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The personality types of key catalytic individuals shape colonies' collective behaviour and success

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Behavioural ecologists often note that one or a few group members appear to shape the collective behaviour of social groups differentially. Our understanding of these keystone individuals is largely taken from meticulous field observations and semi-scientific anecdotes. In this study we experimentally test whether the behavioural tendencies of putative keystone individuals shift the collective behaviour of colonies using the social spider *Stegodyphus dumicola*. Prior studies on *Stegodyphus* demonstrated that the single best predictor of colonies' collective behaviour is the behaviour of colonies' boldest individual. Here, we probe the causal relationship between the traits of extremely bold individuals and colonies' collective behaviour by experimentally creating colonies of identical size and personality composition in the laboratory and then adding a single individual of varying boldness (the putative keystone individual). Experimentally adding just one extremely bold individual increased the foraging aggressiveness of entire colonies and altered the total mass gained by fellow group members, relative to the addition of a less bold individual. Additionally, our data suggest that bold individuals are capable of such influence because they catalyse variation in the behavioural tendencies of fellow group members.

Fastidious observers of animal societies often note that one or a few key individuals appear to exert an inordinately large influence over groups. Dominant males in lekking species (Ballard & Robel, 1974), alpha individuals in primate societies (Alberts, Sapolsky, & Altmann, 1992), queens in social insect colonies (Aron, Passera, & Keller, 1994), and superspreaders in disease transmission networks (Meyers, Pourbohloul, Newman, Skowronski, 2005) all share the common feature that they are thought to affect their groups more strongly than standard, more generic individuals. Here, we term these animals 'keystone individuals' or merely 'keystones', which, analogous to Paine's 'keystone species' concept (Paine, 1966, 1995), are defined as individuals that show an inordinately large influence over their social groups relative to their abundance (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih & Watters, 2005). The ecological effects of these individuals vary wildly among study systems, and their mere presence can become major drivers of social groups' success (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014).

Although behavioural ecologists have often observed the effects of keystone individuals in situ (reviewed in Modlmeier et al., 2014), rigorous and experimental studies of these effects are rare (Flack, Girvan, de Waal, & Krakauer, 2006; Flack, Krakauer, & de Waal, 2005). Instead, the evidence behind the role of keystones is more regularly treated as a series of semi-scientific anecdotes or idiosyncratic field observations (e.g. Pyle, Schramm, Keiper, & Anderson, 1999; Sapolsky & Share, 2004). This is, in part, because manipulating the presence/abundance of putative keystone individuals is intractable for the majority of study systems. For example, predicting which individuals will act as keystones can prove difficult (e.g. during outbreak of severe acute respiratory syndrome, SARS; Shen et al., 2004) and, in some cases, the addition/removal of keystone individuals is impossible (e.g. McComb et al., 2011). Consequently, we maintain a poor understanding of (1) how keystone individuals are maintained within populations, (2) the behavioural and physiological mechanisms by which they exert their influence over their fellow group members and (3) how variation in the traits of the keystone individuals themselves shift the collective behaviour or performance of their associated societies. Exploring these avenues is important for our understanding of animal societies because the data available, although quite limited, suggest that keystones have the potential to become powerful arbiters of collective behaviour and group success (e.g. McComb et al., 2011; Sih & Watters, 2005).

Social spiders, like those of the genus *Stegodyphus,* are a superb model with which to explore the effects of keystone individuals on

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collective behaviour. Social *Stegodyphus* live in cooperative foraging societies characterized by highly female-biased sex ratios, serial within-colony inbreeding and a high incidence of colony turnover (Aviles, 1997; Lubin & Bilde, 2007). Like all social spiders, the majority of colony maintenance tasks are performed by females. Shared colony maintenance tasks include cooperative prey capture, shared web maintenance and alloparental care.

In a previous field study on intercolony variation in collective behaviour, we demonstrated that social *Stegodyphus* colonies show stable, characteristic differences in their collective-foraging behaviour: some colonies attack prey rapidly with numerous attackers, whereas other colonies attack prey more slowly with fewer attackers (Keiser, Jones, Modlmeier, & Pruitt, 2014; Pruitt, Grinsted, & Settepani, 2013). Most notably, the single best predictor of intercolony variation is the behavioural tendency (or 'personality') of colonies' boldest individuals. Boldness, in this context, is defined as the latency for an individual to resume activity after an aversive threatening stimulus. Strikingly, this variable alone explains more than 60% of the naturally occurring variation in colonies' collective-foraging behaviour (Pruitt et al., 2013). This result is intriguing because it implies that the behavioural tendencies of these extremely bold individuals may somehow drive colonies' collective behaviour. Unfortunately, these correlative data were unable to verify a causal relationship between the presence of these extremely bold individuals and colonies' collective behaviour.

In this study, we investigate the presence of extremely bold individuals on colonies' collective behaviour by manipulating colony composition in the laboratory. Specifically, we asked the following questions. (1) Does the presence of a single extremely bold individual predictably change the collective-foraging behaviour of a colony composed of nonbold individuals? (2) Are extremely bold individuals more likely to engage in foraging behaviour than their nonbold colonymates? (3) How does the presence of an extremely bold individual change the behavioural tendencies of other group members? (4) Is colony performance (i.e. change in mass and colony members' survivorship) associated with the phenotypes of their boldest individuals? Together, our studies were designed to probe more deeply into the interplay of animal personality, keystone individuals and collective behaviour than has been achievable to date.

METHODS

Study System

Stegodyphus dumicola (Araneae, Eresidae) is a patchily abundant spider throughout southwestern Africa living in colonies containing 1–2000 individuals (Bilde et al., 2007). Colonies' webs consist of two functionally distinct and connected structures: the capture web and the nest. The nest is composed of a dense three-dimensional matting of silk, dried leafs and prey carcasses, which together serve as the spiders' retreat during the day. In addition, webs contain one or more two-dimensional capture webs composed of sticky cribellate silk that extend out from the nest and serve to intercept prey (Henschel, 1998). When prey make contact with the capture web, one or more spiders emerge from the nest, locate the struggling prey and subdue them. Once subdued, a prey item is either dragged back to the nest and shared with other group members or consumed directly on the capture web.

The spiders used in these experiments were collected as mixture of adults and subadults in the Northern Cape, South Africa along the southern edge of the Kalahari Desert (28°26′S, 21°21′E, 894 m elevation). Colonies were collected by first disturbing the capture web, which resulted in the spiders retreating into their nest. The nest was then plucked off of its substrate in its entirety and placed within a chiffon pillow case. Colonies were transported back to nearby hostels/hotels where they were hand-sorted. The number of colony members and inquilines (i.e. heterospecific arthropods living as social parasites in the nest) were counted and colony members were placed together in a clear 490 ml plastic container for transport to Pittsburgh, PA, U.S.A. In Pittsburgh, we again hard-sorted through colonies, determined the boldness of each individual spider and maintained spiders individually in 2-ounce (6 ml) plastic cups. Animals were kept in isolation for 14 days prior to the experiments outlined herein. Spiders were fed a maintenance diet of one 2-week-old cricket, once per week. Water was provided by misting the webs with a water bottle every 3 weeks.

Procedural Overview

To observe whether the behavioural tendency of a single very bold individual is sufficient to change the collective behaviour of a colony, we created colonies of nine *S. dumicola* with identical low boldness scores ('personality' assay described below). To these colonies we then added one bolder individual from the same source colony (i.e. a putative keystone), determined randomly using statistical software, that varied in its degree of boldness depending on the colony. Some colonies received only a modestly bold individual, while others received a considerably bolder individual, and still other colonies received an extraordinarily bold individual. Care was taken not to mix spiders from multiple source colonies, and thus, relatedness among experimental colony constituents resembled that of naturally occurring colonies. Colonies of *Stegodyphus* are very highly inbred ($r \approx 0.70$) as a consequence of low dispersal among colonies and serial within-colony inbreeding (Smith, Van Rijn, Henschel, Bilde, & Lubin, 2009). The mass of each spider was measured prior to experimental combinations. A total of 36 experimental colonies were created in this way. We then split these colonies among two experimental treatments. In half of these colonies, we tested their collective behavioural response to an unrewarding vibratory stimulus daily for 5 days. In the other half of the colonies, we tested collective-foraging behaviour with an identical vibratory stimulus but, upon attacking the artificial stimulus, we rewarded spiders with a presubdued prey item. We then compared the relationship between the behavioural tendencies of colonies' boldest individuals and colonies' collective-foraging behaviour: the latency for the first spider to bite the vibratory stimulus and the total number of spiders that were out on the capture web during the time of attack. At the end of our assessment of colonies' collective-foraging behaviour, colonies were taken apart and the boldness of each individual was reassessed. To assess the effect of putative keystone individuals on colony performance, we compared the collective mass gain of the nine generic colony members over the duration of our collective-foraging assays (total mass after – total mass before). For this performance metric we restricted our analysis to colonies that received a rewarding prey stimulus.

Personality Assays

Boldness assays were designed to resemble the sensory cue of a rapidly approaching aerial predator (e.g. avian, chiropteran, wasp, etc.), which web-building spiders detect via a sudden, rapidly moving and directional jet of air (Jones et al., 2011; Riechert & Hedrick, 1993). The individual-based assay described below elicits a highly repeatable behavioural response, and is an informative indicator of individuals' behaviour in a social context and predicts survivorship under increased predation risk (Grinsted, Pruitt, Settepani, & Bilde, 2013; Pruitt et al., 2013; Riechert & Hedrick,