Adult presence augments juvenile collective foraging in social spiders

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The presence of a few highly influential individuals, so called 'keystone individuals', is thought to influence group dynamics and success in a diverse variety of animal societies. Although older, experienced individuals often occupy keystone roles such as leader or dominant individual, few studies have performed manipulations to study their impact. Here, we investigate how juvenile collective foraging behaviour is influenced by adult presence in the social spider *Stegodyphus dumicola*. Our manipulation of age demography revealed that the presence of a few mature females drastically increased a groups' foraging aggressiveness, demonstrating that adults indeed act as keystone individuals in juvenile spider groups. Interestingly, the magnitude of their positive impact on collective foraging was mediated by group size: adult presence shortened latency to attack prey more strongly in large groups than in small groups. Conversely, adult presence increased the number of attackers only in small groups. Surprisingly, intergroup variation in collective foraging, which is known to be consistent in mature social spiders, was not repeatable in juvenile groups. Thus, juvenile groups seem to behave more erratically or need more time to develop collective personalities. Together, our results suggest that adult presence can have profound, catalytic effects on juvenile collective foraging behaviour, and that these effects are modulated by group size.

Animal groups often exhibit striking idiosyncrasies in their collective behaviours that not only differentiate one group from another, but moreover influence their fitness and survival (Pruitt & Keiser, 2014; Scharf, Modlmeier, Fries, Tirard, & Foitzik, 2012; Wray, Mattila, & Seeley, 2011). In other words, whether a group thrives or collapses could be tightly linked to its collective behaviour. Consequently, studying the factors that help generate consistent behavioural variation among animal groups, also known as 'collective personality' or 'colony-level personality' (Keiser, Jones, Modlmeier, & Pruitt, 2014; Pruitt & Keiser, 2014; Scharf et al., 2012), is crucial for a deeper understanding of the ecology and evolution of animal societies. Variation in collective behaviours can be generated by the abiotic environment (e.g. weather or habitat structure: Modlmeier, Forrester, & Pruitt, 2014; Pinter-Wollman, Gordon, & Holmes, 2012) and/or demographic factors like group behavioural composition (Aplin, Farine, Mann, & Sheldon, 2014; Brown & Irving, 2014; Hui & Pinter-Wollman, 2014; Keiser & Pruitt, 2014; Modlmeier, Keiser, Shearer, & Pruitt, 2014; Pruitt, Grinsted, & Settepani, 2013).

Astonishingly, even the presence of a few highly influential individuals, so called 'keystone individuals' (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014), can dramatically change the behaviour and dynamics of a group. The keystone individual concept is derived from the keystone species concept (Power et al., 1996) and therefore shares its basic premise: a keystone individual/species has a large effect on its environment relative to its abundance. Although keystone individuals are known to occur in a variety of forms (e.g. dominant, leader and superspreader) and systems, so far few studies have performed the necessary controlled manipulations via removal experiments to unequivocally demonstrate their 'disproportionally large, irreplaceable effect' on group dynamics (Modlmeier, Keiser, Watters, et al., 2014; Sih & Watters, 2005). Here we study how collective behaviour might be driven by the presence of a few experienced older individuals.

The adaptive significance of age demography has long been established for highly structured societies such as the social insects, in which division of labour, a major component for the ecological

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success of social insects, can be guided by age polyethism (Huang & Robinson, 1996; Oster & Wilson, 1978; Seeley, 1982). In African elephants, *Loxodonta africana*, groups with older matriarch leaders are better in social discrimination and assessing predatory threats (McComb, Moss, Durant, Baker, & Sayialel, 2001; McComb et al., 2011). Similarly, Brent et al. (2015) suggested that postreproductive female killer whales, *Orcinus orca*, act as 'ecological repositories' that lead group movement in salmon foraging grounds, especially during years of low salmon abundance. Thus, older individuals might increase group success because they have acquired knowledge that allows the group to perform certain tasks better, or at least differently. For instance, age increases hunting success in spotted hyaenas *Crocuta crocuta*, who do not reach their full hunting proficiency until they are about 5 years old, suggesting that successful hunting is a learned skill that requires practise (Holekamp, Smale, Berg, & Cooper, 1997). This could be driven by adults directly influencing the behaviour of younger individuals, providing them with food and/or defending them against predators. In summary, although it is well established that adult presence can impact group dynamics via a number of established routes, virtually no studies have manipulated age demography to study whether and how adults influence juvenile collective behaviour (but see Huang & Robinson, 1996).

How important a few older individuals are for the overall group dynamics and particularly for collective behaviour may strongly depend on group size. Many studies on the emergence of collective behaviour have demonstrated the importance of group size in influencing collective behaviours (e.g. Avilés & Tufiño, 1998; Creel & Creel, 1995; Dornhaus, Powell, & Bengston, 2012). In general, larger groups are more efficient in problem solving, because they are more likely to contain experienced or otherwise skilled individuals (Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011). However, even without the presence of these few experienced or skilled individuals, larger groups may be able to overcome their lack of keystone individuals: larger groups of passerine birds are more efficient problem solvers, even when the group consists of only inexperienced individuals (Morand-Ferron & Quinn, 2011). Thus, in some circumstances larger group size might diminish the impact of a few experienced or otherwise skilled individuals to a point where they become expendable. The interaction between group size and group composition (i.e. the presence of keystone individuals) may be complex and both factors need to be manipulated in order to determine their influence on collective behaviours.

Social spiders of the species *Stegodyphus dumicola* are an ideal model system to investigate how group composition and group size influence collective foraging. Just like other social spiders, females within a colony cooperate in prey capture, web building and care for the young (Lubin & Bilde, 2007; Salomon & Lubin, 2007). During prey capture, multiple individuals work together to subdue larger prey, but individuals can also try to monopolize prey. Larger individuals in particular have a competitive advantage, because they can sometimes exclude smaller individuals from access to a prey item (Whitehouse & Lubin, 1999). Furthermore, collective prey capture behaviour in *S. dumicola* can be driven by the mere presence of a few highly influential bold individuals that act as catalysts (Pruitt & Keiser, 2014). In this study, we focus on a different aspect of group composition (i.e. not the behavioural mixture, but the age demography of the group). Although *S. dumicola* is an annual species, colonies can range from a single female to several hundred individuals, and persist for multiple generations. Adult females have an average body length of 7.4 mm and can survive for 12−15 months, until they all invariably die at the end of the reproductive season (Wickler & Seibt, 1993). Adults of both sexes typically remain in the parental colony to reproduce (Henschel, Lubin, & Schneider, 1995), which leads to a significant degree of inbreeding (0.69; Wickler & Seibt, 1993). Interestingly, nonbreeding adult and subadult females also remain in the colony and help to raise the young (Salomon & Lubin, 2007). The only overlap in generations occurs during the nursery period, during which females from the parental generation defend the young and provision them with regurgitated food (Henschel et al., 1995; Ulbrich & Henschel, 1999). This period ends with the death of the adults, which liquefy their inner organs and are subsequently eaten by the young ('gerontophagy', Seibt & Wickler, 1987). Notably, nonbreeding adults and subadults of the parental generation also feed the young of other females via regurgitation and gerontophagy (Salomon & Lubin, 2007). This cooperative breeding increases survival, growth and reproductive value of the young (Salomon et al., 2011; Salomon, Schneider, & Lubin, 2005). While previous studies have concentrated on the efficiency of (allo-) parental care in raising young, we will examine whether adult presence may also impact juvenile foraging behaviour.

Adult presence could affect the foraging behaviour of the group in multiple ways: adults might signal prey presence to the young and thereby trigger juvenile foraging behaviour. Adults could also reduce the number of unsuccessful attacks by signalling to the young if the probability of success is too low or there is danger. The magnitude of these effects could depend on group size, being especially pronounced in smaller juvenile groups if the effect of adults diminishes with larger group size. Alternatively, the effect of adults could be more pronounced in larger groups if increased levels of competition for food and subsequent hunger increase spiderlings' motivation to respond to adult signals.

To investigate the influence of age demography and group size on collective foraging, we compared the foraging aggressiveness (i.e. the average latency for groups to attack prey and the number of attackers participating in a foraging bout) in experimentally reconstituted groups of two sizes (20 or 40 juvenile individuals) with zero, one or two mature individuals. We predicted that (1) adult presence would increase juveniles' willingness to attack prey (i.e. groups containing adults would attack prey more quickly and respond with more individuals) and (2) adult influence would be related to group size, being either stronger in smaller groups, if adults' influence diminishes with group size, or stronger in larger groups, if competition for food increases spiderlings' responsiveness to adult signals.

METHODS

Collection and Maintenance

We collected 24 *S. dumicola* colonies along the N10 road between Groblerschoop and Upington in the Northern Cape, South Africa in August 2013. Colonies were collected along roadside fencing and hook bush (*Acacia mellifera*) by trimming of colonies' supporting branches and placing the colony within a cloth pillowcase. Colonies were then transported back to our hut in Griekwastad, Northern Cape, South Africa where they were sorted by hand. We counted the number of colony members and visually assigned them to one of three developmental stages: early instar juveniles (first and second instar), middle instar juveniles (third and fourth instar), and mature individuals. We checked the epigynum of each female used in our experiment to verify its maturity. However, the small size of these spiders makes it inherently difficult to distinguish large subadult females from adult females, so it is possible that some of individuals we classified as mature were actually large subadults. After sorting through the colonies and recording their demographics, we placed colonies in IATA (International Air Transport Association)-approved packaging and

transported them to the laboratory at the University of Pittsburgh, Pittsburgh, PA, U.S.A. Colonies were maintained in 490 ml plastic deli cups and provided a maintenance diet of four adult crickets weekly. Colonies were maintained at ~25 °C near large windows that provided ambient lighting conditions (~13:11 h light:dark cycle).

Experimental Group Establishment

We constructed experimental groups either containing only middle-instar juvenile spiders or middle-instar juveniles with one or two adult females present. For each experimental group, all individuals were randomly chosen from one of the source colonies; each source colony was used to establish more than one experimental group. We manipulated group size and adult presence in a 2 × 2 full factorial design: group size (20 small groups with 21 ± 1 juveniles; 23 large groups with 41 ± 1 juveniles); adult presence × group size (6 small groups with 20 juveniles and 1–2 adults; 9 large groups with 40 juveniles and 1–2 adults). The addition/removal of one juvenile and the addition of one or two adults within the small and large treatments was done to control for shifts in group size from adding one or more adult individuals. One might argue that any shifts in collective behaviour seen in our adult-present treatments were actually not the result of adding an adult, but stemmed merely from a small increase in group size. To control for this possibility, we created treatments where we added one or two juvenile individuals and then observed the consequences that this had on collective behaviour (see Data Analysis for further details).

Groups were established by placing the individuals into a new 490 ml container containing a piece of poultry wiring to facilitate web construction. Groups were given 10 days to establish a web before they were run through a series of collective foraging assays. Experimental groups were provided an ad libitum diet of 6-week-old crickets once weekly. This meant that small groups with 20–22 individuals received roughly two crickets each week and large groups with 40–42 individuals received roughly four crickets each week. Ad libitum feeding helped standardize hunger levels across groups of different sizes and treatments and diminished the likelihood that variation in hunger level (or recent resource acquisition) was responsible for differences among treatment groups.

Collective Foraging Assays

Collective foraging assays occurred 4 days after a routine feeding event. Trials were initiated by removing the lid to the groups' containers and dropping a single 3-week-old cricket (approximately 1 cm body length) centrally within the groups' foraging web. We then noted (1) a groups' latency to attack the prey as indicated by the first individual to attack the cricket and (2) the total number of individuals feeding around the cricket every 15 min for the next 4 h. The maximum number of attackers during this period was used for all subsequent analyses. We also noted whether mature individuals participated in foraging or not. By the end of this 4 h window, the groups had eaten the majority of the cricket, leaving only a largely translucent husk. A groups' collective foraging behaviour was assessed once weekly for 5 consecutive weeks.

Data Analysis

We detected no significant effects of adding one or two additional juvenile individuals to our groups of 20 or 40 juveniles or any difference in the one- versus two-adult addition treatments (data not shown). Therefore, groups that contained 20–22 individuals

were labelled as 'small' whereas those that contained 40–42 individuals were labelled as 'large'. In addition, groups that contained one or two adults were labelled as adults 'present' and those without any adults, 'absent'. Final sample sizes included 43 groups with adults absent (20 small groups, 23 large groups) and 15 groups with adults present (6 small groups, 9 large groups).

To explore the impact of adult presence and group size on collective foraging behaviour, we used linear mixed models with our behaviour of interest (latency to attack or number of attackers) as the response variable and included adult presence (present/absent), group size (small/large) and its interaction as fixed effects. We included the additional fixed effect of observation (1–5) as a covariate and its interactions with adult presence and group size to determine whether behaviour changed differently over time in our treatment groups. Models were then stepwise simplified by removing nonsignificant fixed effects, starting with the highest interaction term; nonsignificant main effects were retained if any interaction including them remained significant. We also included the random effects of source colony and experimental group to account for the nonindependence of the data.

We also tested for evidence of consistent differences among groups in their collective behaviours. To test this, we used a model with the behaviour of interest as the response variable and source colony and experimental group as random effects. We then estimated the repeatability of the behaviour among the experimental groups using the resulting variance components. We included no other fixed effects (other than an intercept) in these models as we wished to have a conservative estimate of the among-group variation; however inclusion of the fixed effects did not alter the results (data not shown). We tested for the significance of the among-group variation by comparing the fit of a model with the experimental group random effect to that of a model without. We compared the deviance information criterion (DIC) of the models to determine fit. DIC is similar to Aikake's information criterion where smaller values indicate a better-supported model.

As both of our behaviours of interest were count variables, we used generalized linear mixed models with Markov chain Monte Carlo (MCMC) estimation and a Poisson error distribution using the MCMCglmm package (Hadfield, 2010) in R (R Core Team, 2014). Inspection of the residual deviance and posterior distributions indicated a Poisson distribution fitted our data. In addition, our results were robust to the type of model: square-root transformation of the variables to approximate a Gaussian distribution and rerunning the models using linear mixed models with REML and Gaussian error distribution produced similar results. We used noninformative proper priors, and preliminary analyses indicated our results were not sensitive to changes in prior information. All models were run with 500 000 iterations, a burn-in of 1000 and thinning every 100 iterations. We ran five chains for each model and inspected posterior distributions to ensure proper mixing and convergence.

RESULTS

All of the adults died by the end of the experiment and were presumed to have been consumed (at least in part) by the young. All of the adults were alive for at least the first 2 weeks of the experiment, although we surprisingly never observed an adult participate in prey capture. However, we found evidence that our manipulation of group size and adult presence influenced both of our collective behaviours of interest, latency to attack and number of attackers. There was a significant interaction between presence of adults and group size on latency to attack (Table 1). Specifically, the presence of adults reduced attack latency times in all groups, but this effect was especially pronounced in the large groups

Table 1
Summary of the retained fixed effects and their influence on colonies' latency to attack as estimated by a generalized linear mixed model

Effect	Estimate	95% CI	P
Observation	−0.008	(−0.088, 0.069)	0.829
Adults: present	−1.662	(−2.245, −1.056)	<0.001
Group size: small	−0.112	(−0.339, 0.121)	0.336
Observation ∗ adults	0.251	(0.098, 0.408)	0.002
Adults ∗ group size	0.509	(0.040, 0.959)	0.033

Main effects were retained in the model when they were part of a significant interaction.

Table 2
Summary of the retained fixed effects and their influence on colonies' total number of attackers as estimated by a generalized linear mixed model

Effect	Estimate	95% CI	P
Observation	−0.084	(−0.133, −0.037)	<0.001
Adults: present	0.126	(−0.108, 0.367)	0.291
Group size: small	−0.217	(−0.378, −0.059)	0.124
Adults ∗ group size	0.464	(0.144, 0.767)	0.004

Main effects were retained in the model when they were part of a significant interaction.

(Fig. 1). We found an additional interaction between the presence of adults and observation number on latency to attack. Groups without adults always took a long time to attack across all observations, whereas groups with adults attacked more quickly at first, but then took longer to attack during subsequent observations (Fig. 2).

The maximum number of attackers that a group committed to prey capture differed depending on our treatments as well. We found a significant interaction between the presence of adults and group size on number of attackers (Table 2). Specifically, the
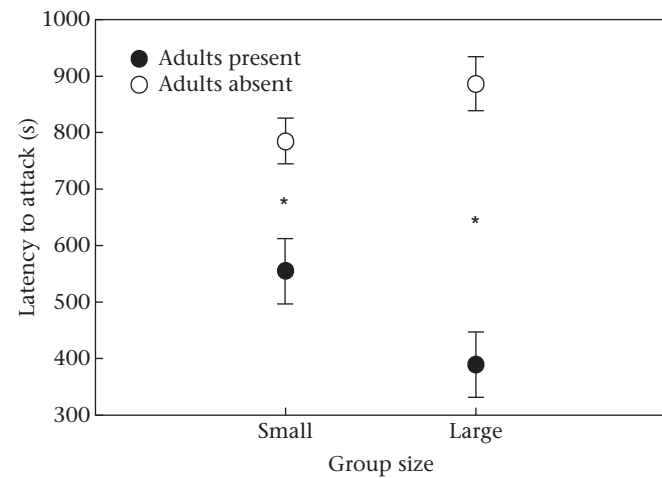
presence of adults in a group increased the maximum number of attackers, but this effect was only found within the small groups; large groups always committed roughly the same number of individuals regardless of whether adults were present (Fig. 3). There was no overall effect of the presence of adults or of group size; however, groups did decrease their number of attackers with repeated observations (Table 2).

We found no evidence for consistent among-group variation in either of our collective behaviours. Repeatability estimates for both behaviours were essentially zero (latency to attack: $r = 3.5 \times 10^{-5}$, 95% CI (0, 0.02); number of attackers: $r = 4.9 \times 10^{-5}$, 95% CI (0, 0.01) and inclusion of the group random effect was not supported by changes in DIC values (latency to attack: $\Delta DIC = +1.5$; number of attackers: $\Delta DIC = +6.03$).

DISCUSSION

The results of our study demonstrate that the presence of a few mature individuals increases juvenile aggressiveness during collective prey capture. Specifically, groups with adults attacked prey much faster than groups lacking mature individuals. Interestingly, this was not driven by adults 'leading the way', as they were never observed joining the collective prey capture. Enhancing foraging has long been considered a primary function of sociality in social spiders (Whitehouse & Lubin, 2005), but our results suggest a previously unknown mechanism (i.e. a catalytic effect of mature individuals on juvenile foraging). One potential explanation may be that the increased foraging aggressiveness of the young during our experiments was a result of adults excluding the young during the maintenance feedings, so that the juvenile spiders were hungrier during the actual experiments.

Figure 1. Influence of adult presence/absence on juvenile social spiders' mean ± SE latency to attack prey (time until first attack) in large and small groups.
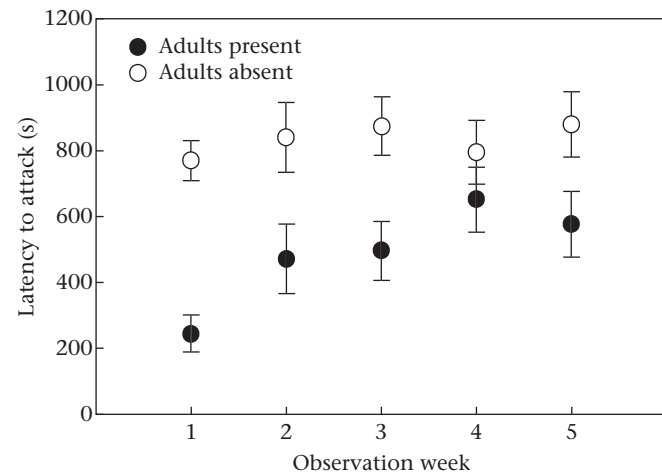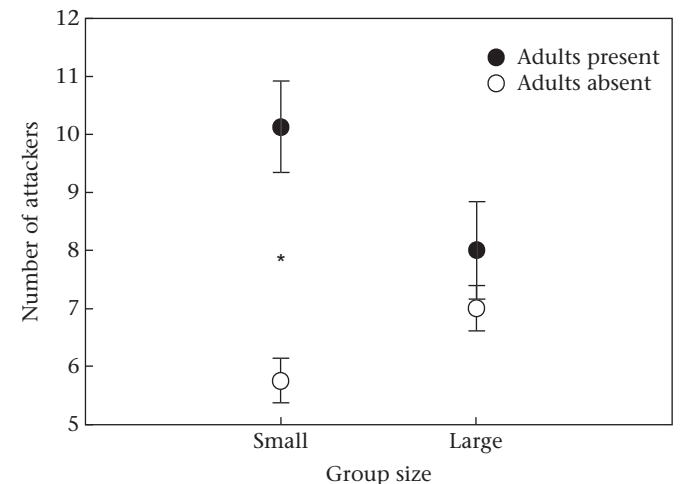

Figure 2. Influence of adult presence/absence on juvenile social spiders' mean ± SE latency to attack prey (time until first attack) after 1−5 weeks of observation.

Figure 3. Influence of adult presence/absence on the mean ± SE number of attackers in large and small groups of juvenile social spiders.

However, at odds with this hypothesis, we never actually observed any adults engage in foraging behaviour of any kind. Surprisingly, group size did not significantly influence any aspect of collective foraging behaviour, but instead only mediated the magnitude with which adult presence impacted juvenile foraging aggressiveness: the adults' positive impact on the latency to attack was much stronger in large groups than in small groups. Conversely, adult presence increased the number of attackers only in small groups. Taken together, group size seems to be a key factor governing the impact of age demography on collective foraging.

In accordance with our first prediction, adult presence increased juvenile foraging aggressiveness, and their attack speed in particular. Importantly, this was driven by mere adult presence and not by adult participation in prey capture. The most likely explanation for our result is that adult presence increased the juveniles' willingness to attack prey. This could be due to a couple of nonmutually exclusive explanations. First, adults might alert juveniles to the presence of prey by causing vibrations in the webbing as has been observed in *Theridion saxatile* (Nørgaard, 1956). Second, adults might have competitively excluded the juveniles from the maintenance feedings, so that the juveniles were hungrier during the experiments. Larger females are known to experience competitive advantages in *S. dumicola* (Whitehouse & Lubin, 1999), so adults would presumably be able to monopolize some prey items. However, it is unknown whether mature females forage during the nursery period and, if so, whether they share prey with the young or not. This competitive exclusion scenario seems unlikely to us because we never observed adults participate in any prey capture events. Regardless of the underlying mechanism, our results suggest that mature social spiders act as keystone individuals during the nursery period by catalysing juvenile collective foraging. The increased foraging aggressiveness should in turn increase juvenile prey capture efficiency, growth and survival (Pasquet & Krafft, 1992; Pruitt & Keiser, 2014).

Although group size by itself did not significantly influence latency to attack or number of attackers in our study, it acted as a key mediator between age demography and both aspects of collective foraging. While adult presence enhanced attack speed regardless of group size, this effect was about 50% stronger in large groups compared to small groups (Fig. 1). The reason for this could be that the combined effects of higher competition in large groups between the young (Schneider, 1995) and adult presence (e.g. adults might have signalled prey presence to the young) increased the spiderlings' willingness to attack prey rapidly. While mature *S. dumicola* groups attack prey with more individuals if the group is larger (Modlmeier, Forrester, et al., 2014), we did not find a significant main effect of group size on the number of attackers in groups composed of juvenile spiders (Fig. 2); large groups always committed about the same number of individuals (~7–8 individuals) to the attack regardless of whether the adults were present or not. Since competition for prey increases with group size in juveniles (Schneider, 1995), it is possible that monopolization and fighting over prey (i.e. a more selfish behaviour) limited the maximum number of attackers in large groups. Surprisingly, small juvenile spider groups reached a higher hunting participation than groups twice their size when adults were present (Fig. 3). Therefore, adult presence could dictate the diversity of prey size classes that smaller groups are able to subdue. This is a vital point because the ability to subdue large, profitable prey is thought to be the primary driver of sociality in social spiders and other cooperative hunters (Creel & Creel, 1995; Guevara, Gonzaga, Vasconcellos-Neto, & Avilés, 2011; Scheel & Packer, 1991). Harwood and Avilés (2013) previously suggested that whether spider colonies realize the full hunting potential of their group size depends on the behaviour of its members. Yet, adult presence did not affect the number of attackers in large groups, suggesting that larger group size might diminish the positive effect that keystone individuals have on their group.

The lack of repeatability in collective foraging behaviour of juveniles is surprising, because mature *S. dumicola* groups show highly consistent differences in their latency to attack prey and in the number of attackers that respond during prey capture (Keiser et al., 2014; Modlmeier, Forrester, et al., 2014). Juvenile groups might behave more erratically than mature groups and/or lack the idiosyncratic intergroup differences in foraging behaviour that mature groups exhibit. Although the development of animal personality on the individual level has received increased attention during the last few years (Laskowski & Pruitt, 2014; Modlmeier, Laskowski, et al., 2014; Stamps & Groothuis, 2010), studies on the development of collective personality throughout a group's lifetime are virtually nonexistent (Bengston & Jandt, 2014; but see Gordon, 1991; McDonald & Topoff, 1986). All groups exhibited decreased prey capture participation with repeated observations. We argue that this could be due to the high abundance of food in the laboratory (Fig. 2), as seen in the desert spider *Seothyra henscheli* (Lubin & Henschel, 1996). This indicates that the influence of adults on the aggressiveness of their groups gradually subsides over time, presumably also due to satiation effects (Ainsworth, Slotow, Crouch, & Lubin, 2002). Alternatively or in addition, gerontophagy might have contributed to the vanishing effect of the adults, because all adults had died by the end of the experiment and were presumed to have been consumed (at least in part) by the young. In fact, the observation that the adults' effect on foraging aggressiveness disappeared as the adults were dying strengthens the idea that behavioural differences in groups with and without adults are due to the adults' presence. In comparison, groups without adults maintained a relatively slow attack speed throughout the 5-week observation period.

In summary, our study suggests a previously unknown effect of adult presence for juvenile social spider groups, that is, their catalytic effect on juvenile foraging aggressiveness. Shorter latencies to attack and higher numbers of attackers can improve prey capture efficiency by reducing the time and effort needed to immobilize prey (Pasquet & Krafft, 1992). Furthermore, a higher number of attackers will allow groups to subdue large and more profitable prey items (Nentwig, 1985; Yip, Powers, & Avilés, 2008). Accordingly, groups with a higher foraging aggressiveness should gain more mass and show a higher survival (Pruitt & Keiser, 2014). Therefore, we argue that this phenomenon could have facilitated the evolution of sociality in social spiders by benefiting groups with late dispersal or philopatry. While extended maternal care via food provisioning is thought to be an important precursor to sociality in cooperative spiders (Whitehouse & Lubin, 2005), no studies have so far quantitatively examined whether adult presence might also influence juvenile foraging behaviour. Surprisingly, adults did not participate in prey capture in our experiments, indicating that food provisioning by the adults influences juvenile behaviour, possibly by modulating their willingness to attack prey. Interestingly, the positive influence of adults on foraging aggressiveness was mediated by group size in opposite directions, either increasing adult impact in large groups (for attack latency) or completely eliminating their influence in large groups (for the number of attackers), depending on the trait considered. This suggests that group size plays a major role in mediating the impact of putative keystone individuals on collective behaviour, further emphasizing the need to study the influence of group composition across different group sizes in this and other systems.

Acknowledgments

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