and Krafft 1992).

54   In addition to coordination through social interactions, groups often rely on particular

55   individuals to expedite collective dynamics (Modlmeier et al. 2014b).

56   Social network analysis provides tools to quantify interaction patterns and has been

57   instrumental in understanding the dynamics and outcomes of interactions within groups

58   (Wey et al. 2008; Kurvers et al. 2014; Pinter-Wollman et al. 2014; Krause et al. 2015) and in

59   predicting group success (Royle et al. 2012). Different network measures can describe

60   interactions occurring at various organizational levels, such as an individual's direct

61   interactions with its neighbours, links within a subgroup, or interactions at the whole group

62   level (Lusseau and Newman 2004; Wittemyer et al. 2005; Krause et al. 2007; Wey et al.

63   2008). The social structure of animal groups often changes over time, and interaction

64   patterns occurring in one period can impact the group later (Blonder et al. 2012; Pinter-

65   Wollman et al. 2014; Krause et al. 2015). For example, social connectivity early in life can

66   predict male mating success several years later in long-tailed manakins (McDonald 2007),

67   social connections to relatives can persist for longer than relationships with non-kin in

68   spotted hyenas (Holekamp et al. 2012), and social stability of subgroups can be maintained

69   over years in sparrows (Shizuka et al. 2014). Thus, temporal dynamics of interactions may

70   occur at different rates at different organization levels (Blonder et al. 2012).

71   Animals within a society often differ from one another in their behaviour, and these

72   differences can be consistent over time, a phenomenon that has been referred to as

73   'personality' (Sih et al. 2004; Bell et al. 2009; Jandt et al. 2014). Behavioural variation

74   among individuals in a social group can have a considerable impact on group functions

75   (Pinter-Wollman 2012). Only a small amount of variation among individuals may be

76   necessary to have large impacts on the entire group. In the most extreme situations just one

77   'keystone' individual, such as a leader or a tutor, may have a disproportionate impact on the

78   group (Conradt and Roper 2003; Modlmeier et al. 2014b). A keystone can be either a

79   particular individual or a role that different individuals assume at different times

80   (Modlmeier et al. 2014b). Keystone individuals can have an increased interaction rate with

81   other group members (Lloyd-Smith et al. 2005) and their behavioural tendencies can

82   influence interaction patterns (Pike et al. 2008; Sih et al. 2009; Krause et al. 2010; Pinter-

83   Wollman et al. 2011; Firth et al. 2015), thus in turn impacting collective actions (Bansal et al.

84   2007; Brown and Irving 2014). It is still unknown how keystone individuals influence the

85   performance of a group. Generally speaking, keystone individuals can either perform the

86   work itself or catalyse the work of other group members (Robson and Traniello 1999), for

87   example through social interactions.

88   Individual differences that are consistent over short time frames may change over

89   longer periods (Stamps and Groothuis 2010). Such changes can alter the relationship

90   between a group's personality composition and collective outcomes over time. For example,

91   in social insects the task that each individual performs can change with age (Seeley 1982;

92   Tripet and Nonacs 2004) potentially altering the distribution of task performance in the

93   colony. Changes to an animal's personality may arise from changes in physiological

94   processes such as growth (Biro and Stamps 2008), metamorphosis (Hedrick and Kortet 2012;

95   Wilson and Krause 2012), or sexual maturation (Stamps and Groothuis 2010). Personality

96   may also develop due to changes in the external physical or social environment over time,

97   i.e. experiential factors (Stamps and Groothuis 2010). For example, as group members

98   become familiar with one another, variation among individuals increases and variation

99   within an individual decreases, thus increasing behavioural repeatability (Laskowski and

100   Pruitt 2014; Modlmeier et al. 2014c; Laskowski et al. 2016).

101   In the social spider *Stegodyphus dumicola* (Araneae, Eresidae) individuals vary in

102   their boldness, and the boldest individual in the colony (referred to as the keystone) affects

103   foraging intensity (attack speed and number of attackers) and mass gain of the entire group

104   (Keiser and Pruitt 2014; Pruitt and Keiser 2014). It is not known how the influence of

105   keystone individuals is imparted in this species, only that keystones have long lasting

106   effects, and that the duration of their impact is proportional to the tenure of the keystone in

107   the group (Pruitt and Pinter-Wollman 2015). A recent model (Pinter-Wollman et al. 2016)

108   predicts that when the boldness of group members is persistent (i.e., is a stable personality

109   trait), social interactions should play a larger role than boldness in shaping collective

110   outcomes. This prediction emerges because who interacts with whom would change more

111   rapidly than boldness if it was highly stable, and boldness does not necessarily determine

112   who interacts with whom (Hunt et al. 2018). In contrast, if boldness is plastic, social

113   interactions may play a smaller role in determining collective outcomes because changes in

114   the collective outcomes can emerge from changes in boldness. Younger animals are often

115   more behaviourally plastic than adults (Scott 1962). Thus, by comparing the social behaviour

116   of both subadult, or juvenile, and adult organisms, we can test when social interactions and

117   when behavioural traits, i.e. boldness, have a larger impact on collective outcomes (Pinter-

118   Wollman et al., 2016).

119   *S. dumicola* spiders live in colonies of up to several hundred individuals of the same

120   age that exhibit cooperative behaviours such as prey capture and allo-maternal care (Bilde

121   et al. 2007; Junghanns et al. 2017). Enhanced foraging success is thought to be a primary

122   driver of sociality in social spiders (Whitehouse and Lubin 2005), to enable subduing of large

123   prey items (Guevara et al. 2011; Harwood and Avilés 2013). More frequent co-feeding

124   interactions of the same prey item has been observed in sibling groups compared with non-

125   sibling groups in group-foraging subsocial spiders, suggesting that social network structure

126   may play a role in the evolution of social behaviour in spiders (Ruch et al. 2015). Colonies

127   composed of bolder spiders attack more rapidly (Keiser et al. 2014; Keiser and Pruitt 2014;

128   Pruitt and Keiser 2014) and with more individuals (Grinsted et al. 2013; Keiser and Pruitt

129   2014; Laskowski and Pruitt 2014; Pruitt and Keiser 2014) than colonies with shy individuals.

130   Here we use social network analysis to determine the temporal scale and the social

131   organization level at which interactions between group members have the most impact on

132   collective prey capture dynamics. We evaluate if the keystone individual influences the

133   group through its role in the group's social network. We also consider whether these social

134   interactions have long-lasting effects on prey capture success, or if the impact of

135   interactions is immediate and ephemeral. Furthermore, we examine if developmental stage

136   (subadults vs. adults) affects the relationships between personality, social interactions, and

137   collective prey attack. Comparing subadults, with more plastic, emergent personalities, to

138   adults, with more established personalities, allows us to test the predictions of the model of

139   keystone influence detailed above (Pinter-Wollman et al. 2016).

140   In sum, we consider whether the speed at which *S. dumicola* colonies of either

141   subadult or adult spiders collectively attack prey depends on: *(i)* interactions occurring at

142   different levels of social organization; *(ii)* temporal changes in social structure; and *(iii)* the

143   behavioural and social attributes of the keystone individual.

144

145   **Methods**

146   *Animal collection and maintenance*

147   Colonies of *S. dumicola* were collected from roadside *Acacia* trees in the Northern Cape of

148   South Africa in November 2015 (subadults) and March 2016 (adults), transported to the

149   laboratory, and fed crickets *ad lib*. The size of collected colonies ranged between 70-300

150   individuals and contained only females - males are short-lived and rare (12%) in natural

151   colonies (Henschel et al. 1995). We created 15 groups of 26-30 sub-adult female spiders,

152   from 4 source colonies of subadults, and 24 groups of 10 adult female spiders each, from 3

153   other source colonies. Individuals from different source colonies were not mixed. Group

154   sizes were larger for subadults because of the small size of those individuals, and because it

155   potentially requires more small individuals to execute a successful attack on large prey (see

156   supplementary Figure S2 for differences in sizes between adults and subadults). The

157   behavioural composition of these groups is detailed below in the '*Group composition*'

158   section. Groups were housed in large round containers (18cm diameter, 8cm depth for

159   subadults and 11cm diameter, 10cm depth for adults) with vertical wire meshes (two 9x6cm

160   sheets positioned 10cm apart for subadults and a 5x5cm sheet for adults) to allow the

161   spiders to build both a retreat and a capture web. Trials were conducted from January until

162   August, 2016.

163

164   *Experimental procedure*

165   To determine the effect of interaction patterns at different time scales on prey attack we

166   observed groups over time. Each group was observed for 6.5 weeks. Boldness and prey

167   capture were measured once a week and resting interactions, as detailed below, were

168   observed three times a week with 2-3 days separating each observation. The first resting

169   network was obtained immediately before measuring boldness on Day 4, numbered as four

170   days before measuring prey attack. The second resting network was observed on Day 2, two

171   days after measuring boldness and two days before measuring prey attack. The third resting

172   network was observed immediately before testing prey attack speed, on Day 0. This spacing

173   of measures allowed ample time for the spiders to recover from disturbances due to

174   removing them from their web to determine boldness. Each group was fed with a single 4-

175   week-old cricket once a week, which provides *ad lib* food, after the prey assay (described

176   below), hence all colonies had an equal opportunity to consume prey, and were at a similar

177   state of hunger. We obtained 7 boldness measures for each individual spider, 6 collective

178   prey capture response measures for each group, and 18 resting networks for each group (19

179   including a final boldness/network observation not used here). We compared the predictive

180   power of the resting networks observed four days, two days, and immediately before each

181   prey capture trial, for explaining the speed of prey attack. This allows us to differentiate

182   between short term (immediately before prey attack), medium (two days), and long (four

183   days) term influences of spider interaction networks.

184

185   *Boldness*

186   To determine individuals' boldness, each spider was tested once a week using an

187   established assay that measured the recovery of a spider from exposure to air puffs, which

188   mimic the approach of an avian predator (Riechert and Hedrick 1993). Spiders react to the

189   air puffs by huddling and remaining still. The faster the spiders resume movement after this

190   simulated threat, i.e., move one body length away from where they were huddled, the

191   bolder they are considered. Bolder spiders tend to participate more in collective prey

192   attacks than shy individuals (Lichtenstein et al. 2017). Boldness is a repeatable behaviour in

193   this species when spiders are kept isolated over days, with a repeatability of 0.63 (Keiser et

194   al. 2014). However, in a social context, boldness is much more plastic and changes as a

195   function of the boldness of the individuals with whom one interacts and over time (Hunt et

196   al. 2018) and may be related with metabolic rate (Lichtenstein et al., 2017). To test

197   boldness, spiders were placed individually in a plastic container (15x15cm) and after 30s of

198   acclimation, two puffs of air were administered to the anterior prosoma using an infant

199   nose-cleaning bulb. Boldness was measured as the latency to resume movement and move

200   one body length. Because bolder individuals resume movement faster, we subtracted the

201   time to resume movement from the maximum duration of the procedure (600s) to create a

202   metric that increases with boldness. We designated as 'shy' individuals those with a latency

203   to resume movement of 400-600s, while 'bold' individuals were those with a latency to

204   resume movement of 0-200s. The abdomen of each spider was marked uniquely with acrylic

205   paint to track their behaviour over time (Figure 1). We examined how many individuals

206   occupied the role of keystone (boldest) in each experimental group over the 7 weeks of the

207   experiment – this ranged from 1 to 7 individuals (same individual throughout, or a different

208   individual each week). A priori, turnover is expected to be higher for the subadults because

209   they have larger group sizes and therefore more individuals that might replace the keystone

210   individual. We compare the keystone turnover for the two developmental stages using a

211   Wilcoxon rank sum (Mann-Whitney) test. We used linear interpolation to obtain an

212   estimate of boldness on Days 0 and 2 and identify a putative boldest individual on those

213   days, which were in between the weekly boldness measurement taken on Day 4.

214

215   *Group composition*

216   To examine the effect of group composition on collective behaviour we assigned spiders to

217   one of three group compositions: all shy, all bold, and 'keystone' (all shy individuals plus one

218   bold individual). For subadults, we established five groups of each composition and for

219   adults we established five groups of all bold, nine of all shy, and ten keystone groups.

220   Individuals that were not assigned to experimental groups, including those with a boldness

221   score of 200-400, were returned to their source colony. After the first week of our study,

222   the average boldness of all group compositions converged, with the 'all bold' groups

223   reducing their average boldness substantially and the other two group types increasing their

224   average group boldness slightly (Figure S1 A, B). Boldness during week 1 was the boldness

225   recorded before creating the experimental groups, thus before individuals interacted with

226   one another. We used a one-way ANOVA to compare mean group boldness of the three

227   different group compositions, for the latter five weeks of our experiment, excluding week

228   one. Because we did not detect a significant difference in average boldness between the

229   three compositions for the latter five weeks (subadults: $F_{2,71}=0.739$, p=0.48; adults:

230    $F_{2,117}=2.076$, p=0.13), we excluded week one and pooled the remaining data across

231   compositions in all analyses (see also distribution analysis in Table S1). Because boldness

232   was found to be more plastic in a social context compared with isolation, and because the

233   artificially manipulated boldness distributions were quickly returned to their natural skewed

234   state by the spiders' collective boldness dynamics, we did not find evidence that our

235   treatments had any long-term effects. For further information on changes in boldness over

236   time in a social context see Hunt et al. 2018.

237

238   *Social interactions*

239   The physical contacts among spiders were manually recorded three times a week:

240   immediately (1-2 hours) before the prey-capture assay, two days prior to the prey capture

241   assay, and four days before to the prey capture assay. Resting interactions were defined as

242   a physical contact between any body parts of two spiders (Figure 1). Interactions were

243   observed during the day, when spiders are resting and inactive, which is their condition

244   most of the time, unless disturbed by a prey in their web or by a destruction of their web

245   that requires maintenance. Care was taken to note each spider in the colony so that all

246   interactions are recorded. These interactions were used to construct social networks and

247   calculate network variables that indicate individual, sub-group, and group level dynamics.

248   The network variables measuring individual level behaviours were keystone degree,

249   keystone closeness, and maximum boldness in the group (i.e., boldness of the keystone); for

250   the sub-group level, modularity; and for the group level, average degree and degree

251   distribution skewness, as detailed in Table 1.

252   To calculate the 2 individual-level network measures (Table 1), we had to first

253   identify which individual was the boldest, i.e. occupying the keystone role each week. In this

254   system, the individual with the highest boldness assumes the keystone role, regardless of its

255   identity (Pinter-Wollman et al. 2017b). Thus, the role of keystone is not necessarily

256   maintained by a specific individual. In a social setting, individuals change their boldness over

257   time (Hunt et al. 2018) and so boldness ranks among individuals may also shift. When more

258   than one spider exhibited the same maximum value, we took the average network value of

259   those individuals (this happened 2 out of 74 times for the subadult spiders and 1 out of 120

260   times for the adults). When all spiders had zero boldness, we identified the keystone

261   individual as the boldest spider in the previous week (this did not occur for the subadults,

262   and 13 out of 120 times for the adults); where this was not possible, we calculated network

263   values as an average across all individuals in the group that week (7 out of 120 times for the

264   adults).

265

266   *Prey response*

267   To determine the speed at which groups attacked prey collectively, we examined the

268   groups' latency to respond to vibrations on their capture web (Grinsted et al. 2013). We

269   used a custom-made vibratory device assembled from an Arduino Uno board, a vibratory

270   motor, and a metal wire, directed at a 1x1cm piece of paper placed in the capture web

271   (Pinter-Wollman et al. 2017b). The stimulus was always placed on the capture web at the

272   same distance (4cm) from the nest retreat, where most spiders were gathered, to control

273   for any effects the distance of the stimulus might have on the response of the group. The

274   Arduino board was programmed to vibrate the piece of paper in pulses that varied

275   randomly between 0.5-1.5 sec in both the duration of the vibration and the pauses between

276   vibrations, to simulate the irregular vibrations that a prey makes when captured in the web

277   (Hedrick and Riechert 1989). The paper was vibrated until a spider touched it, to avoid

278   habituation to our stimulus, or until 10 minutes elapsed, in which case the trial was stopped

279   (Pinter-Wollman et al. 2017b). As the first individual left the retreat, others followed,

280   creating a collective response. The first individual to leave the retreat was not necessarily

281   the one closest to the simulated prey (personal observations). When no attack took place,

282   we set the latency to attack to ten minutes. We noted the identity of the first individual(s)

283   to touch the stimulus, as well as the identity of all the individuals that left the nest during

284   the attack as participants, so that we could assess whether the keystone (boldest) individual

285   participated in prey attack. Both adult and subadult groups responded to the simulated prey

286   in a similar manner (Figure S3).

287

288   *Data analysis*

289   To examine the relationship between social network structure, boldness, and prey attack we

290   used censored mixed regression models. We considered six variables as predictors of

291   latency to attack, as detailed in Table 1. These were included as fixed effects interacting

292   with the effect 'Day' which accounted for the number of days before the attack assay (4, 2,

293   or 0). This approach allowed us to determine the timescale on which social interactions act

294   on prey capture. We constructed separate models for adult and subadult spider behaviour,

295   and each model included 5 weeks of data (weeks 2-6, excluding week 1). For the adult

296   spiders these included N=360 resting network observations (24 colonies x 5 weeks x 3

297   observations per week) and for the subadults N=224 (15 colonies x 5 x 3, except N=74 for

298   Day 0 because of 1 missing network observation). Because latency to attack was right-

299   censored at 600 s, with 76% of subadult trials and 65% of adult trials resulting in an attack,

300   we used censored regression (Tobit) models with the R package 'censReg' (Henningsen,

301   2017). The response variable, latency to attack, was log-transformed to adhere to the model

302   assumption that the error term is normally distributed. To account for variation among

303   groups and source colonies we included group identity as a random effect and source

304   colony identity as a fixed effect. We further included a time-varying residual component as a

305   random effect to account for changes over the 5 weeks. Because we did not have an *a priori*

306   prediction regarding which network variable would best explain collective prey attack, we

307   identified a suitable model for the adults and subadults by first estimating all 63 possible

308   models that linearly combined one or more (i.e., not including interactions) of the 6 fixed

309   effects listed in Table 1. We calculated the Akaike weight of the 63 models (Burnham et al.,

310   2011). These model weights were then used to estimate the relative importance of the six

311   predictor variables under consideration (Table 1). The importance of each predictor is

312   determined by summing the Akaike weights of each model in which it appears (Symonds

313   and Moussalli 2011). If a certain predictor appears in many of the top models, its summed

314   Akaike weight will tend toward 1. On the other hand, if it only appears in the weaker

315   models, its weight will tend toward 0 (Symonds and Moussalli 2011). This procedure results

316   in a ranking of predictor variables in terms of performance, and one can interpret the

317   predictor weight as a probability that it is a component of the best model (Burnham and

318   Anderson 2002; Symonds and Moussalli 2011). We selected the top-ranked predictor

319   variable at the individual level, and the top-ranked predictor at the group or subgroup level,

320   to obtain a parsimonious model for the adult and subadult behaviour with two main

321   predictors in each model (Tables 2, 3, 4). We find this predictor-ranking approach to be

322   preferable to full-model averaging because it allows us to identify a particular model with

323   properly estimated predictor standard errors and without excessive model complexity (full-

324   model averaging results are available in Table S7, S8). We checked for multicollinearity

325   between predictors in the final models by calculating their corrected generalized variance

326   inflation factors (Fox and Monette 1992), using the R package 'car' (Fox and Weisberg 2011).

327   There was low collinearity in both the adult model (Table S3) and subadult model (Table S5).

328   To assess whether the keystone spider's role in the interactions network (closeness and

329   degree) was correlated with its boldness we calculated the Pearson's correlation between

330   these measures.

331

332   **Results**

333   The adult spider model included average degree (predictor weight 46%), as the group or

334   subgroup-level fixed effect, and closeness of the keystone individual (predictor weight 81%),

335   as the individual-level fixed effect (Tables 2, 3). The subadult spider model included average

336   degree (predictor weight 47%), as the group or subgroup-level fixed effect, and maximum

337   boldness (predictor weight 97%), as the individual-level fixed effect (Tables 2, 4).

338   Network measures impacted collective prey attack in groups of adult spiders. Adult

339   spider groups that were overall more connected (high average degree) attacked the prey

340   stimulus more quickly. This relationship was found only for resting networks observed

341   immediately before testing collective prey attack, but not for networks measured earlier

342   (Table 3). At the level of the individual, when the groups' boldest (keystone) individual was

343   more closely connected to all other individuals (closeness centrality), prey attack was

344   slower. This relationship between prey attack and the closeness centrality of the boldest

345   individual was retained for resting networks obtained two days prior to prey attack (Table

346   3).

347   No relationship between the network measure average degree and attack speed was

348   found for the groups of subadult spiders (Tables 4). We also ran an alternative model that

349   included degree of keystone as a second individual-level, network effect (predictor weight

350   52%) but this was also not significant (Table S6). However, the boldness of the boldest

351   individual in the group, i.e., the keystone's boldness, significantly reduced latency to attack

352   i.e., groups with a bolder keystone attacked more quickly (Table 4).

353   In the adult spiders, the boldness of the boldest (keystone) individual was not

354   associated with its degree in the before-prey resting network (Pearson's correlation: r =

355   0.039, t = 0.428, df = 118, p = 0.670), or its closeness (Pearson's correlation: r = -0.007, t = -

356   0.074, df = 118, p-value = 0.941). This was also the case for the subadults' boldest spiders

357   and their degree (Pearson's correlation: r = -0.212, t = -1.837, df = 72, p-value = 0.070) and

358   closeness (Pearson's correlation: r = -0.069, t = -0.5909, df = 72, p = 0.556). There was high

359   turnover in the role of keystone (boldest) individual in both in the adult (4.38 $\pm$ 0.68, mean

360     $\pm$ standard deviation) and subadult (5.67 $\pm$ 0.87) groups (number of different individuals in

361   the role out of a maximum of 7). There was a significant difference between the adult and

362   subadult distributions of keystone turnover (Wilcoxon rank sum test: W=230, p=0.0003).

363   Keystone individuals participated in 7-29% of prey attacks. In the adult groups on the

364   first week, 24 trials resulted in 21 prey attacks. 17 of these attacking groups had a keystone

365   individual (the remainder of the groups were set up as all-shy individuals), and 5 (29.4%) of

366   the attacks by these groups included the keystone individual. In contrast, on weeks 2-6, 73

367   of 120 trials resulted in prey attacks. In 70 of these groups there was an individual that had

368   the highest boldness (i.e., was a keystone), and in only 5 (7.1%) of these groups, the

369   keystone individual participated in the prey attack. This decrease in keystone participation

370   in prey attack after week 1 is consistent with previous findings (Figure S2 of Pruitt and

371   Pinter-Wollman 2015). In the subadult groups, on the first week, 15 trials resulted in 12 prey

372   attacks and only in one (8.3%) of these attacks a keystone individual participated. In weeks

373   2-6, there were 75 trials, 56 resulting in prey attack, 4 (7.1%) of which had keystone

374   participation.

375

376   **Discussion**

377   The structure of resting interaction networks measured immediately before prey

378   attack predicted the attack speed of adult social spiders. Higher overall connectivity

379   (average degree), a group-level measure, led to faster attack, though only in the resting

380   interactions measured pre-stimulus. Furthermore, the more connected to others (greater

381   closeness centrality) was the boldest individual (keystone), the slower the collective prey

382   attack speeds, when considering both the networks observed immediately and two days

383   prior to the prey attack. Therefore, the social connectivity of the keystone to the rest of its

384   group, but not its boldness, was found to be significant in groups of adults. The opposite

385   finding was observed for the subadult spiders: groups with a bolder keystone individual

386   attacked the prey stimulus more quickly, but we did not detect any significant associations

387   between subadult resting network measures and attack speeds. These findings support our

388   hypothesis that subadult spiders will rely on behavioural traits likely because younger

389   animals are often more behaviourally plastic than adults (Scott 1962). Our results further

390   support the hypothesis that adult groups rely on social interactions more than on

391   behavioural changes to modify collective dynamics. We also found that the individual-level

392   predictor had a noticeably higher predictor weight compared to the group-level predictor in

393   both the adults and subadults: 81% vs 46% in the adults, and 97% vs 47% in the subadults

394   (Table 3). This seems to confirm the relevance of the 'keystone individual' concept in this

395   species.

396   Influential 'keystone' individuals in social groups have a large effect on their social

397   environment relative to their abundance (Modlmeier et al. 2014b). While this influence can

398   be mediated through the behavioural traits of the keystone individual, it may also depend

399   on its social interactions. Here we found that the behavioural traits of the keystone are not

400   the only feature that impacts group success. When the boldest individual in an adult spider

401   group had a lower closeness, i.e., was less connected with other resting spiders, the colony

402   attacked prey more quickly. Thus, we find that the impact of the keystone's defining trait –

403   high boldness – was mediated by its interactions with the rest of the social group. Other

404   studies define keystone individuals according to their centrality in an interaction network

405   (Lusseau and Newman 2004; Vital and Martins 2013; Modlmeier et al. 2014b) and deem

406   central individuals as critical for the stability of their society. Our findings suggest that *both*

407   the behavioural traits and role in the social network should be considered when defining

408   keystone individuals in some contexts. The boldness of the keystone individuals was not

409   associated with network closeness or degree in either adults or subadults, which suggests

410   that centrality in an interaction network is not merely a direct consequence of individual

411   behavioural characteristics but may result from a different process.

412   Our results suggest that a keystone individual affects group dynamics either through

413   its own behaviour, or through influencing the formation and dissolution of social

414   interactions. We found low direct participation of keystone individuals in prey attacks (7-

415   29%), which is similar to keystone participation seen in other studies of this system (Pruitt

416   and Pinter-Wollman 2015). Direct keystone participation in prey attack is most common

417   during the first three days after *S. dumicola* colony establishment (Pruitt and Pinter-

418   Wollman 2015) or after a new boldest individual is introduced (Pinter-Wollman et al.

419   2017b). Keystones rarely participate in prey capture directly in established colonies (Pruitt

420   and Keiser 2014). Seismic recruitment signals have been indicated in *S. sarasinorum* (Bradoo

421   1980) and other spider genera such as *Theridion saxatile* (Norgaard 1956). Likewise, adult *S.*

422   *dumicola* are observed to catalyse foraging participation by juvenile spiders without

423   becoming directly involved (Modlmeier et al. 2015). Thus, faster attack speeds may result

424   from keystone individuals signalling information to the rest of the group about the presence

425   of prey through, for example, vibrations on the web. Such signalling does not necessarily

426   require physical proximity, only connection through the capture web, thus it is consistent

427   with the peripheral position of the keystone individual in the proximity networks. In

428   addition, the observed fast attacks in groups with high connectivity that we observed could

429   point to another mechanism underlying the effects of interactions on behaviour. Recent

430   work shows that in this study system boldness is impacted by proximity interactions (Hunt

431   et al. 2018). Thus, it is possible that individuals in groups with high connectivity have more

432   opportunities to modify each other's behaviour and shape overall group boldness

433   composition, which impacts prey attack.

434   Interaction patterns had effects on collective outcomes depending on when they

435   occurred. The closeness of the keystone was a significant predictor of attack speed up to

436   two days before the stimulus. This effect duration may be a result of persistence in

437   occupying certain social roles in the interaction network or, as previous research indicates,

438   because keystone spiders have legacy effects on their social environment (Pruitt and Pinter-

439   Wollman 2015). A keystone individual's long-term influence on its group can result from

440   influencing the behaviour of others or their interactions. For example, in primates the

441   removal of certain individuals who engage in policing behaviour affects the group's social

442   network structure, even in situations, such as play, in which the removed individuals did not

443   participate (Flack et al. 2006). *S. dumicola* colonies containing bolder keystones attack with

444   more spiders, even after the keystone has been removed, suggesting that keystone

445   individuals shape the overall structure of the social network, and/or change the group

446   members' individual characteristics (Pruitt and Pinter-Wollman 2015). The lack of

447   relationship between the boldness of the boldest individual in the group and prey attack

448   speed in the adults, could be due to these long-term effects and the dynamics of boldness

449   that we observed. It is possible that it is the boldness of the boldest individual many days

450   before the prey attack that has the largest impact on group dynamics, rather than the

451   boldness of the currently boldest individual. Bold spiders may actively contribute to a

452   process of social niche construction, whereby repeated social interactions reinforce and

453   enhance inter-individual differences in behaviour such as boldness and prey attack speed

454   (Laskowski and Pruitt 2014).

455   The impact of overall group connectivity (average degree) on the adult spiders'

456   response to prey suggests that most group members have a role to play in coordinating

457   collective predation, even without needing to participate directly in prey attack. For

458   instance, the presence of fellow colony members may catalyse increased foraging

459   aggressiveness in individuals that are already predisposed to participate in prey capture

460   (e.g., bold individuals (Wright et al. 2015, 2016)). Such catalytic effects have been observed

461   in the context of nightly web repair in *S. dumicola* (Keiser et al. 2016). Furthermore, group

462   level interactions impacted collective prey attack only on a short-time scale. The significant

463   effect of group connectivity (average degree) immediately before, but not two and four

464   days prior to prey capture on its speed, suggests that group level measures are important

465   for immediate dynamics, such as the coordination of motion during prey capture (Krafft and

466   Pasquet 1991). For example, it is possible that spatial proximity between individuals

467   facilitates more rapid information through vibrations or allows individuals to better

468   distinguish vibrations from prey and vibrations from colony mates. Such immediate effects

469   of social connectivity are consistent with observations that small and confined artificial nest

470   scaffolds facilitate rapid prey capture (Modlmeier et al. 2014a). Tighter proximity among

471   group members may increase the frequency of social interactions among all group members

472   (Modlmeier et al. 2014a). Future work on the impact of nest architecture on social

473   interactions could uncover a potential mechanism underlying social interaction patterns

474   (Pinter-Wollman et al. 2017a).

475   If individuals are behaviourally flexible, the group may be less reliant on social

476   interactions to coordinate activities. Subadult spider groups attacked the prey stimulus

477   more quickly if they had a bolder keystone individual, however, no association was found

478   between their resting networks and attack speeds. These findings are consistent with

479 previous work showing that groups with bolder keystones attack prey faster and with more

480 attackers (Keiser and Pruitt 2014). The lower importance of social network structure in

481 subadults compared with adult spider groups could be related to greater behavioural

482 plasticity in the subadults. In a new social environment *Stegodyphus* spiders show higher

483 within-individual variation in boldness before becoming more behaviourally consistent with

484 time (Laskowski and Pruitt 2014; Modlmeier et al. 2014c; Laskowski et al. 2016). Earlier

485 developmental stages show more behavioural flexibility in a variety of animal systems

486 (Stamps and Groothuis 2010). Here we found high turnover in keystone identity in both

487 adults and subadults, with higher turnover in the subadults. Because adult spiders are

488 perhaps more constrained in adjusting their behavioural traits, they may be more reliant on

489 social interactions to achieve a beneficial group-level behavioural phenotype, because who

490 interacts with whom can be changed more easily. Thus, effective group-level hunting

491 behaviour, which is a key function of sociality in social spiders (Whitehouse and Lubin 2005),

492 could depend on a balance between the plasticity of individual-level behavioural traits and

493 the ease of modifying social interactions (Pinter-Wollman et al. 2016), which may vary

494 according to developmental stage.

495 Finally, group size may have played a role in the differences we observed between

496 adult and subadult groups. In our experiments, adult groups had 10 individuals and

497 subadults 26-30 and so development stage and group size are not independent of each

498 other in this study. Individuals in smaller groups have been found to participate more in

499 collective prey capture, probably as a consequence of necessity rather than a change in

500 behaviour (Wright et al. 2015). Thus, it is possible that, if not all individuals are required for

501 prey capture in large groups, interactions among all group members are less important than

502 in small groups. Furthermore, larger groups are more likely to contain skilled or experienced

503   individuals, assuming they have greater diversity in ability or experience; this is referred to

504   as the 'pool of competence' hypothesis (Morand-Ferron and Quinn 2011). However,

505   subadults are all likely equally inexperienced and unskilled at hunting and so variation in

506   experience in a large group may not be a suitable explanation for the differences we

507   observed between the adult and subadult groups. Finally, the containers occupied by

508   subadults were somewhat larger than those of the adults (to accommodate the larger

509   number of individuals). However, subadult group members tended to all cluster in one small

510   area and not utilize more space than the adult spiders in their smaller containers.

511   Therefore, we expect group size to have a smaller impact on the differences between

512   subadult and adult groups than the difference in developmental stage.

513

514   **Conclusion**

515   Our study shows that social interactions are important in determining the speed of

516   collective predation in social spiders and that the impact of interactions may differ

517   according to developmental stage, time scale, and level of social organization.

518   Developmental stages may vary in the importance of social interactions versus shifts in

519   individuals' behavioural tendencies (Pinter-Wollman et al. 2016). Furthermore, different

520   types of interactions on different social organizational levels may vary in the duration of

521   their effects. For example, we found that an individual-based network measure had longer

522   lasting effects than a group-level measure. Finally, our results indicate that the social role of

523   keystone individuals within a group can have a longer-term effect on collective hunting

524   success. This finding emphasizes the importance of observing both the social structure of

525   individuals in a group and noting inter-individual differences in personality characteristics,

526   for understanding the success of some animal societies. Although keystone individuals can

527   occupy a wide variety of roles across different taxa (Modlmeier et al. 2014b), our work

528   suggests that a combination of network and behavioural trait characteristics could provide a

529   more precise definition of keystones in many contexts in future work.

530

Data availability

The datasets generated and analysed during the study will be available in an online data

repository upon acceptance of the paper.

Author contributions

ERH analyzed the data and drafted the manuscript, NPW and JNP designed the study, BM,

RG, CF, BW, and NPW collected the data, and all authors contributed to the final version of

the manuscript.

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766 **Figure captions**

767 **Fig. 1.** Close-up photograph of resting spiders in the first week of the experiment. The abdomen of

768 each spider is marked uniquely with acrylic paint to track their behaviour over time. The resting

769 network here corresponds to one connected chain (left) and one unconnected node (right).

770 **Fig. 2.** Interaction networks of three sample adult spider groups, immediately before prey attack

771 speed was examined. Each node represents an individual spider and colour represents boldness –

772 redder indicates higher boldness, with the boldest individual marked as a star. Lower keystone

773 closeness and higher average degree are associated with faster latency to attack. Latencies to attack,

774 average degree, and keystone closeness are noted below each network.

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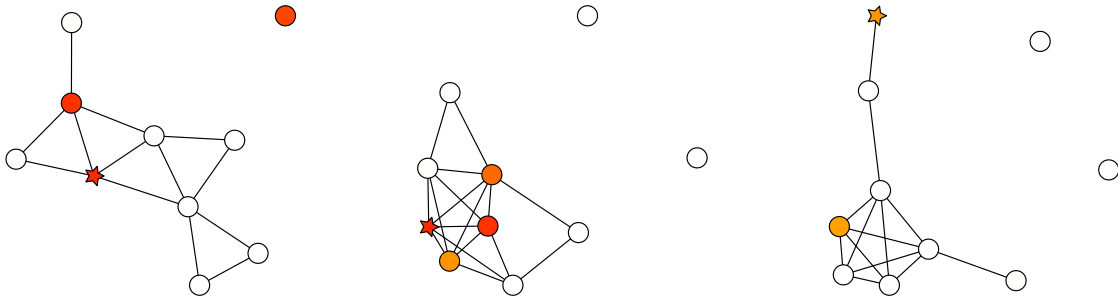776 **Figures and Tables**

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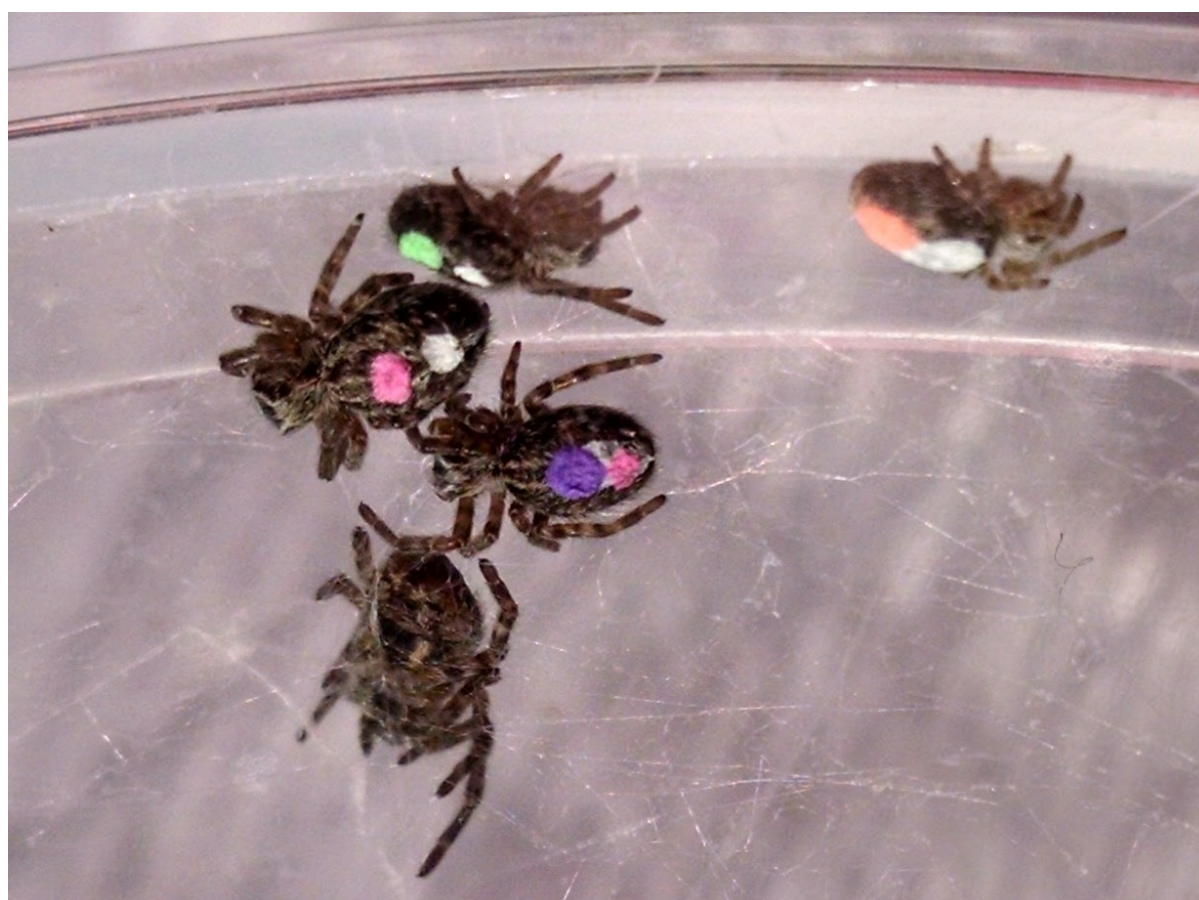
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Latency to attack = 567s
Average degree = 2.6
Keystone closeness = 0.045

Latency to attack = 165s
Average degree = 3.4
Keystone closeness = 0.034

Latency to attack = 46s
Average degree = 2.6
Keystone closeness = 0.023

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785   Table 1. Network measures examined

786

Level of analysis	Network variable	Description
Individual	Keystone degree	Number of individuals interacting with the boldest individual
	Keystone closeness	The sum of reciprocal shortest paths from the boldest individual to all other nodes. Measures how well integrated an individual is in the overall network.
	Maximum boldness	The boldness of the boldest (keystone) individual in the group for that week (not a network measure).
Sub-group	Modularity	The extent to which the network is divided into modules, measured by the ratio between links within a module and links outward to other modules. Modules were defined based on the Optimal Community Structure algorithm (Brandes et al., 2008).
Group	Average degree	The average number of individuals that each individual interacts with. Quantifies overall network connectivity.
	Skewness of degree distribution	The skewness of the degree distribution. Larger absolute values indicate that degree is less evenly distributed among individuals in the group.

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790 Table 2. The Akaike weights for the attack speed predictors, as calculated across all possible models
791 (see Tables S3 and S4). The top two predictors are selected for the final models, one individual and
792 one group or subgroup level.

Level of analysis	Network variable	Predictor weights	
		Adults	Subadults
Individual	Keystone degree	0.14	0.52
	Keystone closeness	**0.81**	0.15
	Maximum boldness	0.29	**0.97**
Subgroup	Modularity	0.36	0.42
Group	Average degree	**0.46**	**0.47**
	Skewness of degree distribution	0.06	0.18

800
801 Table 3. Statistics of the selected model for attack speed in adult spiders. *denotes significance at p
802 < 0.05. See Table S2 for information on random effects and t values.

Level of Analysis	Coefficient	Days before	Estimate log(seconds)	Standard error	p
Individual	Closeness of keystone	4	10.715	6.682	0.109
		2	12.766	6.269	**0.0428 ***
		0	18.842	7.205	**0.0089 ***
Group	Average degree	4	-0.172	0.129	0.182
		2	-0.239	0.150	0.111
		0	-0.367	0.175	**0.036 ***

810 Table 4. Statistics of the selected model for attack speed in subadult spiders. *denotes significance
811 at p < 0.05. See Table S4 for information on random effects and t values.

812

Level of Analysis	Coefficient	Days before	Estimate log(seconds)	Standard error	p
Individual	Maximum boldness	4	-0.0050	0.0015	**< 0.001 ***
		2	-0.0049	0.0016	**0.002 ***
		0	-0.0053	0.0016	**< 0.001 ***
Group	Average degree	4	0.005	0.0247	0.833
		2	-0.041	0.0314	0.192
		0	-0.025	0.0245	0.317