



Original Article

Better safe than sorry: spider societies mitigate risk by prioritizing caution

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Group members often vary in the information that they have about their environment. In this study, we evaluated the relative contribution of information held by the population majority versus new immigrants to groups in determining group function. To do so, we created experimental groups of the social spider *Stegodyphus dumicola* that were either iteratively exposed to a dangerous predator, the ant *Anoplopepis custodiens*, or kept in safety. We then seeded these groups (i.e., the population majority) with an “immigrant” individual that either had or did not have prior experience with the predator and was either shy or bold. Bold group members are argued to be particularly influential for group function in *S. dumicola*. We then evaluated colonies’ response towards predators over multiple trials to determine the effect of the immigrant’s and the majority’s prior experience with the predator and the immigrant’s boldness. We found that groups adopt a “better safe than sorry” strategy, where groups avoided predators when either the group or the immigrant had been previously exposed to risk, regardless of immigrant boldness. These findings suggest that past experience with predators, even if only experienced by a single individual in the group, can alter how groups respond to risk in a potentially advantageous manner.

Key words: information, learning, personality, predation, sociality, spider.

INTRODUCTION

Many animals live in groups, as group living often confers advantages to its constituents (Krause and Ruxton 2002). The advantages of sociality include increased vigilance toward predators (Lima 1995; Roberts 1996), decreased vulnerability to predators via “dilution effects” (Hamilton 1971; Foster and Treherne 1981; Dehn 1990), increased offspring survival (Silk 2007), and higher efficiency in foraging and thermoregulation (Clark and Mangel 1986; Gilbert et al. 2006; Jones and Oldroyd 2007; Kerth 2008). Another crucial, yet cryptic, benefit of group living is the ability of social groups to acquire wide-ranging information about the current state of their environment by collectively accumulating the narrow experiences of many individuals (Pacala et al. 1996; Brodbeck and Greitemeyer 2000; Thornton and Clutton-Brock 2011). When this information is vital for the survival of the individuals in the group, the informed individuals often accurately convey the information to others.

Groups can benefit from assimilating the experiences of individuals in many ways. For instance, in elephants, older females (matriarchs) have had more time to accumulate information over their lifetime, such as the location of seldom used water holes (Foley et al. 2008), or the identities of other elephant groups (McComb et al. 2011). This information increases both the survival and reproductive success of herds led by older matriarchs (McComb et al. 2011). Group members can garner useful information from individuals via social learning (Thornton and Clutton-Brock 2011). The primary benefit of social learning is that it enables individuals to acquire the fitness advantages associated with a behavior without needing to discover it anew or be near the innovator after the behavior is learned. However, these advantages might be impacted by what information is learned and from whom it is learned. For example, groups might receive disparate or conflicting information from different individuals, which then need to be negotiated (Conradt 2012).

Individuals may possess different, sometimes mutually exclusive, information about their environment and thus may have different preferred outcomes (Couzin et al. 2005; Dostalkova and Spinka 2007). For example, individuals could differ in desired food types

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cautious behavior (i.e., attack slower and with fewer individuals) over time, while unexposed bold immigrants will either have no effect or cause exposed colonies to decrease their cautious behavior over time. Shy immigrants under the *dictator hypothesis* will have no influence on colony behavior. Lastly, the *better safe than sorry hypothesis* predicts that colonies will behave in a manner that mitigates overall risk and respond with caution if either the immigrant or colony has experience with predators, regardless of immigrant keystone (personality) status. Under this hypothesis, we would expect colonies to exhibit cautious behavior if either the colony, immigrant, or both have previously been exposed to predators, and remain unaffected only if neither the colony nor the immigrant have been exposed to predators, regardless of immigrant personality.

METHODS

Colony collection and behavioral assays

Colonies of *S. dumicola* were collected around Upington, in the Northern Cape of South Africa, and brought into the lab the same day in summer 2016. Each spider was individually isolated from its nest mates in small 30 mL plastic condiment containers. We then measured each spider's boldness by placing them into an arena, allowing them to acclimate to the new container for 60 s, and administering 2 gentle puffs of air to their anterior prosoma using a rubber squeeze-bulb. These air puffs resemble an attack from an avian predator, and cause the spider to cease activity and pull its legs in against their body in a "huddle" position (Riechert and Hedrick 1990; Pruitt et al. 2013). The latency to unhuddle and move one whole body length following these air puffs is our measure of boldness. Boldness is defined as the propensity of an individual to engage in risky behavior (Sloan Wilson et al. 1994), and resuming normal activity quickly after interacting with a mock predator (air puffs) is here deemed risky or "bold" behavior. These latencies scores are then subtracted from 600 (the maximum value) so that higher numbers reflect greater boldness scores. Spiders with intermediate boldness values were not used in the present study. We used maximally shy spiders for our colony constituents and for the shy immigrants (i.e., spiders that never unhoodled during boldness trials and had a boldness score of zero). Bold immigrants all had latencies to resume movement under 60 s (i.e., boldness scores greater than 540).

Colony creation

Following individual boldness trials, we constructed 80 experimental colonies containing 9 shy spiders each. Each colony was housed in a separate 250 mL clear, plastic parfait cup containing several twigs of acacia hookbush (*Acacia mellifera*) for the spiders to use as nesting substrate. One bold or shy future "immigrant" spider from the same source colony was kept separately in a 30 mL plastic condiment cup until its addition to the 9-individual colony after 7 days. Each experimental colony, and its respective immigrant, was derived from a single source colony from an area where ants were not observed to ensure little to no previous experience with these predators. Spiders from different source colonies were never combined so that within-group relatedness and familiarity was maintained (Laskowski and Pruitt 2014; Modlmeier, Laskowski, et al. 2014; Laskowski et al. 2016). Half of the experimental colonies ($N = 40$) were exposed to predatory *A. custodiens* ant workers twice a day for 7 days prior to immigrant additions, and the other 40 colonies were not exposed to ants prior to immigrant additions. Details of ant exposures

are outlined in the following section. Within each of the above exposure groups, half ($N = 20$) of the colonies received a bold immigrant and the other half a shy immigrant. Half of the immigrants in each of these groups were pre-exposed to predatory ant cues, and the other half were not. Thus, we established 8 treatments in total, 10 replicates in each, which were deployed in a fully factorial $2 \times 2 \times 2$ design: colony experience (ant presence +/-), immigrant experience (ant presence +/-), and immigrant personality (shy/bold).

Immigrant predator exposure treatments

To expose immigrant spiders to predators, we punctured small holes in the bottom of their 30 mL container and nested it within another identical cup with 2 predatory ants that were free to move around in the space between the stacked cups. Spiders were continuously exposed to these predators in this manner for 7 days, and dead ants were replaced with live ones immediately when discovered. This setup allowed chemical cues from the ants to reach the spiders, while protecting them from predation by the ants. Previous work has shown that *S. dumicola* responds to ant cues using the same setup by decreasing their foraging activity and increasing their latency to attack ants that encounter their webs (Wright et al. 2017). The other half of the immigrant spiders experienced an identical but ant-free procedural control treatment.

Colony predator exposure treatments

Colonies were exposed to the ant predators similarly to the immigrant exposure of immigrants outlined in the previous section, but with minor differences. We punctured small holes in the bottom of the containers of the experimental colonies and nested them within other identical cups. To half of the experimental colonies we added, 5 *A. custodiens* workers to the space between the nested cups for 7 days. In addition, we directly exposed colonies to ants twice daily, 6 h apart, over the course of the same 7-day period by placing a single *A. custodiens* worker in the capture web of the colony and allowing the spiders to briefly interact with the ant. Ants were removed after we observed spiders interacting with them so that the colonies were unable to consume the ants as food, and the ants could not harm the spiders.

Collective attack of innocuous vs. dangerous prey

Prior to exposing colonies to ants, we evaluated each colony's initial aggressiveness towards innocuous prey by placing a 1×1 cm piece of paper (representing an innocuous prey item) in the center of the capture web and vibrating the paper with a small handheld vibrator. This causes the paper to flutter, mimicking the vibrations that a small winged insect might make while struggling in the capture web. We recorded the latency for the first spider to attack (make physical contact with the paper) and the number of spiders that were recruited to the capture web during the attack sequence. This was performed twice a day over 2 consecutive days, equaling 4 trials total. These measures give us an estimate of both the speed and magnitude of an attack. All 4 trials were then averaged to get an estimate of initial average colony aggressiveness. This initial measurement was taken to verify that the initial behavior of these colonies was not significantly different from one another, so that we could track how exposure to predators altered their behavior over time. On the day following these initial aggressiveness trials to innocuous prey, we began the ant exposures to half the colonies as outlined above.

RESULTS

Response towards a dangerous predator (ants)

Colony experience

Exposure to predators decreased aggressiveness towards them over time. Unexposed colonies were faster to attack ants in the capture web than predator-exposed colonies early (colony experience: $P < 0.0001$; Figure 1: C1 and C2). Furthermore, unexposed colonies deployed up to 260% more attackers than exposed colonies over time (colony experience: $P < 0.0001$; Figure 1: D1 and D2). Colony experience with the predatory ants had no influence on the number of defensive cribellate silk spinners observed (colony experience: $P = 0.92$; Figure 1: E1 and E2).

Immigrant experience

Immigrant experience with predatory ants had large effects on colony collective behavior in unexposed colonies on both latency to attack (colony experience \times immigrant experience: $P = 0.0074$) and number of attackers (colony experience \times immigrant experience: $P = 0.038$). Unexposed colonies that received exposed immigrants dramatically increased their latency to attack ants (i.e., exhibited increased cautious behavior) over time resembling attack latencies (cautious behavior) comparable to those of exposed colonies by days 4 and 5. In contrast, attack latencies of unexposed colonies that received unexposed immigrants did not exhibit a similar shift (Figure 1: C1 and C2). A nearly identical pattern emerged for the number of attackers deployed in those colonies: unexposed colonies that received exposed immigrants radically decreased the number of attackers to resemble the attack numbers of exposed colonies (Figure 1: D1 and D2). Thus, immigrant experience, rather than immigrant personality, influenced group collective behavior, supporting the better-safe-than-sorry hypothesis. We did not detect an influence of immigrant experience on the number of defensive cribellate silk spinners observed in both exposed and unexposed colonies (immigrant experience: $P = 0.51$; colony experience \times immigrant experience: $P = 0.12$).

Response towards innocuous prey (paper)

Colony experience

Exposure to predators had no observable influence on colonies' latency to attack ($P = 0.19$) or on the number of attackers deployed ($P = 0.41$) to an innocuous prey stimulus.

Immigrant experience

When bold immigrants were introduced into unexposed colonies the colonies attacked with increasingly more individuals than when shy immigrants were introduced to colonies (immigrant experience: $P = 0.0044$; immigrant BT: $P < 0.0001$; colony experience \times immigrant BT: $P = 0.019$). We did not detect a difference among any of the treatments in latency to respond to mock prey (immigrant experience: $P = 0.91$; immigrant BT: $P = 0.89$; colony experience \times immigrant BT: $P = 0.12$). Thus, the presence of bold individuals increases collective aggressiveness towards innocuous prey in spite of ongoing experiences with predators.

See Table 2 for the complete results of our model.

DISCUSSION

Our results support the *better safe than sorry hypothesis* by demonstrating that colonies exhibit an increasingly cautious behavioral phenotype

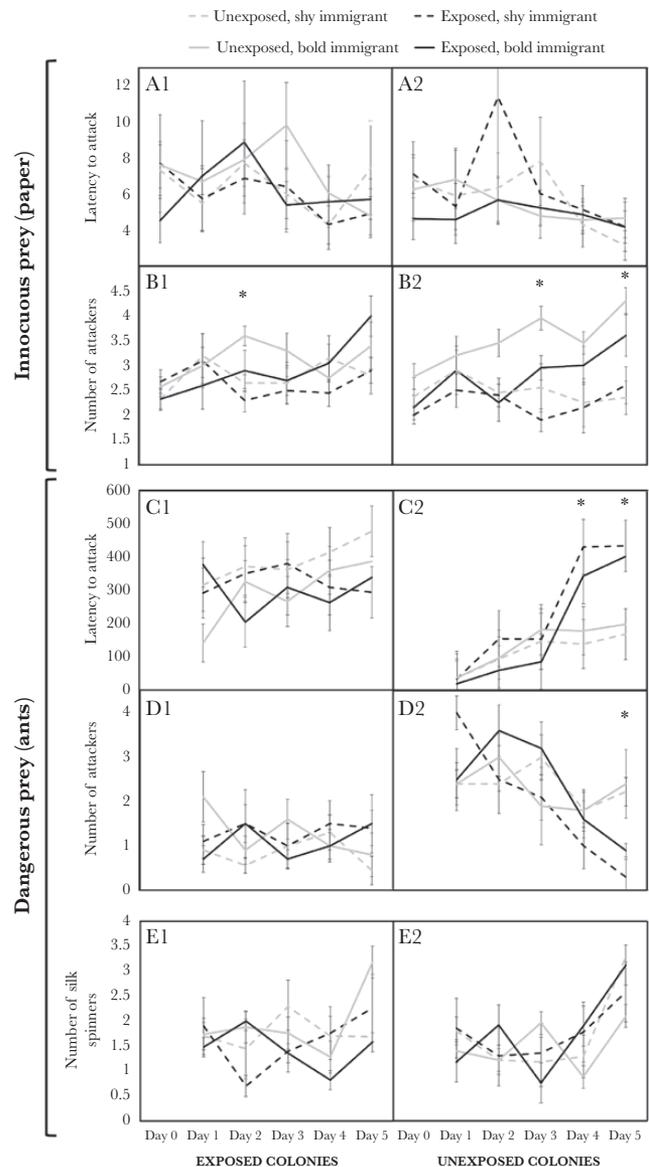


Figure 1

Colony collective responses over time. Latency to attack and number of attackers on innocuous prey (paper) over time when colonies were previously exposed to ants (A1, B1) or not previously exposed to ants (A2, B2). Latency to attack and number of attackers on dangerous prey (ants) over time when colonies were previously exposed to ants (C1, D1) or not previously exposed to ants (C2, D2). Number of spiders participating in defensive cribellate silk-making over time when colonies were previously exposed to ants (E1) or not previously exposed to ants (E2). Immigrants added to colonies on day 1 differed in predator experience (experienced = black; unexperienced = gray) and personality (bold = solid; shy = dashed). Asterisks indicate statistically significant differences between at least 2 treatments via post-hoc analysis (see Supplementary Table S1 for a full breakdown).

(i.e., attacking slower and with fewer individuals) when either the group majority or singleton immigrants were previously exposed to predators, and that immigrant personality had no effect on this outcome. Specifically, immigrants that had previous exposure to predator cues caused unexposed colonies to exhibit more cautious behavior and reduce their attack speeds toward ants and attacker numbers on ants, yielding attack speeds and numbers indistinguishable from those of exposed colonies (Figure 1: C2 and

Table 2

The 2 × 2 × 2 fully factorial LMM for each behavioral trial, showing degrees of freedom (df), adjusted R-Squares, F-ratios, and P-values

| | df | Adj. R-square | F-ratio | P-value |
|---|----|---------------|---------|-------------------|
| Latency to attack innocuous prey (paper) | | | | |
| Whole model | 11 | 0.014 | 1.52 | 0.12 |
| Colony experience | 1 | - | 1.72 | 0.19 |
| Immigrant experience | 1 | - | 0.011 | 0.91 |
| Immigrant BT | 1 | - | 0.019 | 0.89 |
| Colony experience × Immigrant experience | 1 | - | 0.34 | 0.56 |
| Colony experience × Immigrant BT | 1 | - | 2.43 | 0.12 |
| Immigrant experience × Immigrant BT | 1 | - | 0.48 | 0.49 |
| Colony experience × Immigrant experience × Immigrant BT | 1 | - | 0.21 | 0.65 |
| Day # | 4 | - | 2.86 | 0.023 |
| Latency to attack dangerous prey (ants) | | | | |
| Whole model | 11 | 0.17 | 8.49 | <0.0001 |
| Colony experience | 1 | - | 46.7 | <0.0001 |
| Immigrant experience | 1 | - | 0.62 | 0.43 |
| Immigrant BT | 1 | - | 3.21 | 0.074 |
| Colony experience × Immigrant experience | 1 | - | 7.26 | 0.0074 |
| Colony experience × Immigrant BT | 1 | - | 0.72 | 0.39 |
| Immigrant experience × Immigrant BT | 1 | - | 0.031 | 0.86 |
| Colony experience × Immigrant experience × Immigrant BT | 1 | - | 3.65 | 0.057 |
| Day # | 4 | - | 7.88 | <0.0001 |
| No. of attackers to innocuous prey (paper) | | | | |
| Whole model | 11 | 0.11 | 5.28 | <0.0001 |
| Colony experience | 1 | - | 0.67 | 0.41 |
| Immigrant experience | 1 | - | 8.19 | 0.0044 |
| Immigrant BT | 1 | - | 29.9 | <0.0001 |
| Colony experience × Immigrant experience | 1 | - | 1.27 | 0.26 |
| Colony experience × Immigrant BT | 1 | - | 5.49 | 0.019 |
| Immigrant experience × Immigrant BT | 1 | - | 0.99 | 0.32 |
| Colony experience × Immigrant experience × Immigrant BT | 1 | - | 1.81 | 0.18 |
| Day # | 4 | - | 2.45 | 0.045 |
| No. of attackers to dangerous prey (ants) | | | | |
| Whole model | 11 | 0.14 | 6.86 | <0.0001 |
| Colony experience | 1 | - | 54.7 | <0.0001 |
| Immigrant experience | 1 | - | 0.85 | 0.36 |
| Immigrant BT | 1 | - | 0.49 | 0.48 |
| Colony experience × Immigrant experience | 1 | - | 4.34 | 0.038 |
| Colony experience × Immigrant BT | 1 | - | 0.042 | 0.84 |
| Immigrant experience × Immigrant BT | 1 | - | 0.8 | 0.37 |
| Colony experience × Immigrant experience × Immigrant BT | 1 | - | 2.71 | 0.1 |
| Day # | 4 | - | 2.98 | 0.019 |
| No. of defensive silk spinners | | | | |
| Whole model | 11 | 0.048 | 2.83 | 0.0014 |
| Colony experience | 1 | - | 0.0099 | 0.92 |
| Immigrant experience | 1 | - | 0.42 | 0.51 |
| Immigrant BT | 1 | - | 0.094 | 0.76 |
| Colony experience × Immigrant experience | 1 | - | 2.45 | 0.12 |
| Colony experience × Immigrant BT | 1 | - | 0.27 | 0.6 |
| Immigrant experience × Immigrant BT | 1 | - | 0.038 | 0.84 |
| Colony experience × Immigrant experience × Immigrant BT | 1 | - | 1.05 | 0.31 |
| Day # | 4 | - | 6.72 | <0.0001 |

Significant results are shown in bold. BT = behavioral type (i.e., shy vs. bold).

D2). Immigrant personality (bold vs. shy), which reflects their status as a keystone (Pruitt et al. 2013), had no influence on response to dangerous ants. For innocuous prey (paper), we did not find any relationship between immigrant experience and collective behavior. We did however find a strong positive relationship between immigrant boldness and the number of attackers deployed to innocuous (but not dangerous) prey, which is corroborative of the keystone dynamics that have been described previously in this system (Pruitt and Keiser 2014; Pinter-Wollman et al. 2016; Pruitt et al. 2016). Our findings further demonstrate that predator presence eliminates keystone effects, consistent with a previous study

that showed predator presence eliminated the link between colony behavioral composition and collective behavior (Wright et al. 2017). Thus, we found no evidence that colonies preferentially base collective decisions on majority information or on immigrant keystone status in the presence of predators, and therefore we reject both the *democracy hypothesis* and the *dictator hypothesis*. Colonies, however, remained cautious when constituents had prior experience with predators and became more cautious when immigrants with prior predator experience were introduced to unexposed colonies. This result supports the *better safe than sorry hypothesis*, where colonies act based on any source of information to mitigate risk.

Our results demonstrate high levels of behavioral plasticity in *S. dumicola* colonies, where groups can modify their behavior in response to information regarding risk. The presence of behavioral plasticity in *S. dumicola* is not entirely surprising, as several studies have shown high levels of behavioral plasticity in this species in other contexts, such as in foraging and defensive cribellate silk spinning behavior (Wright et al. 2016; Wright et al. 2017). However, this plasticity has always been linked to the collective personalities of the groups, or the personality of “keystone” individuals due to their ability to alter the collective behavior of groups containing shy individuals (Pruitt et al. 2013; Pruitt and Keiser 2014). The present study differs from these in its focus on information and personality rather than personality per se, and demonstrates that information can over-ride majority experience and personality effects when the information is pertinent for colony survival. A past study on how colonies respond to keystone information/misinformation demonstrated that colonies are less susceptible to mistakes when responding to predators vs. innocuous prey (Pruitt et al. 2016), perhaps mirroring the cautious behavior revealed in this study. The ability of uninformed colonies to shift their behavioral phenotypes to match those of informed colonies hints at a long evolutionary history with predatory ants, and at the possible benefits of being forewarned to their presence (Henschel 1998; Keiser et al. 2015). Colonies thus appear to adopt a “better safe than sorry” strategy. This is likely because preparing for an ant raid that never comes is considerably less costly than failing to adequately prepare when a raid occurs, especially when raids are common and typically result in total colony annihilation (Keiser et al. 2015; Wright et al. 2016).

Bold immigrants do have a pronounced effect on colony foraging behavior directed towards innocuous prey, and this was retained even in predator-exposed colonies. This retention of keystone effects was not expected, as a previous study (Wright et al. 2017) had shown that exposure to predators appeared to over-ride the link between colony personality composition and collective foraging on innocuous prey. In the previous study, groups containing a higher proportion of bold individuals attacked innocuous prey in larger numbers than those containing more shy spiders (Wright et al. 2017). However, this positive relationship between the proportion of bold individuals and attack magnitude vanished when colonies were exposed to predatory ants as in the present study. Given that the addition of bold keystones to shy colonies alters colony composition, we predicted that predator presence would nullify keystone effects (Wright et al. 2017). Yet, surprising, adding a bold individual increased colony aggressiveness to some degree even in predator-exposed colonies. Our previous study admittedly used larger colony sizes (20 vs. 10 here) and colonies in that study often contained multiple bold individuals. To what degree either of these factors contribute to these contrasting results is presently unclear. Although, these differences raise a number of new hypotheses regarding how keystone influence might change with contrasting group sizes and the presence of multiple socially influential individuals. It is also unclear why colony-level differences in behavior appeared to lag for several days, and only emerged on days 4 and 5. Some possible explanation are that colonies have a fixed temporal response threshold for exposure, or that it takes time for immigrant information to pass between individuals and that a certain quorum must be reached before colonies respond collectively to new information.

Given their limited mobility and inability to fly, social spider colonies are generally fixed to a single location for their entire lives, save for rare and extremely risky instances of ballooning (Schneider et al. 2001). Among social spiders, *S. dumicola* is a

particularly immobile species, as they live in sparsely vegetated arid environments. Immobility, combined with high colony extinction rates due to predatory ants, suggests that these colonies must remain hyper vigilant to outside threats. Therefore, information sharing about risks in immobile and extinction-prone societies may be much more frequent than in societies where relocation or temporary retreat is possible and group-level extinction is uncommon. If true, then it is not surprising that *S. dumicola* colonies appear to prioritize safety by adopting a *better safe than sorry* strategy when any individual in the group is privy to indications of predator presence. Future studies comparing information sharing proficiency on a variety of social species that vary in their mobility and group-level extinction rates due to predation could illuminate the effects of life history and environment on information sharing. We would predict that mobile species, populations, or colony types with low extinction rates due to predators will exhibit the least amount of information sharing, and immobile, extinction-prone societies would exhibit the most information sharing. This is an area of research wide open for discovery.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Wright et al (2019).

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