Animal Behaviour 109 (2015) 9–14

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Adult presence augments juvenile collective foraging in social spiders

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ARTICLE INFO

Article history:
Received 24 February 2015
Initial acceptance 2 April 2015
Final acceptance 20 July 2015
Available online
MS. number: A15-00152R

Keywords:
age demography
collective behaviour
foraging
group size
keystone individual
social spider

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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http://dx.doi.org/10.1016/j.anbehav.2015.07.033
0003-3472/

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 post-reproductive 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