Author for correspondence:
Jonathan N. Pruitt
e-mail: agelenopsis@gmail.com

THE ROYAL SOCIETY
PUBLISHING

The Achilles' heel hypothesis: misinformed keystone individuals impair collective learning and reduce group success

Jonathan N. Pruitt[1,2], Colin M. Wright[1], Carl N. Keiser[1], Alex E. DeMarco[3], Matthew M. Grobis[4] and Noa Pinter-Wollman[5]

[1]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA
[2]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, USA
[3]Department of Biological Sciences, East Tennessee State University, Johnson City, TN, USA
[4]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA
[5]BioCircuits Institute, University of California San Diego, La Jolla, CA, USA

Many animal societies rely on highly influential keystone individuals for proper functioning. When information quality is important for group success, such keystone individuals have the potential to diminish group performance if they possess inaccurate information. Here, we test whether information quality (accurate or inaccurate) influences collective outcomes when keystone individuals are the first to acquire it. We trained keystone or generic individuals to attack or avoid novel stimuli and implanted these trained individuals within groups of naive colony-mates. We subsequently tracked how quickly groups learned about their environment in situations that matched (accurate information) or mismatched (inaccurate information) the training of the trained individual. We found that colonies with just one accurately informed individual were quicker to learn to attack a novel prey stimulus than colonies with no informed individuals. However, this effect was no more pronounced when the informed individual was a keystone individual. In contrast, keystones with inaccurate information had larger effects than generic individuals with identical information: groups containing keystones with inaccurate information took longer to learn to attack/avoid prey/predator stimuli and gained less weight than groups harbouring generic individuals with identical information. Our results convey that misinformed keystone individuals can become points of vulnerability for their societies.

1. Introduction

A group's composition often determines its success. Factors such as group size [1], sex ratio [2,3], relatedness [4], demography [5], body size distribution [6] and behavioural composition [7–9] result in emergent group phenotypes [10] that, in turn, help to determine their fate. This relationship is well recognized in behavioural ecology [11–13]. Yet the effects of group composition can often be subtle, non-additive and counterintuitive, especially in societies harbouring keystone individuals, which are defined as individuals that exhibit a disproportionately large influence over groups' collective behaviour or success [14].

Keystone individuals are a common and often volatile social phenomenon present in a variety of systems. Movement leaders [15,16], knowledgeable tutors [17,18], disease super-spreaders [19,20], hyperaggressive males [21] and social arbitrators [22,23] represent just some of the ways in which one or a few individuals can influence entire societies. Interestingly, evidence from dozens of field studies indicates that the effects of keystone individuals on group success can range from beneficial to disastrous, depending on numerous circumstances [14]. Thus, the same group members that are invaluable in one context can prove problematic in another. For example, individuals that are responsible for

rapid transmission of beneficial substances, such as food, may also cause accelerated disease spread [24]. Unfortunately, much of our understanding of how keystones operate comes from descriptive studies [25]. We therefore maintain a relatively weak mechanistic understanding of how keystones exert their influence and/or which factors can cause a keystone's impacts to switch from positive to negative.

Social interaction networks have the potential to spread the impact of keystone individuals throughout the colony quickly. In particular, theory and some empirical work suggest that highly connected [26] and socially influential [27,28] individuals might spread information quickly and thoroughly throughout their group. If this is true, and if information accuracy is important for group success, then the impacts of keystone individuals could change drastically depending on whether they possess accurate or inaccurate information. Notably, network centrality is just one mechanism by which keystone individuals can come to wield social influence. In this study, we test the hypothesis that the group-level consequences of information (accurate or inaccurate) will vary depending on whether or not its original bearer is a keystone individual. Specifically, we predict that the effects of both accurate and inaccurate information will be most pronounced when the keystone individual is its original bearer. We liken any instance where singularly influential individuals enhance group performance under some conditions at the cost of performance during others to an idiomatic Achilles' heel, defined as an attribute that renders its bearer vulnerable in spite of an overall strength [29]. We hypothesize that any society that relies on keystone individuals for success renders itself vulnerable to manipulation if such individuals depart, perish or become compromised. In contrast, if societies lacked such individuals and were instead composed of equivalent group members, the effect of compromising any one individual would be comparatively small. We term this hypothesis the Achilles' heel hypothesis.

In the social spider Stegodyphus dumicola (Araneae, Eresidae), a group's boldest individual has a disproportionately large influence over group hunting behaviour and success [30,31]. Boldness is defined as an individual's tendency to place themselves in a threatening situation [32], which in S. dumicola is expressed as a short latency to resume normal activity after being presented with an aversive stimulus. Links between personality and probability of becoming keystone individuals are fairly common [14,33]. In S. dumicola, the link between boldness and keystone-ness is particularly strong ($R^2 = 0.36-0.67$) [30,31]: simply adding one very bold individual to a colony increases the number of attackers that respond to live prey by 300–600% and increases the mass gained by societies as a whole by 300%, and these effects linger for weeks after a keystone individual's removal [34]. No such effects are observed when the presence of shy individuals is manipulated. These bold individuals appear to exert their disproportionately large influence over group behaviour (i.e. act as keystone individuals) by catalysing aggressive foraging behaviour in their otherwise shy colony mates [31,34]. The longer that keystone individuals remain in a group, the more dramatic their effects become and the longer their effects linger following their departure or death [34].

In S. dumicola, particularly bold individuals, which previous work indicates function as keystone individuals [30,31], are often the first individuals to interact with both prey and predators following dispersal. For a few days after colony establishment, keystone individuals initiate and complete a disproportionately large number of prey capture and web repair events [31,35]. This means that keystone individuals are potentially the first individuals to obtain information about their new environment, and these individuals may be more adept at spreading such information because of their enhanced social influence. We posit that the accuracy of this information could shape both colony performance and the speed at which whole societies learn about changing environments.

To examine how keystone individuals influence the rate at which their groups collectively learn about their environment, we created experimental colonies in which one individual was trained to associate one vibratory stimulus with a profitable prey item and a second stimulus with that of a predator. We then subjected colonies to conditions that either matched or mismatched the trained individual's training. We subsequently tested how the tendency of colonies to attack either stimulus changed over time. Specifically, we predict (i) that the speed at which colonies learn to respond to either stimulus appropriately will depend on whether the trained individual possesses accurate or inaccurate information, and (ii) that these effects will be more pronounced when the trained individual is a putative keystone individual. (iii) Finally, we predict that colonies will gain the most mass when keystone individuals harbour accurate information, and the least amount of mass when keystone individuals harbour inaccurate information. In contrast, we predict relatively minor colony-level effects when generic individuals harbour accurate versus inaccurate information. We define *generic* individuals as any non-keystone individual. In *S. dumicola*, generic individuals standardly represent 80–95% of all colony members and exhibit a shy behavioural tendency (N.P.-W. & J.N.P. 2016, unpublished data).

2. Material and methods

(a) Natural history

The social spider *S. dumicola* inhabits arid and semi-arid environments throughout southwestern Africa. This species lives in inbred colonies containing one to several thousand individuals [36,37]. Within these colonies, individuals cooperate in web maintenance, prey capture and alloparental care [38]. This species also exhibits a highly female-biased sex ratio, which is thought to be the outcome of historic patterns of colony-level selection for enhanced colony growth rate [3,39,40]. *Stegodyphus dumicola* webs are composed of two functional components: a dense three-dimensional labyrinthine retreat, where individuals reside for the majority of their time, and several two-dimensional capture webs that radiate out from the retreat, which serve to intercept prey [41]. Individuals rarely move between colonies in this species and new colonies are initiated by either one or a small group of gravid foundresses [37,42,43].

(b) Procedural overview

We collected 10 large *S. dumicola* colonies (240–689 females, average colony size = 30 spiders) along the southern Kalahari Basin in Upington, South Africa (28°49.094′ S, 21°52.034′ E) in February 2015. Colonies were collected by placing the entire colony within a cotton pillowcase and then trimming off the supporting branches. Colonies were then transported back to our camp at Koekais in Griekwastad, Northern Cape, South Africa. Colonies were hand-sorted and all of the resident individuals were counted and sexed. Only mature females were used for the

2

rspb.royalsocietypublishing.org   Proc. R. Soc. B 283: 20152888

present studies. The weight and body size (prosoma width) of all colony constituents were obtained using a portable balance and digital callipers. We then ran each spider through a behavioural assay (described below) to determine its 'boldness'. We subsequently assigned 10 females to each experimental colony: nine shy individuals and one bold individual that represented the putative keystone individual. This behavioural composition closely approximates those of naturally occurring colonies; most colonies contain 60–95% shy individuals [44]. Individuals were distinguished by an individualized sequence of paint markings atop their abdomens.

We used each source colony to make one experimental colony for each of nine treatments in a balanced split-colony design. We never mixed individuals from multiple source colonies, in order to preserve natural levels of within-colony relatedness and familiarity [36,45]. Before placing individuals together in an experimental colony, we selected either the bold individual or one shy individual haphazardly for training. Spiders selected for training were taught to associate one of two novel vibratory stimuli (stimulus A or stimulus B) with prey and the other with a predator. The vibratory stimulus that was paired with each outcome (prey or predator) was alternated among colonies. Training sessions occurred in individual 30 ml deli cups. Training sessions occurred twice daily for four days. After these training sessions, we placed all 10 individuals (one trained individual and nine naive individuals) within an experimental colony. The colony was allowed 24 h to construct a web. We subsequently assayed their collective response towards either stimulus twice daily for the next 6 days. We removed the trained individual from each colony prior to conducting the last two assays (nos. 11–12).

Half of the experimental colonies were maintained in an environment that matched the training of the trained individual ('informed' treatment), and the other half of the colonies were subjected to a reversal treatment, where the associations experienced by the colony mismatched the training of the trained individual ('misinformed' treatment).

(c) Boldness assays

Boldness is defined as an individual's willingness to place itself in a threatening or high-risk situation [32,46]. We assessed individuals' boldness as their latency to resume movement following an aversive stimulus, which is a commonly used metric in spiders [47,48] and other arthropods [49,50]. Individual spiders were taken from their home containers and placed in the centre of a circular open-topped arena. After 30 s of acclimation, two rapid puffs of air were applied to the anterior prosoma of the spider using an infant nose-cleaning bulb. This procedure resulted in the spider drawing its legs in tight against its body in a death-feigning posture. We then recorded the amount of time it took for the individual to resume its normal posture and traverse one body length. Trials were terminated after the spider moved one body length or after 600 s, whichever occurred first. Individuals with shorter latencies to resume movement were deemed 'bolder' than other individuals.

For our analyses, we create a boldness index by subtracting individuals' latency to resume movement following the aversive stimulus from 600 s (the maximum time), thus creating a boldness index where larger values represent higher degrees of boldness. This boldness metric is repeatable in all three species of social *Stegodyphus* and is associated with individuals' propensity to participate in prey capture and collective escape behaviour [31,35]. For these experiments, we operationally defined 'shy' individuals as those with a boldness score between 0 and 200, and 'bold' individuals as those with a boldness score between 400 and 600. This boldness metric exhibits a very high statistical repeatability (ICC = 0.60–0.80), thus individuals scored as bold remain behaviourally distinct from their shy counterparts [45,51].

(d) Individual training trials

Spiders were allowed 3 days to build a web individually in their 30 ml container before beginning their training regime. Training trials were initiated by removing the lid to the spider's container and placing a 1.5×1.5 cm piece of computer paper in the web. We then allowed 10 s of acclimation before gently touching the paper with a metal prod attached to a handheld vibratory device (GoVibe, Fun Factory). Two settings which varied in vibration frequency were used; which setting was associated with a predator and which with a prey item was alternated among individuals. The first stimulus was a consistent low amplitude vibration (stimulus A) and the second was a pulse setting characterized by pulses of high amplitude and brief pauses in between (stimulus B). We administered the stimulus for 90 s or until the spider emerged from its retreat and made contact with the paper. For our rewarding prey treatment, we provided attacking spiders with a small fragment of a karoo moth (*Loxostege trustalis*), which is a common prey item found in *S. dumicola* capture webs. For our unrewarding predator treatment, we touched attacking spiders with the anterior end of a live predatory ant, *Anoplolepis custodiens*, held by the thorax with a pair of tweezers. *Anoplolepis* is one of *S. dumicola*'s most significant predators [41].

For some colonies, the trained individual was a keystone (bold) individual and in others the trained individual was a generic (shy) individual. Individual learning trials were conducted in the morning and early evening hours each day for four consecutive days. We also implemented a set of control trials where individuals received an equal number of encounters with predator and prey as the treatment individuals, but there was no reliable (i.e. randomized) association between the stimulus and outcome (hereafter 'control individuals'). Control colonies contained one such spider and nine naive spiders. In half of the cases, the control spider was a keystone (bold) individual and in half it was a generic (shy) individual.

(e) Collective learning trials

Experimental colonies were constructed with nine shy individuals and one bold individual. Nine of these individuals were untrained naive individuals and one was a trained individual. Experimental colonies were constructed with one of nine treatments: colonies contained a trained individual with accurate or inaccurate information (i.e. matched or mismatched the trained individual's training); the trained individual was either a keystone (bold) individual or a generic (shy) individual; the experienced individual was trained to associate stimulus A with prey and stimulus B with predators, or vice versa. This constituted a fully factorial $2 \times 2 \times 2$ (eight treatments) experimental design, plus a set of control colonies in which a control individual was added to a group of naive spiders. We constructed five to seven colonies of each combination plus a set of 12 control colonies (total $n = 63$). We were prevented from having more colonies per treatment because some individuals died during the course of their training.

Colonies were constructed by placing all 10 spiders within a 490 ml plastic cup containing several clippings of dried red thorn acacia (*Vachellia reficiens*) to facilitate web construction. Colonies were given 24 h to construct a web before collective learning trials were initiated. As with the individual training trials, first a 1.5×1.5 cm piece of computer paper was placed onto the web. We then vibrated the paper with one of the two vibratory stimuli. If and when the colonies attacked, we administered the appropriate prey/predator outcome to the responding individuals' according to the treatment. Although only the responding individuals interacted with the predator, prey items were typically dragged back towards the nest and shared with other colony members. We recorded whether or not the colony attacked and their latency of attack for each interaction. Colonies were permitted 600 s to attack the prey, after which time we terminated the trial

and scored the colony as not having attacked the prey. One set of trials was performed in the morning and a second set at night for six consecutive days. On the evening prior to the last day, we experimentally removed the trained individual to determine whether the patterns observed over the course of our experiment were contingent on the trained individual's continued presence within the colony. In control colonies, we removed one randomly selected individual, to control for alterations to group size.

At the end of the sixth day, we randomly selected four untrained individuals per colony and re-determined their mass. We used their average change in mass as our metric of colony success. We deemed colonies that gained more mass (or those that lost less mass) per capita as being more successful.

(f) Statistical methods

To assess whether our individual training regime impacted individuals' latency to attack various stimuli, we used a GLMM. We included trial number, whether the individual was a keystone or not, treatment (stimulus A prey and stimulus B predator, stimulus A predator and stimulus B prey, control treatment) and a treatment × trial number interaction term as predictor variables in our model. We included source colony ID and individual ID nested within source colony ID as random effects. A significant interaction term between trial number and treatment (trained versus control individuals) indicates that individuals' response towards either stimulus changes over time as a result of their training. A separate analysis was run for the prey and predator outcomes, and thus we used a modified alpha of 0.025.

To test whether the influence of information quality changed depending on the social influence of its bearer, we used two GLMMs. We included information quality (informed, misinformed or control), whether the trained individual was a keystone versus generic individual, trial number, and all possible interaction terms as predictor variables in our models. Colonies' latency to attack was used as our response variable. Instances where colonies failed to attack were provided the maximum score of 600 s. We included source colony ID, experimental colony ID nested within source colony ID, and stimulus association (stimulus A prey and stimulus B predator, or vice versa) as random effects in our analysis. Again, a separate analysis was run for the prey and predator outcome, and thus we used a modified alpha of 0.025 for all of our statistics.

To determine the effects that our various treatments had on mass gain, we averaged the change in mass of the four exemplar individuals taken from each experimental colony and used this metric as our response variable. We included information quality (informed versus misinformed), whether or not the trained individual was a keystone, and the interaction term information quality × keystone/generic as predictor variables. Here again, we included source colony ID and stimulus association (stimulus A prey and stimulus B predator or vice versa) as random effects in our model.

For all of our analyses, we first considered models containing all of the random effect variables mentioned above. In cases where the random effect(s) did not explain a significant proportion of the variation (i.e. the 95% CI overlapped zero), we removed the effect(s) from the final analysis. The stimulus association pattern failed to explain a significant portion of the variation in any of our models so was excluded entirely from the final models. Effect sizes are given in terms of parameter estimates $\pm$ s.e. All of our analyses were run using JMP PRO v. 10.0.

3. Results

(a) Individual learning proficiency

Individuals learned to associate novel vibratory stimuli with prey. Our model predicting individuals' latency to attack the prey stimulus detected significant main effects of trial number ($F_{1,503.8} = 6.58$, $p = 0.011$, estimate $= -1.14 \pm 0.44$), whether or not the focal individual was a keystone individual ($F_{1,502.3} = 6.36$, $p = 0.011$, estimate $= 2.46 \pm 0.97$), treatment ($F_{2,484.4} = 8.08$, $p = 0.0004$, estimate $= -3.9 \pm 1.34$) and a near-significant interaction term, treatment × trial number ($F_{2,503.8} = 3.54$, $p = 0.03$, estimate $= -1.25 \pm 0.04$). This interaction term became non-significant when we removed the control treatment from the analysis ($F_{1,404.2} = 0.63$, $p = 0.42$, estimate $= 0.35 \pm 0.43$), indicating that whether the prey was associated with stimulus A or stimulus B had little bearing on outcome. All other main effects were non-significant ($p > 0.42$). Individuals of the control treatment tended to exhibit a similar, albeit erratic latency to attack the prey stimulus over time, whereas individuals that received a consistent association between the stimulus and prey reward attacked prey more quickly over time (electronic supplementary material, appendix 1). Overall, keystone individuals exhibited a latency to attack the prey stimulus 9–10 s faster than generic individuals ($F_{1,355} = 12.72$, $p = 0.0004$, estimate $= -2.46 \pm 0.97$). Such a different might seem trivial at first glance, but subtle differences in colonies' latency to attack doubtlessly translate into prey won or lost.

Individuals also learned to associate novel vibratory stimuli with a predator. Our model assessing individuals' latency to attack the predator stimulus detected significant main effects of trial number ($F_{1,502.1} = 44.50$, $p < 0.0001$, estimate $= 4.34 \pm 0.65$) and the interaction term treatment × trial number ($F_{2,502.1} = 10.7$, $p < 0.0001$, estimate $= 2.71 \pm 0.86$). Here again, this interaction term became non-significant when the control treatment was removed from the analysis ($F_{1,400.2} = 0.41$, $p = 0.51$, estimate $= 0.33 \pm 0.51$), indicating again that whether the predator outcome was associated with stimulus A or stimulus B had little bearing on the observed pattern. All other main effects were non-significant ($p > 0.47$). For the predator stimulus, control individuals again failed to exhibit any striking temporal pattern in their latency to attack. In contrast, individuals that received a consistent association between stimulus and predator outcome exhibited progressively longer latencies to attack the stimulus (electronic supplementary material, appendix 1).

(b) Collective learning proficiency

Colonies' latency to attack prey generally decreased with experience, and colonies containing an informed individual, keystone or otherwise, attacked prey more quickly and sooner during the experiment. Our model predicting colonies' latency to attack the prey stimulus detected main effects of information quality ($F_{2,565} = 12.71$, $p < 0.0001$, estimate $= -81.28 \pm 21.8$) and trial number ($F_{9,562.8} = 3.98$, $p < 0.0001$, estimate $= -63.28 \pm 23.21$). All other main effects were non-significant (all $p > 0.18$; figure 1). Notably, the effect of an informed individual lingered even after it was removed from the colony after trial no. 10 (figure 1). We further noted that colonies containing a misinformed keystone individual attacked prey more slowly than control colonies (figure 1), but no such effect was observed in colonies containing a misinformed generic individual. Here again, colonies containing misinformed keystones exhibited this pattern throughout the majority of the experiment, even after the misinformed individual's departure.
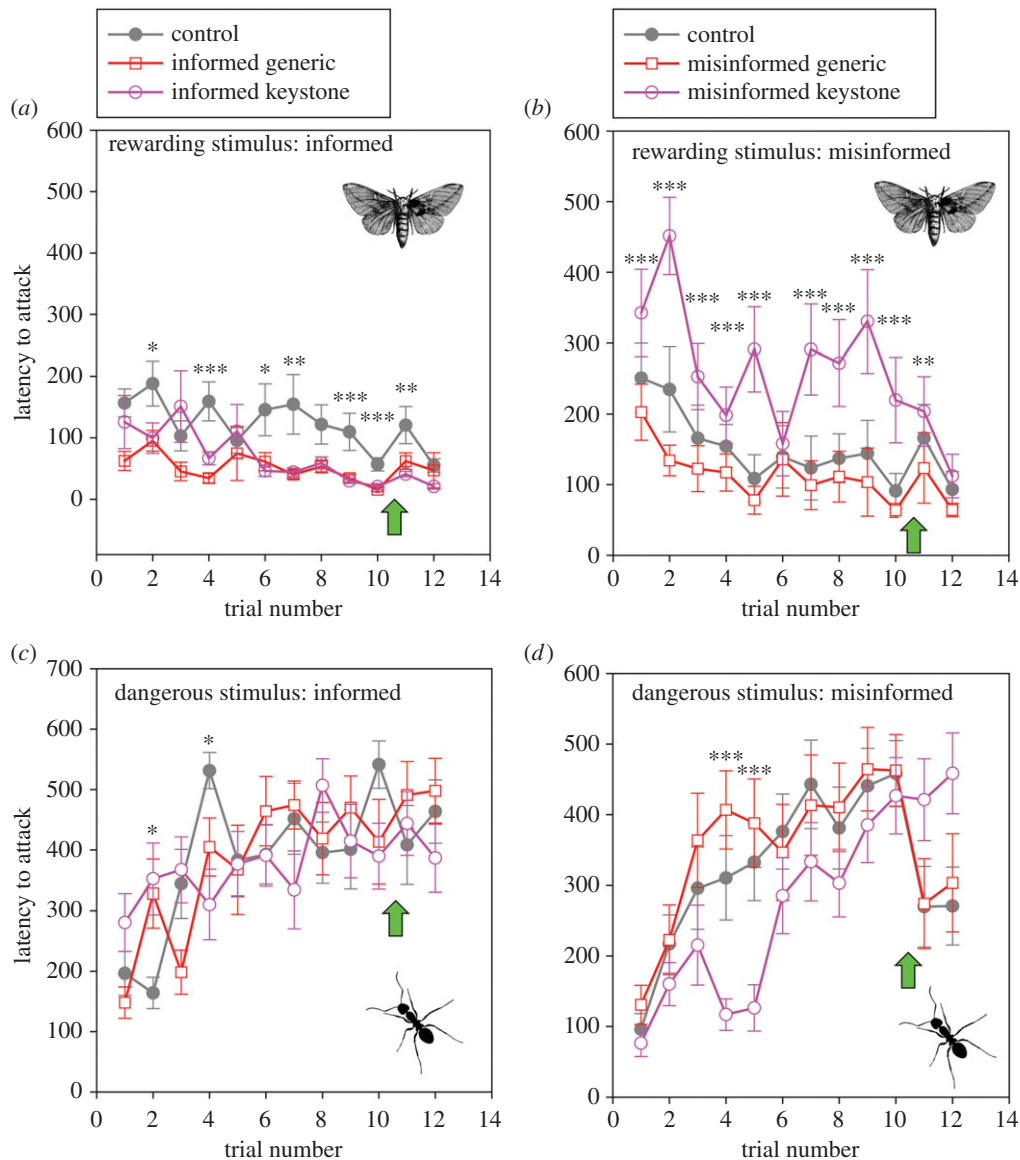
Figure 1. Time series of colonies' latency to attack novel vibratory stimuli that are consistently paired with either a prey reward outcome (a,b) or the approach of an ant predator (c,d). Colonies were composed of nine naive spiders and one trained individuals whose training either matched ('informed', a,c) or mismatched ('misinformed', b,d) colonies' current environment. In half of these colonies, the trained individual was a keystone individual (purple) and in half of the colonies the trained individual was a generic individual (dark red). Control colonies (grey) did not contain informed or misinformed individuals. Green arrows depict the moment when trained individuals were removed from the colony. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

In the predator stimulus treatment, we failed to detect a significant difference between control colonies and colonies containing informed individuals, keystones or otherwise. In contrast, we detected a significant effect of misinformed keystone individuals, where colonies containing misinformed keystones attacked predator stimuli more rapidly during the early portion of our experiment. Our model predicting colonies' latency to attack the predator stimulus detected significant main effects of trial number ($F_{9,562.4} = 14.12$, $p < 0.0001$, estimate $= 81.73 \pm 34.25$), information quality $\times$ trial number ($F_{18,562.4} = 1.91$, $p = 0.01$, estimate $= -116.36 \pm 53.85$) and trial number $\times$ keystone status ($F_{9,562.4} = 2.22$, $p = 0.02$, estimate $= 115.34 \pm 34.25$). All other main effects were non-significant (all $p > 0.09$) (figure 1).

(c) Mass gain

Colonies containing misinformed keystone individuals tended to lose 200–400% more mass than any other treatment group and 280% more than the control group (Levene's test for

HoV: $F_{5,54} = 1.88$, $p = 0.11$). Our model predicting mass gain of untrained colony members detected significant main effects of information quality ($F_{2,52.35} = 5.92$, $p = 0.005$, estimate $= 0.0034 \pm 0.002$), keystone status ($F_{1,52.69} = 6.25$, $p = 0.02$, estimate $= 0.0033 \pm 0.001$) and the interaction term information quality $\times$ keystone status ($F_{2,52.18} = 5.67$, $p = 0.006$, estimate 0.0046 ± 0.0011) (figure 2).

4. Discussion

One common benefit of group living is the potential of individuals in groups to learn about their environment through social interactions, and thus make more swift, accurate and/or effective decisions than solitary individuals [52,53]. Such social learning has been noted in a variety of animal societies [17,18,54–57] and has profound theoretical ramifications for how societies function [58]. In this study, we show that the effects of information quality on group performance differ based on the identity of its original bearer. In the social
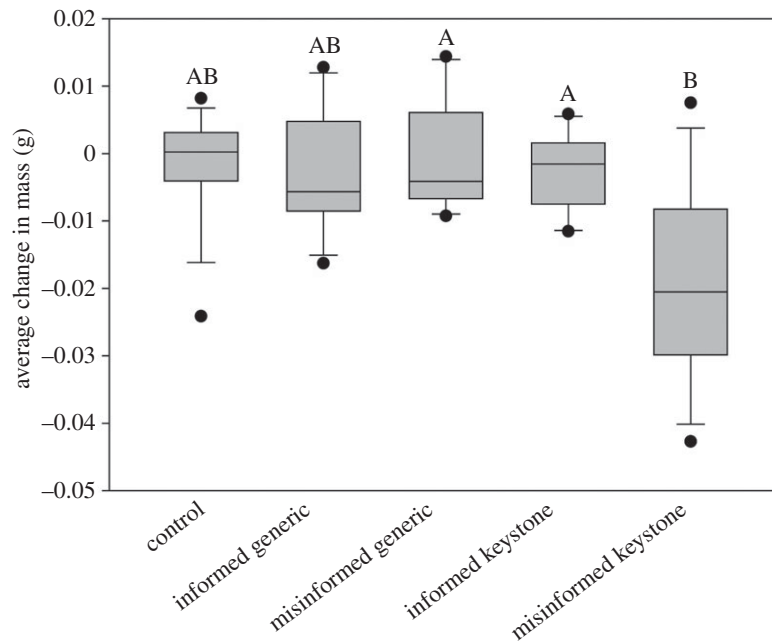
Figure 2. Per capita change in mass of untrained individuals within colonies housing an informed or misinformed individual that was either a keystone or a generic individual. Treatment groups not sharing a letter flagging were deemed significantly different using post hoc Tukey's HSD tests (corrected p-value < 0.05).

spider *S. dumicola*, misinformation in the tarsal claws) of keystone individuals decreased the rate that colonies learned to attack or avoid novel prey and predator stimuli, respectively. In contrast, accurate information in the hands of keystone individuals had similar effects to accurate information in the hands of generic individuals. Thus, keystone individuals appear more likely to hurt their societies by harbouring inaccurate information than to help their societies by harbouring accurate information, at least under dynamic conditions where the association between stimulus and outcome vary temporally. This is in contrast to previous studies on *S. dumicola* using live prey only: when colonies are iteratively subjected to a single stimulus that always conveys food (crickets), colonies containing keystone individuals gain 300% more mass and have 30–40% higher survivorship than colonies lacking keystones [31]. Taken together, these results suggest that keystone individuals have the propensity to become 'Achilles' heels' for their societies, leading to enhanced group vulnerability (under some conditions) because of their propensity to diminish societal performance when they harbour inaccurate information. Notably, in *S. dumicola*, as in other systems, an individual's probability of becoming a keystone individual is linked with its personality type [31,34]. This further highlights the value of considering individual variation in behaviour when exploring collective outcomes.

When colonies were subjected to conditions that matched the training of trained individuals, they learned to attack profitable prey stimuli sooner than control colonies. A similar magnitude of effect was observed regardless of whether or not the trained individual was a keystone individual, and these effects lasted for a moderate number of trials (trial nos. 4–10). All colonies, regardless of treatment, eventually converged on a similar latency to attack the prey stimulus by the end of our experiment (figure 1). In contrast, we did not detect a significant effect of accurately informed trained individuals (keystone or not) on the rate with which colonies learned to avoid the predator stimulus. By trial nos. 4–5, all colonies, regardless of treatment, took four times as long to attack the predator stimulus as compared with control colonies

at the start of the experiment (figure 1). Thus, it seems that colonies change their behaviour more drastically in response to encounters with predators than with prey. This rapid response may obscure any subtle effects of having just one or two informed individuals present within the colony. Although, it is possible that we may have detected a significant effect if the ratio of demonstrators to naive individuals had been larger [55]. The tendency for these societies to learn rapidly about their predators has important fitness implications, because an error with a voracious predator like *A. custodiens* could not only result in the death of the attacking individuals, but the demise of the entire society [41,59].

Inaccurate information only had a detectable effect when keystones were the first to harbour it. Under no conditions did we see an adverse effect of inaccurate information in the hands of generic individuals (figure 1), yet misinformation in the hands of keystone individuals had pronounced effects. Colonies containing just one misinformed keystone exhibited longer latencies to attack prey stimuli for nearly the entirety of our experiment (figure 1), which resulted in fewer foraging opportunities for the whole colony and greater collective weight loss (figure 2). Likewise, containing just one misinformed keystone individual resulted in colonies continuing to attack predator stimuli; this effect was somewhat ephemeral and all colonies quickly learned to avoid the predator stimuli. While these effects were fleeting, we emphasize that the primary driver of colony extinction at many sites is predation by ants [41]. Thus, even one mistaken response towards these predators may result in the annihilation of an entire colony [59]. Taken together, although informed keystones failed to exhibit any enhanced benefits for their societies relative to informed generic individuals, misinformed keystones resulted in the loss of foraging opportunities for their colony and may place them at greater risk of attack by their most serious predator [41].

Although this study was not aimed at exploring the behavioural mechanisms underlying the ill effects of misinformed keystones, we will take a moment here to speculate about just some of the putative mechanisms. One plausible

explanation for the ill effects of misinformed keystone individuals on collective learning is that they might have engaged in a disproportionately large number of attacks. If keystone individuals tended to perform a large amount of work for their society, then it follows that they might have been particularly influential in determining colony-level outcomes. This does not appear to be the case in the patterns observed here (figure 1; electronic supplementary material, appendix 2). As found in previous studies, keystone individuals do engage in a disproportionately large number of attacks shortly after colony initiation (electronic supplementary material, appendix 2). However, their involvement decreases over time, regardless of treatment, and eventually their involvement ceases entirely. This point of cessation precedes the moment at which colonies harbouring misinformed keystones approximate the behaviour and performance of other treatment groups (figure 1; electronic supplementary material, appendix 2). It is therefore unlikely that the patterns observed can be attributed to the direct involvement of keystone individuals. Instead, this suggests that transmission of information is responsible for the observed patterns.

Our data also highlight the importance of individual variation for group success. In *S. dumicola*, inaccurate information had little or no effect in the hands of generic individuals, which constitute the vast majority of individuals in these societies. Thus, if we had ignored individual variation, we might have mistakenly concluded that inaccurate information had no effect on colony performance. However, the effects of misinformation merely depend on the phenotypes (and the social influence) of the individuals that initially harbour it. In *S. dumicola*, as in some other systems [14,33], individuals' probability of emerging as a keystone individual is tightly linked with their personality type [31,34]. This provides further rationale for considering individual variation in personality in any complex society. Surprisingly, the effects of keystone individuals appear to be unidirectional in this system: keystones only seem to have a particularly large influence when they harbour inaccurate information to potentially disastrous effect, but not when they possess accurate information. We posit that a moderate or high rate of prey community turnover across the course of a season or year could result in a mismatch between a colony's experience and its contemporary environment. However, the data here raise unanswered questions regarding the frequency with which keystone individuals acquire misinformation in nature, and the fitness consequences of such keystone individuals in the wild.

5. Conclusion

In the social spider *S. dumicola*, inaccurate information has its greatest effects when it is in the hands of keystone individuals. Misinformed keystones slow the rate at which colonies learn to

attack/avoid novel prey or predator stimuli, resulting in greater weight loss across the entire colony, and the propagation of misinformation that results in other individuals mistakenly attacking some of their most dangerous predators. Keystone individuals are often the first to disperse [60], and therefore are likely to be the first individuals to learn about novel environments and may possess the necessary social influence to spread their findings to fellow colony members. We therefore propose that keystone individuals may, at times, become points of susceptibility within their societies, providing powerful benefits for their societies under some conditions [31] but decreasing group performance during others. This leads us to ask, with what regularity do key group members become idiomatic Achilles' heels of their society?

6. Significance statement

It stands to reason that the efficacy of information spread may change based on the social influence of the information's original bearers. This has been hypothesized by other investigators but rarely, if ever, confirmed outside of human societies. Our data demonstrate that information quality has its greatest effects in the hands of singularly influential keystone individuals, which tend to exhibit unique personality types. Disturbingly, these effects are ratcheted in a way that predisposes keystone individuals to hurt their societies: keystone individuals only appear to have particularly large effects when they harbour inaccurate information and these effects are disastrous. Keystone individuals with inaccurate information literally cause their societies to wither and slow the rate with which groups learn about their environment.

References

1. Aviles L, Tufino P. 1998 Colony size and individual fitness in the social spider *Anelosimus eximius*. *Am. Nat.* **152**, 403–418. (doi:10.1086/286178)

2. Reece SE, Drew DR, Gardner A. 2008 Sex ratio adjustment and kin discrimination in malaria parasites. *Nature* **453**, 609–614. (doi:10.1038/nature06954)

3. Aviles L. 1993 Interdemic selection and the sex-ratio—a social spider perspective. *Am. Nat.* **142**, 320–345. (doi:10.1086/285540)

4. Hamilton WD. 1964 The genetical evolution of social behaviour I and II. *J. Theor. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90038-4)

5. Oster G, Wilson EO. 1978 *Castes and ecology in the social insects.* Princeton, NJ: Princeton University Press.

6. Beshers SN, Traniello JFA. 1994 The adaptiveness of worker demography in the attine ant *Trachymyrmex septentrionalis*. *Ecology* **75**, 763–775. (doi:10.2307/1941733)

7. Aplin LM, Farine DR, Mann RP, Sheldon BC. 2014 Individual-level personality influences social foraging and collective behaviour in wild birds. *Proc. R. Soc. B* **281**, 20141016. (doi:10.1098/rspb.2014.1016)

8. Pruitt JN, Goodnight CJ. 2014 Site-specific group selection drives locally adapted colony compositions. *Nature* **28**, 1248–1256.

9. Hui A, Pinter-wollman N. 2014 Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants. *Anim. Behav.* **93**, 261–266. (doi:10.1016/j.anbehav.2014.05.006)

10. Gardner A. 2015 The genetical theory of multilevel selection. *J. Evol. Biol.* **28**, 305–319. (doi:10.1111/jeb.12566)

11. Burns JG, Dyer AG. 2008 Diversity of speed-accuracy strategies benefits social insects. *Curr. Biol.* **18**, R953–R954. (doi:10.1016/j.cub.2008.08.028)

12. Dyer JRG, Croft DP, Morrell LJ, Krause J. 2009 Shoal composition determines foraging success in the guppy. *Behav. Ecol.* **20**, 165–171. (doi:10.1093/beheco/arn129)

13. Pruitt JN, Riechert SE. 2011 How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proc. R. Soc. B* **278**, 1209–1215. (doi:10.1098/rspb.2010.1700)

14. Modlmeier AP, Keiser CN, Watters JV, Sih A, Pruitt JN. 2014 The keystone individual concept: an ecological and evolutionary overview. *Anim. Behav.* **89**, 53–62. (doi:10.1016/j.anbehav.2013.12.020)

15. Couzin ID, Krause J, Franks NR, Levin SA. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)

16. Couzin ID, Ioannou CC, Demirel G, Gross T, Torney CJ, Hartnett A, Conradt L, Levin SA, Leonard NE. 2011 Uninformed individuals promote democratic consensus in animal groups. *Science* **334**, 1578–1580. (doi:10.1126/science.1210280)

17. Farine DR, Aplin LM, Sheldon BC, Hoppitt W. 2015 Interspecific social networks promote information transmission in wild songbirds. *Proc. R. Soc. B* **282**, 20142804. (doi:10.1098/rspb.2014.2804)

18. Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015 Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541. (doi:10.1038/nature13998)

19. Hawley DM, Altizer SM. 2011 Disease ecology meets ecological immunology: understanding the links between organismal immunity and infection dynamics in natural populations. *Funct. Ecol.* **25**, 48–60. (doi:10.1111/j.1365-2435.2010.01753.x)

20. 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:10.1038/nature04153)

21. Chang AT, Sih A. 2013 Multilevel selection and effects of keystone hyperaggressive males on mating success and behavior in stream water striders. *Behav. Ecol.* **24**, 1166–1176. (doi:10.1093/beheco/art044)

22. Flack JC, Krakauer DC, de Waal FBM. 2005 Robustness mechanisms in primate societies: a perturbation study. *Proc. R. Soc. B* **272**, 1091–1099. (doi:10.1098/rspb.2004.3019)

23. 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)

24. Naug D. 2008 Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behav. Ecol. Sociobiol.* **62**, 1719–1725. (doi:10.1007/s00265-008-0600-x)

25. Robson SK, Traniello JFA. 1999 Key individuals and the organisation of labor in ants. In *Information processing in social insects* (eds DC Deneubourg, JM Pasteels), pp. 239–259. Basel, Switzerland: Birkhauser Verlag.

26. 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. *J. R. Soc. Interface* **8**, 1562–1573. (doi:10.1098/rsif.2011.0059)

27. Krause J, James R, Croft DP. 2010 Personality in the context of social networks. *Phil. Trans. R. Soc. B* **365**, 4099–4106. (doi:10.1098/rstb.2010.0216)

28. Rosenthal SB, Twomey CR, Hartnett AT, Wu HS, Couzin ID. 2015 Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proc. Natl Acad. Sci. USA* **112**, 4690–4695. (doi:10.1073/pnas.1420068112)

29. Homer. 1999 *The iliad*. Cambridge, MA: Harvard University Press.

30. Pruitt JN, Grinsted L, Settepani V. 2013 Linking levels of personality: personalities of the 'average' and 'most extreme' group members predict colony-level personality. *Anim. Behav.* **86**, 391–399. (doi:10.1016/j.anbehav.2013.05.030)

31. Pruitt JN, Keiser CN. 2014 The personality types of key catalytic individuals shape colonies' collective behaviour and success. *Anim. Behav.* **93**, 87–95. (doi:10.1016/j.anbehav.2014.04.017)

32. Sloan Wilson D, Clark AB, Coleman K, Dearstyne T. 1994 Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446. (doi:10.1016/0169-5347(94)90134-1)

33. Sih A, Watters JV. 2005 The mix matters: behavioural types and group dynamics in water striders. *Behaviour* **142**, 1417–1431. (doi:10.1163/156853905774539454)

34. Pruitt JN, Pinter-wollman N. 2015 The legacy effects of keystone individuals on collecitve behavior scale to how long they remain within a group. *Proc. R. Soc. B* **282**, 20151766. (doi:10.1098/rspb.2015.1766)

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

36. Wickler W, Seibt U. 1993 Pedogenetic sociogenesis via the sibling-route and some consequences for stegodyphus spiders. *Ethology* **95**, 1–18. (doi:10.1111/j.1439-0310.1993.tb00452.x)

37. Lubin Y, Birkhofer K, Berger-Tal R, Bilde T. 2009 Limited male dispersal in a social spider with extreme inbreeding. *Biol. J. Linn. Soc.* **97**, 227–234. (doi:10.1111/j.1095-8312.2009.01190.x)

38. Lubin Y, Bilde T. 2007 The evolution of sociality in spiders. *Adv. Study Behav.* **37**, 83–145. (doi:10.1016/s0065-3454(07)37003-4)

39. 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. *J. Evol. Biol.* **20**, 2412–2426. (doi:10.1111/j.1420-9101.2007.01407.x)

40. Aviles L, Maddison W. 1991 When is the sex-ratio biased in social spiders—chromosome-studies of embryos and male meiosis in Anelosimus species (Araneae, Theridiidae). *J. Arachnol.* **19**, 126–135.

41. Henschel JR. 1998 Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). *J. Arachnol.* **26**, 61–69.

42. Henschel JR, Schneider J, Lubin YD. 1995 Dispersal mechanisms of *Stegodyphus* (Eresidae): do they balloon? *J. Arachnol.* **23**, 202–204.

43. Schneider JM, Roos J, Lubin Y, Henschel JR. 2001 Dispersal of *Stegodyphus dumicola* (Araneae, Eresidae): they do balloon after all! *J. Arachnol.* **29**, 114–116. (doi:10.1636/0161-8202(2001)029[0114:dosdae]2.0.co;2)

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

45. Modlmeier AP, Laskowski KL, DeMarco AE, Coleman A, Zhao K, Brittingham HA, McDermott DR, Pruitt JN. 2014 Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. *Biol. Lett.* **10**, 20140419. (doi:10.1098/rsbl.2014.0419)

46. Coleman K, Wilson DS. 1998 Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* **56**, 927–936. (doi:10.1006/anbe.1998.0852)

47. Berning AW, Gadd RDH, Sweeney K, MacDonald L, Eng RYY, Hess ZL, Pruitt JN. 2012 Sexual cannibalism is associated with female behavioural type, hunger state and increased hatching success. *Anim. Behav.* **84**, 715–721. (doi:10.1016/j.anbehav.2012.06.030)

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

49. Wilson ADM, Whattam EM, Bennett R, Visanuvimol L, Lauzon C, Bertram SM. 2010 Behavioral correlations across activity, mating, exploration, aggression, and antipredator contexts in the European house cricket, *Acheta domesticus*. *Behav.*

Ecol. Sociobiol. **64**, 703 – 715. (doi:10.1007/s00265-009-0888-1)

50. Niemela PT, DiRienzo N, Hedrick AV. 2012 Predator-induced changes in the boldness of naive field crickets, gryllus integer, depends on behavioural type. *Anim. Behav.* **84**, 129 – 135. (doi:10.1016/j.anbehav.2012.04.019)

51. Laskowski KL, Pruitt JN. 2014 Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. *Proc. R. Soc. B* **281**, 20133166. (doi:10.1098/rspb.2013.3166)

52. Hoppitt W, Boogert NJ, Laland KN. 2010 Detecting social transmission in networks. *J. Theor. Biol.* **263**, 544 – 555. (doi:10.1016/j.jtbi.2010.01.004)

53. Franz M, Nunn CL. 2009 Network-based diffusion analysis: a new method for detecting social learning. *Proc. R. Soc. B* **276**, 1829 – 1836. (doi:10.1098/rspb.2008.1824)

54. Hobaiter C, Poisot T, Zuberbuhler K, Hoppitt W, Gruber T. 2014 Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biol.* **12**, e1001960. (doi:10.1371/journal.pbio.1001960)

55. Chivers DP, Ferrari MCO. 2015 The effect of group size and tutor-to-observer ratio on socially learned antipredator responses in woodfrog tadpoles. *Anim. Behav.* **104**, 25 – 29. (doi:10.1016/j.anbehav.2015.03.003)

56. Crane AL, Mathiron AGE, Ferrari MCO. 2015 Social learning in a high-risk environment: incomplete disregard for the 'minnow that cried pike' results in culturally transmitted neophobia. *Proc. R. Soc. B* **282**, 20150934. (doi:10.1098/rspb.2015.0934)

57. Battesti M, Moreno C, Joly D, Mery F. 2012 Spread of social information and dynamics of social transmission within *Drosophila* groups. *Curr. Biol.* **22**, 309 – 313. (doi:10.1016/j.cub.2011.12.050)

58. Heyes CM, Galef BG. 1996 *Social learning in animals: the roots of culture*, 1st edn. New York, NY: Academic Press.

59. Keiser CN, Wright CM, Pruitt JN. 2015. Warring arthropod societies: social spider colonies can delay annihilation by predatory ants via reduced apparency and increased group size. *Behav. Process* **119**, 14 – 21. (doi:10.1016/j.beproc.2015.07.005)

60. Grinsted L, Pruitt JN, Settepani V, Bilde T. 2013 Individual personalities shape task differentiation in a social spider. *Proc. R. Soc. B* **280**, 20131407. (doi:10.1098/rspb.2013.1407)

9

rspb.royalsocietypublishing.org Proc. R. Soc. B 283: 20152888