

# Warring arthropod societies: Social spider colonies can delay annihilation by predatory ants via reduced apparency and increased group size



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## ABSTRACT

Sociality provides individuals with benefits via collective foraging and anti-predator defense. One of the costs of living in large groups, however, is increased apparency to natural enemies. Here, we test how the individual-level and collective traits of spider societies can increase the risk of discovery and death by predatory ants. We transplanted colonies of the social spider *Stegodyphus dumicola* into a habitat dense with one of their top predators, the pugnacious ant *Anoplolepis custodiens*. With three different experiments, we test how colony-wide survivorship in a predator-dense habitat can be altered by colony apparency (i.e., the presence of a capture web), group size, and group composition (i.e., the proportion of bold and shy personality types present). We also test how spiders' social context (i.e., living solitarily vs. among conspecifics) modifies their behaviour toward ants in their capture web. Colonies with capture webs intact were discovered by predatory ants on average 25% faster than colonies with the capture web removed, and all discovered colonies eventually collapsed and succumbed to predation. However, the lag time from discovery by ants to colony collapse was greater for colonies containing more individuals. The composition of individual personality types in the group had no influence on survivorship. Spiders in a social group were more likely to approach ants caught in their web than were isolated spiders. Isolated spiders were more likely to attack a safe prey item (a moth) than they were to attack ants and were more likely to retreat from ants after contact than they were after contact with moths. Together, our data suggest that the physical structures produced by large animal societies can increase their apparency to natural enemies, though larger groups can facilitate a longer lag time between discovery and demise. Lastly, the interaction between spiders and predatory ants seems to depend on the social context in which spiders reside.

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## 1. Introduction

The evolution of sociality has afforded group-living predators ample benefits, including advantages gleaned by cooperative hunting (e.g., Lührs et al., 2012; Boesch 1994; Creel and Creel, 1995) and anti-predator defenses via increased group vigilance (Roberts, 1996 e.g., the 'many eyes' effect; Powell, 1974). Thus, sociality undoubtedly plays a major role in mediating countless predator-prey interactions in nature. Arguably some of the most spectacular species interactions that animal groups experience arise when societies collide. Examples of these have been documented for over

a century; for example, intergroup combat between chimpanzee troops (Goodall et al., 1979; Wilson et al., 2002, mass-attacks by Vespidae wasps decimating honey bee colonies (Matsuura 1988), and the "legendary" wars between insect societies like carpenter ants (Fielde et al., 1904) and wood ants (Elton 1932; Wallis, 1962). In fact, eusocial Hymenoptera have served as models for inter-group contests for over a century, even for testing principles of human combat (i.e., Lanchester's "laws of combat"; Whitehouse and Jaffe, 1996). Given that animal societies often require abundant resources to persist, they must exhibit diverse lines of defenses across multiple organizational scales to protect those resources from other societies and to defend themselves from predatory social groups.

For many social units, simple dilution effects (Foster and Treherne, 1981), selfish herd dynamics (Hamilton, 1971), or early warning effects (i.e., the "Trafalgar effect"; Treherne and Foster, 1981) reduce predation risk for individuals despite an increased

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encounter rate with predators (Mooring and Hart, 1992). For example, larger groups of the colonial spider *Metepheira incrassata* experience increased encounter rates with predatory wasps, though per capita predation risk decreases with group size via early warning effects (Uetz et al., 2002). Because these colonial spiders live in three-dimensional colonies, the surface area to volume ratio of colonies decreases as they grow, allowing individuals to escape predation at centrally located sites (Rayor and Uetz, 1993) and thus, predation risk scales non-linearly with group size (Uetz and Hieber, 1994). While the biomaterials produced by many animal societies (i.e., termites, wasps, social spiders) offer survival advantages, we argue that they might also increase the group's apparency to natural enemies in the same way that large, long-lived plants are 'bound to be found' by herbivores (Feeny, 1976).

Just like Feeny's (1976) plant apparency hypothesis, which predicts that plants that are more "apparent" to their herbivores should invest broadly in functional defenses, so too should animal societies with conspicuous architecture exhibit more complex defenses against their enemies. For example, dynamic social groups like fish shoals often exhibit intricate collective anti-predator escape behaviours (Hall et al., 1986) and social groups of red colobus monkeys live in larger groups and exhibit specialized defensive behaviours when in proximity of predatory chimpanzee troops (Stanford, 1995). But, how do high-apparency animal societies which live in stationary, perennial physical structures (e.g., most arthropod societies) survive in predator-dense habitats, and what collective anti-predator mechanisms mediate their survival?

Evidence from multiple gregarious or social arthropods suggests that smaller domiciles can allow groups greater survivorship by evading detection by predators (gregarious spiny lobster: Eggleston and Lipcius, 1992; social spider mites: Mori and Saito, 2004). Thus, domicile size and colony traits jointly determine predation risk in some diverse social groups. Two collective traits in particular may likely decrease the risk of mortality for high-apparency groups in predator-dense habitats: increased group size (i.e., a dilution effect) and achieving the appropriate phenotypic composition within the group. For example, predation risk can be decreased by the presence of leaders in elephant herds and fish dyads (Milinski et al., 1997; McComb et al., 2011) and groups of social spiders and ant colonies containing more aggressive individuals can thwart invasion by social parasites (Pruitt, 2013; Pamminger et al., 2012). Here, we test how three collective traits (colony apparency, group size, and colony behavioural composition) jointly influence colony mortality in regards to predation by a voracious social forager.

*Stegodyphus dumicola* is a social spider that lives in groups of up to several hundred individuals in arid Southern Africa. These social spiders are philopatric, living in long-term colonies which can last several generations. They live in colonies that consist of two main physical units: a three-dimensional silken retreat labyrinth with tunnels where the spiders spend the majority of the day, and a large two-dimensional capture web which radiates from the retreat. These colonies experience strong top-down pressure from *Anoplolepis* spp. ants, causing up to 90% colony extinction rates in some populations in the Namib desert (Henschel 1998). Predation events on *S. dumicola* colonies are characterized by a sequence of events where one or a few scout ants discover the colony, more individuals are then recruited to the raid, and the workers tear apart the capture web and retreat silk to retrieve the spiders inside (Fig. 1). In response to an ant raid, spiders either evacuate the colony or begin to produce a defensive layer of cribellate silk to block the entrance of ants (Henschel, 1998). As opposed to the non-linear scaling of group size and colony size in the colonial spider *M. incrassata*, capture web size in *S. dumicola* appears to scale linearly with group size (Keiser and Pruitt, 2014). Thus, web apparency and predation risk might similarly increase linearly with group size in these spider societies.

Although the ant *A. steingroveri* will attack *S. dumicola* colonies of any size, multi-individual colonies are more likely to be discovered than individuals which are living solitarily (Henschel, 1998). Further, ant raids on *S. dumicola* nests are less common in populations where more *S. dumicola* live solitarily (Henschel 1998). Given the observation that some spider colonies appear to persist for many years in proximity to aggressively foraging *Anoplolepis*, we aim to identify the collective traits and individual behavioral mechanisms that allow some colonies subsist/linger while others are destroyed.

Here, using three different experiments, we address the following four hypotheses: (1) colonies whose physical structures are larger and, thus, more apparent to top predators will have decreased survivorship, (2) larger groups will have increased survivorship, perhaps due to dilution effects, (3) colonies containing more bold individuals (a "proactive" behavioural phenotype important for foraging in these societies) will have increased survivorship, (4) the behavioural interactions between predatory ants and spiders will differ between solitary individuals and social groups (i.e., their social context).

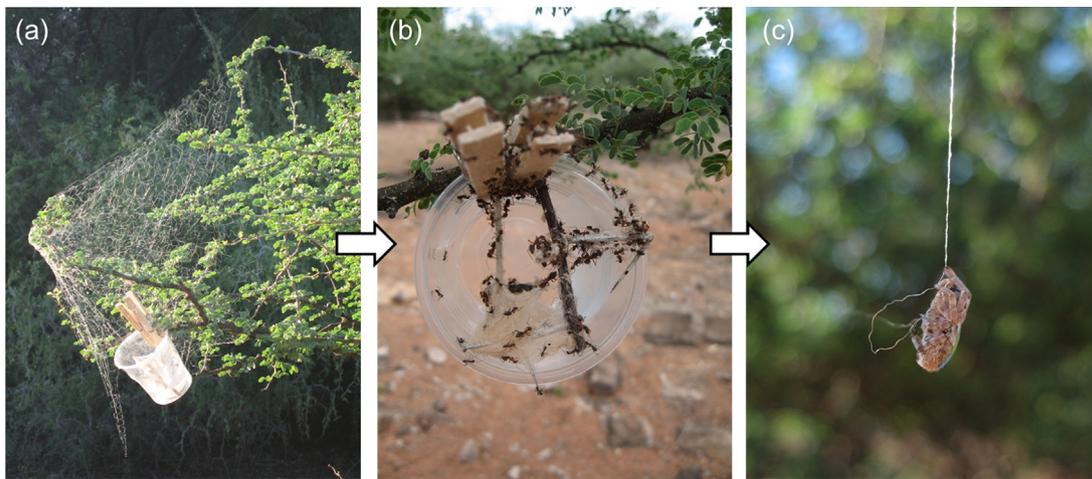
## 2. Materials and methods

### 2.1. Field site and study species

Colonies of *S. dumicola* were collected in February 2014 along roadside fences near Upington, South Africa (S28°27'24.9" E21°24'09.0"). All three experiments took place in an arid thornveld near Griekwastad, Northern Cape, South Africa (S28°54'32.0" E23°24'33.7"). This habitat was dominated by *Acacia mellifera* trees, similar to the sites where the spider colonies were originally collected. However, this particular site contained an abundance of an aggressive, ground-nesting predatory ant, *Anoplolepis custodiens*. This site contained 2–8 nest entrances per m<sup>2</sup> near *Acacia* trees and pitfall traps indicate that >95% of the insects surveyed were *A. custodiens*. Sites where spiders were collected, however, contained approximated 85% fewer *A. custodiens* during pitfall trap collections. These ants are voracious diurnal foragers (Addison and Samways, 2000; Löhr, 1992) and, although they exist in sympatry with *S. dumicola*, large spider colonies are rarely found at sites that contain high densities of *A. custodiens* (Henschel 1998).

#### 2.1.1. Web apparency and group size

We collected 16 different source colonies ranging in size from 4 to 200 individuals, and divided each colony into two groups of equal size, each in a 240 ml clear plastic cup containing a piece of an *Acacia* branch to facilitate web construction. These cups are an appropriate volume for *Stegodyphus* colonies surveyed in the field containing these group sizes (Pruitt et al., 2013). Spiders from different source colonies were not mixed in attempts to preserve natural levels of within-group familiarity (Schneider and Bilde, 2008; Modlmeier et al., 2014). This provided us with 36 colonies, ranging in size from 2 to 100 adult female spiders. Experimental groups were allowed 24 h to produce a retreat in their cup before they were fastened to a branch of an *A. mellifera* tree with two clothespins at 8pm. This time-frame for retreat construction does not alter the survivorship of artificial colonies in this habitat compared to those that are allowed up to one month to do so, and all of these retreats perform about as well as naturally-occurring retreats that can be more than a year old (*unpubl. data*). Every colony built a capture web overnight (avg. web area: 1486 cm<sup>2</sup> ± 255) and thus contained the two functional units of *Stegodyphus* colonies: a 3-dimensional retreat and a large 2-dimensional capture web. No more than three colonies were placed on a single tree, with at least 2 m between each colony, and we did not observe colonies constructing capture webs that were in contact with each other (i.e., "polydomous" colonies).



**Fig. 1.** Predation events on *S. dumicola* colonies by *Anoplolepis* ants are characterized by a sequence of events where (a) scouts discover the colony, likely via contact chemical cues from the capture web, (b) then more individuals are recruited to the raid where the workers chew through the capture web and nest to subsequently attack the spiders inside. (c) During the raid, some individual spiders escape attack by dropping from the substrate on a strand of silk and waiting through the duration of the raid.

We only fastened colonies onto trees on which we had previously observed *A. custodiens* foraging. One of the benefits of social *Stegodyphus* spiders is that individuals in experimentally constituted colonies reliably remain at the location where the colony is placed in the field and very rarely disperse to other sites (Pruitt et al., 2013; Grinsted et al., 2013; Keiser and Pruitt, 2014).

At 6am the next morning, we measured the approximate area of each capture web and then removed the capture web from one of each of the pairs of colonies (chosen haphazardly). Web area was calculated by estimating the approximate shape of the capture web (e.g., rectangle, triangle, etc.) and then measuring the length in cm of each of the sides using a tape measurer and calculating the total area of the web (Higgins and Buskirk, 1992) (but see Blackledge and Gillespie, 2002). We then visually surveyed the colonies every hour and recorded (1) the time until each colony was discovered by ants, (2) the time until the colony collapsed (i.e., all individuals had been removed from the plastic cup, either via extirpation by ants or evacuation into the capture web or adjacent branches), and (3) the time until each colony was “extinct” (every individual was killed). We distinguish collapse from extinction (i.e., whether spiders had fled or been killed) by inspecting the area around experimental colonies for the silk dragline *S. dumicola* readily leaves whilst traversing their environment. Thus, if no evidence for evacuation was found, it is likely that all spiders had been killed by ants. Any colony that was discovered before 6am (i.e., less than 10 h after placement in the field,  $n=8$  colonies) was removed from further analysis because we did not know the exact time that the colony was discovered.

### 2.1.2. Group size and personality composition

For this experiment, adult female spiders were obtained from 12 different source colonies collected at the same sites as before (source colony sizes: 45–182 spiders, 1375 spiders in total). To determine spiders' individual behavioural phenotypes (i.e., “personalities”), we quantified their boldness, defined as the latency to resume activity after an aversive stimulus (Sloan Wilson et al., 1994), where bold individuals resumed activity quickly and shy individuals had longer latencies to resume activity. In *S. dumicola* collected from these populations, boldness is highly consistent across time (repeatability = 0.63; Modlmeier et al., 2014; Keiser et al., 2014a,b,c) and, in some cases, has been shown to predict an individual's propensity to participate in colony tasks (Pruitt and Keiser, 2014). Further, the composition of personality types in the group has been shown to predict collective behaviour and group stability in *S. dumicola* and two social congeners (Laskowski and

Pruitt, 2014; Settepani et al., 2013; Pruitt et al., 2013; Grinsted et al., 2013; Keiser et al., 2014a,b,c).

Spiders were each placed in a black plastic arena (12 cm diameter  $\times$  4 cm height) and provided a 30 s acclimation period. Then, two rapid puffs of air (the aversive stimulus) were administered to the spider's anterior prosoma using an infant nose-cleaning bulb. We then measured the time until the spider resumed activity by moving one full body length. Individuals were then classified as “bold”, “shy”, or “average” based on earlier procedures (Keiser and Pruitt, 2014). Spiders here ranged in their latency to resume movement from 1 s–600 s. We then constructed artificial colonies of two different sizes (10 or 30 individuals) and four personality compositions (all bold, all shy, 50/50 bold and shy, or all individuals of “average” boldness) in 240 ml clear plastic cups. Each experimental colony contained spiders originating from a single source colony (i.e., spiders were never mixed from different source colonies). Colony composition  $\times$  size treatment groups were fully factorial ( $n=64$  experimental colonies), though each source colony varied in the number of experimental colonies which could be arranged into each treatment group. We chose these group sizes because they represent real colony sizes that can be found commonly in the Kalahari, especially for younger colonies, and we reasoned that younger colonies may be more susceptible to ant raids. Colonies were allowed 24 h to produce a retreat in their cup before they were fastened to an *A. mellifera* tree at 8pm as before. We checked these colonies at 6am and 6pm every day for 9 days. At each time point, we recorded if each colony had been discovered by ants, and then calculated the time in hours until the colony collapsed after discovery and until all individuals were killed. Any colony that was discovered before 10 h was removed from further analysis ( $n=5$ ).

### 2.1.3. Social context

Individual mature female spiders from three different source colonies were starved for 10 days and then randomly assigned to one of two social environments: isolated spiders in 30 ml clear plastic condiment cups ( $n=20$ ) or groups of three spiders in 240 ml clear plastic containers ( $n=20$  groups), each containing a fragment of *Acacia* branch to facilitate web building. Although we cannot rule out variation in housing volume as an explanatory force between these two treatment groups, these volumes fall within the size ranges of naturally-occurring colonies and approximate natural conditions. Further, singletons readily produce distinct “retreats” and capture webs in 30 ml containers, as do 3 spiders in 240 ml cups (pers. obs.). Groups of spiders were gathered from the same

source colony (i.e., spiders were not mixed from different source colonies). We allowed spiders 24 h to build a capture web in in the plastic housing containers.

The following day, we recorded the behavioural reaction of spiders to the presence of either a single, live pugnacious ant (*A. custodiens*) or Karoo moth (*Loxostege frustalis*) in the capture web. The order of presentation was alternated among spiders, and a fresh ant/moth was used for each trial. We placed a single *A. custodiens* worker in the center of the capture web and recorded whether the spiders approached the prey item, if they attacked the prey item, and subsequently if they retreated after contact. Trials lasted 10 min. If the spider(s) attacked, we removed the ant immediately to deny any consumption, to ensure that their hunger state remained the same for the foraging trial the following day. During early stages of ant raids on naturally-occurring colonies, a few to several dozen ants can become caught in the capture web of the colony under attack. Thus, we reason that the presence of ants in the web might not represent a “dangerous” prey item (for instance, the average mass of an ant worker is  $\sim 0.06\%$  that of an adult female *S. dumicola*; unpubl. data), but rather a reliable cue of an oncoming ant raid.

Spiders’ interactions with moths were observed for one hour because the moth’s movements were more irregular, characterized by long periods of motionlessness punctuated by short bursts of fluttering. Consequently, spiders received little prey stimulus for sustained periods of time, and thus, this increased their latency to respond to moths caught in the web. Ants, in contrast, struggled continuously in the capture webs and spiders responded more readily.

We randomly selected and recorded the mass (g) of 10 additional unused worker ants ( $x=0.004$  g) and 10 unused adult moths ( $x=0.0146$  g), and the moths weighed nearly four times more than ants. This is important, because if ants were on average larger than the Karoo moths, it would be difficult to infer whether any avoidance of ants was the result of anything other than their larger size.

## 2.2. Statistical analyses

### 2.2.1. Web apparency and group size

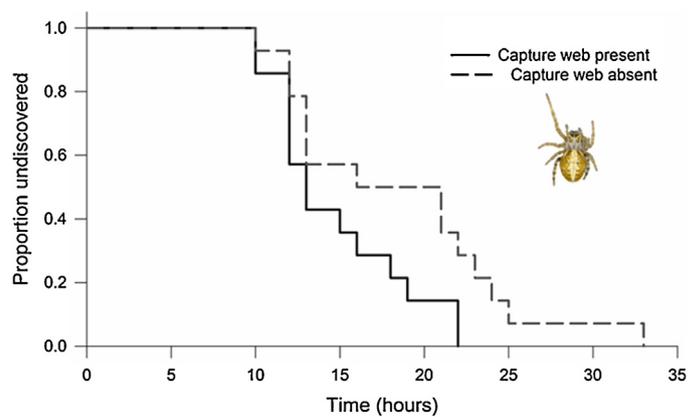
To determine whether capture web presence vs. absence influenced the time until colonies were discovered by ants, we used a Kaplan–Meier survival log-rank test. We analyzed the latency between colony discovery and collapse and between discovery and extinction using generalized linear mixed models (log link function). To test the joint effects of group size and capture web presence on the time until colonies were discovered, we used a general linear mixed model with group size and capture web presence/absence as fixed effects and source colony ID as a random effect to account for the non-independence of these paired colonies (identity link function). The relationship between capture web area, group size, and time until discovery were analyzed with a non-parametric Spearman’s correlation, because the data did not fit the model assumptions for parametric statistics.

### 2.2.2. Group size and personality composition

As we only checked these colonies twice daily, we used a general linear mixed model to test the effects of group size and group composition on the time until colonies’ discovery and collapse, including source colony ID as a random effect.

### 2.2.3. Social context

We used chi-square tests to determine the tendency of spiders in different social contexts to approach, attack, and retreat from ants in the capture web. To test if spider body size influenced their propensity to approach and retreat from prey, we used a standard one-way ANOVA with spider mass as an independent variable



**Fig. 2.** Colonies with capture webs intact were discovered by predatory ants on average 25% faster than colonies with the capture web removed. 8 colonies were discovered before 10 h. These colonies were not included in our analysis, nor are they represented in this figure.

**Table 1**

Results from a series of models predicting the time until colonies were discovered, collapsed, and completely consumed (i.e., “extinction”) by predatory ants, and also the lag time between discover and collapse and between discovery and extinction. See the Statistical analyses section for descriptions of specific models. Significant *p*-Values are denoted with an asterisk.

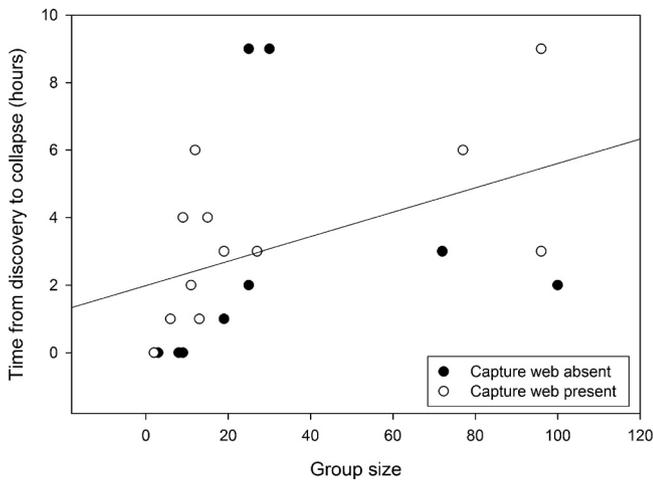
Time until discovery			
Source	DF	Test statistic	<i>P</i> -Value
Web present/absent	1	$\chi^2 = 4.61$	0.03*
Colony size	26	Spearman’s $\rho = -0.59$	0.003*
Web area (cm <sup>2</sup> )	26	Spearman’s $\rho = -0.66$	0.0006*
Time until collapse			
Web present/absent	1	$\chi^2 = 6.09$	0.01*
Colony size	26	Spearman’s $\rho = -0.37$	0.12
Web area (cm <sup>2</sup> )	26	Spearman’s $\rho = -0.48$	0.04*
Time until extinction			
Web present/absent	1	$\chi^2 = 1.52$	0.22
Colony size	26	Spearman’s $\rho = -0.18$	0.45
Web area (cm <sup>2</sup> )	26	Spearman’s $\rho = -0.24$	0.33
Time from discovery to collapse			
Web present/absent	1	$\chi^2 = 0.38$	0.54
Colony size	26	Spearman’s $\rho = 0.64$	0.0005*
Web area (cm <sup>2</sup> )	26	Spearman’s $\rho = 0.24$	0.30
Time from discovery to extinction			
Web present/absent	1	$\chi^2 = 3.02$	0.08
Colony size	26	Spearman’s $\rho = 0.57$	0.003*
Web area (cm <sup>2</sup> )	26	Spearman’s $\rho = 0.27$	0.23

and the proportion of trials where spiders approached, attacked, and retreated from each prey type as dependent variables. Due to the non-independence of our dependent variables, we tested these *p*-Values against Bonferroni-corrected  $\alpha$ -values to reduce the likelihood of Type I error (corrected  $\alpha = 0.008$ ; Rice, 1989). All statistical analyses were performed in JMP version 10 (SAS Institute Inc., Cary, NC, USA).

## 3. Results

### 3.1. Web apparency and group size

Colonies containing more individuals produced larger capture webs overnight ( $F_{1,27} = 32.2, p < 0.0001$ ) and colonies whose capture webs were intact were discovered by predatory ants, on average, 25% faster than colonies without capture webs (log-rank statistic = 4.61,  $df=N1, p = 0.03$ ; Fig. 2). Further, colonies whose present capture webs had a larger approximate area (cm<sup>2</sup>) were discovered by ants faster (Spearman’s  $\rho = -0.66, p = 0.0006$ ; Table 1;



**Fig. 3.** The lag time from discovery by ants to colony collapse was greater for colonies containing more individuals. Although colonies with and without capture web are denoted differently, the regression line represents the relationship between group size and lag time for all colonies together.

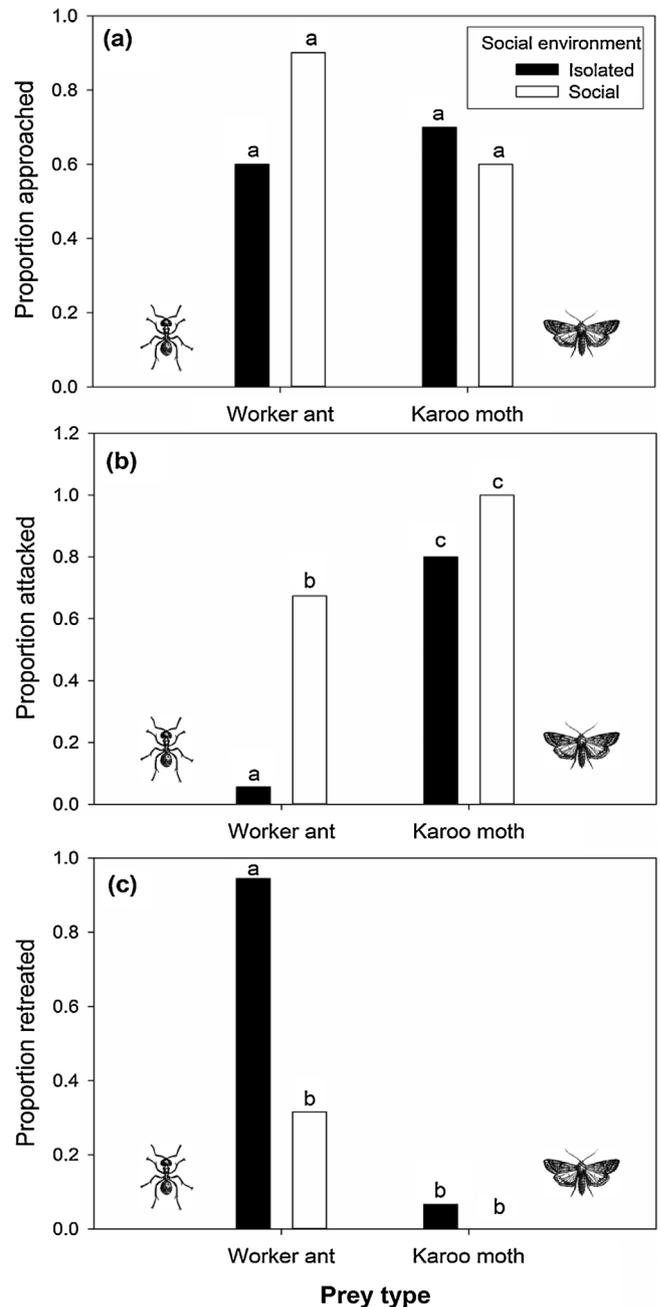
$n = 14$  colonies). Most importantly, although the initial presence or absence of a capture web did not influence the time for all individuals to die ( $p = 0.56$ ), all colonies that were discovered by ants eventually collapsed within 9 h. The latency for a colony to collapse (Spearman's  $\rho = 0.64$ ,  $p = 0.0005$ ; Table 1, Fig. 3) and go extinct (Spearman's  $\rho = 0.57$ ,  $p = 0.003$ ; Table 1) after it had been discovered was greater for colonies containing more individuals, regardless of web presence (Table 1). The 95% confidence intervals indicate that source colony ID did not account for a significant amount of variation in the model. Neither the time until discovery by ants nor survivorship were affected by the height of the colony from the ground (all  $p > 0.45$ ).

### 3.2. Group size and composition

Small changes to group size (10 vs. 30 spiders) did not influence the time until colonies were discovered by ants ( $F_{1,37} = 0.008$ ,  $p = 0.93$ ), nor did personality composition ( $F_{3,34} = 1.97$ ,  $p = 0.14$ ). Further, neither group size ( $F_{1,30} = 0.08$ ,  $p = 0.78$ ) nor personality composition ( $F_{3,37} = 0.42$ ,  $p = 0.74$ ) influenced the time until the colony experienced group-wide mortality. Remarkably, two of our colonies (one of “mixed” and one of “average” composition, both groups of 10 spiders) were never discovered by ants through the duration of this experiment, surviving at least 28 days or longer in this highly predator-dense habitat.

### 3.3. Social context

Neither isolated nor grouped spiders differed in their tendency to approach ants or moths caught in the capture web, though there was a trend for grouped spider to approach more readily ( $\chi^2 = 4.8$ ,  $df = 1$ ,  $p = 0.03$ ,  $\alpha = 0.008$ ; Fig. 4a). Isolated spiders were 14.3 times more likely to attack moths over ants (80% vs. 5.6%, respectively) ( $\chi^2 = 18.9$ ,  $df = 1$ ,  $p < 0.0001$ ,  $\alpha = 0.008$ ; Fig. 4b), and social groups attacked ants at much higher rates than did isolated spiders ( $\chi^2 = 9.8$ ,  $df = 1$ ,  $p = 0.0017$ ,  $\alpha = 0.008$ ; Fig. 4b), however neither group differed in their tendency to attack moths ( $p > 0.05$ ). Isolated spiders were 14.2 times more likely to retreat from ants than moths (94% vs. 6.6%, respectively) ( $\chi^2 = 25.4$ ,  $df = 1$ ,  $p < 0.0001$ ,  $\alpha = 0.008$ ; Fig. 4c) while grouped spiders did not differ in their tendency to retreat from ants or moths after an approach ( $\chi^2 = 4.7$ ,  $df = 1$ ,  $p = 0.03$ ,  $\alpha = 0.008$ ; Fig. 4c). Lastly, we found no indication that the spider's mass influenced a spider's tendency to approach



**Fig. 4.** (a) Neither isolated nor grouped spiders differed in their tendency to approach ants or moths caught in the capture web. (b) Additionally, singleton spiders were more likely to attack moths over ants after the approach while social groups attacked ants at much higher rates than did isolated spiders. (c) Isolated spiders were more likely to retreat from ants than were spiders in a group, while spiders rarely retreated from moths regardless of social context. Significantly different values are denoted by separate letters (Bonferroni corrected  $\alpha = 0.008$ ).

or retreat from ants, but we did find a trend where smaller spiders were less likely to approach moths ( $F_{1,19} = 4.4$ ,  $p = 0.048$ ).

## 4. Discussion

The apparency of large animal societies to their natural enemies could be a determinant of group longevity in the face of predation, which, in turn, could play a substantial role in shaping the evolution of collective anti-predator defenses. Here, we demonstrate that more apparent social spider colonies (those with capture webs present) are indeed at higher risk of discovery by voracious preda-

tors that drive the collapse and extinction of entire groups. For example, astonishingly, one colony containing 100 spiders, with a capture web present, collapsed within 2 h after discovery by predatory *A. custodiens* ants. In many cases, however, larger group sizes facilitated a longer latency between discovery and collapse. Though, neither personality composition nor small differences in group size (i.e., 10 vs. 30 individuals) influenced the time until discovery by ants. We also demonstrate that the social environment, i.e., whether an individual is isolated or among colony-mates, can change the way individuals interact with these voracious predators.

The physical structures produced by large animal societies increase their apparency to natural enemies (e.g., large termite mounds; Kruuk and Sands, 1972) and, as such, highly-apparent social groups must exhibit especially effective anti-predator mechanisms (Prestwich, 1984; Hall et al., 1986). Here, scout ants discover *S. dunicola* colonies by antennating the capture web silk where it anchors to the substrate (Keiser, Wright, and Pruitt, pers. obs.), similar to the chemical detection of underground termite colonies by predatory ants (Longhurst and Howse, 1978) or the attraction of araneophagous wasps to prey spider silk (Craig et al., 2001; Rayor, 1996). Ants may also be recruiting conspecifics to the raid via chemical alarm signaling upon detection of silk or after ensnarement (Vander Meer and Alonso, 1998). Admittedly, our experimentally reconstituted colonies were only allowed 24 h to produce a retreat in the plastic cups, and naturally-occurring, multi-generational colonies contain much more physical complexity (e.g., tunnels, polydomous colonies). This could provide better physical protection against ant raids (Evans, 1998) and/or increase their predation risk via greater visual and chemical apparency (stronger release of chemical cues from nest material and prey remains; (Rypstra and Tirey 1991; Leborgne et al., 2011). Observational and manipulation experiments on naturally-occurring colonies will help resolve these questions.

Despite increased apparency via the presence of a capture web, larger groups experienced a longer lag time between discovery by ants and the time at which the colony went extinct. Thus, larger spider colonies produce larger capture webs that attract their predators, but larger groups also experience a rescuing lag effect. Larger colonies take longer to collapse and go extinct because there are simply more individuals for the ants to encounter. We did not detect a relationship between colony size and the time from collapse to extinction ( $p=0.57$ ), so we are yet unsure the degree to which colony size can influence the number of individuals that escape the siege by evacuating the colony and hanging from a strand of silk away from the ants (e.g., Fig. 1c). However, we observed 1–5 individuals escaping sieges in this manner across 6 colonies of varying sizes, so this should warrant further precise study. Since spiders within a colony are highly related (Johannesen et al., 2002), if these surviving individuals can disperse away from the enemy-dense habitat (e.g., via ballooning; Schneider et al., 2001), only a few surviving individuals could mean the continuity of the matrilineage. It should be noted, however, that spiders living solitarily or in very small groups could also escape predation via this strategy, so perhaps the propensity for individuals to evacuate/disperse is a consequence of individual traits (i.e., personality, body condition, etc.) rather than group size. We also observed spiders immediately producing thick cribellate silk at the entrance of the retreat after coming into contact with ants stuck in the capture web. This may represent a collective defensive response that was, here, unsuccessful against large groups of predators, but may be more effective for very large colonies or in areas of lesser predator pressure (Henschel, 1998).

Despite numerous discoveries in the literature revealing strong relationships between group composition and collective traits (Brown and Irving, 2014; Keiser, Jones et al., 2014; Dyer et al., 2009) and group life history (Modlmeier et al., 2012; Pruitt, 2013, 2012),

we demonstrate here that group personality composition had no rescuing effect on survival for social spider colonies in a predator-dense habitat. Thus, interactions with predatory ants and this social spider do not parallel the interactions between the North American socially polymorphic spider *Anelosimus studiosus* and its parasitic inquilines, where groups composed of more aggressive colony compositions experience prolonged survivorship (Pruitt, 2013). Since we transplanted colonies from sites where top-down pressure from ants was less intense, we speculate that the defensive properties of certain group compositions could still be effective against lower rates of predator encounters. The spiders in our social context experiment appeared to engage these ants with a behavioural repertoire different from that of encountering prey and very similar to those reported in prior studies (Henschel, 1998); likewise, the ants responded very aggressively to *Stegodyphus* silk. Together, these behaviors, hint at a history of bidirectional interactions.

In Central and South America, top-down pressure from ants can limit the geographic range of sub-social *Anelosimus* spiders to low-predation habitats (Purcell and Avilés, 2008). In these environments, ant predation favors larger colonies. In contrast, very large *S. dunicola* colonies are nearly absent in habitats where *Anoplolepis* ants are abundant. In these high-predation environments, spiders are more likely to live solitarily (or in small colonies), perhaps because individuals and smaller groups produce smaller and less conspicuous colonies (Henschel 1998). It is, as of yet, difficult to suggest with any certainty why such divergent trends emerge in across systems, but variation in ant diversity vs. abundance might provide some clues. Predatory ants in tropical rainforests are tremendously diverse (Longino et al., 2002; Philpott and Armbrrecht, 2006), while pitfall trap surveys of the ant communities at our site reveal that >95% of the individuals surveyed are *A. custodiens* and hundreds of individuals can be collected in a matter of hours. Future studies should test the hypothesis that intermediate levels of predation from a variety of ant species favors escalatory defensive behaviors like those in New World *Anelosimus*, whereas, more intense levels of predation favor strategies that allow colonies to go unnoticed. Yip (2014) also recently described bull ants, *Myrmecia pyriformis*, engaging in interference competition with the Australian social huntsman spider *Delena cancerides*, where the ants invade and extirpate spiders from their nest sites. In this new system, however, it yet unclear whether or how ant predation impacts the selective advantage of living in groups of various sizes. Taken together, although the precise dynamics vary across systems (species and continents), it is clear that interactions with ants are a major ecological pressure for spider societies across the world.

The behavioural interaction between *S. dunicola* and ants differed depending on whether spiders were living solitarily or among conspecifics. Social groups attacked ants caught in the web more readily than isolated spiders. Further, spiders were more likely to retreat after contact with an ant when living solitarily compared to grouped spiders, while spiders rarely retreated from moths regardless of the social context. Although solitary *S. dunicola* can exhibit greater boldness after experiencing a stressor compared to spiders in social groups (Keiser, Modlmeier et al., 2014), it seems here that living among conspecifics can facilitate an aggressive/defensive interaction with ants as opposed to the evasive strategy of solitary individuals. We reason that the different behaviours exhibited by individuals in isolation vs. within a group may represent two optimal strategies: a solitary spider's best option may be to simply retreat and relocate in response to the forthcoming raid, while organized relocation may not be possible for groups. Thus, a social group may instead attack and kill ant scouts more readily in order to decrease the likelihood of a raid; after all, a dead and ensnared scout rarely returns to its colony. In the social huntsman *D. cancerides*, adult and subadult females are more likely to attack predatory bull ants after an encounter, though these spiders rarely attack ants

collectively (Yip and Rayor, 2011). Future studies should evaluate whether and how other collective metrics like colony composition, size, and demography of both spiders and ants alters the nature of these interactions.

For high-apparency social groups that experience extraordinary rates of colony extinction, achieving certain group traits (i.e., large group sizes) might be pivotal in determining local persistence in predator-dense habitats. Some of our colonies were never discovered by ants, regardless of their apparency or group size, despite extreme mortality events occurring all around them. This suggests that there may be some yet undiscovered traits about colonies, or perhaps the locations at which they establish their colony (Birkhofer et al., 2014), which reduces the risk of predation and perhaps conceals them from their enemies. Future studies should jointly consider the collective traits of predator and prey simultaneously, along with aspects of their habitat use and varying levels of predator density, in order to glean a deeper understanding of group-on-group predation.

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