Resting networks and personality predict attack speed in social spiders

Edmund R. Hunt[1*], Brian Mi[2], Rediet Geremew[2], Camila Fernandez[2], Brandyn M. Wong[2], Jonathan N. Pruitt[3], and Noa Pinter-Wollman[1]

[1] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095
[2] BioCircuits Institute, University of California, San Diego, La Jolla CA 92093
[3] Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106
*Corresponding author: Edmund R. Hunt, edmund.hunt@bristol.ac.uk, +44 (0)117 331 4760

ORCIDS: ERH, 0000-0002-9647-124X; JNP, 0000-0003-0326-6755; NP-W, 0000-0002-0448-8037
Keywords: Collective behaviour, Foraging, Keystone individual, Boldness, Social network analysis, *Stegodyphus dumicola*

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

reduce the time and effort needed to capture prey, and increases the probability of success, thus conferring important fitness benefits to all group members (Pasquet and Krafft, 1992). At the same time, social groups often rely on particular individuals to expedite group dynamics; such individuals have been termed 'keystone' individuals (Modlmeier et al., 2014b).

It is still unknown how keystone individuals influence the performance of a group. Generally speaking, keystone individuals can either perform the work itself or catalyse the work of other group members (Robson and Traniello, 1999), for example through social interactions. A recent model predicts that when the behaviour of group members is persistent, social interactions play a larger role than behaviour in shaping collective outcomes. This prediction emerges because who interacts with whom can change more rapidly than behaviour, and behaviour does not necessarily determine who interacts with whom. In contrast, if behaviour is plastic, social interactions may play a smaller role in determining collective outcomes because behaviour is malleable (Pinter-Wollman et al., 2016). Younger animals are often more behaviourally plastic than adults (Scott, 1962). Thus, by comparing the social behaviour of both subadult, or juvenile, and adult organisms, we can test when social interactions and when behavioural traits have a larger impact on collective outcomes (Pinter-Wollman et al., 2016).

Social network analysis provides tools to quantify interaction patterns and has been instrumental in understanding the dynamics and outcomes of interactions within groups (Krause et al., 2015; Kurvers et al., 2014; Pinter-Wollman et al., 2014; Wey et al., 2008) and in predicting group success (Royle et al., 2012). Different network measures can describe interactions occurring at various organizational levels, such as an individual's direct interactions with its neighbours, links within a subgroup, or interactions at the whole group

level (Krause et al., 2007; Lusseau and Newman, 2004; Wey et al., 2008; Wittemyer et al., 2005). The social structure of animal groups often changes over time, and interaction patterns occurring in one period can impact the group later (Blonder et al., 2012; Krause et al., 2015; Pinter-Wollman et al., 2014). For example, social connectivity early in life can predict male mating success several years later in long-tailed manakins (McDonald, 2007), social connections to relatives can persist for longer than relationships with non-kin in spotted hyenas (Holekamp et al., 2012), and social stability of subgroups can be maintained over years in sparrows (Shizuka et al., 2014). Thus, temporal dynamics of interactions may occur at different rates at different organization levels (Blonder et al., 2012).

Animals within a society often differ from one another in their behaviour, and these differences can be consistent over time, a phenomenon that has been referred to as 'personality' (Bell et al., 2009; Jandt et al., 2014; Sih et al., 2004). Behavioural variation among individuals in a social group can have a considerable impact on group functions (Pinter-Wollman, 2012). Only a small amount of variation among individuals may be necessary to have large impacts on the entire group. In the most extreme situations just one 'keystone' individual, such as a leader or a tutor, may have a disproportionate impact on the group (Conradt and Roper, 2003; Modlmeier et al., 2014b). A keystone can be either a particular individual or a role that different individuals assume at different times (Modlmeier et al., 2014b). Keystone individuals can have an increased interaction rate with other group members (Lloyd-Smith et al., 2005) and their behavioural tendencies can influence interaction patterns (Firth et al., 2015; Krause et al., 2010; Pike et al., 2008; Pinter-Wollman et al., 2011; Sih et al., 2009), thus in turn impacting collective actions (Bansal et al., 2007; Brown and Irving, 2014).

99 Individual differences that are consistent over short time frames may change over
100 longer periods (Stamps and Groothuis, 2010). Such changes can alter the relationship
101 between a group's personality composition and collective outcomes over time. For example,
102 in social insects the task that each individual performs can change with age (Seeley, 1982;
103 Tripet and Nonacs, 2004) potentially altering the distribution of task performance in the
104 colony. Changes to an animal's personality may arise from changes in physiological
105 processes such as growth (Biro and Stamps, 2008), metamorphosis (Hedrick and Kortet,
106 2012; Wilson and Krause, 2012), or sexual maturation (Stamps and Groothuis, 2010).
107 Personality may also develop due to changes in the external physical or social environment
108 over time, i.e. experiential factors (Stamps and Groothuis, 2010). For example, spiders
109 placed in a group of unfamiliar individuals show initial high individual variation in boldness
110 that becomes more consistent over time, as group members become familiar with one
111 another (Laskowski et al., 2016; Laskowski and Pruitt, 2014; Modlmeier et al., 2014c).
112 In the social spider *Stegodyphus dumicola* (Araneae, Eresidae) individuals vary in
113 their boldness, and the boldest individual in the colony (referred to as the keystone)
114 determines the foraging intensity and mass gain of the entire group (Keiser and Pruitt, 2014;
115 Pruitt and Keiser, 2014). It is not known how the influence of keystone individuals is
116 imparted in this species, only that keystones have long lasting effects, and that the duration
117 of their impact is proportional to the tenure of the keystone in the group (Pruitt and Pinter-
118 Wollman, 2015). *S. dumicola* spiders live in colonies of up to several hundred individuals
119 that exhibit cooperative behaviours such as prey capture and allo-maternal care (Bilde et al.,
120 2007; Junghanns et al., 2017). Enhanced foraging success is thought to be a primary driver
121 of sociality in social spiders (Whitehouse and Lubin, 2005), to enable subduing of large prey
122 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

146 Colonies of *S. dumicola* were collected from roadside *Acacia* trees in the Northern Cape of
147 South Africa in November 2015 (subadults) and March 2016 (adults), transported to the
148 laboratory, and fed crickets *ad lib*. The size of collected colonies ranged between 70-300
149 individuals and contained only females - males are short-lived and rare (12%) in natural
150 colonies (Henschel et al., 1995). We created 15 groups of 26-30 female spiders, from 4
151 source colonies of subadults, and 24 groups of 10 adult female spiders each, from 3 other
152 source colonies. Group sizes were larger for subadults because of the small size of those
153 individuals, and because it potentially requires more small individuals to execute a
154 successful attack on large prey (see supplementary Figure S2 for differences in sizes
155 between adults and subadults). Groups were housed in large round containers (18cm
156 diameter, 8cm depth for subadults and 11cm diameter, 10cm depth for adults) with vertical
157 wire meshes (two 9x6cm sheets positioned 10cm apart for subadults and a 5x5cm sheet for
158 adults) to allow the spiders to build both a retreat and a capture web. Trials were conducted
159 from January until August, 2016.
160
161 *Experimental procedure*
162 To determine the effect of interaction patterns at different time scales on prey attack we
163 observed groups over time. Each group was observed for 6.5 weeks. Boldness and prey
164 capture were measured once a week and resting interactions, as detailed below, were
165 observed three times a week with 2-3 days separating each observation. The first resting
166 network was obtained immediately before measuring boldness on Day 4, numbered as four
167 days before measuring prey attack. The second resting network was observed on Day 2, two
168 days after measuring boldness and two days before measuring prey attack. The third resting
169 network was observed immediately before testing prey attack speed, on Day 0. This spacing

170 of measures allowed ample time for the spiders to recover from disturbances due to
171 removing them from their web to determine boldness. Each group was fed with a single 4-
172 week-old cricket once a week, which provides *ad lib* food, after the prey assay (described
173 below), hence all colonies had an equal opportunity to consume prey, and were at a similar
174 state of hunger. We obtained 7 boldness measures for each individual spider, 6 collective
175 prey capture response measures for each group, and 18 resting networks for each group (19
176 including a final boldness/network observation not used here). We compared the predictive
177 power of the resting networks observed four days, two days, and immediately before each
178 prey capture trial, for explaining the speed of prey attack. This allows us to differentiate
179 between short term (immediately before prey attack), medium (two days), and long (four
180 days) term influences of spider interaction networks.
181
182 *Boldness*
183 To determine individuals' boldness, each spider was tested once a week using an
184 established assay that measured the recovery of a spider from exposure to air puffs, which
185 mimic the approach of an avian predator (Riechert and Hedrick, 1993). Spiders react to the
186 air puffs by huddling and remaining still. The faster the spiders resume movement after this
187 simulated threat, i.e., move one body length away from where they were huddled, the
188 bolder they are considered. Boldness is a repeatable behaviour in this species when spiders
189 are kept isolated over days, with a repeatability of 0.63 (Keiser et al., 2014). However, in a
190 social context, boldness is much more plastic and changes as a function of the boldness of
191 the individuals with whom one interacts (Hunt et al., 2018). To test boldness, spiders were
192 placed individually in a plastic container (15x15cm) and after 30s of acclimation, two puffs
193 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 adults we established five groups of all bold, nine of all shy, and ten keystone groups. Individuals that were not assigned to experimental groups, including those with a boldness score of 200-400, were returned to their source colony. After the first week of our study, the average boldness of all group compositions converged, with the 'all bold' groups

218 reducing their average boldness substantially (Figure S1 A, B). We used a one-way ANOVA to
219 compare mean group boldness of the three different group compositions, for the latter five
220 weeks of our experiment, excluding week one. Because we did not detect a significant
221 difference in average boldness between the three compositions for the latter five weeks
222 (subadults: $F_{2,71}$=0.739, p=0.48; adults: $F_{2,117}$=2.076, p=0.13), we excluded week one and
223 pooled the remaining data across compositions in all analyses (see also distribution analysis
224 in Table S1). Because boldness was found to be more plastic in a social context compared
225 with isolation, and because the artificially manipulated boldness distributions were quickly
226 returned to their natural skewed state by the spiders' collective boldness dynamics, we did
227 not find evidence that our treatments had any long-term effects. For further information on
228 changes in boldness over time in a social context see Hunt et al., 2018.
229
230 *Social interactions*
231 The physical contacts among spiders were manually recorded three times a week:
232 immediately (1-2 hours) before the prey-capture assay, two days prior to the prey capture
233 assay, and four days before to the prey capture assay. Resting interactions were defined as
234 a physical contact between any body parts of two spiders (Figure 1). Interactions were
235 observed during the day, when spiders are resting and inactive. Care was taken to note each
236 spider in the colony so that all interactions are recorded. These interactions were used to
237 construct social networks and calculate network variables that indicate individual, sub-
238 group, and group level dynamics. The network variables measuring individual level
239 behaviours were keystone degree, keystone closeness, and maximum boldness in the group
240 (i.e., boldness of the keystone); for the sub-group level, modularity; and for the group level,
241 average degree and degree distribution skewness, as detailed in Table 1.

To calculate the 2 individual-level network measures (Table 1), we had to first identify which individual was the boldest, i.e. occupying the (keystone role each week. In this system, the individual with the highest boldness assumes the keystone role, regardless of its identity (Pinter-Wollman et al., 2017b). Thus, the role of keystone is not necessarily maintained by a specific individual. In a social setting, individuals change their boldness over time (Hunt et al., 2018) and so boldness ranks among individuals may also shift. When more than one spider exhibited the same maximum value, we took the average network value of those individuals (this happened 2 out of 74 times for the subadult spiders and 1 out of 120 times for the adults). When all spiders had zero boldness, we identified the keystone individual as the boldest spider in the previous week (this did not occur for the subadults, and 13 out of 120 times for the adults); where this was not possible, we calculated network values as an average across all individuals in the group that week (7 out of 120 times for the adults).

Prey response

To determine the speed at which groups attack prey, we examined the spiders' 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 spiders. 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

266 irregular vibrations that a prey makes when captured in the web (Hedrick and Riechert,
267 1989). The paper was vibrated until a spider touched it, to avoid habituation to our stimulus,
268 or until 10 minutes elapsed, in which case the trial was stopped (Pinter-Wollman et al.,
269 2017b). As the first individual left the retreat, others followed, creating a collective
270 response. The first individual to leave the retreat was not necessarily the one closest to the
271 simulated prey (personal observations). When no attack took place, we set the latency to
272 attack to ten minutes. We noted the identity of the first individual(s) to touch the stimulus,
273 as well as the identity of all the individuals that left the nest during the attack as
274 participants, so that we could assess whether the keystone (boldest) individual participated
275 in prey attack. Both adult and subadult groups responded to the simulated prey in a similar
276 manner (Figure S3).
277
278 *Data analysis*
279 To examine the relationship between social network structure, boldness, and prey attack we
280 used censored mixed regression models. We considered six variables as predictors of
281 latency to attack, as detailed in Table 1. These were included as fixed effects interacting
282 with the effect 'Day' which accounted for the number of days before the attack assay (4, 2,
283 or 0). This approach allowed us to determine the timescale on which social interactions act
284 on prey capture. We constructed separate models for adult and subadult spider behaviour,
285 and each model included 5 weeks of data (weeks 2-6, excluding week 1). For the adult
286 spiders these included N=360 resting network observations (24 colonies x 5 weeks x 3
287 observations per week) and for the subadults N=224 (15 colonies x 5 x 3, except N=74 for
288 Day 0 because of 1 missing network observation). Because latency to attack was right-
289 censored at 600 s, with 76% of subadult trials and 65% of adult trials resulting in an attack,

290 we used censored regression (Tobit) models with the R package 'censReg' (Henningsen,
291 2017). The response variable, latency to attack, was log-transformed to adhere to the model
292 assumption that the error term is normally distributed. To account for variation among
293 groups and source colonies we included group identity as a random effect and source
294 colony identity as a fixed effect. We further included a time-varying residual component as a
295 random effect to account for changes over the 5 weeks. Because we did not have an *a priori*
296 prediction regarding which network variable would best explain collective prey attack, we
297 identified a suitable model for the adults and subadults by first estimating all 63 possible
298 models that linearly combined one or more of the 6 fixed effects listed in Table 1. We
299 calculated the Akaike weight of the 63 models (Burnham et al., 2011). These model weights
300 were then used to estimate the relative importance of the six predictor variables under
301 consideration (Table 1). The importance of each predictor is determined by summing the
302 Akaike weights of each model in which it appears (Symonds and Moussalli, 2011). If a
303 certain predictor appears in many of the top models, its summed Akaike weight will tend
304 toward 1. On the other hand, if it only appears in the weaker models, its weight will tend
305 toward 0 (Symonds and Moussalli, 2011). This procedure results in a ranking of predictor
306 variables in terms of performance, and one can interpret the predictor weight as a
307 probability that it is a component of the best model (Burnham and Anderson, 2002;
308 Symonds and Moussalli, 2011). We selected the top-ranked predictor variable at the
309 individual level, and the top-ranked predictor at the group or subgroup level, to obtain a
310 parsimonious model for the adult and subadult behaviour with two main predictors in each
311 model (Tables 2, 3, 4). We find this predictor-ranking approach to be preferable to full-
312 model averaging because it allows us to identify a particular model with properly estimated
313 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, was a significant predictor of latency to attack; 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 the role out of a maximum of 7). There was a significant difference between the adult and subadult distributions of keystone turnover (Wilcoxon rank sum test: $W=230$, $p=0.0003$).

Keystone individuals participated in 7-29% of prey attacks. In the adult groups on the first week, 24 trials resulted in 21 prey attacks. 17 of these attacking groups had a keystone individual (the remainder of the groups were set up as all-shy individuals), and 5 (29.4%) of the attacks by these groups included the keystone individual. In contrast, on weeks 2-6, 73 of 120 trials resulted in prey attacks. In 70 of these groups there was an individual that had the highest boldness (i.e., was a keystone), and in only 5 (7.1%) of these groups, the keystone individual participated in the prey attack. This decrease in keystone participation in prey attack after week 1 is consistent with previous findings (Figure S2 of Pruitt and

361 Pinter-Wollman, 2015). In the subadult groups, on the first week, 15 trials resulted in 12
362 prey attacks and only in one (8.3%) of these attacks a keystone individual participated. In
363 weeks 2-6, there were 75 trials, 56 resulting in prey attack, 4 (7.1%) of which had keystone
364 participation.
365
366 **Discussion**
367 The structure of resting interaction networks measured immediately before prey
368 attack predicted the attack speed of adult social spiders. Higher overall connectivity
369 (average degree), a group-level measure, led to faster attack, though only in the resting
370 interactions measured pre-stimulus. Furthermore, the more connected to others (greater
371 closeness centrality) was the boldest individual (keystone), the slower the collective prey
372 attack speeds, when considering both the networks observed immediately and two days
373 prior to the prey attack. Therefore, the social connectivity of the keystone to the rest of its
374 group, but not its boldness, was found to be significant in groups of adults. The opposite
375 finding was observed for the subadult spiders: groups with a bolder keystone individual
376 attacked the prey stimulus more quickly, but we did not detect any significant associations
377 between subadult resting network measures and attack speeds. These findings support our
378 hypothesis that subadult spiders will rely on behavioural traits likely because they have
379 greater behavioural plasticity than adults, owing to their relative lack of prior exposure to
380 social contact, over their lifetime, not just within the experiment. Our results further
381 support the hypothesis that adult groups rely on social interactions more than on
382 behavioural changes to modify collective dynamics. We also found that the individual-level
383 predictor had a noticeably higher predictor weight compared to the group-level predictor in
384 both the adults and subadults: 81% vs 46% in the adults, and 97% vs 47% in the subadults

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

387 Influential 'keystone' individuals in social groups have a large effect on their social
388 environment relative to their abundance (Modlmeier et al., 2014b). While this influence can
389 be mediated through the behavioural traits of the keystone individual, it may also depend
390 on its social interactions. Here we found that the behavioural traits of the keystone are not
391 the only feature that impacts group success. When the boldest individual in an adult spider
392 group had a lower closeness, i.e., was less connected with other resting spiders, the colony
393 attacked prey more quickly. Thus, we find that the impact of the keystone's defining trait –
394 high boldness – was mediated by its interactions with the rest of the social group. Other
395 studies define keystone individuals according to their centrality in an interaction network
396 (Lusseau and Newman, 2004; Modlmeier et al., 2014b; Vital and Martins, 2013) and deem
397 central individuals as critical for the stability of their society. Our findings suggest that *both*
398 the behavioural traits and role in the social network should be considered when defining
399 keystone individuals in some contexts. The boldness of the keystone individuals was not
400 associated with network closeness or degree in either adults or subadults, which suggests
401 that centrality in an interaction network is not merely a direct consequence of individual
402 behavioural characteristics but may result from a different process.

403 Our results suggest that the effect of the keystone individual on group dynamics that
404 have been previously observed (Keiser and Pruitt, 2014; Pruitt and Keiser, 2014; Pruitt and
405 Pinter-Wollman, 2015), could be made directly through its own behaviour, or through
406 influencing the formation and dissolution of social interactions. Here, there was low direct
407 participation of keystone individuals in prey attacks (7-29%), which is similar to keystone
408 participation seen in other studies of this system (Pruitt and Pinter-Wollman, 2015). Direct

409 keystone participation in prey attack is most common during the first three days after *S.*
410 *dumicola* colony establishment (Pruitt and Pinter-Wollman, 2015) or after a new boldest
411 individual is introduced (Pinter-Wollman et al., 2017b). Keystones rarely participate in prey
412 capture directly in established colonies (Pruitt and Keiser, 2014). Seismic recruitment signals
413 have been indicated in *S. sarasinorum* (Bradoo, 1980) and other spider genera such as
414 *Theridion saxatile* (Norgaard, 1956). Likewise, adult *S. dumicola* are observed to catalyse
415 foraging participation by juvenile spiders without becoming directly involved (Modlmeier et
416 al., 2015). Thus, faster attack speeds may result from keystone individuals signalling
417 information to the rest of the group about the presence of prey through, for example,
418 vibrations on the web. Such signalling does not necessarily require physical proximity, only
419 connection through the capture web, thus it is consistent with the peripheral position of the
420 keystone individual in the proximity networks. In addition, the observed fast attacks in
421 groups with high connectivity that we observed could point to another mechanism
422 underlying the effects of interactions on behaviour. Recent work shows that in this study
423 system boldness is impacted by proximity interactions (Hunt et al., 2018). Thus, it is possible
424 that individuals in groups with high connectivity have more opportunities to modify each
425 other's behaviour and shape overall group boldness composition, which impacts prey
426 attack.

427 The closeness of the keystone was a significant predictor of attack speed up to two
428 days before the stimulus. This effect duration may be a result of persistence in occupying
429 certain social roles in the interaction network or, as previous research indicates, because
430 keystone spiders have legacy effects on their social environment (Pruitt and Pinter-
431 Wollman, 2015). A keystone individual's long-term influence on its group can result from
432 influencing the behaviour of others or their interactions. For example, in primates the

433 removal of certain individuals who engage in policing behaviour affects the group's social
434 network structure, even in situations, such as play, in which the removed individuals did not
435 participate (Flack et al., 2006). *S. dumicola* colonies containing bolder keystones attack with
436 more spiders, even after the keystone has been removed, suggesting that keystone
437 individuals shape the overall structure of the social network, and/or change the group
438 members' individual characteristics (Pruitt and Pinter-Wollman, 2015). For example, bold
439 spiders may actively contribute to a process of social niche construction, whereby repeated
440 social interactions reinforce and enhance inter-individual differences in behaviour such as
441 boldness and prey attack speed (Laskowski and Pruitt, 2014).

442 The impact of overall group connectivity (average degree) on the adult spiders'
443 response to prey suggests that most group members have a role to play in coordinating
444 collective predation, even without needing to participate directly in prey attack. For
445 instance, the presence of fellow colony members may catalyse increased foraging
446 aggressiveness in individuals that are already predisposed to participate in prey capture
447 (e.g., bold individuals (Wright et al., 2015, 2016)). Such catalytic effects have been observed
448 in the context of nightly web repair in *S. dumicola* (Keiser et al., 2016). Furthermore, group
449 level interactions impacted collective prey attack only on a short-time scale. The significant
450 effect of group connectivity (average degree) immediately before, but not two and four
451 days prior to prey capture on its speed, suggests that group level measures are important
452 for immediate dynamics, such as the coordination of motion during prey capture (Krafft and
453 Pasquet, 1991). Such immediate effects are consistent with observations that small and
454 confined artificial nest scaffolds facilitate rapid prey capture (Modlmeier et al., 2014a).
455 Tighter proximity among group members may increase the frequency of social interactions
456 among all group members (Modlmeier et al., 2014a). Future work on the impact of nest

457 architecture on social interactions could uncover a potential mechanism underlying social
458 interaction patterns (Pinter-Wollman et al., 2017a).
459 If individuals are behaviourally flexible, the group may be less reliant on social
460 interactions to coordinate activities. Subadult spider groups attacked the prey stimulus
461 more quickly if they had a bolder keystone individual, however, no association was found
462 between their resting networks and attack speeds. These findings are consistent with
463 previous work showing that groups with bolder keystones attack prey faster and with more
464 attackers (Keiser and Pruitt, 2014). The lower importance of social network structure in
465 subadults compared with adult spider groups could be related to greater behavioural
466 plasticity in the subadults. In a new social environment *Stegodyphus* spiders show higher
467 within-individual variation in boldness before becoming more behaviourally consistent with
468 time (Laskowski et al., 2016; Laskowski and Pruitt, 2014; Modlmeier et al., 2014c). Earlier
469 developmental stages show more behavioural flexibility in a variety of animal systems
470 (Stamps and Groothuis, 2010). Here we found high turnover in keystone identity in both
471 adults and subadults, with higher turnover in the subadults. Because adult spiders are
472 perhaps more constrained in adjusting their behavioural traits, they may be more reliant on
473 social interactions to achieve a beneficial group-level behavioural phenotype, because who
474 interacts with whom can be changed more easily. Thus, effective group-level hunting
475 behaviour, which is a key function of sociality in social spiders (Whitehouse and Lubin,
476 2005), could depend on a balance between the plasticity of individual-level behavioural
477 traits and the ease of modifying social interactions (Pinter-Wollman et al., 2016), which may
478 vary according to developmental stage.
479 Finally, group size may have played a role in the differences we observed between
480 adult and subadult groups. In our experiments, adult groups had 10 individuals and

481 subadults 26-30 and so development stage and group size are not independent of each
482 other in this study. Individuals in smaller groups have been found to participate more in
483 collective prey capture, probably as a consequence of necessity rather than a change in
484 behaviour (Wright et al., 2015). Thus, it is possible that, if not all individuals are required for
485 prey capture in large groups, interactions among all group members are less important than
486 in small groups. Furthermore, larger groups are more likely to contain skilled or experienced
487 individuals, assuming they have greater diversity in ability or experience; this is referred to
488 as the 'pool of competence' hypothesis (Morand-Ferron and Quinn, 2011). However,
489 subadults are all likely equally inexperienced and unskilled at hunting and so variation in
490 experience in a large group may not be a suitable explanation for the differences we
491 observed between the adult and subadult groups. Finally, the containers occupied by
492 subadults were somewhat larger than those of the adults (to accommodate the larger
493 number of individuals). However, subadult group members tended to all cluster in one small
494 area and not utilize more space than the adult spiders in their smaller containers.
495 Therefore, we expect group size to have a smaller impact on the differences between
496 subadult and adult groups than the difference in developmental stage.
497

498 **Conclusion**

499 Our study shows that social interactions are important in determining the speed of
500 collective predation in social spiders and that the impact of interactions may differ
501 according to developmental stage, time scale, and level of social organization.
502 Developmental stages may vary in the importance of social interactions versus shifts in
503 individuals' behavioural tendencies (Pinter-Wollman et al., 2016). Furthermore, different
504 types of interactions on different social organizational levels may vary in the duration of

their effects. For example, we found that an individual-based network measure had longer lasting effects than a group-level measure. Finally, our results indicate that the social role of keystone individuals within a group can have a longer-term effect on collective hunting success. This finding emphasizes the importance of observing both the social structure of individuals in a group and noting inter-individual differences in personality characteristics, 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.

Acknowledgements

We thank the South Africa Department of Tourism, Environment, and Conservation for providing permits for animal collection (FAUNA 1072/2013 and 1691/2015) and Colin Wright and James Lichtenstein for collecting spiders in the field. We further thank Arne Henningsen for guidance on the 'censReg' R package.

Data availability

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

Funding

This work was supported by the National Science Foundation IOS grants 1456010 to NPW and 1455895 to JNP, and National Institutes of Health grant GM115509 to NPW and JNP.

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.

References

Bansal S, Grenfell BT, Meyers LA, 2007. When individual behaviour matters: homogeneous and network models in epidemiology. Journal of The Royal Society Interface 4:879-891. doi: 10.1098/rsif.2007.1100.

Bednarz JC, 1988. Cooperative hunting in Harris' hawks (Parabuteo unicinctus). Science 239:1525.

Bell AM, Hankison SJ, Laskowski KL, 2009. The repeatability of behaviour: a meta-analysis. Anim Behav 77:771-783. doi: DOI 10.1016/j.anbehav.2008.12.022.

Bilde T, Coates KS, Birkhofer K, Bird T, Maklakov AA, Lubin Y, Aviles L, 2007. Survival benefits select for group living in a social spider despite reproductive costs. Journal of Evolutionary Biology 20:2412-2426. doi: 10.1111/j.1420-9101.2007.01407.x.

Biro PA, Stamps JA, 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology & Evolution 23:361-368. doi: 10.1016/j.tree.2008.04.003.

Blonder B, Wey TW, Dornhaus A, James R, Sih A, 2012. Temporal dynamics and network analysis. Methods in Ecology and Evolution 3:958-972. doi: 10.1111/j.2041-210X.2012.00236.x.

Boesch C, 2002. Cooperative hunting roles among taï chimpanzees. Human Nature 13:27-46. doi: 10.1007/s12110-002-1013-6.

Bradoo B, 1980. Feeding behaviour and recruitment display in the social spider *Stegodyphus sarasinorum* Karsch (Araneae, Eresidae). Tijdschrift voor entomologie 123.

Brandes U, Delling D, Gaertler M, Gorke R, Hoefer M, Nikoloski Z, Wagner D, 2008. On Modularity Clustering. IEEE Transactions on Knowledge and Data Engineering 20:172-188. doi: 10.1109/TKDE.2007.190689.

Brown C, Irving E, 2014. Individual personality traits influence group exploration in a feral guppy population. Behav Ecol 25:95-101. doi: DOI 10.1093/beheco/art090.

Burnham KP, Anderson DR, 2002. Model selection and multimodel inference, 2nd edn. Springer, New York.

Burnham KP, Anderson DR, Huyvaert KP, 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23-35. doi: 10.1007/s00265-010-1029-6.

Conradt L, Roper TJ, 2003. Group decision-making in animals. Nature 421:155-158. doi: 10.1038/Nature01294.

Creel S, Creel NM, 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour 50:1325-1339. doi: 10.1016/0003-3472(95)80048-4.

Firth JA, Voelkl B, Farine DR, Sheldon BC, 2015. Experimental Evidence that Social Relationships Determine Individual Foraging Behavior. Curr Biol 25:3138-3143. doi: 10.1016/j.cub.2015.09.075.

Flack JC, Girvan M, de Waal FBM, Krakauer DC, 2006. Policing stabilizes construction of social niches in primates. Nature 439:426-429. doi: 10.1038/nature04326.

Fox J, Monette G, 1992. Generalized Collinearity Diagnostics. Journal of the American Statistical Association 87:178-183. doi: 10.1080/01621459.1992.10475190.

Fox J, Weisberg S, 2011. An R Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.

Grinsted L, Pruitt JN, Settepani V, Bilde T, 2013. Individual personalities shape task differentiation in a social spider. Proceedings of the Royal Society B: Biological Sciences 280. doi: 10.1098/rspb.2013.1407.

Guevara J, Gonzaga MO, Vasconcellos-Neto J, Avilés L, 2011. Sociality and resource use: insights from a community of social spiders in Brazil. Behavioral Ecology 22:630-638. doi: 10.1093/beheco/arr022.

Harwood G, Avilés L, 2013. Differences in group size and the extent of individual participation in group hunting may contribute to differential prey-size use among social spiders. Biology Letters 9. doi: 10.1098/rsbl.2013.0621.

Hedrick AV, Kortet R, 2012. Sex differences in the repeatability of boldness over metamorphosis. Behavioral Ecology and Sociobiology 66:407-412. doi: 10.1007/s00265-011-1286-z.

Hedrick AV, Riechert SE, 1989. Genetically-based variation between two spider populations in foraging behavior. Oecologia 80:533-539. doi: 10.1007/bf00380078.

Henningsen A, 2017. censReg: Censored Regression (Tobit) Models.

Henschel JR, Lubin YD, Schneider J, 1995. Sexual competition in an inbreeding social spider, *Stegodyphus dumicola* (Araneae: Eresidae). Insectes Sociaux 42:419-426. doi: 10.1007/BF01242170.

Holekamp KE, Smith JE, Strelioff CC, Van Horn RC, Watts HE, 2012. Society, demography and genetic structure in the spotted hyena. Molecular Ecology 21:613-632. doi: 10.1111/j.1365-294X.2011.05240.x.

Hunt ER, Mi B, Fernandez C, Wong BM, Pruitt JN, Pinter-Wollman N, 2018. Social interactions shape individual and collective personality in social spiders. P R Soc B 285. doi: 10.1098/rspb.2018.1366.

Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A, 2014. Behavioural syndromes and social insects: personality at multiple levels. Biological Reviews 89:48-67. doi: Doi 10.1111/Brv.12042.

Junghanns A, Holm C, Schou MF, Sørensen AB, Uhl G, Bilde T, 2017. Extreme allomaternal care and unequal task participation by unmated females in a cooperatively breeding spider. Animal Behaviour 132:101-107. doi: 10.1016/j.anbehav.2017.08.006.

Keiser CN, Jones DK, Modlmeier AP, Pruitt JN, 2014. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. Behavioral Ecology and Sociobiology 68:839-850. doi: DOI 10.1007/s00265-014-1696-9.

Keiser CN, Pruitt JN, 2014. Personality composition is more important than group size in determining collective foraging behaviour in the wild. P R Soc B 281:20141424. doi: 10.1098/rspb.2014.1424.

Keiser CN, Wright CM, Pruitt JN, 2016. Increased bacterial load can reduce or negate the effects of keystone individuals on group collective behaviour. Animal Behaviour 114:211-218. doi: 10.1016/j.anbehav.2016.02.010.

Krafft B, Pasquet A, 1991. Synchronized and rhythmical activity during the prey capture in the social spider *Anelosimus eximius* (Araneae, Theridiidae). Insectes Sociaux 38:83-90. doi: 10.1007/bf01242716.

Krause J, Croft DP, James R, 2007. Social network theory in the behavioural sciences: potential applications. Behavioral Ecology and Sociobiology 62:15-27.

Krause J, James R, Croft DP, 2010. Personality in the context of social networks. Philos T R Soc B 365:4099-4106. doi: 10.1098/rstb.2010.0216.

Krause J, James R, Franks DW, Croft DP, 2015. Animal social networks: Oxford University Press, USA.

Krause J, Ruxton GD, 2002. Living in groups: Oxford University Press.

Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M, 2014. The evolutionary and ecological consequences of animal social networks: emerging issues. Trends in Ecology & Evolution 29:326-335. doi: 10.1016/j.tree.2014.04.002.

Laskowski KL, Montiglio P-O, Pruitt JN, 2016. Individual and Group Performance Suffers from Social Niche Disruption. The American Naturalist 187:776-785. doi: 10.1086/686220.

Laskowski KL, Pruitt JN, 2014. Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. P Roy Soc B-Biol Sci 281. doi: 10.1098/rspb.2013.3166.

Lloyd-Smith JO, Schreiber SJ, Kopp PE, Getz WM, 2005. Superspreading and the effect of individual variation on disease emergence. Nature 438:355-359. doi: Doi 10.1038/Nature04153.

Lusseau D, Newman MEJ, 2004. Identifying the role that animals play in their social networks. Proceedings Biological sciences / The Royal Society 271 Suppl:S477-481. doi: 10.1098/rsbl.2004.0225.

McDonald DB, 2007. Predicting fate from early connectivity in a social network. Proceedings of the National Academy of Sciences 104:10910-10914. doi: 10.1073/pnas.0701159104.

Modlmeier AP, Forrester NJ, Pruitt JN, 2014a. Habitat structure helps guide the emergence of colony-level personality in social spiders. Behavioral Ecology and Sociobiology 68:1965-1972. doi: 10.1007/s00265-014-1802-z.

Modlmeier AP, Keiser CN, Watters JV, Sih A, Pruitt JN, 2014b. The keystone individual concept: an ecological and evolutionary overview. Anim Behav 89:53-62.

Modlmeier AP, Laskowski KL, Brittingham HA, Coleman A, Knutson KA, Kuo C, McGuirk M, Zhao K, Keiser CN, Pruitt JN, 2015. Adult presence augments juvenile collective foraging in social spiders. Animal Behaviour 109:9-14. doi: 10.1016/j.anbehav.2015.07.033.

Modlmeier AP, Laskowski KL, DeMarco AE, Coleman A, Zhao K, Brittingham HA, McDermott DR, Pruitt JN, 2014c. Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. Biology Letters 10. doi: 10.1098/rsbl.2014.0419.

Morand-Ferron J, Quinn JL, 2011. Larger groups of passerines are more efficient problem solvers in the wild. Proceedings of the National Academy of Sciences 108:15898-15903. doi: 10.1073/pnas.1111560108.

Norgaard E, 1956. Environment and Behaviour of Theridion Saxatile. Oikos 7:159-192. doi: 10.2307/3564917.

O'Brien RM, 2007. A Caution Regarding Rules of Thumb for Variance Inflation Factors. Quality & Quantity 41:673-690. doi: 10.1007/s11135-006-9018-6.

Pasquet A, Krafft B, 1992. Cooperation and Prey Capture Efficiency in a Social Spider, *Anelosimus eximius* (Araneae, Theridiidae). Ethology 90:121-133. doi: 10.1111/j.1439-0310.1992.tb00826.x.

Pike TW, Samanta M, Lindstrom J, Royle NJ, 2008. Behavioural phenotype affects social interactions in an animal network. P R Soc B 275:2515-2520. doi: DOI 10.1098/rspb.2008.0744.

Pinter-Wollman N, 2012. Personality in social insects: How does worker personality determine colony personality? Curr Zool 58:580-588. doi: 10.1093/czoolo/58.4.580.

Pinter-Wollman N, Fiore SM, Theraulaz G, 2017a. The impact of architecture on collective behaviour. Nature Ecology & Evolution:0111. doi: DOI: 10.1038/s41559-017-0111.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, de Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, Fewell J, McDonald DB, 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behavioural Ecology 25:242–255.

Pinter-Wollman N, Hubler J, Holley J-A, Franks NR, Dornhaus A, 2012. How is activity distributed among and within tasks in Temnothorax ants? Behavioral Ecology and Sociobiology 66:1407-1420. doi: 10.1007/s00265-012-1396-2.

Pinter-Wollman N, Keiser CN, Wollman R, Pruitt JN, 2016. The Effect of Keystone Individuals on Collective Outcomes Can Be Mediated through Interactions or Behavioral Persistence. American Naturalist 188:240-252. doi: 10.1086/687235.

Pinter-Wollman N, Mi B, Pruitt JN, 2017b. Replacing bold individuals has a smaller impact on group performance than replacing shy individuals. Behavioral Ecology 28:883-889. doi: 10.1093/beheco/arx054.

Pinter-Wollman N, Wollman R, Guetz A, Holmes S, Gordon DM, 2011. The effect of individual variation on the structure and function of interaction networks in harvester ants. Journal of the Royal Society Interface 8:1562-1573. doi: DOI 10.1098/rsif.2011.0059.

Pitman RL, Durban JW, 2012. Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. Marine Mammal Science 28:16-36. doi: 10.1111/j.1748-7692.2010.00453.x.

Pruitt JN, Keiser CN, 2014. The personality types of key catalytic individuals shape colonies' collective behaviour and success. Anim Behav 93:87–95.

Pruitt JN, Pinter-Wollman N, 2015. The legacy effects of keystone individuals on collective behaviour scale to how long they remain within a group. P R Soc B 282:89-96. doi: 10.1098/rspb.2015.1766.

Riechert SE, Hedrick AV, 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). Animal Behaviour 46:669-675. doi: 10.1006/anbe.1993.1243.

Robson SK, Traniello JFA, 1999. Key individuals and the organization of labor in ants. In: Detrain C, Deneubourg JL, Pasteels JM, editors. Information processing in social insects Basel Boston, Berlin: Birkhauser. p. 239-260.

Royle NJ, Pike TW, Heeb P, Richner H, Kolliker M, 2012. Offspring social network structure predicts fitness in families. P Roy Soc B-Biol Sci 279:4914-4922. doi: 10.1098/rspb.2012.1701.

Scott JP, 1962. Critical Periods in Behavioral Development. Science 138:949-958.

Seeley TD, 1982. Adaptive significance of the age polyethism schedule in honeybee colonies. Behavioral Ecology and Sociobiology 11:287-293. doi: 10.1007/bf00299306.

Shizuka D, Chaine AS, Anderson J, Johnson O, Laursen IM, Lyon BE, 2014. Across-year social stability shapes network structure in wintering migrant sparrows. Ecology Letters 17:998-1007. doi: 10.1111/ele.12304.

Sih A, Bell A, Johnson JC, 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372-378. doi: DOI 10.1016/j.tree.2004.04.009.

Sih A, Hanser SF, McHugh KA, 2009. Social network theory: new insights and issues for behavioral ecologists. Behavioral Ecology and Sociobiology 63:975-988. doi: DOI 10.1007/s00265-009-0725-6.

Stamps J, Groothuis TGG, 2010. The development of animal personality: relevance, concepts and perspectives. Biological Reviews 85:301-325. doi: 10.1111/j.1469-185X.2009.00103.x.

Stander PE, 1992. Cooperative hunting in lions: the role of the individual. Behavioral Ecology and Sociobiology 29:445-454. doi: 10.1007/bf00170175.

Symonds MRE, Moussalli A, 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13-21. doi: 10.1007/s00265-010-1037-6.

Tripet F, Nonacs P, 2004. Foraging for Work and Age-Based Polyethism: The Roles of Age and Previous Experience on Task Choice in Ants. Ethology 110:863-877. doi: 10.1111/j.1439-0310.2004.01023.x.

Vital C, Martins EP, 2013. Socially-Central Zebrafish Influence Group Behavior More than Those on the Social Periphery. PLOS ONE 8:e55503. doi: 10.1371/journal.pone.0055503.

Wey T, Blumstein DT, Shen W, Jordan F, 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav 75:333-344. doi: DOI 10.1016/j.anbehav.2007.06.020.

Whitehouse MEA, Lubin Y, 1999. Competitive foraging in the social spider Stegodyphus dumicola. Animal Behaviour 58:677-688. doi: 10.1006/anbe.1999.1168.

Whitehouse MEA, Lubin Y, 2005. The functions of societies and the evolution of group living: spider societies as a test case. Biological Reviews 80:347-361. doi: 10.1017/S1464793104006694.

Wilson ADM, Krause J, 2012. Personality and metamorphosis: is behavioral variation consistent across ontogenetic niche shifts? Behavioral Ecology 23:1316-1323. doi: 10.1093/beheco/ars123.

Witte V, Schliessmann D, Hashim R, 2010. Attack or call for help? Rapid individual decisions in a group-hunting ant. Behavioral Ecology 21:1040-1047. doi: 10.1093/beheco/arq100.

Wittemyer G, Douglas-Hamilton I, Getz WM, 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. Animal Behaviour 69:1357-1371. doi: 10.1016/j.anbehav.2004.08.018.

Wright CM, Keiser CN, Pruitt JN, 2015. Personality and morphology shape task participation, collective foraging and escape behaviour in the social spider *Stegodyphus dumicola*. Animal Behaviour 105:47-54. doi: 10.1016/j.anbehav.2015.04.001.

Wright CM, Keiser CN, Pruitt JN, 2016. Colony personality composition alters colony-level plasticity and magnitude of defensive behaviour in a social spider. Animal Behaviour 115:175-183. doi: 10.1016/j.anbehav.2016.03.002.

Figures and Tables

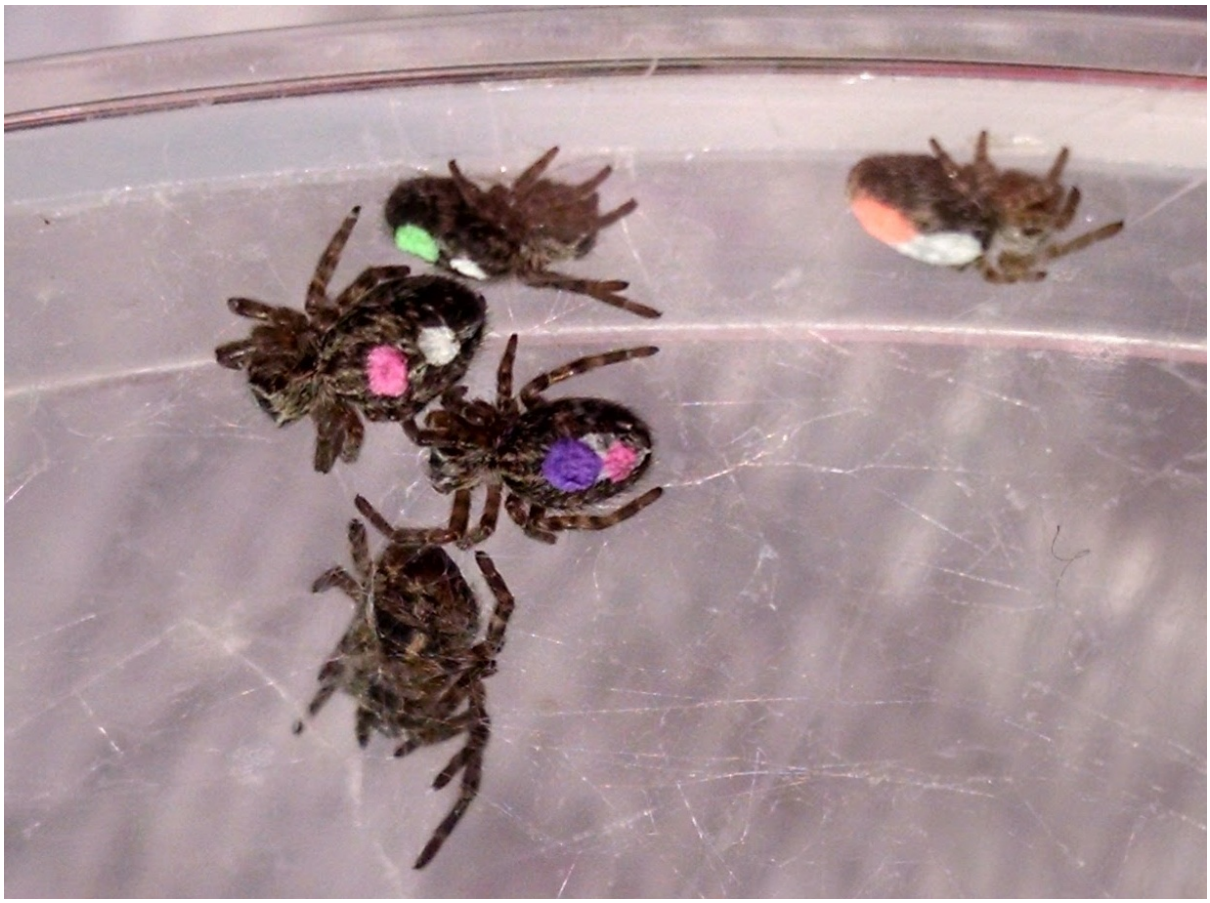
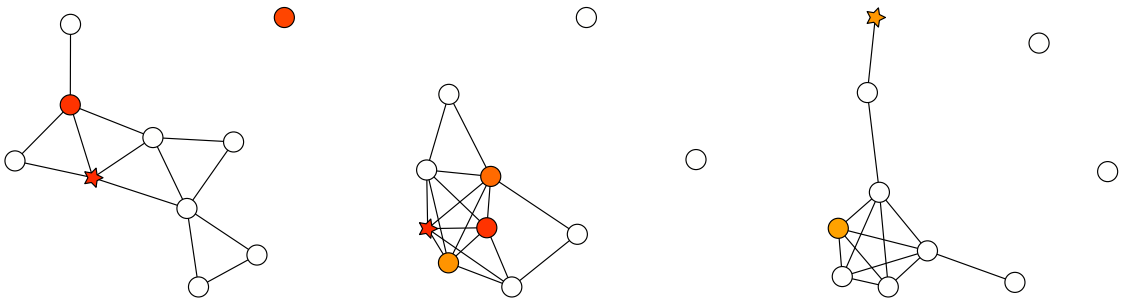


Fig. 1. Close-up photograph of resting spiders in the first week of the experiment. The abdomen of each spider is marked uniquely with acrylic paint to track their behaviour over time. The resting network here corresponds to one connected chain (left) and one unconnected node (right).



Latency to attack = 567s	Latency to attack = 165s	Latency to attack = 46s
Average degree = 2.6	Average degree = 3.4	Average degree = 2.6
Keystone closeness = 0.045	Keystone closeness = 0.034	Keystone closeness = 0.023

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.

773 Table 1. Network measures examined

774

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.

775
776
777

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	**0.0427** *
		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	0.192
		0	-0.025	0.0245	0.317