Original Article

Replacing bold individuals has a smaller impact on group performance than replacing shy individuals

Noa Pinter-Wollman,[a,b] Brian Mi,[b] and Jonathan N. Pruitt[c]

[a]Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095–1606, USA, [b]BioCircuits Institute, University of California San Diego, 9500 Gilman Dr., Mail Code 0328, La Jolla, CA 92093, USA, and [3]Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106–9610, USA

In many animal societies, just one or few individuals referred to as keystone individuals can have a disproportionately large impact on collective outcomes. Despite ongoing interest in the consequences of losing a keystone individual on group performance, little is known about whether other individuals with an appropriate behavioral type can readily assume the keystone role. Here, we examine if the identity of a keystone individual impacts its influence on the collective behavior of its group in a society of social spiders. We find that the repeated replacement of a keystone individual, which is typically a group's boldest constituent, has little impact on the collective prey capture of the colony. However, repeatedly replacing a shy, generic, individual in the group reduces prey capture success. Groups in which the keystone individual is repeatedly replaced increase their overall boldness, thus potentially collectively substituting the bold behavioral type that they lost. Furthermore, newly replaced keystone individuals participate in a greater proportion of prey attacks than established keystone individuals in undisturbed colonies, as seen in prior work on colony social development, suggesting that the repeated replacement of a keystone individual maintains colonies in an early stage of social succession. By uncovering the mechanisms that underlie a group's robustness to social perturbations, our work sheds light on how social dynamics dictate colony-level phenotypes in animal groups.

Key words: **collective behavior, keystone individual, personality, social niche, *Stegodyphus dumicola*.**

INTRODUCTION

The collective actions of social groups are shaped by the groups' behavioral composition. Group members vary widely in their behavior (Jandt et al. 2014) and the distribution of behaviors that are represented in a group impacts how well the group performs (Pinter-Wollman 2012; Farine et al. 2015). For example, the proportion of aggressive (Pruitt and Riechert 2011a, 2011b), exploratory (Aplin et al. 2014; Hui and Pinter-Wollman 2014), sociable (Cote et al. 2012), or bold individuals (Dyer et al. 2009; Cote et al. 2011) in a group can impact how well it collectively finds and defends food and shelter. In some cases, just one or few individuals can have a disproportionately large impact on collective outcomes, either by performing more of the work than other group members or by changing the behavior of others (Robson

and Traniello 1999). Such individuals are referred to as 'keystone individuals' (Modlmeier, Keiser, et al. 2014) and examples include leaders (Sumana and Sona 2013; Smith et al. 2016), tutors (Hare et al. 2001; Franz and Nunn 2009), and disease super-spreaders (Lloyd-Smith et al. 2005).

Because keystone individuals have a large impact on a group's success, losing those individuals, for example, because they die or disperse, can have dire consequences for the entire group (Modlmeier, Keiser, et al. 2014). For example, the removal of a keystone individual in primates (Flack et al. 2006) and whales (Williams and Lusseau 2006) results in an unstable social structure, African elephant groups that lose their matriarch cannot find scarce water holes during droughts, which leads to higher mortality (Foley et al. 2008) and the loss of a keystone individual in ant colonies reduces nest relocation efficiency (Sumana and Sona 2013). Notably, some or all of the effects of the keystone individual may linger after its disappearance (Pruitt and Pinter-Wollman 2015). One possible mechanism that may underlie such lingering effects is that another

Address correspondence to N. Pinter-Wollman. E-mail: nmpinter@ucla.edu.

group member assumes the role of the keystone individual that disappeared. In social insects, when workers are removed from a colony, their vacant positions are filled by other workers who were previously engaged in different tasks (Gordon 1989; Gordon 1996; O'Donnell 1998; Breed et al. 2002; O'Donnell 2006; Gardner et al. 2007; Beverly et al. 2009; Pinter-Wollman et al. 2012). Flexibility in the roles that individuals play within their groups helps to fortify social groups against environmental perturbation. Still, to date, only little is known about whether keystone individuals, who are a rare phenotype in groups, are replaceable. Here we examine if a certain individual needs to persist in its colony for its social influence to emerge, or whether any individual with the same behavioral attributes can assume the keystone's role.

In the social spider *Stegodyphus dumicola*, keystone individuals play an important role in determining group performance. *S. dumicola* spiders live in colonies of up to several hundred individuals that exhibit cooperative behaviors such as prey capture and alloparental care (Henschel et al. 1995; Henschel 1998; Avilés et al. 1999; Bilde et al. 2007). Individuals in a colony vary in their boldness—measured as the latency of an individual to recover from an adverse stimulus—such that most individuals in a colony are shy and only few are bold (Pinter-Wollman et al. 2016). Providing just one bold individual to a group of all shy individuals greatly improves the group's ability to capture prey (Keiser and Pruitt 2014; Pruitt and Keiser 2014; Pruitt et al. 2016) and to defend itself from predators (Wright et al. 2016). This positive effect of a keystone individual will persist even after it is removed from the colony, provided that its tenure in the group was longer than 10 days (Pruitt and Pinter-Wollman 2015).

Here, we test if the effects of a keystone individual on group performance can be maintained after its removal by providing the group with a new bold individual from outside the group but from the same source colony. We hypothesize that such a new bold individual will quickly assume the role of a keystone and will maintain the high collective performance of the group. However, a turnover in the identity of the boldest individual in the group reduces the group's social stability, defined as the consistent identity of individuals comprising a group. Previous studies have shown that disrupting social stability by manipulating the identity of shy individuals in a group results in a decrease in the repeatability of boldness (Laskowski and Pruitt 2014; Modlmeier, Laskowski, et al. 2014) and in overall group performance (Laskowski et al. 2016). Therefore, we alternatively hypothesize that disrupting the group's social stability by replacing the keystone individual with a different bold individual will reduce the collective performance of the group, as does the perturbation of shy individuals. We evaluate these 2 hypotheses by iteratively replacing the boldest individual in the group with bold individuals from the same source colony but who were not previously integrated in the experimental group and subsequently examining the groups' collective prey capture behavior. We compare the group's performance when capturing prey with the collective performance of groups 1) in which a shy individual was iteratively replaced and 2) no individuals were replaced. We predict that if a new bold individual quickly assumes the keystone individual's role, groups in which the boldest individual was iteratively replaced will exhibit little change over time in their collective performance, similarly to groups in which no social perturbations occurred. Alternatively, if any disruption to the social stability of a group reduces its performance, we predict that both the bold and the shy replacement procedures will reduce group performance over time and that the control groups, in which no social perturbations

occurred, will outperform the groups in both replacement treatments. We further examine if any effects on group performance emerge from the actions of the keystone individual or from changes to the behavior of all other group members.

METHODS

Animal collection and maintenance

Colonies of *S. dumicola* were collected from roadside *Acacia* trees in the Northern Cape of South Africa in November 2015. Colonies were transported to the laboratory at the University of California, San Diego where they were fed with crickets weekly. In April-May 2016, we created 27 groups of 10 individually marked subadult females. We used acrylic paint to uniquely mark the abdomen of each spider. All individuals in each group came from one source colony, that is, individuals from different source colonies were not mixed. We measured the boldness (as described below) and mass (to 0.001 g) of all the spiders at the beginning and end of the experiment. We assigned 9 shy (latency to resume movement 400–600 s) individuals and one bold (latency to resume movement 0–200 s) individual to each group. Group size and composition followed previous work in this species that showed that the boldest individual in a group of 10 individuals acts as a keystone individual (Pruitt and Keiser 2014). Individuals that were not assigned to the experimental groups, including those with a boldness score of 200–400, were returned to the source colony. This distribution of many shy individuals, few or no intermediate individuals, and a small number of very bold individuals is typical for *S. dumicola* colonies (Pinter-Wollman et al. 2016). Groups were housed in 710 ml round plastic deli containers with a 5 × 5 cm chicken wire sheet that allowed the spiders to build both a retreat and a capture web. For the social perturbation experiments described below, we further isolated a large number of bold and shy individuals in 60 ml containers, where they were fed ad lib until they were added to the experimental groups.

Social perturbation experiments

To determine how social stability influences the effects of a keystone individual on group performance, we assigned the 27 groups to 3 different treatments with 9 groups in each treatment. Each source colony contributed evenly to the 3 treatments. In our experimental treatment, we replaced the boldest individual twice a week (i.e., every 3–4 days) for 3 weeks. Replacement was conducted by identifying the boldest individual in the group according to its unique paint marking, removing it from the group, and adding a previously isolated bold individual from the same source colony into the group. Isolated individuals maintain their boldness for up to 90 days (Pinter-Wollman et al. 2016). Individuals that were removed from the group were returned to their source colony and were not reused in the experiment. As a control for the replacement procedure, we replaced a shy individual twice a week for 3 weeks in another 9 groups, using isolated shy individuals from the same source colony to replace them. Shy individuals were replaced on the same days as the bold individuals in the experimental treatment. To ensure that the shy- and bold-replacement treatments were similar, we replaced just 1 of the shy individuals such that the boldest individual and 8 of the shy individuals remained in the group for the entire duration of the study. Only 1 shy individual was repeatedly replaced, using a different individual for each replacement, as in the bold-replacement treatment. Finally, 9 groups were assigned to a "socially stable" control in which no individuals were removed

from or added to the group. To control for the disturbance caused by replacing spiders in the other 2 treatments, the containers of the groups in the "socially stable" treatment were handled in the same way as the containers of the groups in the other 2 treatments but without changing group composition. Because we did not aim to test the well documented (Keiser and Pruitt 2014; Pruitt and Keiser 2014; Pruitt and Pinter-Wollman 2015; Pruitt et al. 2016; Wright et al. 2016) effects of the presence or absence of a keystone individual on group performance, we did not include groups in which there were no bold individuals.

Boldness assays

To determine the boldness of spiders we used an established assay (Riechert and Hedrick 1993). Boldness was measured by placing a spider in a plastic container (15 × 15 cm) and after a 30 s acclimation period, administering 2 puffs of air to the anterior prosoma using an infant nose-cleaning bulb. In response to this stimulus, spiders stand still and pull their legs close to the body. Boldness was measured as the latency to resume movement and move one body length from their original position after the air puffs. Because bold individuals resume movement faster, we subtracted the latency to resume movement from the maximum duration of the procedure (600 s) to provide an intuitive metric that increases with boldness. This boldness measure is highly repeatable in this species ($r > 0.62$) (Keiser, Modlmeier, et al. 2014; Laskowski and Pruitt 2014).

Prey response

To determine the speed with which groups attacked prey, we examined their latency of response to vibrations on their capture web. We used a custom-made vibratory device assembled from an Arduino Uno board, a vibratory motor, and a metal wire to vibrate a 1 × 1 cm piece of paper that we placed in the capture web. The Arduino board was programmed to vibrate the piece of paper in pulses that varied randomly between 0.5 and 1.5 s in the duration of the vibration and the pauses between vibrations, to most closely simulate the irregular vibrations that a prey makes when it is captured in the web (Hedrick and Riechert 1989). We continued to vibrate the paper until a spider touched it, or until 10 min elapsed. We noted the latency of the first individual to attack the simulated prey (i.e., make physical contact with the piece of paper) and its identity. Information on the identity of the first attacker allowed us to determine the proportion of prey attacks in which the keystone individual participated. If none of the individuals in the colony responded to the vibrations for 10 min, we stopped the trial and did not include it in further analysis. We tested prey response once a week for 3 weeks such that the first trial was performed after one spider replacement, the second after 3 replacements, and the third prey trial after 5 replacements. We chose to conduct the experiment for 3 weeks because the effects of a keystone individual on prey attack can linger after it is removed from a colony for up to 3 weeks (Pruitt and Pinter-Wollman 2015). Thus, if the first replacement of the keystone individual had a substantial impact on group behavior, we would likely observe it by the end of 3 weeks.

Relationship between response to simulated prey and weight gain

To reduce the likelihood of mortality from starvation during the study, all experimental groups received a 4-week old live cricket (*Acheta domestica*) after the prey trials, regardless of their response to the simulated vibrations. This procedure ensured that all individuals had an opportunity to feed, resulting in nonsignificant differences among treatments in weight gain, as detailed below. To determine if a colony's response to a simulated prey can be used as a proxy for the direct benefits of individuals' weight gain, we examined the relationship between these 2 measures when colonies were not provided with food ad lib. We conducted these trials with colonies of adult females, which are more robust than subadults to food limitation (Lichtenstein et al. 2017). We measured the weight of each individual in 18 groups, each comprised of 9 shy and 1 bold adult females. We tested colonies' latency to attack prey using a vibratory stimulus, as described above, 3 times over the course of 3 days to establish the average colonies' response to prey. The containers in which these groups were housed had an opening at the bottom, which allowed crickets that were not captured to writhe through the silk and escape, as in Pruitt and Riechert (2011a). We provided colonies with feeding opportunities twice per week for 3 weeks to allow for sufficient opportunities to capture the crickets and feed. After 3 weeks, we reweighed the spiders and measured the relative weight gained by each individual (change in mass/starting mass). Colonies used for this component of the study were not used in any other experiments.

Data analysis

To determine if latency to attack prey differed among social stability treatments and whether it changed over time, we used a Linear Mixed Model (LMM) with estimates chosen to optimize the log-likelihood criterion, because our data were normally distributed—determined by investigating the qqplot fits to 5 different distributions. The response variable was latency to attack prey (seconds) and the independent variables were social stability treatment, week, and the interaction term treatment × week as fixed effects, and group ID nested in source colony ID as a random effect. To examine how changes in boldness or in weight were affected by social stability treatment, we used 2 LMM tests with the response variable being either the average change in boldness across all colony members or the average proportion of weight gained between the beginning and end of the study. The independent variables in both these models were treatment as a fixed effect and colony origin as a random effect. LMMs were implemented using the "lme4" package (Bates et al. 2015). To determine the confidence of our estimates, we ran a Wald Chi-squared test using the Anova R function on the LMM results. Post-hoc tests of these models were implemented in the "lsmeans" package using the "lsmeans" and "lstrends" functions (Lenth 2016) in R version 3.1.2 (R Core Team 2014). To determine if the proportion of trials in which the keystone individual participated differed among social stability treatments each week, we used a chi-squared test. Finally, we tested for an association between colonies' average mass gain and their latency to attack using a Pearson's correlation.

RESULTS

The 3 treatments differed in how latency to attack prey changed over time. Latency to attack prey increased in groups where a shy individual was iteratively replaced but did not change significantly over time in the other 2 treatments (Table 1, Supplementary Table S1, Figure 1). A post-hoc test of the change in latency to attack over time revealed a significant linear trend only for the shy replacement treatment ($P = 0.004$) but no significant changes over time for the other 2 treatments. Furthermore, by the third week, the groups in which a shy individual was iteratively replaced performed

Table 1

Results from a linear mixed model of the effects on colonies' latency to attack prey

| Effect	df	χ^2	$P > \chi^2$
Treatment	2	1	0.61
Week	1	6.45	**0.01**
Treatment × week	2	6.17	**0.04**

Values in bold indicate $P < 0.05$.
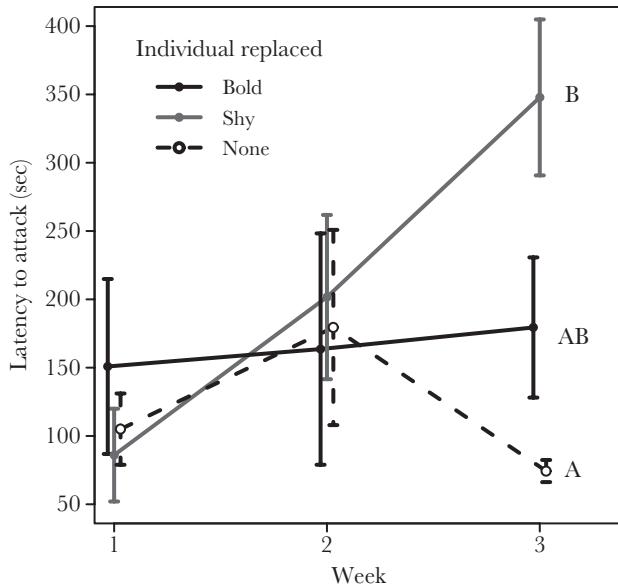
Figure 1
Latency to attack a simulated prey over 3 weeks for 3 treatments of social stability: bold individual replaced (solid black), shy individual replaced (solid gray), and no replacements (dashed black). Points represent the mean of 9 treatment replicates and bars represent standard errors. Data points are slightly jittered along the x axis to improve visibility. Treatments in the third week that do not share a letter are statistically different according to a post-hoc Tukey test (P value < 0.05).

significantly worse during prey capture than the control groups in which no individuals were replaced (post-hoc Tukey test: $P < 0.05$, Figure 1). The random effect "source colony" accounted for 16% of the variance in the model and "group ID" for 10%.

We found that latency to attack prey is a reliable proxy for group performance. Undisturbed groups that attacked a simulated prey the fastest gained the most weight in situations where prey were permitted to escape (Pearson correlation: $r = -0.66$, $P = 0.003$, Figure 2). However, the social stability treatments did not differ in the proportion of weight gained over the 3 weeks of the experiment (LMM of proportion of mass gained as a function of social stability treatment: $\chi^2 = 2.25$, df = 2, $P > \chi^2 = 0.32$, Supplementary Table S2).
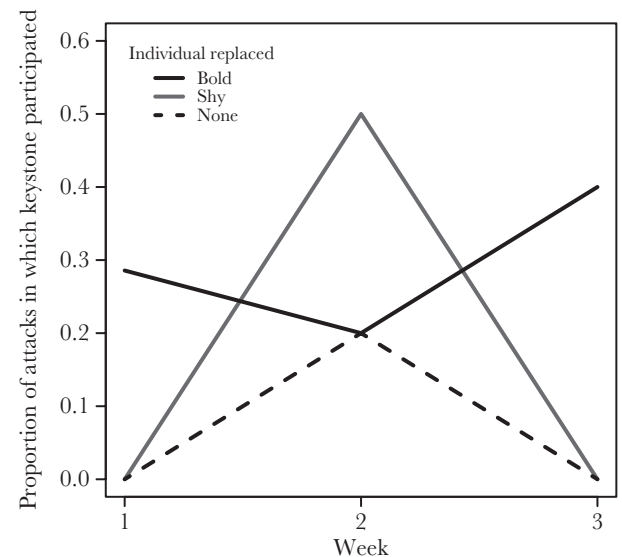
Social stability treatments differed in the proportion of attacks in which the boldest individual participated. The boldest individual in the group participated in significantly more attacks when the bold individual was repeatedly replaced, as compared with the shy replacement and socially stable treatments in the first and third weeks (χ^2: $P < 0.0001$, Figure 3). There was no significant difference among the treatments on the second week (Figure 3).

Treatments differed in how individuals changed their boldness over the 3 weeks of the experiment. The boldness of individuals in groups where the boldest individual was iteratively replaced
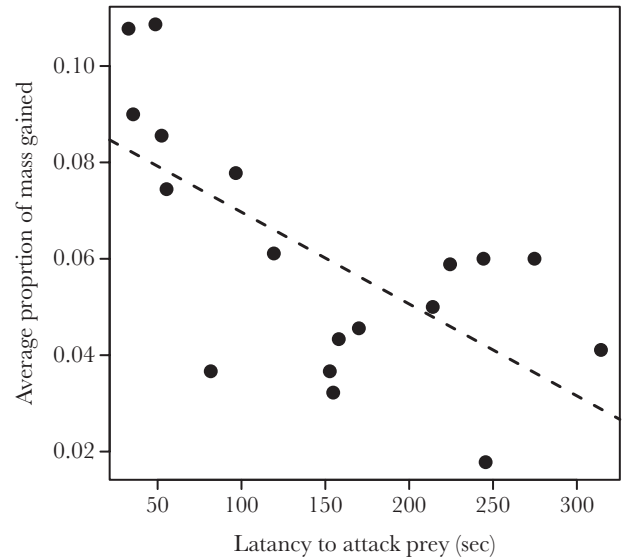
Figure 2
Relationship between the average latency of a group to attack prey and the average proportion of mass gained by the individuals in the group. The dashed line represents a linear fit to the data (Pearson correlation: $r = -0.66$, $P = 0.003$).
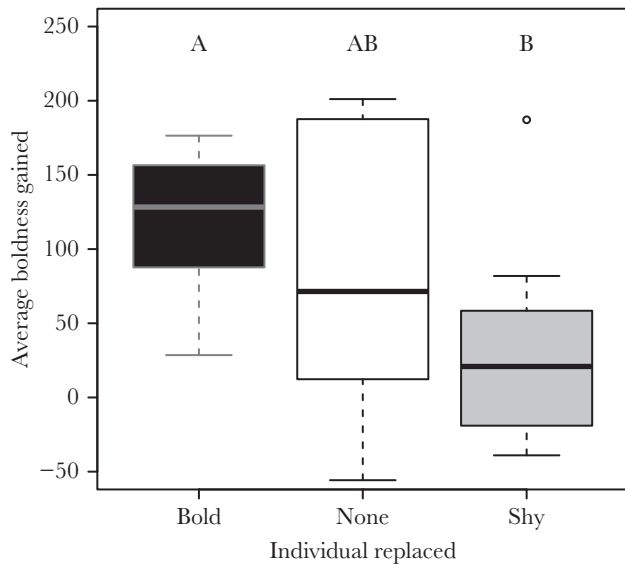

Figure 3
Proportion of attacks in which the boldest individual in the group participated in each of the 3 weeks and 3 treatments of social stability: bold individual replaced (solid black), shy individual replaced (solid gray), and no replacements (dashed black).

increased over the course of the experiment. This change was significantly greater than the change in boldness in groups in which a shy individual was iteratively replaced, where boldness changed very little (LMM of change in boldness in response to social stability treatment: $\chi^2 = 9.02$, df = 2, $P > \chi^2 = 0.011$, Supplementary Table S3, Figure 4).

DISCUSSION

Colonies were more sensitive to the repeated replacement of a shy individual than the repeated replacement of a bold individual, as exhibited by a reduction in colonies' speed of collective prey attack

Figure 4
Change in boldness, averaged for each group, over the 3 weeks of the study in groups where a bold (black), shy (gray), or no (white) individual was iteratively replaced. Boxes indicate the lower and upper quartiles; horizontal lines within boxes indicate the median; whiskers extend to the 1.5 interquartile range from the box; and open circles indicate outliers. Boxes that do not share a letter are statistically different according to a post-hoc Tukey test (*P*-value < 0.03).

over time. These differences in how colonies responded to turnover in group membership of shy versus bold constituents can potentially be explained by changes in the boldness of other group members (Figure 4) and/or by differences in the participation of the keystone individual in collective prey attacks (Figure 3), as discussed below.

Iteratively replacing the boldest individual in a group only slightly decreased the well-documented positive effects that keystones have on their colony's collective aggressiveness (Keiser, Jones, et al. 2014; Keiser and Pruitt 2014; Pruitt and Keiser 2014). Consistent with previous work (Laskowski et al. 2016), after 3 weeks, our control groups outperformed the groups in which shy individuals were repeatedly replaced (Figure 1). We further observed slower collective response to prey over time for the shy-replacement treatment but no significant change over time in the bold-replacement treatment. These findings support our hypothesis that a new bold individual can assume the role of a keystone individual. In social insects, replacing individuals that are removed from one task with individuals engaged in another task can lead to diminished collective performance (Pinter-Wollman et al. 2012). Perhaps here because we provided *S. dumicola* colonies with a substitute bold individual after removing the keystone, the new bold individual was able to quickly assume the role of the former keystone and recover its positive impacts on group behavior. If indeed an unfamiliar individual was able to assume the keystone role, our findings suggest that individually recognizing the boldest individual by other group members is not essential for the bold individual to positively impact group foraging behavior. In contrast, we predict that for species in which individual recognition is an important driver of social dynamics (Silk et al. 2010; Hobson et al. 2015), turnover of keystone individuals may have more pronounced social effects. However, a recent study on African elephants, *Loxodonta africana*, showed that groups who lost their matriarch inherit the social bonds of the lost individuals (Goldenberg et al. 2016), suggesting

that there may be social properties that transcend the identity of the individuals who instigated them, even in animals with very high cognitive capabilities (Hart et al. 2008) and in species that can distinguish among individuals (Mccomb et al. 2000, 2003). Our data demonstrating colony-wide robustness to the replacement of bold keystone individuals suggests that the effects of keystone individuals on social dynamics might not require individual recognition in this and other systems.

Despite the importance of bold keystone individuals for collective prey capture, which leads to benefits in the form of mass gain (Figure 2), iteratively replacing a shy individual reduced collective performance over time but replacing a bold individual did not (Figure 1). A possible explanation for this surprising result is the observed change in boldness of all group members. When the boldest individual was replaced repeatedly, other group members increased their boldness, compared to the shy replacement treatment (Figure 4). Previous work has shown that bolder groups are more aggressive than shy ones in collective prey attacks (Keiser, Jones, et al. 2014; Wright et al. 2015). Thus, any decrease in group-wide aggressiveness during foraging as a result of keystone removal may be offset by the increase in the boldness of otherwise shy colony members (Figure 4). Furthermore, it has been shown that *S. dumicola* groups become more timid when a few shy individuals are replaced (Laskowski et al. 2016), which is consistent with our observation of longer latencies to attack in these colonies (Figure 1). It is possible that because bold individuals tend to perform riskier tasks (Wright et al. 2015, 2016), they are also more likely to perish. It thus stands to reason that colonies of *S. dumicola* may have been subjected to an evolutionary history where the disappearance of bold group members is common. *If* this is true and *if* the effects of such members on group performance are positive, as our data suggest, then individuals within these colonies should evolve mechanisms of resilience in the face of the disappearance or demise of their boldest group members. Social spider groups are indeed quite robust to the disappearance of their boldest individuals (Pruitt and Pinter-Wollman 2015). However, repeatedly losing shy individuals might signal to the group that the threat of predation is high, which could then lead to more cautious behavior in the form of lower average boldness and an increased latency to attack at the colony level, as was observed here. Another nonmutually exclusive explanation of our results is that shy individuals interact more with one another than bold individuals and thus, removing and replacing these individuals has a large effect on the social dynamics of the colony. Consistent with this interpretation, shy individuals in this species tend to spend the majority of their time nestled together within their nests (Wright et al. 2015, 2016). Likewise, in other species of social spiders (Riechert and Jones 2008; Holbrook et al. 2014) and in some mammals (Fuong et al. 2015), shy individuals have different interaction patterns than their bold counterparts. Thus, it is possible that the replacement of a highly interactive shy individual was more conspicuous to the other group members than the replacement of a bold individual, given that bold individuals may not interact with other individuals as frequently. Further detailed examination of the interactions among spiders could shed light on these possibilities.

The faster response to the simulated prey in the bold-replacement groups compared with the shy-replacement groups in the last week of the study could further be explained by the participation of the keystone individual in the prey attacks. In the last week of the study, the keystone individual did not participate in any attacks of the shy-replacement or the control, no-replacement, groups. However,

the keystone individual participated in 40% of attacks by the bold-replacement groups (Figure 3). Previous work on this species has shown that the percentage of prey attacks in which the keystone individual participates is 30–40% only for the first 3 days after colony establishment and then goes down to less than 10% after the sixth day (Pruitt and Pinter-Wollman 2015). Prey trials in the current study were conducted 3 days after the most recent individual replacement, effectively maintaining colonies in a constant state of early development. Bold individuals perform a great deal of work shortly after colony establishment (Keiser and Pruitt 2014; Pruitt and Pinter-Wollman 2015; Wright et al. 2016), thus constantly providing the colonies with a new bold individual potentially prevented them from moving into later organizational stages in which bold individuals decrease their involvement in collective actions.

Our work highlights the flexibility and robustness of social systems by showing that the keystone individual does not necessarily have to be a specific, familiar, or socially integrated individual to serve its role. We found that societies can be robust to social perturbations by replacing key individuals with new ones and that colonies are flexible in accepting novel individuals into the keystone role, specifically when the new individuals have the appropriate behavioral type. Our work suggests that the ways in which keystone individuals impact collective outcomes differ between socially stable groups and those that experience social instability. When groups experience instability in the keystone individual, the behavior of other group members—boldness in our study system—begins to resemble that of the keystone individual. Furthermore, a new keystone individual participates in more collective prey attacks than established keystone individuals in stable groups. Experimental manipulations of social composition are fundamental for uncovering how the identity of individuals impacts a group's collective actions. However, such manipulations are not always possible or ethical. By uncovering how social spider groups overcome repeated losses of keystone individuals, our work can shed light on the mechanisms that underlie social robustness in other systems that are less amenable to experimental manipulations but go through repeated losses of leaders, for example, due to poaching or management actions.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

Handling editor: Louise Barrett

REFERENCES

Aplin LM, Farine DR, Mann RP, Sheldon BC. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. Proc Biol Sci. 281:20141016.

Avilés L, Varas C, Dyreson E. 1999. Does the African social spider *Stegodyphus dumicola* control the sex of individual offspring?. Behav Ecol Sociobiol. 46:237–243.

Bates D, Mächler M, Bolker BM, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67:1–48.

Beverly BD, McLendon H, Nacu S, Holmes S, Gordon DM. 2009. How site fidelity leads to individual differences in the foraging activity of harvester ants. Behav Ecol. 20:633–638.

Bilde T, Coates K, Birkhofer K, Bird T, Maklakov A, Lubin Y, Aviles L. 2007. Survival benefits select for group living in a social spider despite reproductive costs. J Evol Biol. 20:2412–2426.

Breed MD, Williams DB, Queral A. 2002. Demand for task performance and workforce replacement: undertakers in honeybee, *Apis mellifera*, colonies. J Insect Behav. 15:319–329.

Cote J, Fogarty S, Brodin T, Weinersmith K, Sih A. 2011. Personality-dependent dispersal in the invasive mosquitofish: group composition matters. Proc Biol Sci. 278:1670–1678.

Cote J, Fogarty S, Sih A. 2012. Individual sociability and choosiness between shoal types. Anim Behav. 83:1469–1476.

Dyer JRG, Croft DP, Morrell LJ, Krause J. 2009. Shoal composition determines foraging success in the guppy. Behav Ecol. 20:165–171.

Farine DR, Montiglio PO, Spiegel O. 2015. From individuals to groups and back: the evolutionary implications of group phenotypic composition. Trends Ecol Evol. 30:609–621.

Flack JC, Girvan M, De Waal FBM, Krakauer DC. 2006. Policing stabilizes construction of social niches in primates. Nature. 439:426–429.

Foley C, Pettorelli N, Foley L. 2008. Severe drought and calf survival in elephants. Biol Lett. 4:541–544.

Franz M, Nunn CL. 2009. Network-based diffusion analysis: a new method for detecting social learning. Proc Biol Sci. 276:1829–1836.

Fuong H, Maldonado-Chaparro A, Blumstein DT. 2015. Are social attributes associated with alarm calling propensity?. Behav Ecol. 26:587–592.

Gardner KE, Foster RL, O'Donnell S. 2007. Experimental analysis of worker division of labor in bumblebee nest thermoregulation (*Bombus huntii*, Hymenoptera: Apidae). Behav Ecol Sociobiol. 61:783–792.

Goldenberg SZ, Douglas-Hamilton L, Wittemyer G. 2016. Vertical transmission of social roles drives resilience to poaching in elephant networks. Curr Biol. 26:75–79.

Gordon DM. 1989. Dynamics of task switching in harvester ants. Anim Behav. 38:194–204.

Gordon DM. 1996. The organization of work in social insect colonies. Nature. 380:121–124.

Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know?. Anim Behav. 61:139–151.

Hart BL, Hart LA, Pinter-Wollman N. 2008. Large brains and cognition: Where do elephants fit in?. Neurosci Biobehav Rev. 32:86–98.

Hedrick AV, Riechert SE. 1989. Genetically-based variation between 2 spider populations in foraging behavior. Oecologia. 80:533–539.

Henschel J, Lubin Y, Schneider J. 1995. Sexual competition in an inbreeding social spider, *Stegodyphus dumicola* (Araneae: Eresidae). Insectes sociaux. 42:419–426.

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

Hobson EA, John DJ, Mcintosh TL, Avery ML, Wright TF. 2015. The effect of social context and social scale on the perception of relationships in monk parakeets. Curr Zool. 61:55–69.

Holbrook CT, Wright CM, Pruitt JN. 2014. Individual differences in personality and behavioural plasticity facilitate division of labour in social spider colonies. Anim Behav. 97:177–183.

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.

Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A. 2014. Behavioural syndromes and social insects: personality at multiple levels. Biol Rev. 89:48–67.

Keiser CN, Jones DK, Modlmeier AP, Pruitt JN. 2014. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. Behav Ecol Sociobiol. 68:839–850.

Keiser CN, Modlmeier AP, Singh N, Jones DK, Pruitt JN. 2014. Exploring how a shift in the physical environment shapes individual and group behavior in two social contexts. Ethology. 120:825–833.

Keiser CN, Pruitt JN. 2014. Personality composition is more important than group size in determining collective foraging behaviour in the wild. Proc Biol Sci. 281:20141424.

Laskowski KL, Montiglio PO, Pruitt JN. 2016. Individual and group performance suffers from social niche disruption. Am Nat. 187:776–785.

Laskowski KL, Pruitt JN. 2014. Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. Proc Biol Sci. 281: 20133166.

Lenth RV. 2016. Least-squares means: the R package lsmeans. J Stat Softw. 69:1–33.

Lichtenstein JL, Wright CM, Luscuskie LP, Montgomery GA, Pinter-Wollman N, Pruitt JN. 2017. Bold individuals generate aggressive foraging behavior and greater mass gain in shy group mates in a social spider. Curr Zool. 1–7. doi: 10.1093/cz/zow097.

Lloyd-Smith JO, Schreiber SJ, Kopp PE, Getz WM. 2005. Superspreading and the effect of individual variation on disease emergence. Nature. 438:355–359.

Mccomb K, Moss C, Sayialel S, Baker L. 2000. Unusually extensive networks of vocal recognition in African elephants. Anim Behav. 59:1103–1109.

Mccomb K, Reby D, Baker L, Moss C, Sayialel S. 2003. Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav. 65:317–329.

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.

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.

O'Donnell S. 1998. Effects of experimental forager removals on division of labour in the primitively eusocial wasp *Polistes instabilis* (Hymenoptera: Vespidae). Behaviour. 135:173–193.

O'Donnell S. 2006. Polybia wasp biting interactions recruit foragers following experimental worker removals. Anim Behav. 71:709–715.

Pinter-Wollman N. 2012. Personality in social insects: How does worker personality determine colony personality?. Curr Zool. 58:580–588.

Pinter-Wollman N, Hubler J, Holley JA, Franks NR, Dornhaus A. 2012. How is activity distributed among and within tasks in *Temnothorax* ants? Behav Ecol Sociobiol. 66:1407–1420.

Pinter-Wollman N, Keiser CN, Wollman R, Pruitt JN. 2016. The effect of keystone individuals on collective outcomes can be mediated through interactions or behavioral persistence. Am Nat. 188:240–52.

Pinter-Wollman N, Mi B, Pruitt JN. 2017. Data from: replacing bold individuals has a smaller impact on group performance than replacing shy individuals. Dryad Digital Repository. http://doi.org/10.5061/dryad.5q6s3

Pruitt JN, Keiser CN. 2014. The personality types of key catalytic individuals shape colonies' collective behaviour and success. Anim Behav. 93:87–95.

Pruitt JN, Pinter-Wollman N. 2015. The legacy effects of keystone individuals on collective behaviour scale to how long they remain within a group. Proc Biol Sci. 282:89–96.

Pruitt JN, Riechert SE. 2011a. How within-group behavioural variation and task efficiency enhance fitness in a social group. Proc Biol Sci. 278:1209–1215.

Pruitt JN, Riechert SE. 2011b. Within-group behavioral variation promotes biased task performance and the emergence of a defensive caste in a social spider. Behav Ecol Sociobiol. 65:1055–1060.

Pruitt JN, Wright CM, Keiser CN, DeMarco A, Grobis MM, Pinter-Wollman N. 2016. The Achilles heel hypothesis: misinformed keystone individuals impair collective learning and reduce group success. Proc Biol Sci. 283:20152888.

R Core Team. 2014. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. http://www.R-project.org/.

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.

Riechert SE, Jones TC. 2008. Phenotypic variation in the social behaviour of the spider *Anelosimus studiosus* along a latitudinal gradient. Anim Behav. 75:1893–1902.

Robson SK, Traniello JFA. 1999. Key individuals and the organization of labor in ants. In: Detrain C, Deneubourg JL, Pasteels JM, editors. Information processing in social insects Basel Boston. Berlin: Birkhauser. p. 239–260.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010. Female chacma baboons form strong, equitable, and enduring social bonds. Behav Ecol Sociobiol. 64:1733–1747.

Smith JE, Gavrilets S, Mulder MB, Hooper PL, El Mouden C, Nettle D, Hauert C, Hill K, Perry S, Pusey AE, et al. 2016. Leadership in mammalian societies: emergence, distribution, power, and payoff. Trends Ecol Evol. 31:54–66.

Sumana A, Sona C. 2013. Key relocation leaders in an Indian queenless ant. Behav Process. 97:84–89.

Williams R, Lusseau D. 2006. A killer whale social network is vulnerable to targeted removals. Biol Lett. 2:497–500.

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.

Wright CM, Keiser CN, Pruitt JN. 2016. Colony personality composition alters colony-level plasticity and magnitude of defensive behaviour in a social spider. Anim Behav. 115:175–183.