



Colony personality composition alters colony-level plasticity and magnitude of defensive behaviour in a social spider



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The ways in which animal societies respond to threat has enormous consequences for their success. In the present study, we investigated how group personality composition in social spiders (*Stegodyphus dumicola*) alters groups' average response towards predators and how their responses change with experience with important predators, *Anoplolepis custodiens* ants. We found that colonies composed of a mixture of 'bold' and 'shy' personality types exhibited twice as much defensive web-making behaviour as other colony compositions. Colony defensive behaviour was also more temporally stable following experience with predators for 'mixed' colonies than for either monotypic composition (all shy or all bold). Colonies composed of bold individuals were particularly erratic in their defensive behaviour over time. Thus, colony composition altered colony-level plasticity in response to experience with one of their most voracious predators. We additionally observed the behaviour of marked individuals within colonies to determine which individual traits were associated with task participation during encounters with predators. Individual morphology and boldness both predicted task participation at the individual level, with boldness being negatively associated with participation in the attack sequence, but positively associated with defensive silk making. Low body condition also proved to be important for predicting participation in any task. Lastly, despite a tight association between colony composition and colony defensive behaviour, we found no evidence that colony composition affected colony survival during ant attacks in situ. Instead, older and more established nests were positively associated with colony persistence during attacks.

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Animals commonly behave differently in the presence of predators in ways that reduce their chance of being detected and eaten (David, Salignon, & Perrot-Minnot, 2014; Lima & Dill, 1990). This is no surprise, as the risk of predation is one of the most ubiquitous selective pressures experienced by any animal. There are many ways in which an organism can avoid predation: camouflage (Merilaita, Tuomi, & Jormalainen, 1999; Stevens & Merilaita, 2009), aposematic coloration (Mappes, Marples, & Endler, 2005), nonoverlapping activity times (Lima & Dill, 1990; Suselbeek et al., 2014), to name a few. However, there is perhaps nothing more readily amenable to selection and more immediately advantageous to the organism than modifications to behaviour (Nonacs & Blumstein, 2010). Behaviours, unlike other modes of defence, are rarely constitutive traits and therefore have the ability to be deployed immediately in response to cues of threat via behavioural

plasticity (Dingemanse, Kazem, Réale, & Wright, 2010; Holbrook, Wright, & Pruitt, 2014; Sih, Bell, & Johnson, 2004). Hence, anti-predator behaviour is nearly universal in nature, while morphological adaptations and weapons are, in comparison, less common.

Social organisms provide us with a particularly intriguing landscape for predator–prey interactions. Social organisms can modify their behaviour in response to threat, and have the added complexity of a two-tiered system where behaviour can be simultaneously considered at both the individual and group level. Social organisms often gain protection in numbers, as groups composed of many individuals often exhibit defensive behaviours that would be impotent if performed alone (Breed, Guzman-Novoa, & Hunt, 2004; Judd, 1998; Tener, 1954). Such effects often positively scale with group size (Elgar, 1989; Hermann & Blum, 1981). Social organisms have also been shown to exhibit varying degrees of behavioural plasticity in response to threat of predation (Holbrook et al., 2014). For instance, some ants (*Lasius pallitarsis*) reduce foraging at sites where they risk predation by larger ant species (Nonacs & Dill, 1990, 1991), and paper wasps often build more nest-defensive structures in areas where predation risk is higher (Furuichi &

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Kasuya, 2014). Here we explore how the phenotypic composition of social groups influences their collective defensive behaviour and how groups' defensive behaviour changes as a consequence of experience (i.e. repeated exposure to predators). In particular, we consider to what degree a group's personality composition affects how groups respond to repeated interactions with predators.

A group's personality composition often has a large effect on its collective behaviour (Jandt et al., 2014; Modlmeier, Keiser, Wright, Lichtenstein, & Pruitt, 2015). Here we define animal 'personality' as temporally consistent individual differences in behaviour (Sih et al., 2004). The ratios of different personality types within groups are often major determinants of group behaviour in various contexts, as well as group survival and reproductive output (Pruitt, 2013; Pruitt & Goodnight, 2014; Wray, Mattila, & Seeley, 2011). For example, personality variation within a group often helps streamline the performance of collective tasks (Chittka & Muller, 2009; Pruitt & Riechert, 2011; Waibel, Floreano, Magnenat, & Keller, 2006; Wright, Holbrook, & Pruitt, 2014). In some extreme cases, the effects of personality composition on collective behaviour can outweigh the effects of even large differences in group size (Keiser & Pruitt, 2014). Yet, the majority of the studies published on this topic to date have focused on foraging tasks or interactions with social parasites (Aplin, Farine, Mann, & Sheldon, 2014; Burns & Dyer, 2008; Dyer, Croft, Morrell, & Krause, 2009; Gordon, 2013; Hui & Pinter-Wollman, 2014), with infrequent regard for predator–prey interactions, which are arguably some of the most dire interactions that groups are likely to endure.

The African social spider, *Stegodyphus dumicola* (Araneae: Eresidae), lives in groups ranging from one to several thousand individuals. They build webs that consist of a three-dimensional, tough silken retreat permeated with a complex series of tunnels, and two-dimensional capture webs radiating away from this retreat in one or more directions (Seibt & Wickler, 1990). Spiders typically reside within the retreat until they are alerted to prey caught in the capture web via vibrational cues. Unlike the social hymenoptera and termites, *S. dumicola* does not exhibit morphological castes, nor does it seem to display reproductive division of labour. However, this species does exhibit strongly repeatable 'bold–shy' personality variation between individuals within the colony. This variation has been shown to predict foraging and escape behaviour at the individual and colony level (Grinsted, Pruitt, Settepani, & Bilde, 2013; Keiser & Pruitt, 2014; Wright, Keiser, & Pruitt, 2015). Here we assess how a group's personality composition influences its repeated interactions with their most voracious predators, ants of the genus *Anoplolepis*: *Anoplolepis custodiens* (Keiser, Wright, & Pruitt, 2015) and *Anoplolepis steingroveri* (Henschel, 1998). Ant raids of spider nests are extremely common where ant and spider ranges overlap, and can often lead to 90–100% colony eradication at sites where ants are active (Henschel, 1998). During ant raids, *S. dumicola* can be observed producing special cribellate silk (Henschel, 1998), which is used to make a tangled silken barrier during attacks. Cribellate silk is a very fine silk that is extruded from the cribellum and combed out using a specialized structure called the calamistrum. This silk is woolly in nature, making it efficient at ensnaring insect prey and is therefore commonly used to line capture webs (Vollrath, 2006). In *S. dumicola*, cribellate silk is most commonly produced during the construction and repair of their capture web, but it is also produced defensively during ant raids. Here the silk is laid down on the attachment points of the colony to the surrounding substrate in areas where predatory ants are abundant (Henschel, 1998).

In the present study we subjected colonies to staged encounters with ant predators to examine (1) whether colonies of different behavioural compositions differ in their antipredator behaviour and (2) whether colony composition influences how

colonies alter their behaviour as a single unit (i.e. collective behavioural plasticity) following repeated exposure to predators. Then, we placed colonies within sites with moderate levels of predator density to examine (3) whether differences in colonies' defence behaviour translate to increased persistence during attacks and (4) whether the time available to spider colonies to build their retreats is positively associated with their ability to withstand ant raids.

Our independent (predictor) variable for both individual-level and colony-level behaviour was boldness, which is a measure of the propensity of an individual, or a colony, to engage in risky behaviour. We use a well-vetted and common boldness assay for our study organism, however, boldness has been measured in myriad ways in a wide variety of species (Sloan Wilson, Clark, Coleman, & Dearstyne, 1994). This raises the question of the generality of these methods, and whether one measure of boldness in a certain context and species is really comparable to measures of boldness in different contexts and in different species. This concern is particularly noteworthy given the evolutionary distance and consequent differences in physiology between various taxa. While we realize this as an area of concern (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; Carter, Marshall, Heinsohn, & Cowlshaw, 2012), we do not view this as overly problematic so long as researchers are explicit in their methods and nuanced in their definitions. Thus, while we may define our spiders as being 'bold' or 'shy' according to our initial diagnostic assay, this is not meant to imply that this assessment is not in some way context specific. We do find it fascinating, however, when simple behaviours measured in one context appear enormously consequential across many contexts and have the power to reliably predict ecologically important outcomes.

METHODS

Collection and Boldness Assays

Spiders were collected near Upington, Northern Cape, South Africa in January and February of 2015 along roadside bushes and fences. Colonies were placed into cloth bags for transport to our field site near Griekwastad, South Africa. Once at the field site, colonies were sorted and spiders were counted and placed into 500 ml plastic containers. Spiders from different source colonies were never mixed, in order to preserve natural levels of within-group relatedness and familiarity (Laskowski & Montiglio, in press; Laskowski & Pruitt, 2014; Modlmeier, Laskowski, et al., 2014). Following colony sorting, we recorded the mass, prosoma width and boldness of each spider. Measures of mass and prosoma width allowed us to determine whether any of our behavioural responses were associated with morphological traits or body condition, which is a measure of how massive a spider is for any given prosoma width. Given that prosoma width does not fluctuate with hunger level, spiders that are on average less massive for a given prosoma width are considered to be in poorer body condition, while higher average mass for any given prosoma width is an indicator of good body condition (Jakob, Marshall, & Uetz, 1996). Boldness is a measure of the propensity of individuals to engage in risky behaviour (Sloan Wilson et al., 1994). Individual boldness here was estimated by administering two rapid puffs of air anteriorly to their prosoma of an isolated spider using a rubber squeeze-bulb. This puff of air simulates attack from a flying predator, and elicits a death-feigning huddle response in *S. dumicola* and other spiders (Lohrey, Clark, Gordon, & Uetz, 2009; Pruitt, Grinsted, & Settepani, 2013; Riechert & Hedrick, 1990). Given that web-building spiders generally have poor vision, they rely heavily on vibrational cues and air currents to detect the approach of predators (Foelix, 2011). Thus,

the length of time a spider feigns death is a measure of boldness, as recovering too early in proximity to predators can be risky. Spiders were given a maximum of 600 s to resume normal activity and move one body length following the air puff. We defined bold spiders as those that resumed activity within 0–200 s, and shy spiders as those taking 400 s or more to resume activity (Keiser & Pruitt, 2014). Boldness has been shown to be highly repeatable in *S. dumicola* ($r > 0.60$) and related species (Keiser, Jones, Modlmeier, & Pruitt, 2014; Keiser, Modlmeier, Singh, Jones, & Pruitt, 2014). Each spider was then marked with a unique colour combination using fast-drying acrylic modelling paint.

Colony Construction

Once morphology (mass and prosoma width) and boldness of all spiders had been recorded, we placed individual spiders (20 spiders per colony) into new 250 ml plastic containers with spiders taken from the same source colony. Colonies were constructed with one of three different behavioural compositions: 100% bold ($N = 6$), 100% shy ($N = 27$) and 50% bold/50% shy ($N = 20$). Each colony was given a small *Acacia mellifera* branch to provide substrate for web building. Colonies were then given 24 h to construct a capture web and retreat prior to their staged interactions with ants.

Colony Behaviour during Staged Predator–Prey Encounters

We performed colony behavioural assays twice a day for 3 days between 0800 and 1500 hours, totalling six replicates per colony. Each assay was performed as follows. We removed the lid from the colony's container and allowed the colony to sit undisturbed for 1 min. We then placed a live *A. custodiens* worker in the centre of the colony's capture web and recorded the colour ID and latency of the first spider to emerge and attack the ant. The web of *S. dumicola* is composed of two parts: a retreat and a capture web. We defined latency to emerge as the time it took the first spider to be recruited to the capture web after the ant was added to the capture web. We defined latency to attack the ant as the total time it took for the spider to attack the ant once it was placed in the capture web, which included the latency to emerge. In addition, every 2 min for 10 min (five time points total) we recorded the number and colour ID of each spider (1) pinning down the ant's legs, (2) attacking the ant's body and (3) participating in defensive cribellate silk-making behaviour.

Colony Survival Experiment: Colony Composition

Following completion of our staged predator–prey encounters, we placed these same colonies haphazardly in the field on *A. mellifera* trees after dusk at a site with moderate ant densities. This site was chosen to help ensure that ant raids were common, but not too overwhelming, thus avoiding immediate and total annihilation of all colonies. We tracked colony survival beginning the following morning when ant activity commenced (roughly 0700 hours). Colonies were checked every hour during daylight to determine when ant raids began for each colony, and the time between the beginning of a raid and colony collapse was recorded. Raids were identified by the presence of many ants gathering outside the colony and biting at silk but not yet infiltrating the spiders' capture web. A colony was considered 'collapsed' when ant raids progressed to the point where ants were present inside the spider's retreat, forcing the resident spiders to evacuate.

Colony Survival Experiment: Retreat Density

An outstanding question in social *Stegodyphus* pertains to the function of their dense retreat (Seibt & Wickler, 1990). We reasoned that these retreats might be important in mitigating risk during ant raids. To address the question of whether older and, consequently, thicker and denser retreats provide better defence against ant raids, we constructed colonies composed of 100 individuals each that varied in the amount of time that they were allowed to construct retreats. The spiders for this experiment were chosen at random from larger colonies, and thus the experimental colonies were composed of natural nestmates of unknown mixed behavioural composition. The treatment durations were as follows: 1 day ($N = 11$), 1 week ($N = 10$), 2 weeks ($N = 12$), 1 month ($N = 12$) and approximately 1 year ($N = 18$). The 1-year-old colonies were small to medium colonies collected in the field that approximated the size of our artificially constructed colonies (80–120 individuals). All colonies (+their retreats) were placed within identical plastic containers and attached to *A. mellifera* trees during the night. The following morning we recorded the latency between the start of an ant raid and total colony collapse for retreats of different ages. Colony status observations were made every hour during the day when ants were active.

Statistical Methods

We used generalized linear mixed models (GLMMs) with a Poisson distribution and log-link function to analyse changes in colony defensive behaviour over behavioural trials (across-trial analysis). Our predictor variables were trial number, colony behavioural composition and a trial number*behavioural composition interaction term. Response variables included latency to emerge and attack, the average number of leg and body attackers and the average number defensive cribellate silk makers. We also used GLMMs, but with a normal distribution and identity-link function, to analyse the behavioural changes observed every 2 min over the course of a single trial (within-trial analysis). The predictor variables for within-trial analyses were the three colony behavioural compositions: shy, bold and mixed. Response variables included the number of spiders pinning legs, the number of spiders attacking the ant's body and the number of colony members engaged in defensive cribellate silk making. Colonies' behaviours at each 2 min check were averaged together for our analysis of colonies' change in behaviour across trials. Colony ID and source colony ID were included as random effects in both of these analyses. Post hoc comparisons were performed between each colony composition (shy, bold, mixed) within each trial and time point, as well as between each trial and time point for each behaviour measured. Post hoc comparisons for latency to emerge and attack were performed using Tukey's HSD, and comparisons between the number of leg attackers, body attackers and cribellate silk makers were analysed using Wilcoxon signed-ranks tests.

For individual task participation analysis, we used GLMMs (Poisson distribution and log-link function) with the following predictor variables: individual mass, prosoma width and boldness as fixed effects and source colony ID and experimental colony ID as random effects. Our individual-level response variables were the number of trials where each individual was the first to emerge and attack and the number of trials where each individual participated in leg pinning, body attacking or defensive cribellate silk-making behaviour.

Survival of colonies in the field was analysed using a Kaplan–Meier survival function and Mantel–Cox tests in SPSS (IBM, Armonk, NY, U.S.A.). All other statistics were run in JMP 12 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

Across-trial Analysis

Latency to emerge and attack

Over six iterative encounters with predatory ants, all colonies showed a trend towards increased emergence latencies ($P \leq 0.0001$), with shy and mixed colonies significantly increasing their average latency to emerge by nearly 600% (shy: $P = 0.0040$; mixed: $P = 0.049$; [Table 1](#)). Additionally, colonies' latency to emerge was associated with their personality compositions ($P < 0.0001$), with bold colonies emerging over twice as quickly as both shy and mixed colonies, although this effect dissipated with time. Lastly, we found a significant trial number*personality composition interaction ($P < 0.0001$; [Fig. 1a](#), [Table 2](#)).

Likewise, latency to attack for all colonies increased over time ($P < 0.0001$), with mixed and shy colonies showing a 400% increase over the six trials. Bold colonies also followed this pattern, although the differences between the first and last trials were not significant ([Table 1](#)). On average, bold colonies took about twice as long to attack predatory ants as both shy and mixed colonies (bold versus shy: $P = 0.011$; bold versus mixed: $P = 0.019$; [Table 3](#)). Here again, we found a significant trial number*personality composition interaction ($P < 0.0001$; [Fig. 1b](#), [Table 1](#)).

Leg pinning

Over six trials with predatory ants, all colonies showed a 75% decrease in the number of individuals that pinned the ant's legs (trial number: $P < 0.0001$; [Table 1](#)). This effect was associated with colonies' personality composition, with bold colonies on average attacking the ant's legs with half as many spiders as mixed colonies in total ($P = 0.027$; [Table 3](#)). We did not detect a significant time*personality composition interaction ($P = 0.40$; [Fig. 1c](#), [Table 2](#)).

Body attacking

Over the six trials, the number of participants that responded by attacking the predator's body decreased by more than 45% in shy and mixed colonies (trial number: $P < 0.0001$; [Table 1](#)). In addition, nearly twice as many individuals attacked the ant's body in shy and mixed colonies as in bold colonies (shy versus bold: $P = 0.0015$; mixed versus bold: $P = 0.020$; [Table 3](#)). This result is in stark

contrast to the patterns observed when colonies attack prey; when attacking prey, bold colonies attack with 200–400% more individuals than shy or mixed colonies ([Keiser & Pruitt, 2014](#); [Wright et al., 2015](#)). The interaction term time*personality composition was not significant ($P = 0.62$; [Fig. 1d](#), [Table 2](#)).

Defensive cribellate silk making

Over six trials, colonies showed disparate responses to ants in terms of their defensive cribellate silk-making behaviour (trial number: $P < 0.0001$; [Table 1](#)). For example, over the six trials, the number of cribellate makers was relatively stable in shy and mixed colonies but erratic and unpredictable in bold colonies (trial number*personality composition: $P < 0.0001$; [Fig. 1e](#), [Table 3](#)). Colonies with mixed personality compositions also differed as well, having twice as many cribellate silk makers on average than either shy or bold colonies (personality composition: $P < 0.0001$; [Fig. 1e](#), [Table 3](#), see [Supplementary Table S1](#) for GLMM output).

Within-trial Analysis

Descriptive summary

Early on, spiders immediately attacked the legs of ant predators, seemingly in order to subdue the predator and to inject venom from a safer distance. Over time, the spiders moved from the legs to attacking the ant's body, where they eventually partially consumed the predator. Defensive cribellate making, in contrast, had few participants early on, but the number of individuals engaged in this activity sharply increased about 6 min into the trials ([Fig. 2](#)).

Leg pinning

For leg-pinning behaviour, all colonies showed a nearly 75% decrease in the number of individuals pinning the predator's legs over the course of a trial (time: $P < 0.0001$; [Supplementary Tables S2 and S3](#)). The number of leg-pinning individuals did not differ based on a colony's personality composition ($P = 0.76$), nor did we detect a time*personality composition interaction ($P = 0.29$; [Supplementary Table S3](#)).

Body attacking

All colonies steadily increased the number of spiders that participated in attacking the ant's body over 10 min trials (time:

Table 1
Comparisons of each colony composition between consecutive trials as well as between the first and last trial

Trials	Composition	Latency to		Number of		
		Emerge	Attack	Leg attackers	Body attackers	Silk makers
T1–T2	Bold	0.98	0.52	0.75	0.58	0.25
	Shy	0.012	0.023	0.0008	0.016	0.51
	Mixed	0.014	0.29	0.38	0.64	0.50
T2–T3	Bold	0.11	0.17	0.99	0.99	0.37
	Shy	0.38	0.9	0.28	0.10	0.36
	Mixed	0.18	0.2	0.044	0.23	0.82
T3–T4	Bold	0.25	0.25	0.56	0.99	0.12
	Shy	0.41	0.4	0.31	0.85	0.86
	Mixed	0.82	0.82	0.30	0.68	0.81
T4–T5	Bold	0.98	0.98	0.99	0.99	0.62
	Shy	0.12	0.11	0.57	0.10	0.11
	Mixed	0.92	0.92	0.53	0.96	0.30
T5–T6	Bold	0.35	0.69	0.99	0.99	0.048
	Shy	0.74	0.49	0.035	0.53	0.81
	Mixed	0.54	0.53	0.37	0.44	0.061
T1–T6	Bold	0.16	0.23	0.0021	0.99	0.75
	Shy	0.0040	0.0003	<0.0001	0.0012	0.89
	Mixed	0.049	0.0070	<0.0001	0.0049	0.44

Comparisons were made using post hoc Tukey's HSD for latency to emerge and attack, and Wilcoxon signed-ranks tests for the number of leg and body attackers and the number of defensive cribellate silk makers. Significant outcomes ($P < 0.05$) are shown in bold.

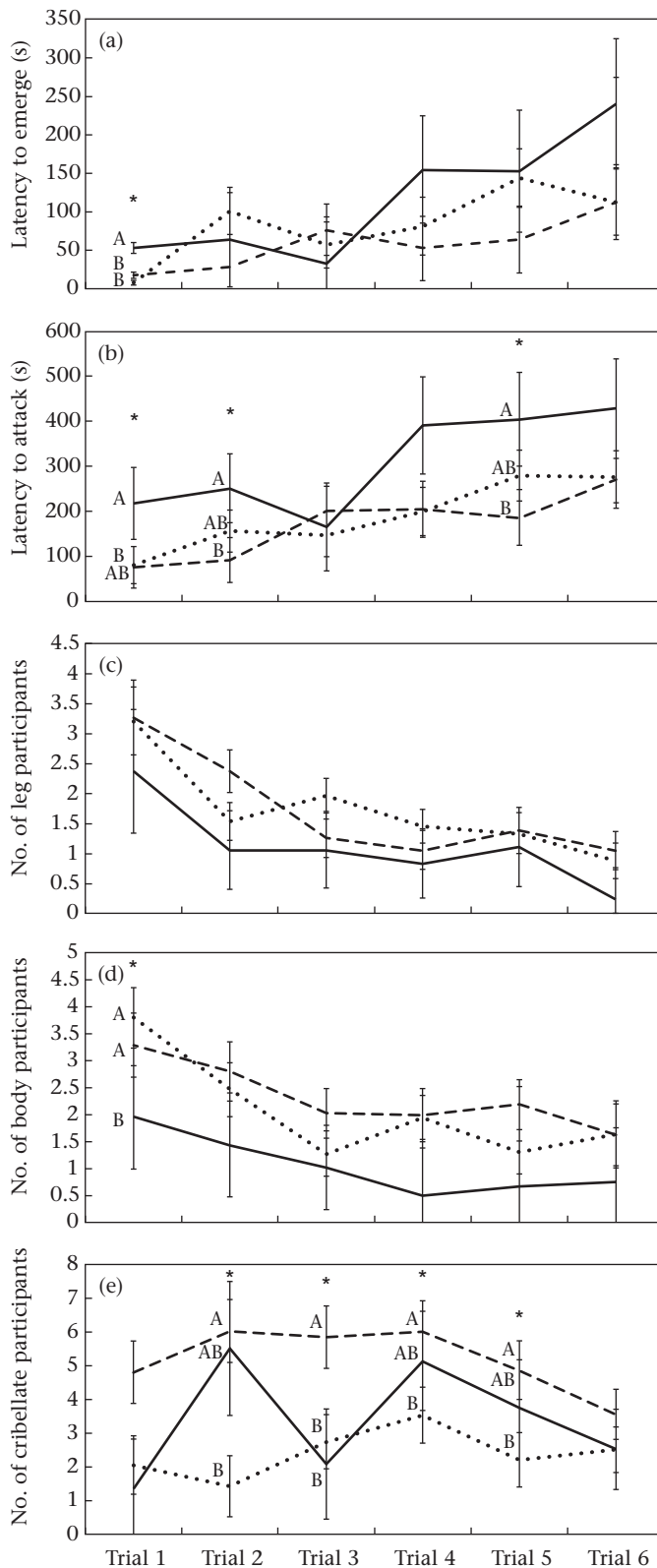


Figure 1. Changes in response to predatory ants over time by colony composition for (a) latency to emerge from the retreat, (b) latency to attack and the propensity to participate in (c) leg pinning, (d) body attacking and (e) defensive cribellate making behaviour. Solid lines correspond to bold colonies, dashed lines correspond to mixed colonies and dotted lines correspond to shy colony compositions. Error bars show standard errors. Significant differences at each trial number are indicated with an asterisk and further broken down with letters (different uppercase letters denote significant differences; see Table 3).

Table 2
Overview of GLMM results for within-trial and across-trial analyses

Predictor variable	Across trials			Within trials		
	df	χ^2	Prob> χ^2	df	χ^2	Prob> χ^2
Leg pinning						
Whole model	17	115.5	<0.0001	14	108.9	<0.0001
Trial no.	5	37.44	<0.0001	4	51.9	<0.0001
Composition	2	7.19	0.027	2	0.53	0.76
Trial no.*composition	10	10.41	0.40	8	9.55	0.29
Body attacking						
Whole model	17	109.7	<0.0001	14	136.9	<0.0001
Trial no.	5	13.07	0.023	4	64.23	<0.0001
Composition	2	17.61	<0.0001	2	10.62	0.0049
Trial no.*composition	10	8.08	0.62	8	6.34	0.61
Cribellate making						
Whole model	17	232.6	<0.0001	14	118.2	<0.0001
Trial no.	5	45.51	<0.0001	4	39.42	<0.0001
Composition	2	23.45	<0.0001	2	22.2	<0.0001
Trial no.*composition	10	35.43	<0.0001	8	12.73	0.12
Latency to emerge						
Whole model	17	9200.8	<0.0001	–	–	–
Trial no.	5	5475.2	<0.0001	–	–	–
Composition	2	359.8	<0.0001	–	–	–
Trial no.*composition	10	1698.6	<0.0001	–	–	–
Latency to attack						
Whole model	17	12872.9	<0.0001	–	–	–
Trial no.	5	6019.1	<0.0001	–	–	–
Composition	2	1515.3	<0.0001	–	–	–
Trial no.*composition	10	1498.6	<0.0001	–	–	–

Includes the predictor variables trial number, colony composition, a trial number* composition interaction term, as well as a whole model estimate. Results include degrees of freedom (*df*), chi-square test statistics and *P* values. Significant outcomes ($P < 0.05$) are shown in bold.

$P < 0.0001$; [Supplementary Tables S2 and S3](#)), from an average of 0.09 individuals at 2 min to an average of 1.46 individuals at 10 min. Colonies also differed in participation by composition, with shy and mixed colonies deploying twice as many individuals to attack the ant's body as bold colonies (personality composition: $P < 0.0001$; [Supplementary Tables S2 and S4](#)). Here again, this pattern is opposite that observed when colonies attack prey; when foraging on safe prey, bold colonies attack more rapidly and with many more attackers than shy or mixed colonies (Keiser & Pruitt, 2014; Wright et al., 2015). Lastly, the interaction term between time and personality composition was not significant ($P = 0.0049$; Table 3).

Defensive cribellate silk making

All colonies generally increased the number of cribellate silk-making participants by about 200% over 10 min (time: $P < 0.0001$; [Supplementary Tables S2 and S3](#)). Colony compositions also differed in defensive cribellate participation, with mixed colonies having twice as many participants as both bold and shy colonies (personality composition: $P < 0.0001$; [Supplementary Tables S2 and S4](#)). The time*personality composition interaction term was not significant ($P = 0.12$; Table 2).

Survival

Colony personality composition was not a significant predictor of persistence in a habitat of moderate predatory density ($\chi^2_{2,53} = 0.57$, $P = 0.75$; Fig. 3a). In contrast, the age of the colonies' retreat did have a significant impact on their persistence, with individuals taking longer to evacuate older nests ($\chi^2_{4,63} = 24.8$, $P < 0.0001$; Fig. 3b).

Individual task participation

Boldness did not predict the propensity for an individual to be the first to emerge ($P = 0.73$) or attack ants. However, less massive

Table 3
Comparisons between each colony composition for each trial and across all trials

Trial no.	Comparison	Latency to		Number of		
		Emerge	Attack	Leg attackers	Body attackers	Silk makers
Total	Bold–Shy	0.52	0.011	0.054	0.0015	0.14
	Bold–Mix	0.2	0.019	0.042	0.020	0.37
	Mix–Shy	0.55	0.98	0.68	0.73	0.0002
Trial 1	Bold–Shy	<0.0001	0.049	0.074	0.0064	0.69
	Bold–Mix	0.0002	0.51	0.11	0.014	0.84
	Mix–Shy	0.53	0.99	0.68	0.31	0.31
Trial 2	Bold–Shy	0.26	0.023	0.38	0.089	0.091
	Bold–Mix	0.7	0.054	0.094	0.061	0.71
	Mix–Shy	0.96	0.76	0.13	0.82	0.0020
Trial 3	Bold–Shy	0.91	0.88	0.25	0.23	0.61
	Bold–Mix	0.93	0.98	0.82	0.46	0.042
	Mix–Shy	0.99	0.9	0.069	0.69	0.022
Trial 4	Bold–Shy	0.53	0.21	0.35	0.2	0.13
	Bold–Mix	0.42	0.31	0.72	0.13	0.94
	Mix–Shy	0.93	0.96	0.37	0.75	0.011
Trial 5	Bold–Shy	0.98	0.061	0.14	0.23	0.12
	Bold–Mix	0.57	0.038	0.25	0.091	0.48
	Mix–Shy	0.41	0.89	0.73	0.34	0.0003
Trial 6	Bold–Shy	0.49	0.47	0.19	0.35	0.99
	Bold–Mix	0.37	0.5	0.093	0.42	0.47
	Mix–Shy	0.91	0.99	0.55	0.86	0.11

Comparisons were made using post hoc Tukey's HSD for latency to emerge and attack, and Wilcoxon signed-ranks tests for the number of leg and body attackers, and the number of defensive cribellate silk makers. Significant outcomes ($P < 0.05$) are shown in bold.

spiders with larger prosomas (an indicator of low body condition) were more likely to emerge first (mass: $P = 0.022$; prosoma: $P = 0.016$) but not more likely to attack first. Additionally, boldness was negatively associated with leg pinning ($P = 0.0018$) and body attacking ($P < 0.0001$) but positively associated with defensive cribellate-making behaviour ($P < 0.0001$). Lastly, low body condition was positively associated with leg pinning (mass: $P = 0.019$; prosoma: $P = 0.0022$), body attacking (mass: $P < 0.0001$; prosoma: $P < 0.0001$) and defensive cribellate silk making (mass: $P < 0.0001$; prosoma: $P < 0.0001$). Thus, shyer individuals were most likely to take part in an aspect of the attack sequence (leg pinning and body attacking), while bolder spiders tended to participate more in defensive cribellate making. Furthermore, poor body condition seems to be positively associated with task participation generally, where spiders in better condition were less likely to participate in any task. See Table 4 for a more detailed account of our statistics.

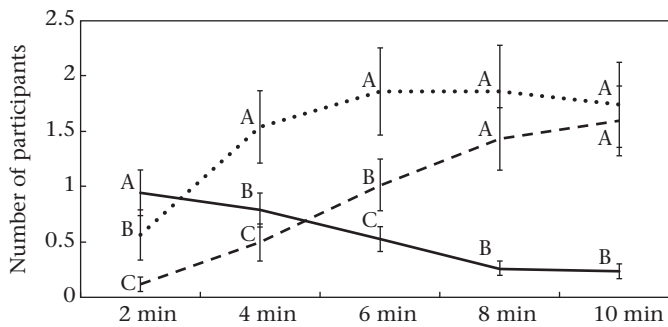


Figure 2. Attack sequence of *S. dumicola* against a threatening insect showing the change in the average number of spiders participating in leg pinning (solid line), body attacking (dashed line) and defensive cribellate making (dotted line) over time averaged across all compositions. Error bars show standard errors. Different letters indicate significant differences in the number of individuals performing that task (see Supplementary Table S5).

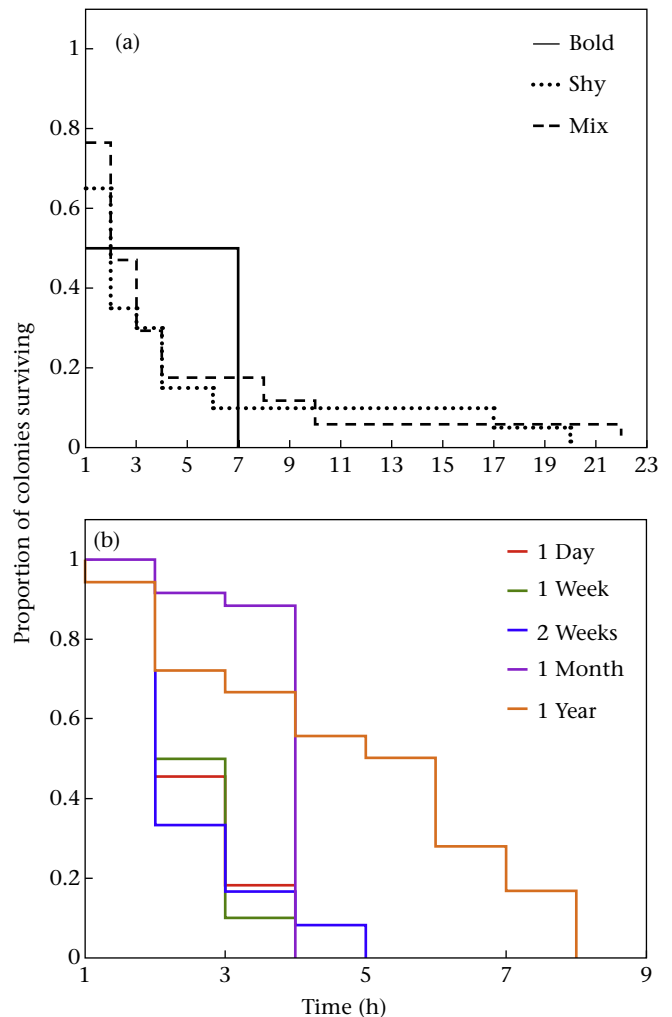


Figure 3. Kaplan–Meier survival curves depicting the proportion of colonies surviving over time based on (a) colony composition and (b) time allowed to construct retreats.

Table 4
Individual task participation results from GLMM analysis

Predictor variable	df	Estimate	SE	Lower CL	Upper CL	χ^2	Prob> χ^2
Leg participation							
Whole model	3	–	–	–	–	20.3	<0.0001
Boldness	1	–0.0004	0.00013	–0.00066	–0.00015	9.71	0.0018
Mass (g)	1	–3.67	1.59	–6.83	–0.58	5.45	0.0195
Prosoma width (mm)	1	0.36	0.12	0.13	0.59	9.4	0.0022
Body participation							
Whole model	3	–	–	–	–	64.2	<0.0001
Boldness	1	–0.00059	0.00014	–0.00086	–0.00032	19.1	<0.0001
Mass (g)	1	–7.16	1.69	–10.5	–3.88	18.8	<0.0001
Prosoma width (mm)	1	0.79	0.12	0.55	1.04	41.7	<0.0001
Cribellate participation							
Whole model	3	–	–	–	–	304.4	<0.0001
Boldness	1	0.0013	9.30E-05	0.0011	0.0015	204.1	<0.0001
Mass (g)	1	–13.4	1.46	–16.3	–10.5	92.6	<0.0001
Prosoma width (mm)	1	0.41	0.1	0.21	0.6	16.9	<0.0001
First to emerge							
Whole model	3	–	–	–	–	6.56	0.087
Boldness	1	0.00011	0.00032	–0.00053	0.00072	0.12	0.73
Mass (g)	1	–9.56	4.33	–18.31	–1.34	5.25	0.022
Prosoma width (mm)	1	0.74	0.31	0.13	1.35	5.8	0.016
First to attack							
Whole model	3	–	–	–	–	2.54	0.47
Boldness	1	–0.00011	0.00033	–0.00079	0.00052	0.12	0.72
Mass (g)	1	–3.39	4.14	–11.7	4.45	0.69	0.4
Prosoma width (mm)	1	0.46	0.31	–0.13	1.07	2.26	0.13

Predictor variables include mass, prosoma width and individual boldness. Results from the entire model are also provided. Output included degrees of freedom (*df*), parameter estimate, standard error, upper and lower confidence intervals and *P* values. Significant outcomes ($P < 0.05$) are shown in bold.

DISCUSSION

Our study reveals a complex relationship between group personality composition, individual body size indices and experiential effects in determining how colonies respond to encounters with predators. A multitude of other studies have shown that a group's personality composition can influence its collective behaviour, although the majority of these studies pertain to foraging tasks (e.g. Aplin et al., 2014; Chang & Sih, 2013; Cote, Fogarty, Brodin, Weinersmith, & Sih, 2011; Dyer et al., 2009; Hui & Pinter-Wollman, 2014; Modlmeier & Foitzik, 2011; Modlmeier, Keiser, Shearer, & Pruitt, 2014). Our results add the more nuanced component that a group's personality composition can also change how groups respond to experience, a sort of personality composition*environment interaction at the group level. More specifically, colonies of social spiders composed of a mixture of bold and shy spiders showed twice as much defensive cribellate silk-making behaviour in response to predators as monotypic compositions. Mixed colonies were also the most consistent in their response across multiple encounters. Bold colonies, in contrast, varied erratically over time in how they responded to predators and they were less responsive to predators overall (i.e. slower to emerge and attack; Fig. 1). In contrast, bolder colonies are always more responsive to prey (Keiser & Pruitt, 2014; Pruitt & Keiser, 2014; Wright et al., 2015). Thus, the way a colony behaves over time can flip depending on both the colony composition and the environmental context (i.e. attacking innocuous prey versus dangerous predators). At the level of the individual, we observed that morphological traits and state variables were generally better predictors of task participation.

Our study is the first to demonstrate that a group's personality composition can alter both its collective behaviour and its behavioural plasticity. While experiential effects on behavioural tendencies are well known at the individual level (Dingemans et al., 2010; Stamps & Groothuis, 2010a, 2010b), relatively little is known about what drives variation in group-level sensitivity or responsiveness to experience (Bengston & Jandt, 2014; Jandt et al.,

2014). Our results demonstrate that group personality composition is one driver in *S. dumicola*. At the individual level, it is often true that more aggressive or bold personality types are less responsive to changes in their environment (Dingemans et al., 2010; Holbrook et al., 2014; Koolhaas, de Boer, Buwalda, & van Reenen, 2007), and there is some evidence of this pattern in social spiders (Holbrook et al., 2014; Modlmeier, Laskowski, et al., 2014). However, our results reveal that colonies composed of bolder (more inflexible) personality types actually show greater flexibility in their emergent group-level plasticity, at least, in their defensive cribellate silk-making response to experience with ant predators. This result hints at the possibility that a group of inflexible behavioural types can still produce behaviourally flexible societies. By parallel logic, colonies composed of flexible individuals might show inflexible, stable collective behaviour. This hypothesis receives some circumstantial support from the relatively common finding that behaviourally diverse societies often show greater homeostasis in a variety of collective traits, including behaviour (Burns & Dyer, 2008; Oldroyd & Fewell, 2007). Therefore, we argue that a hypothesized trade-off in behavioural flexibility at the individual versus group level is deserving of additional scrutiny in this and other test systems. We readily admit, however, that our small sample size for bold colonies ($N = 6$) may partially contribute to the fluctuations observed in these colonies.

At the individual level, we found a nuanced relationship between an individual's boldness and its body condition. Simply put, personality appears to influence whether or not individuals participate in an attack sequence or whether they contribute to defence in a less violent manner, such as producing cribellate silk. A large prosoma-to-mass ratio is widely considered to reflect poor body condition in spiders (Jakob et al., 1996). Thus, it appears that spiders in poor condition are those that participate more frequently in the majority of tasks, possibly reflecting hunger (Beleyur, Bellur, & Somanathan, 2015). Shyer individuals and those in poor condition tend to perform the majority of tasks associated with an attack sequence (leg pinning and body attacking), while bolder spiders tend to participate more in defensive cribellate silk

making, suggesting some role of personality in organizing task differentiation in heterogeneous groups. This is an intriguing result, because mixed colonies have twice as many cribellate participants as colonies composed of only bold individuals, and bold individuals tend to be cribellate silk-making specialists. Thus, one would predict that an entire colony of bold individuals would deploy more cribellate silk makers, not fewer. We therefore propose that something about the presence of shy phenotypes in mixed colonies seems to catalyse greater participation by bold individuals. This seems counterintuitive because foraging data have repeatedly shown that bold individuals usually enhance the responsiveness of shy individuals, and not vice versa (Pruitt & Keiser, 2014; Pruitt & Pinter-Wollman, 2015). This result further echoes a general thread innervating our entire study: the relationships between personality composition, social organization and collective behaviour in *S. dumicola* appear to switch based on whether colonies are responding to predators or prey. The question of why the patterns appear to reverse when colonies encounter predators is fascinating but yet unknown.

Although we detected no relationship between colony personality composition and survival during ant attacks, we are hesitant to make any impassioned claims about this result, given that no colony survived more than 22 h. Despite being chosen for its intermediate predation levels, predation pressure at this site is perhaps still too intense to detect any subtle effect of personality composition on colony persistence. Ongoing long-term studies at sites with varying ant densities will provide us with the final critical test. Nest age, however, proved to be somewhat important in determining colony persistence in the field. We reason that this effect is likely robust, as we managed to detect it despite intense levels of predation.

In conclusion, we have demonstrated that colony personality composition can alter both a group's average response and the way in which a colony responds to experience. We therefore offer that variation in group composition may represent a general factor underlying the way that groups behave from moment to moment and their collective behavioural trajectories through time. We again note patterns of task differentiation in *S. dumicola*, this time with regard to the handling of ant predators. As with foraging tasks, a combination of spider's morphological traits and body state are the most consistent contributors to task differentiation, with personality contributing to these patterns in colonies harbouring greater within-colony behavioural variation. Lastly, the available data suggest that colony personality composition may not be important for determining colony survival in situ, at least at intermediate or high predation sites (Keiser et al., 2015). We see no reasons to suggest that our findings should be unique to this system, and we encourage other researchers to explore the effects of colony personality composition on collective behaviour and plasticity in their own systems.

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Supplementary Material

Supplementary Material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.03.002>.

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