



Increased bacterial load can reduce or negate the effects of keystone individuals on group collective behaviour



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In many societies certain individuals play a central role in the execution of collective behaviours and group success, termed 'keystone individuals'. To date, most studies on keystone individuals have focused on their mere presence/absence and have failed to consider how their influence changes as a function of their condition or recent experiences. Here we explore how the influence of putative keystone individuals on group collective behaviour changes as a function of recent increases in cuticular bacterial load. In the spider *Stegodyphus dumicola*, individuals that exhibit the greatest 'boldness' are important determinants of colony foraging behaviour and success. We topically exposed individual spiders that varied in their boldness to a combination of naturally occurring cuticular bacteria (*Bacillus thuringiensis*, *Microbacterium oxydans*, *Pantoea* sp.) known to be harmful to *S. dumicola*, and then tracked the effects that this exposure had on their colonies' foraging and web-building behaviour. We found that colonies with unexposed keystones attacked prey more quickly and with more attackers than colonies in which the keystone was exposed to bacteria. Moreover, the relationship between keystone individuals' boldness and colonies' attack speed differed based on whether or not the keystone was recently exposed. The number of spiders that participated in nightly web building was greater in colonies containing unexposed keystones than in colonies lacking a keystone, whereas colonies containing recently exposed keystones deployed an intermediate number of individuals. This trend, however, disappeared after the second night of observation. Together, our results suggest that a group's collective behaviour can be altered based on a single individual's recent experience with microbes.

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The collective behaviours of animal societies are more than just a stunning display of biological organization; they are also a key determinant of the success or collapse of societies across the animal kingdom. The transition from solitary living to multilevel sociality has been described as one of the great evolutionary transitions in biological organization, by allowing animal societies to perform feats that are unachievable by solitary individuals (Maynard Smith & Szathmáry, 1997). Although theorists have classically maintained an egalitarian view regarding the organization of collective behaviours for many animal societies, behaviourists are becoming increasingly aware of the role that certain key individuals play in the execution and performance of collective traits. These range from well-established examples like leaders in fish schools (Bumann & Krause, 1993) to lesser-known examples like tutors in bat roosts (Knörnschild, Nagy, Metz, Mayer, & von Helversen, 2010)

or knowledgeable matriarchs in elephant herds (McComb, Moss, Durant, Baker, & Sayialel, 2001). These individuals that, in some instances, exert an inordinately large effect on the success of their social group have been termed 'keystone individuals' (henceforth referred to as 'keystones'), akin to the keystone species concept of community ecology (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014; Paine, 1969).

There are myriad examples demonstrating how the presence of keystones can augment collective behaviours or enhance group productivity and survivorship (reviewed in Modlmeier, Keiser, et al., 2014). However, circumstances also exist where the presence of key individuals can dampen collective behaviours or even incite the demise of the entire group. In fact, the term 'keystone individual' was first coined to describe a particular case of destructive keystones, where the presence of so-called 'hyperaggressive males' can depress the reproductive success of entire groups of water striders (*Aquarius remiges*: Chang & Sih, 2013; Sih & Watters, 2005). A similar phenomenon had also previously been observed in yellow baboons, *Papio cynocephalus* (Alberts, Sapolsky, & Altmann, 1992). Other examples exist where the collective

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exploratory behaviour of feral guppy (*Poecilia reticulata*) schools is restricted by the least active member of the group (Brown & Irving, 2014), and the foraging preferences of dominant pairs of brant geese, *Branta bernicla*, can monopolize preferred food plants for up to 2 years (Prop & Deerenberg, 1991). Even more intriguing, however, are instances where the effects of keystones shift from positive to negative (or vice versa) as a consequence of their condition (e.g. via ageing, injury, or reproductive status; Brent et al., 2015; Horner, Proctor, Bonnie, Whiten, & de Waal, 2010; McComb et al., 2011). These cases are particularly informative because they can help us identify the factors driving the tipping point between when keystones become advantageous, disadvantageous, or entirely impotent. Unfortunately, our present understanding of how keystones' condition alters their social influence remains limited because of a scarcity of experimental evaluation. Many of the case studies mentioned above are correlative and/or unreplicated.

One instance where keystone individuals might lose their influence or where their presence may become disadvantageous is when they suffer microbial infection or an altered resident microbial community, given that infection risk is often associated with functionally important behavioural traits like social dominance (Sapolsky, 2005), aggressiveness (Jin, Su, Tao, Guo, & Yu, 2013) and exploratory behaviour (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010). Perhaps coincidentally, the most well-publicized examples of disadvantageous keystones come from epidemiology, where 'superspreader' individuals generate a disproportionately large number of secondary infection cases relative to other 'generic' infected individuals (Lloyd-Smith, Schreiber, Kopp, & Getz, 2005). Unfortunately, superspreaders are often only identified a posteriori as the index cases of larger epidemics or local transmission events in human (Gahr et al., 2014; Gibbins, 1998; Shen et al., 2004) and animal populations (Hampson et al., 2009; Kao et al., 2007; Matthews et al., 2006). Furthermore, cases where formerly influential keystone individuals, such as leaders or elites, develop microbial infections and thus potentially become detrimental (or at least impotent) to their group are almost entirely absent (but see Sapolsky & Share, 2004).

In social spiders of the genus *Stegodyphus*, the collective performance of an entire society (which can contain a few dozen to several hundred individuals) can hinge on the behaviour of one or a few key individuals (Pruitt, Grinsted, & Settepani, 2013; Pruitt & Keiser, 2014). The magnitude by which keystones augment collective foraging and group success is positively associated with the keystone's boldness, defined as the latency to resume normal activity after an aversive stimulus (Sloan Wilson, Clark, Coleman, & Dearstyne, 1994). Pruitt and Keiser (2014) recently demonstrated that the presence of just one extremely bold individual can enhance the foraging aggressiveness of an entire colony, increasing the average mass gained by their colony-mates. These keystone individuals initiate more foraging bouts than their less bold colony-mates, although their presence seems to eventually catalyse increased foraging aggressiveness in their previously shy colony-mates. Given our knowledge of the role that these keystone individuals play in their colonies, and the ease by which *Stegodyphus* spp. colonies can be manipulated experimentally in both the laboratory and field (Grinsted, Pruitt, Settepani, & Bilde, 2013; Keiser, Jones, Modlmeier, & Pruitt, 2014; Keiser & Pruitt, 2014; Pruitt et al., 2013; Pruitt & Keiser, 2014), this system represents a superb model to test questions on how interactions between keystone individuals and microbes can change the collective behaviour of their colonies. In *Stegodyphus dumicola*, experimental increases in resident cuticular bacterial load can, depending on the bacteria under consideration, result in depressed weight gain and increased mortality in some individuals, although there is no evidence that cuticular microbes alter host behaviour (Keiser et al., 2016).

Here, we test the collective behaviours of *S. dumicola* colonies containing keystones of varying boldness and bacterial exposure by presenting them with a pair of ecological challenges: prey capture and web construction/repair. We aimed to address the following three questions. (1) To what degree will a putative keystone individual's prior exposure to harmful bacteria alter the collective behaviour of the colony? (2) To what extent will the personality type (boldness) of the keystone alter the association between its bacterial exposure history and its colony's collective behaviour? (3) Does a putative keystone individual's propensity to participate in collective behaviour change based on prior exposure to harmful bacteria? Addressing these questions is important because their answers will help probe the robustness of complex systems that rely on just one or a few highly influential individuals.

METHODS

Collection and Maintenance

Stegodyphus dumicola is an Old World social spider that lives in female-biased, age-structured colonies of a few dozen to several hundred individuals throughout southwestern Africa (Avilés, Varas, & Dyreson, 1999; Henschel, 1998; Henschel, Lubin, & Schneider, 1995). Female *S. dumicola* cooperate with colony-mates in collective foraging, web maintenance and alloparental care (Bilde et al., 2007). *Stegodyphus dumicola* colonies are composed of two discrete functional units: a three-dimensional, dense silken retreat and one or a few two-dimensional capture webs where spiders interact with prey. Spiders repair damage to this capture web nightly (Keiser, Jones, et al., 2014). We collected 19 colonies of *S. dumicola* along roadside *Acacia* trees in the Northern Cape of South Africa in January 2015. Spiders were transported back to our research site near Griekwastad, Northern Cape (28°54'32.0"S, 23°24'33.7"E) where the colonies were maintained indoors in 500 ml plastic cups at ambient temperature and natural light:dark cycle. Prior to experimentation, we isolated each adult female from the colony in 1 ml plastic condiment cups.

Bacteria Collection, Identification and Maintenance

We collected bacteria from the cuticles of adult female spiders in the field following aseptic technique by swabbing the cuticle of a haphazardly chosen spider with a sterile cotton-tipped swab and plating these isolates directly on Luria-Bertani (LB) broth. Bacteria were identified using 300 bp 16S ribosomal DNA sequencing and MicroSeq[®] BLAST Software (SeqWright Genomic Services Houston, TX, U.S.A.). From the cuticles of three different spiders, we identified *Microbacterium oxydans*, *Bacillus thuringiensis* and *Pantoea* sp., among others not used in the present study. Bacteria were stored in 25% glycerol at –80 °C until the onset of experimentation. Resurrected bacteria were maintained on LB agar, and liquid cultures were prepared by isolating a single colony with a sterile micropipette tip and placing it in 1 ml of LB broth overnight at ambient room temperature. Directly prior to experimental application, equal parts of the three bacterial liquid monocultures were mixed to form a bacterial 'cocktail'. Although we were unable to estimate cell densities for these bacterial solutions, previous experiments have verified that the cell density of this cocktail (estimated via optical density) when grown in this way is not significantly different from that of each bacterial species contained therein when grown in monoculture (Keiser et al., 2016).

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