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ORIGINAL ARTICLE

Exposure to predators reduces collective foraging aggressiveness and eliminates its relationship with colony personality composition

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Abstract
Predation is a ubiquitous threat that often plays a central role in determining community dynamics. Predators can impact prey species by directly consuming them, or indirectly causing prey to modify their behavior. Direct consumption has classically been the focus of research on predator-prey interactions, but substantial evidence now demonstrates that the indirect effects of predators on prey populations are at least as strong as, if not stronger than, direct consumption. Social animals, particularly those that live in confined colonies, rely on coordinated actions that may be vulnerable to the presence of a predator, thus impacting the society's productivity and survival. To examine the effect of predators on the behavior of social animal societies, we observed the collective foraging of social spider colonies (*Stegodyphus dumicola*) when they interact with dangerous predatory ants either directly, indirectly, or both. We found that when colonies were exposed directly and indirectly to ant cues, they attacked prey with approximately 40–50% fewer spiders, and 40–90% slower than colonies that were not exposed to any predator cues. Furthermore, exposure to predatory ants disassociated the well-documented positive relationship between colony behavioral composition (proportion of bold spiders) and foraging aggressiveness (number of attackers) in *S. dumicola*, which is vital for colony growth. Thus, the indirect effects of predator presence may limit colony success. These results suggest that enemy presence could compromise the organizational attributes of animal societies.

Significance statement
This study demonstrates that predator presence can compromise the organizational structure of complex animal societies. Indirect cues of predators proved to be most effective at eliminating the relationship between colony personality composition and group foraging. These results suggest that colonies may only incur the foraging benefits associated with particular personality compositions in habitats where their main predator does not occur. It is true that most, if not all, animals must respond at some time to the threat of predation, and shifts in behavior are often used as a first line of defense. Therefore, given the fact that individual differences in behavior are important in determining collective outcomes in many species, we feel our findings could have implications for a broad range of social taxa.

Keywords Behavioral syndrome · Personality · Predation · Trait-mediated interaction · Temperament

Introduction

Predator-prey interactions are one of the most widely studied phenomena in ecology because of their importance in driving community dynamics (Berryman 1992; Murdoch et al. 2003; Williams et al. 2004). Traditionally, studies of predator-prey interactions have focused on how predators capture and consume prey and the effects of this consumption on prey

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populations. The effects of direct consumption on prey populations are referred to as *consumptive* effects or *density-mediated interactions*. An alternative approach to examining predator-prey interactions was to address the *non-consumptive* effects of predators. These indirect effects include changes to the behaviors of prey species, such as dispersal, foraging times, and general activity level (Lima and Dill 1990; Lima 1998; Bell and Sih 2007; Cote et al. 2013), or induced morphological, developmental, or physiological costs (Barry 1994; Downes 2001; Werner and Peacor 2003; Orrock et al. 2008) in response to perceived predation risk or intimidation. These *non-consumptive* effects can influence prey populations directly and through changes to trophic interactions. Non-consumptive predator effects are sometimes called *trait-mediated interactions*. Evidence from several meta-analyses that each estimated the magnitude of consumptive and non-consumptive effects, and total effects of predators on prey survival and density, have demonstrated that the non-consumptive effects on predator-prey interactions can be at least as strong as, or even substantially stronger than, consumptive effects (Werner and Peacor 2003; Preisser et al. 2005; Orrock et al. 2008). Both density-mediated and trait-mediated interactions, taken together, now form an integrative approach regarding how predators and prey interact, and the effects these interactions have on population dynamics.

The field of animal personalities, which investigates the ecological effects of consistent individual differences in behavior within a population or group, has proven effective at explaining many inter- and intra-specific interactions (Sih et al. 2004; Sih et al. 2012; Modlmeier et al. 2015), including predator-prey dynamics (Sih et al. 1990; Bell and Sih 2007; Cote et al. 2013). Common personality axes include aggressiveness/docility, boldness/shyness (or the degree to which individuals engage in risky behavior), sociability, activity level, or the degree to which individuals explore novel environments. Most studies on predator-prey interactions are performed on species of solitary or gregarious animals (Castellanos and Barbosa 2006; Bell and Sih 2007; Clinchy et al. 2013; Cote et al. 2013; David et al. 2014). However, personality studies investigating social taxa have revealed the presence of stable differences in behavior at both the individual and group level (Jandt et al. 2013; Bengston and Jandt 2014; Wright et al. 2016b). The extent to which behavioral variation at either or both of these levels influences predator-prey interactions, or any other kind of species interaction for that matter, has been little explored.

Predator-prey interactions where the predator, prey, or both are cooperative organisms offer an intriguing case study for examining how the collective personalities of either predator or prey might impact species interactions and outcomes. For instance, when a colony of social organisms is the target of predation, the outcome can range from colony annihilation to successful predator evasion, without or with individual casualties. Notably, the losses that a group sustains during an attack by a predator may reduce its capacity to combat future predation attempts or to reproduce, akin to leg or tail autonomy in response to predation in individual organisms. Such losses may further curtail a group's ability to effectively perform the various tasks necessary for colony function and growth, such as resource acquisition and care for offspring (Oster 1978). Losses sustained by cooperative hunting groups while attacking prey may reduce their ability to successfully overwhelm future prey. Recent data on colony-level personality in fish (Jolles et al. 2015), social arachnids (Keiser and Pruitt 2014), and eusocial insects (Modlmeier and Foitzik 2011; Wright et al. 2016a) suggest that the way prey colonies respond to such attacks might vary across groups and, conversely, that the mere presence of predators may alter colonies' behavioral tendencies in ways that impact their performance in other contexts (e.g., foraging efficiency, hygienic behavior).

While the effect of predators on group size (direct consumption) has been examined (Krause and Godin 1995), there has been little work on whether the presence of a predator may indirectly disrupt the organization and coordination of group activities. Given that groups can possess traits that individuals cannot (such as adaptive personality ratios and emergent behaviors), observing how predator presence impacts these collective traits could prove illuminating. For instance, many groups rely on complex organization and cooperation to successfully meet an array of ecological challenges and perform tasks such as collective foraging (Deneubourg et al. 1990; Robinson 1992; Bonabeau et al. 1998; Beshers and Fewell 2001; Camazine et al. 2001). Examining how predators affect the collective traits of their prey could therefore enhance our understanding of the ecology of social animals in particular, as well as why the broader ecological impacts of social animals may vary through space and time.

Study system and questions

The African desert social spider, *Stegodyphus dumicola*, is abundant and occurs throughout southern Africa. These spiders build dense three-dimensional silken retreats that are permeated with numerous tunnels where the spiders lay their eggs and reside for protection (Seibt and Wickler 1990). Multiple two-dimensional capture webs radiate away from this central retreat, and spiders are recruited to the capture webs through vibrational cues produced by ensnared and struggling prey (Whitehouse and Lubin 1999; Amir et al. 2000). These spiders are a tractable system for evaluating the magnitude of non-consumptive effects on group behavior because spider groups rely on the ability of their constituents to organize hunting groups to subdue large and occasionally dangerous prey (Keiser and Pruitt 2014; Wright et al. 2015). This species also exhibits a high degree of intracolony behavioral (or personality) variation that is predictive of colony performance in foraging (Grinsted et al. 2013), defensive behavior (Wright et al. 2016a), web repair (Keiser et al. 2016c), bacterial transmission rates (Keiser et al. 2016a, b), and task differentiation among colony constituents (Wright et al. 2015). In fact, colony behavioral composition is more important than colony size for predicting foraging aggressiveness and efficiency in this species (Keiser and Pruitt 2014). Additionally, *S. dumicola* colonies are frequently raided by pugnacious ants (*Anoplolepis custodiens*), a voracious social predator that is the main cause of death for established *S. dumicola* colonies in nature wherever these species' ranges overlap (Henschel 1998; Keiser et al. 2015; Wright et al. 2016a).

The defensive behavior of *S. dumicola* toward *Anoplolepis* ants hints at an important evolutionary history between these species. *S. dumicola* colonies exhibit a unique, stereotyped defensive behavior when ants lay siege to the colony: the spiders immediately begin producing cribellate silk that they then use to ensnare individual ants and to construct tangled silken barriers that help prevent the advancement of ant workers into the spiders' vulnerable retreat (Henschel 1998; Wright et al. 2016a). Cribellate barriers are constructed prophylactically at the attachment points of colonies to the surrounding substrate in regions where ant raids are particularly common (Henschel 1998). Previous studies have shown that the magnitude of this defensive response depends on the colony's personality composition, where colonies composed of a mixture of bold and shy spiders exhibited twice as much defensive cribellate making as monotypic colonies (Wright et al. 2016a). *S. dumicola* colonies attack *A. custodiens* workers progressively slower and with fewer individuals after repeated exposures to dangerous ants in the lab, and colonies receiving ant treatments exhibit a reduction in mass gain (Pruitt et al. 2016; Wright et al. 2016a). This stands in contrast to how colonies behave when they forage on an innocuous prey item, such as a moth. Under these conditions, colonies attack progressively faster after repeated exposures and do not lose significant mass (Pruitt et al. 2016). Thus, it is clear that *S. dumicola* colonies can acquire information about their environment during foraging bouts and are able to adjust their foraging behavior depending on the representation of innocuous vs. dangerous prey in their environment. Yet, it is unknown whether *S. dumicola* colonies can acquire information about predator presence/absence using indirect methods (e.g., via chemical cues), without physically interacting with the predator. Such an ability could have substantive benefits if early detection proves important in preparation for a raid or (Kleeberg et al. 2014), conversely, this ability could have appreciable costs if predator presence causes individuals or groups to behave suboptimally.

The fact that *S. dumicola* relies so heavily on complex and well-orchestrated collective behaviors to execute important tasks make this species ideal to evaluate the effects that predator presence may have on colony organization and performance. Here, we hypothesize that the threat of predation may negatively impact any number of these organizational traits, such as decreasing colony responsiveness towards prey vibratory cues or the number of attackers that respond to prey (Harwood and Aviles 2013), thus adversely impacting colony performance.

To uncover how predators influence the collective behavior of their prey, we constructed experimental colonies that varied continuously in their proportion of bold versus shy individuals that composed them. We tested the collective prey capture of groups of different behavioral composition before subjecting them to either direct, indirect, direct + indirect, or no predatory cues and reevaluated their collective behavior every 5 days to assess whether and how interactions with ants altered spiders' foraging aggressiveness. In addition to tracking colony behavior over time, we also collected data on membership mortality, and the average change in mass in colony constituents.

Methods

Collection and measurement

Spider colonies were collected from Upington, South Africa, in October 2015. Colonies were brought into the lab, and each spider was individually isolated from its nestmates in 30-ml plastic condiment containers. Once isolated, we measured the boldness of each spider by administering two puffs of air to their anterior prosoma using a rubber squeeze-bulb. Boldness is defined as the propensity for an individual to engage in risky behavior (Sloan Wilson et al. 1994). The puffs of air simulate an attack from an avian predator and cause the spider to pull its legs toward its body and huddle (Riechert and Hedrick 1990; Pruitt et al. 2013). The latency to unhuddle and move one whole body length following this aversive stimulus is our measure of boldness. We operationally define *bold*, *intermediate*, and *shy* individuals as those having latencies between 0 and 199, 200–399, and 400–600 s, respectively (Keiser et al. 2014). These boldness scores are then subtracted from 600 (the maximum value) so that higher numbers reflect greater boldness scores.

Following boldness assays, we measured the mass and prosoma width of each spider. The body condition of each spider was estimated as its residual from a linear regression of mass versus body size, measured as prosoma width, for all spiders in our study (Jakob et al. 1996). Using this technique, positive values indicate spiders that are heavier for any given prosoma width, and negative values indicate spiders that are relatively lighter for their prosoma width. At the end of the experiment, we remeasured the mass and prosoma width of each spider to examine whether predator-exposure treatment had an effect on average body condition.

Colony composition

Following boldness, mass, and prosoma measurements, we constructed a total of 84 colonies (21 colonies per treatment group) containing 20 spiders each. Each experimental colony was derived from a single source colony, and spiders from different source colonies were never mixed in order to preserve natural levels of within-group relatedness and familiarity (Laskowski and Pruitt 2014; Modlmeier et al. 2014b; Laskowski et al. 2016). Each of the 21 colonies per treatment group varied along a gradient in the proportion of *bold* and *shy* individuals contained within the colony (from 100% *bold* to 100% *shy* and every composition in-between). For example, the first colony contained 20 bold spiders only, the next colony contained 1:19 shy:bold, followed by 2:18 shy:bold, and so on, ending with a colony containing 20 shy spiders only. Each colony was housed in a 230-ml plastic cup with a lid and contained three *Acacia mellifera* twigs as web-building substrate. We assigned each colony to one of the following four treatment groups: (1) exposed to ants indirectly, (2) daily direct exposure to ants in the capture webs, (3) both direct and indirect exposure to ants, and (4) neither direct nor indirect cues (control) (in a 2 × 2 design). Colonies were provided 24 h to construct capture webs prior to any ant exposures providing sufficient time to construct a retreat structure and a small capture web within the enclosure.

To expose colonies indirectly to ants, five *A. custodiens* workers were placed in a 230-ml cup with water and sugar. The cup of the experimental spider colony was then stacked on top of the ant cup, confining the ants to the small space (10 mm high) between the two stackable cups. We punched many small holes in the bottom of the spider colony cup to allow indirect cues, such as chemical compounds, to permeate into the spider colony. For treatments that were allowed to interact only directly with ants, a single *A. custodiens* worker was placed in the center of the capture web once daily. Spiders were allowed to attack and subdue the ant, but the ant was removed from the colony before the spiders were able to consume them. These colonies were stacked on top of cups containing water and sugar, but no ants. Colonies exposed simultaneously to both direct and indirect ant cues were stacked on cups containing ants, sugar, and water, and received an ant in their capture web once daily. Lastly, our control colonies were stacked inside cups that contained only sugar and water, and never received direct or indirect ant cues.

Colony aggressiveness

To assess each colony's baseline aggressiveness in response to prey prior to manipulation, all colonies were assayed for colony level aggressiveness in prey capture four times over 2 days prior to setting up our treatment groups. To assess colony aggressiveness, we placed a small piece of white paper (1 × 1 cm) in the center of the colony's capture web. Colonies were given a 30-s acclimation period following this initial disturbance. We then vibrated the paper using a handheld vibrator, which causes the paper to flutter about, resembling a struggling winged insect. We recorded the latency for the first spider to attack the paper, as well as the number of attacking spiders on the capture web at the moment the paper was first attacked. These values give us a measure of both the speed and magnitude of prey attack exhibited by each colony. After assigning colonies to the various predator-exposure treatments, we re-measured colony level aggressiveness four more times every 5 days to determine the impact of our predator-exposure treatments on colony aggressiveness over time (i.e., whether differences were exacerbated or perhaps attenuated through habituation). Colonies were given a maximum of 5 min to attack the simulated prey item. All colonies were fed a single, dead, previously frozen and thawed termite worker (to ensure termites did not damage capture webs), every 3 days over the course of the experiment. We removed termite corpses the following day to reduce clutter in the capture webs, which could subtly influence colony behavior due to their propensity to vibrate during mock prey trials using the vibratory device.

Blinded methods across treatments were not used, given that it was necessary to spatially separate treatment groups so as not to inadvertently contaminate other treatments with indirect (chemical) ant cues. Therefore, we knew which treatment groups we were testing during observations. However, within each treatment group, the experimenter was blind to colony ID during observations, and thus data obtained relating to group composition was gathered blind. Please see Supplementary Table (S1) for the complete experimental timeline.

Statistical analysis

To assess whether our treatment groups impacted colonies' aggressiveness, measured as their latency to attack or the number of attackers deployed in response to a novel prey stimulus over time, we used normally distributed GLMMs with an identity-link function. Inspection of Q-Q plots and the distribution of the model residuals conveyed a strong fit for this model structure. We included time (day number), treatment, and a treatment × time interaction term as predictor variables in our model. "Time" is a categorical variable denoting the day number the behavioral assessments occurred, such as colony aggressiveness on day 0, day 5, day 10, and day 15. Source colony ID and experimental colony ID nested within source colony ID were included as random effects. A significant interaction term between trial number and treatment indicates that colonies change in their response over time as a result of their treatment group. Post hoc comparisons for latency to attack and number of attackers were performed between each treatment group at each time point using Tukey's HSD groupings. We performed an additional analysis at each time point using two-way ANOVAs to determine whether any interaction exists between direct and indirect effects, and their relative importance.

Previous studies have shown a strong correlation between the proportion of bold spiders within a colony and both the latency to attack and average number of attackers. We used multiple bivariate linear regressions to verify this relationship in each treatment group prior to any ant exposures, and again at each time point to observe how this relationship may change with exposure to predators. We compared our initial observations (day 0) to our final observations (day 15) using ANCOVAs in order to determine whether the relationship between colony composition and foraging aggressiveness changed before vs. after extended exposure to predatory ants.

To determine the potential effects of predator-exposure treatments on spider mortality (measured as the number of dead individual spiders found in each colony at the end of the experiment), and change in body condition, we again used GLMMs with a normal distribution and identity-link function with source colony ID and experimental colony ID nested within source colony ID included as random effects. All statistics were performed in JMP 12, by SAS. An independent model was created for both of these colony performance metrics (mortality and change in body condition).

Results

Effects of treatment on number of attackers and latency to attack

Exposure to any predator cues decreased the magnitude of prey attacks over time, which could impair the colony's ability to capture large prey. All colonies that received direct, indirect, or both predator cues displayed a decrease of up to 50% in the number of attackers that responded to simulated prey relative to the control colonies (whole model: $p < 0.0001$) (Fig. 1). Indirect cues were also over 2.5 times more effective than direct cues in influencing colony behavior when comparing LogWorth, which is defined as –log(p value), and is used to show the relative strengths of predictor variables (direct vs. indirect effects in this case). All colonies, including the control treatment, showed an increase in latency to attack the simulated prey over time (day no.: $p = 0.0001$). However, treatments that received any ant cue attacked slower on average than control colonies (treatment: $p = 0.0077$). The interaction term time × treatment was not significant ($p = 0.29$) indicating that treatments only differed in their average attack latencies, and these differences did not change over time (Fig. 2). Post hoc comparisons between treatment groups at each time point did not reveal significant differences in latency to attack at any one time point. See Table 1 for the full model outputs, Table 2 for comparisons between treatment groups at each time point, and Table 3 for 2 × 2 analyses. In short, exposure to any predatory cue reduced the magnitude and speed at which colonies attack prey, and indirect cues proved to be over 2.5 times more important than direct cues in influencing colony behavior.

Effects of personality composition and treatment on prey attack

The well-documented, positive association between the proportion of bold spiders in a colony and collective foraging disappeared over time for colonies that were exposed to predator cues. On day 0, prior to exposing any colonies to predator cues, all colonies displayed the characteristic positive relationship between the proportion of bold spiders within the colony and the number of attackers that were deployed in response to prey (Keiser et al. 2014). However, this positive relationship gradually diminished in all experimental colonies over time following exposure to ants (indirectly, directly, or both), while the relationship was maintained in control colonies (Fig. 3). Comparisons between the slopes at day 0 versus day 15 for each treatment group independently using ANCOVA further suggests that the effect of colony personality composition on the number of individuals that respond to prey decays over time in some treatments groups (control: $F_{1,\ 42} = 0.23$, $p = 0.63$; indirect cues: $F_{1,\ 42} = 12.2$, $p = 0.0012$; direct cues: $F_{1,\ 42} = 0.75$, $p = 0.39$; both direct and indirect cues: $F_{1,\ 42} = 6.02$, $p = 0.018$). Most notably, this change over time was only significant for treatments where ants were placed beneath the colony (i.e., those colonies provided with indirect cues) but not for control colonies or colonies that only interacted with ants directly on the capture web. This result conveys that the persistent exposure to indirect cues of nearby ants is key in ablating the collective aggressiveness of *S. dumicola* societies composed of bold spiders. For latency to attack, no clear patterns emerged over time or between treatments.

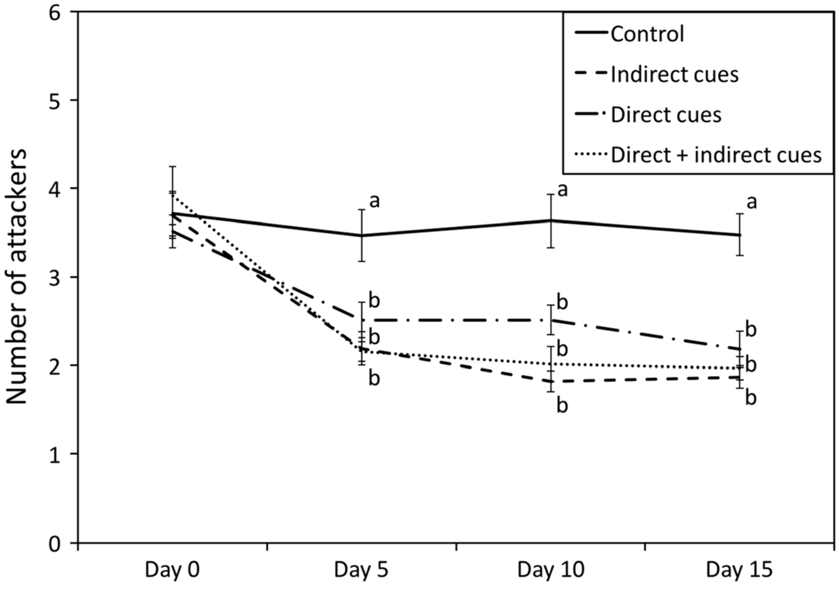

Fig. 1 Mean number of spider attackers observed over time in the four predator-exposure treatment groups. *Different letters* depict significant differences between treatments ($p < 0.05$). When no letters are present, treatments do not significantly differ. *Error bars* show standard error

Mortality and body condition

We did not observe any significant differences between ant exposure treatment groups in mortality rate ($\chi^2_3 = 1.86$, $p = 0.60$), or change in body condition ($\chi^2_3 = 0.76, p = 0.85$).

Discussion

Our study demonstrates that the non-consumptive effects of predatory ants impairs the foraging efficiency of *S. dumicola* colonies, which may in turn reduce colony success in nature. When spider colonies were exposed directly or indirectly to ant cues, *S. dumicola* colonies attacked prey with 40–50% fewer spiders, and at speeds that were 40 to 90% slower than control colonies. This finding is important because *S. dumicola* colonies, like other social spiders, require quick attack speeds to reach prey before they can escape, and colonies rely on deploying large numbers of spiders to successfully overwhelm large or dangerous prey items (Pruitt and Riechert 2011; Harwood and Aviles 2013). More broadly, spider societies are thought to have evolved because of their ability to subdue large and particularly profitable prey that are unavailable to singleton spiders (Nentwig 1985; Agnarsson et al. 2006; Powers and Aviles 2007; Yip et al. 2008; Aviles and Purcell 2012). In fact, large colonies *require* very large prey to persist (Yip et al. 2008). We consequently reason that exhibiting a 40–90% reduction in attack speed and a 40–50% reduction in the number of attackers could diminish a colony's ability to capture prey and,

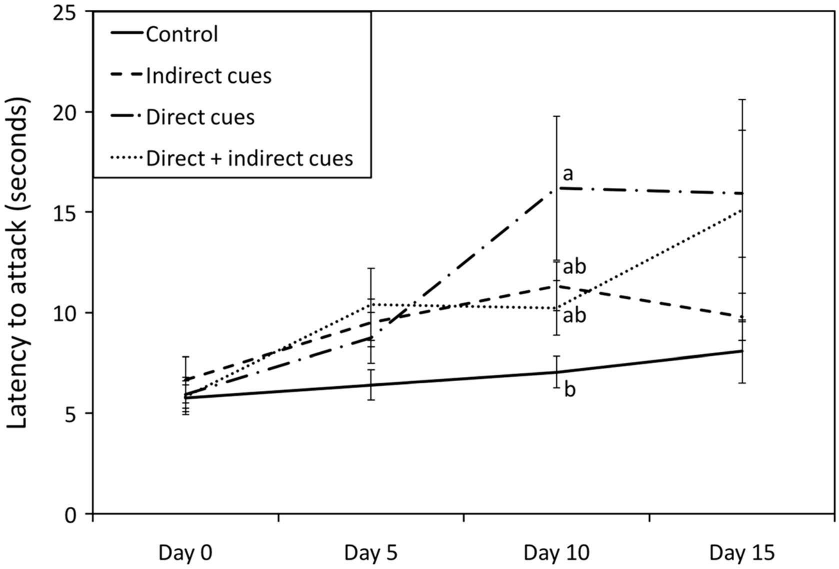

Fig. 2 Mean latency to attack over time in the four predator-exposure treatment groups. *Different letters* depict significant differences between treatments ($p < 0.05$). When no letters are present, treatments do not significantly differ. *Error bars* show standard error

Table 1 Results of the GLMM examining the effects on response to a simulated prey including degrees of freedom (df), chi-square test statistic, and *p* values

Predictor variable	*df*	χ2	*p* value
No. of attackers			
Day no.	3	90.4	<0.0001*
Treatment	3	69.7	<0.0001*
Day no. × treatment	9	30.6	0.0003*
Whole model	15	165.2	<0.0001*
Latency to attack			
Day no.	3	20.7	0.0001*
Treatment	3	11.9	0.0077*
Day no. × treatment	9	10.7	0.29
Whole model	15	41.7	0.0002*

consequently, reduce colony growth and overall fitness. Furthermore, indirect exposure to ant cues alone was sufficient to drastically reduce colonies' responsiveness towards prey and proved to be more than 2.5 times more important than indirect cues in influencing colony behavior. Therefore, colonies that never directly experience an ant raid may still suffer by simply residing in proximity to these predators.

Our results further revealed that ant presence, in addition to their negative effects on colony foraging speed and intensity (Figs. 1 and 2), weakens the relationship between colony personality composition and foraging aggressiveness (number of attackers) in *S. dumicola* (Fig. 3). Past studies have demonstrated a strong positive relationship between the proportion of bold spiders within a colony and the number of attackers that respond during foraging events. Our results demonstrate that this effect vanishes when *S. dumicola* colonies are exposed to cues of predatory ants. In particular, it seems that persistent, indirect cues are necessary and sufficient for weakening this well-established relationship: indirect cues proved more consequential than direct cues in diminishing the link between colony composition and foraging aggressiveness (Fig. 3). The sufficiency of indirect cues to alter colony behavior hints at a long evolutionary history with these predators.

These findings suggest that the presence of predatory ants could weaken the role of bold spiders in *S. dumicola* colonies as "keystone individuals" (Modlmeier et al. 2014a). Adding a single, highly bold spider into a colony composed of only shy spiders dramatically decreases colonies' latency to attack and increases the number of attackers that respond to prey (Pruitt et al. 2013; Pruitt and Keiser 2014). Bold spiders appear to achieve this social influence by catalyzing aggressiveness in

Table 2 Results of a GLMM examining the changes in number of attackers and latency to attack in the different treatment groups over time

Independent variable treatment	Number of attackers			Latency to attack		
	Indirect	Direct	Indirect + direct	Indirect	Direct	Indirect + direct
Day 0						
Indirect cues	–	–	–	–	–	–
Direct cues	0.96	–	–	0.93	–	–
Direct + indirect cues	0.92	0.68	–	0.9	0.99	–
Control (no ants)	0.99	0.94	0.94	0.88	0.99	1
Day 5						
Indirect cues	–	–	–	–	–	–
Direct cues	0.69	–	–	0.97	–	–
Direct + indirect cues	0.99	0.61	–	0.95	0.81	–
Control (no ants)	0.0002*	0.0088*	0.0001*	0.34	0.58	0.14
Day 10						
Indirect cues	–	–	–	–	–	–
Direct cues	0.097	–	–	0.34	–	–
Direct + indirect cues	0.91	0.33	–	0.98	0.17	–
Control (no ants)	<0.0001*	0.0016*	<0.0001*	0.45	0.012*	0.68
Day 15						
Indirect cues	–	–	–	–	–	–
Direct cues	0.62	–	–	0.56	–	–
Direct + indirect cues	0.98	0.83	–	0.67	0.99	–
Control (no ants)	<0.0001*	<0.0001*	<0.0001*	0.98	0.34	0.44

Table 3 Results from two-way ANOVAs comparing direct and indirect effects, as well as the interaction between these two modalities

Day no. and cue	Number of attackers			Latency to attack		
	F Ratio	*p*	LogWorth	*F* Ratio	*p*	LogWorth
Day 0						
Direct	0.0021	0.96	0.016	0.14	0.71	0.15
Indirect	0.54	0.46	0.33	0.19	0.66	0.18
Direct × indirect	0.684	0.41	0.39	0.32	0.57	0.24
Day 5						
Direct	5.71	0.019*	1.71	1.56	0.21	0.67
Indirect	15.6	0.0002*	3.77	3.27	0.074	1.13
Direct × indirect	4.91	0.029*	1.53	0.29	0.58	0.23
Day 10						
Direct	4.95	0.029*	1.54	3.87	0.052	1.28
Indirect	30.6	<0.0001*	6.42	0.17	0.68	0.16
Direct × indirect	9.85	0.0024*	2.65	6.22	0.0146*	1.83
Day 15						
Direct	11.1	0.0013*	2.87	3.89	0.052	1.28
Indirect	25.3	<0.0001*	5.53	0.017	0.89	0.048
Direct × indirect	14.8	0.0002*	3.62	0.14	0.71	0.15

their otherwise shy, non-aggressive group mates, eventually leading to a lasting shift in colonies' behavioral composition (Pruitt et al. 2013; Pruitt and Keiser 2014; Pruitt and Pinter-Wollman 2015). The degree to which keystones catalyze this behavioral variation is directly proportional to the magnitude of their boldness scores (Pruitt and Keiser 2014) and the length of time these individuals remain in the group (Pruitt and Pinter-Wollman 2015). Having just one bold individual also increases colonies' collective mass gain and survival in laboratory conditions (Pruitt and Keiser 2014; Lichtenstein et al. 2016). Thus, *S. dumicola* colonies may only gain the benefits of bold keystone individuals in environments where *Anoplolepis* ants (or perhaps a wide range of other predators or risky cues) do not occur, or are rare. Populations of *S. dumicola* and *A. custodiens* are both ephemeral and patchy, so many regions exist where one, both, or neither species occur. Field studies that span across a diversity of environments are needed to critically evaluate these hypotheses.

Ant presence did not appear to affect any measure of colony growth that we considered, including individual mortality rates, or average changes in body condition. However, given the short duration of our study (2 weeks), we are hesitant to state definitively that ant presence does not influence any of these elements. It might merely take more time, or the ill effects might only appear under a limited set of conditions. For instance, high stress environments have been known to shorten life spans and generate weight loss in many species (Perez-Tris et al. 2004; Thomson et al. 2010; Clinchy et al. 2013). It is possible that our feeding regime, a termite every 3 days, was overly generous and consequently negated any predator-induced stress effects on colony performance. More restricted diets, longer-term experiments, or both might reveal nuanced performance effects. Alternatively, ant presence *per se* might not cause spiders sufficient physiological stress to reduce their body condition.

In summary, we provide experimental evidence that the mere presence of predators can alter and possibly impair the collective foraging traits of complex animal societies. Specifically, indirect cues from a prominent predator—*Anoplolepis* ants—were necessary and sufficient to reduce participation in collective prey capture and attack speed during staged foraging events. Furthermore, predator cues, and indirect cues in particular, nullified the well-documented effects of colony personality composition on collective foraging behavior. So, while colony predation rates on *S. dumicola* by *Anoplolepis* ants are high, it appears that *S. dumicola* colonies might also pay an additional price for ants being present in the vicinity of their nests in the form of depressed foraging aggressiveness and, therefore, foraging efficacy (Pinter-Wollman et al. 2017). This further suggests that these ant predators could suppress the positive effects of bold individuals on group success, even if *S. dumicola* colonies are lucky enough not to be subjected to a physical raid, which are typically lethal for the entire spider colony (Henschel 1998; Keiser et al. 2015; Wright et al. 2016a).

Given the diversity and abundance of species spanning varying degrees of sociality and complexity, from herding animals to eusocial insect societies, the findings herein could have far-reaching implications. Consistent individual differences in behavior that impact collective outcomes, like those seen in *S. dumicola*, have been discovered in countless

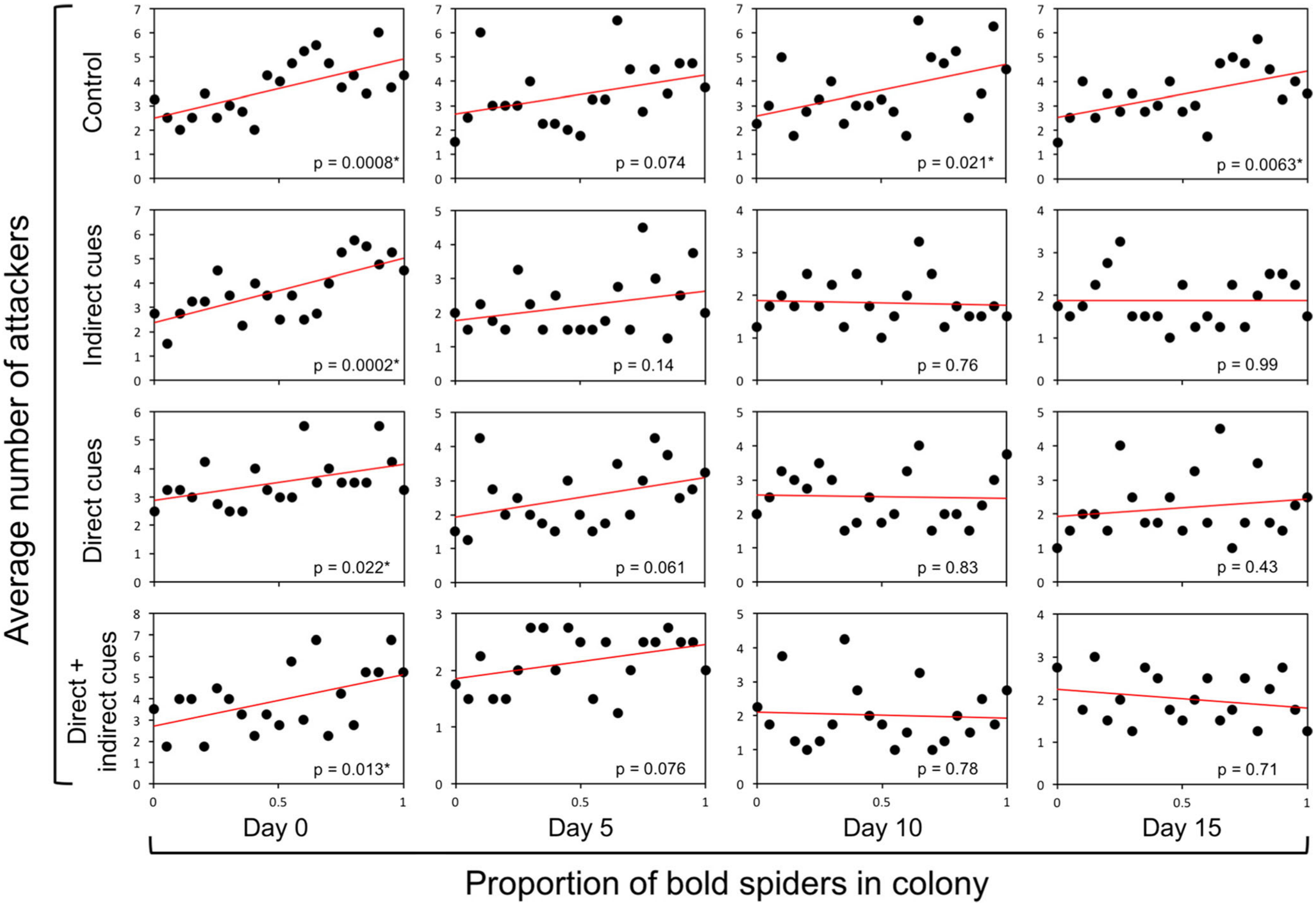

Fig. 3 Mean number of attackers vs. the proportion of bold individuals in the group over time for the four predator-exposure treatment groups. *p* values indicating the significance of the linear relationship from a regression analysis are noted on each plot

animal species such as spiders (Johnson and Sih 2005), water striders (Sih et al. 1990), ants (Modlmeier et al. 2012), bees (Wray et al. 2011), wasps (Wright et al. 2016b; Wright et al. 2017), fish (Bell and Sih 2007), rodents (Daly et al. 1992), birds (Aplin et al. 2014), primates (Flack et al. 2006), and more. For many animals, such variation has proven to be of great ecological importance (Sih et al. 2004; Sih et al. 2012; Jandt et al. 2013; Modlmeier et al. 2015). The ratios of different personality types within groups often predict group behavior (Pinter-Wollman 2012), survival and reproductive output (Wray et al. 2011; Pruitt 2013; Pruitt and Goodnight 2014), and can be associated with societal efficiency (Waibel et al. 2006; Chittka and Muller 2009; Pruitt and Riechert 2011; Modlmeier et al. 2012; Wright et al. 2014; Wright et al. 2015). Most, if not all, animals must respond at some time to the threat of predation, and shifts in prey behavior are often used as a first line of defense (Nonacs and Blumstein 2010). Our findings that predators may disrupt the effects of group composition on group function suggest that the mere presence of predators could negatively impact the performance of a diversity of animal societies.

Data availability statement The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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