Resting networks and personality predict attack speed in social spiders

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Significance statement

Certain animals in a group, such as leaders, may have a more important role than other group members in determining their collective behavior. Often these individuals are defined by their behavioral attributes, for example, being bolder than others. We show that in social spiders both the behavioral traits of the influential individual, and its interactions with other group members, shape its role in affecting how quickly the group collectively attacks prey.

Abstract

Groups of social predators capture large prey items collectively, and their social interaction patterns may impact how quickly they can respond to time-sensitive predation opportunities. We investigated whether various organizational levels of resting interactions (individual, sub-group, group), observed at different intervals leading up to a collective prey attack, impacted the predation speed of colonies of the social spider *Stegodyphus dumicola*. We found that in adult spiders overall group connectivity (average degree) increased group

attack speed. However, this effect was detected only immediately before the predation event; connectivity two and four days before prey capture had little impact on the collective dynamics. Significantly, lower social proximity of the group's boldest individual to other group members (closeness centrality) immediately prior and two days before prey capture was associated with faster attack speeds. These results suggest that for adult spiders, the long-lasting effects of the boldest individual on the group's attack dynamics are mediated by its role in the social network, and not only by its boldness. This suggests that behavioural traits and social network relationships should be considered together when defining keystone individuals in some contexts. By contrast, for subadult spiders, while the group maximum boldness was negatively correlated with latency to attack, no significant resting network predictors of latency to attack were found. Thus, separate behavioural mechanisms might play distinctive roles in determining collective outcomes at different developmental stages, timescales, and levels of social organization.

Introduction

Group living can benefit group members through access to mates, protection from predators, and increased foraging opportunities (Krause and Ruxton 2002). A variety of animals engage in cooperative hunting to capture prey that is larger than what they could capture alone. Examples of cooperative hunting can be seen in chimpanzees (Boesch 2002), lions (Stander 1992), wild dogs (Creel and Creel 1995), hawks (Bednarz 1988), killer whales (Pitman and Durban 2012) and invertebrates such as ants (Witte et al. 2010), and social spiders (Whitehouse and Lubin 1999). During collective prey capture, individuals often coordinate their behaviour through social interactions, to maximize their capture success (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

prey items (Guevara et al. 2011; Harwood and Avilés 2013). More frequent co-feeding interactions of the same prey item has been observed in sibling groups compared with non-sibling groups in group-foraging subsocial spiders, suggesting that social network structure may play a role in the evolution of social behaviour in spiders (Ruch et al. 2015). Colonies composed of bolder spiders attack more rapidly (Keiser et al. 2014; Keiser and Pruitt 2014; Pruitt and Keiser 2014) and with more individuals (Grinsted et al. 2013; Keiser and Pruitt 2014; Laskowski and Pruitt 2014; Pruitt and Keiser 2014) than colonies with shy individuals.

Here we use social network analysis to determine the temporal scale and the social organization level at which interactions between group members have the most impact on collective prey capture dynamics. We evaluate if the keystone individual influences the group through its role in the group's social network. We also consider whether these social interactions have long-lasting effects on prey capture success, or if the impact of interactions is immediate and ephemeral. Furthermore, we examine if developmental stage (subadults vs. adults) affects the relationships between personality, social interactions, and collective prey attack. Comparing subadults, with more plastic, emergent personalities, to adults, with more established personalities, allows us to test the predictions of the model of keystone influence detailed above (Pinter-Wollman et al. 2016).

In sum, we consider whether the speed at which *S. dumicola* colonies of either subadult or adult spiders collectively attack prey depends on: *(i)* interactions occurring at different levels of social organization; *(ii)* temporal changes in social structure; and *(iii)* the behavioural and social attributes of the keystone individual.

Methods

Animal collection and maintenance

Colonies of *S. dumicola* were collected from roadside *Acacia* trees in the Northern Cape of South Africa in November 2015 (subadults) and March 2016 (adults), transported to the laboratory, and fed crickets *ad lib*. The size of collected colonies ranged between 70-300 individuals and contained only females - males are short-lived and rare (12%) in natural colonies (Henschel et al. 1995). We created 15 groups of 26-30 sub-adult female spiders, from 4 source colonies of subadults, and 24 groups of 10 adult female spiders each, from 3 other source colonies. Individuals from different source colonies were not mixed. Group sizes were larger for subadults because of the small size of those individuals, and because it potentially requires more small individuals to execute a successful attack on large prey (see supplementary Figure S2 for differences in sizes between adults and subadults). The behavioural composition of these groups is detailed below in the '*Group composition*' section. Groups were housed in large round containers (18cm diameter, 8cm depth for subadults and 11cm diameter, 10cm depth for adults) with vertical wire meshes (two 9x6cm sheets positioned 10cm apart for subadults and a 5x5cm sheet for adults) to allow the spiders to build both a retreat and a capture web. Trials were conducted from January until August, 2016.

Experimental procedure

To determine the effect of interaction patterns at different time scales on prey attack we observed groups over time. Each group was observed for 6.5 weeks. Boldness and prey capture were measured once a week and resting interactions, as detailed below, were observed three times a week with 2-3 days separating each observation. The first resting network was obtained immediately before measuring boldness on Day 4, numbered as four 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

function of the boldness of the individuals with whom one interacts and over time (Hunt et al. 2018) and may be related with metabolic rate (Lichtenstein et al., 2017). To test boldness, spiders were placed individually in a plastic container (15x15cm) and after 30s of acclimation, two puffs of air were administered to the anterior prosoma using an infant nose-cleaning bulb. Boldness was measured as the latency to resume movement and move one body length. Because bolder individuals resume movement faster, we subtracted the time to resume movement from the maximum duration of the procedure (600s) to create a metric that increases with boldness. We designated as 'shy' individuals those with a latency to resume movement of 400-600s, while 'bold' individuals were those with a latency to resume movement of 0-200s. The abdomen of each spider was marked uniquely with acrylic paint to track their behaviour over time (Figure 1). We examined how many individuals occupied the role of keystone (boldest) in each experimental group over the 7 weeks of the experiment – this ranged from 1 to 7 individuals (same individual throughout, or a different individual each week). A priori, turnover is expected to be higher for the subadults because they have larger group sizes and therefore more individuals that might replace the keystone individual. We compare the keystone turnover for the two developmental stages using a Wilcoxon rank sum (Mann-Whitney) test. We used linear interpolation to obtain an estimate of boldness on Days 0 and 2 and identify a putative boldest individual on those days, which were in between the weekly boldness measurement taken on Day 4.

Group composition

To examine the effect of group composition on collective behaviour we assigned spiders to one of three group compositions: all shy, all bold, and 'keystone' (all shy individuals plus one 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*

To determine the speed at which groups attacked prey collectively, we examined the groups' latency to respond to vibrations on their capture web (Grinsted et al. 2013). We used a custom-made vibratory device assembled from an Arduino Uno board, a vibratory motor, and a metal wire, directed at a 1x1cm piece of paper placed in the capture web (Pinter-Wollman et al. 2017b). The stimulus was always placed on the capture web at the same distance (4cm) from the nest retreat, where most spiders were gathered, to control for any effects the distance of the stimulus might have on the response of the group. The Arduino board was programmed to vibrate the piece of paper in pulses that varied randomly between 0.5-1.5 sec in both the duration of the vibration and the pauses between vibrations, to simulate the irregular vibrations that a prey makes when captured in the web (Hedrick and Riechert 1989). The paper was vibrated until a spider touched it, to avoid habituation to our stimulus, or until 10 minutes elapsed, in which case the trial was stopped (Pinter-Wollman et al. 2017b). As the first individual left the retreat, others followed, creating a collective response. The first individual to leave the retreat was not necessarily the one closest to the simulated prey (personal observations). When no attack took place, we set the latency to attack to ten minutes. We noted the identity of the first individual(s) to touch the stimulus, as well as the identity of all the individuals that left the nest during the attack as participants, so that we could assess whether the keystone (boldest) individual participated in prey attack. Both adult and subadult groups responded to the simulated prey in a similar manner (Figure S3).

Data analysis

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

models, its weight will tend toward 0 (Symonds and Moussalli 2011). This procedure results in a ranking of predictor variables in terms of performance, and one can interpret the predictor weight as a probability that it is a component of the best model (Burnham and Anderson 2002; Symonds and Moussalli 2011). We selected the top-ranked predictor variable at the individual level, and the top-ranked predictor at the group or subgroup level, to obtain a parsimonious model for the adult and subadult behaviour with two main predictors in each model (Tables 2, 3, 4). We find this predictor-ranking approach to be preferable to full-model averaging because it allows us to identify a particular model with properly estimated predictor standard errors and without excessive model complexity (full-model averaging results are available in Table S7, S8). We checked for multicollinearity between predictors in the final models by calculating their corrected generalized variance inflation factors (Fox and Monette 1992), using the R package 'car' (Fox and Weisberg 2011). There was low collinearity in both the adult model (Table S3) and subadult model (Table S5). To assess whether the keystone spider's role in the interactions network (closeness and degree) was correlated with its boldness we calculated the Pearson's correlation between these measures.

Results

The adult spider model included average degree (predictor weight 46%), as the group or subgroup-level fixed effect, and closeness of the keystone individual (predictor weight 81%), as the individual-level fixed effect (Tables 2, 3). The subadult spider model included average degree (predictor weight 47%), as the group or subgroup-level fixed effect, and maximum boldness (predictor weight 97%), as the individual-level fixed effect (Tables 2, 4).

Network measures impacted collective prey attack in groups of adult spiders. Adult spider groups that were overall more connected (high average degree) attacked the prey stimulus more quickly. This relationship was found only for resting networks observed immediately before testing collective prey attack, but not for networks measured earlier (Table 3). At the level of the individual, when the groups' boldest (keystone) individual was more closely connected to all other individuals (closeness centrality), prey attack was slower. This relationship between prey attack and the closeness centrality of the boldest individual was retained for resting networks obtained two days prior to prey attack (Table 3).

No relationship between the network measure average degree and attack speed was found for the groups of subadult spiders (Tables 4). We also ran an alternative model that included degree of keystone as a second individual-level, network effect (predictor weight 52%) but this was also not significant (Table S6). However, the boldness of the boldest individual in the group, i.e., the keystone's boldness, significantly reduced latency to attack i.e., groups with a bolder keystone attacked more quickly (Table 4).

In the adult spiders, the boldness of the boldest (keystone) individual was not associated with its degree in the before-prey resting network (Pearson's correlation: $r = 0.039$, $t = 0.428$, $df = 118$, $p = 0.670$), or its closeness (Pearson's correlation: $r = -0.007$, $t = -0.074$, $df = 118$, p-value = 0.941). This was also the case for the subadults' boldest spiders and their degree (Pearson's correlation: $r = -0.212$, $t = -1.837$, $df = 72$, p-value = 0.070) and closeness (Pearson's correlation: $r = -0.069$, $t = -0.5909$, $df = 72$, $p = 0.556$). There was high turnover in the role of keystone (boldest) individual in both in the adult (4.38 ± 0.68, mean $\pm$ standard deviation) and subadult (5.67 ± 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

finding was observed for the subadult spiders: groups with a bolder keystone individual attacked the prey stimulus more quickly, but we did not detect any significant associations between subadult resting network measures and attack speeds. These findings support our hypothesis that subadult spiders will rely on behavioural traits likely because younger animals are often more behaviourally plastic than adults (Scott 1962). Our results further support the hypothesis that adult groups rely on social interactions more than on behavioural changes to modify collective dynamics. We also found that the individual-level predictor had a noticeably higher predictor weight compared to the group-level predictor in both the adults and subadults: 81% vs 46% in the adults, and 97% vs 47% in the subadults (Table 3). This seems to confirm the relevance of the 'keystone individual' concept in this species.

Influential 'keystone' individuals in social groups have a large effect on their social environment relative to their abundance (Modlmeier et al. 2014b). While this influence can be mediated through the behavioural traits of the keystone individual, it may also depend on its social interactions. Here we found that the behavioural traits of the keystone are not the only feature that impacts group success. When the boldest individual in an adult spider group had a lower closeness, i.e., was less connected with other resting spiders, the colony attacked prey more quickly. Thus, we find that the impact of the keystone's defining trait – high boldness – was mediated by its interactions with the rest of the social group. Other studies define keystone individuals according to their centrality in an interaction network (Lusseau and Newman 2004; Vital and Martins 2013; Modlmeier et al. 2014b) and deem central individuals as critical for the stability of their society. Our findings suggest that *both* the behavioural traits and role in the social network should be considered when defining 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

opportunities to modify each other's behaviour and shape overall group boldness composition, which impacts prey attack.

Interaction patterns had effects on collective outcomes depending on when they occurred. The closeness of the keystone was a significant predictor of attack speed up to two days before the stimulus. This effect duration may be a result of persistence in occupying certain social roles in the interaction network or, as previous research indicates, because keystone spiders have legacy effects on their social environment (Pruitt and Pinter-Wollman 2015). A keystone individual's long-term influence on its group can result from influencing the behaviour of others or their interactions. For example, in primates the removal of certain individuals who engage in policing behaviour affects the group's social network structure, even in situations, such as play, in which the removed individuals did not participate (Flack et al. 2006). *S. dumicola* colonies containing bolder keystones attack with more spiders, even after the keystone has been removed, suggesting that keystone individuals shape the overall structure of the social network, and/or change the group members' individual characteristics (Pruitt and Pinter-Wollman 2015). The lack of relationship between the boldness of the boldest individual in the group and prey attack speed in the adults, could be due to these long-term effects and the dynamics of boldness that we observed. It is possible that it is the boldness of the boldest individual many days before the prey attack that has the largest impact on group dynamics, rather than the boldness of the currently boldest individual. Bold spiders may actively contribute to a process of social niche construction, whereby repeated social interactions reinforce and enhance inter-individual differences in behaviour such as boldness and prey attack speed (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

occupy a wide variety of roles across different taxa (Modlmeier et al. 2014b), our work suggests that a combination of network and behavioural trait characteristics could provide a more precise definition of keystones in many contexts in future work.

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Data availability

The datasets generated and analysed during the study will be available in an online data repository upon acceptance of the paper.

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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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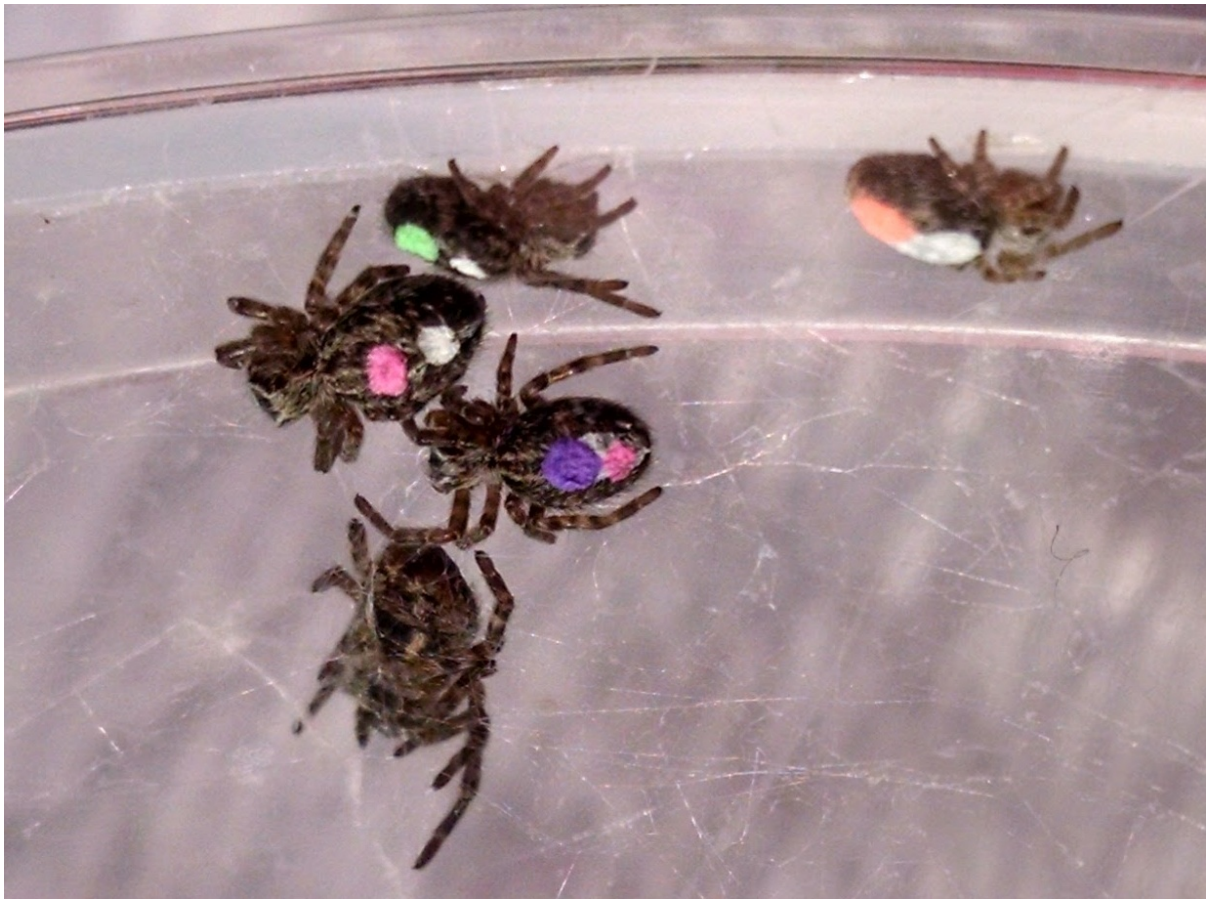
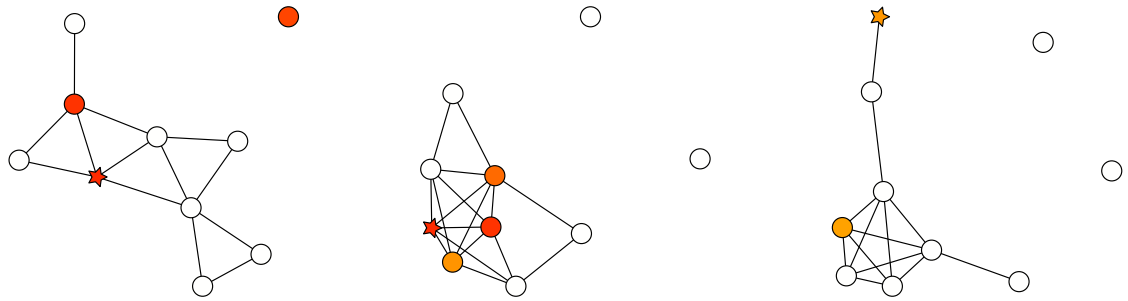
Figure captions

Fig. 1. Close-up photograph of resting spiders in the first week of the experiment. The abdomen of each spider is marked uniquely with acrylic paint to track their behaviour over time. The resting network here corresponds to one connected chain (left) and one unconnected node (right).

Fig. 2. Interaction networks of three sample adult spider groups, immediately before prey attack speed was examined. Each node represents an individual spider and colour represents boldness – redder indicates higher boldness, with the boldest individual marked as a star. Lower keystone closeness and higher average degree are associated with faster latency to attack. Latencies to attack, average degree, and keystone closeness are noted below each network.

Figures and Tables





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

Table 1. Network measures examined

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.

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

Table 3. Statistics of the selected model for attack speed in adult spiders. *denotes significance at p < 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** *

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

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	0.191
		0	-0.025	0.0245	0.317