



# Personality and morphology shape task participation, collective foraging and escape behaviour in the social spider *Stegodyphus dumicola*



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Determining the drivers of complex systems is a major challenge felt by virtually all of biology. For complex societies, there is considerable interest in how individuals' traits determine their social roles and how the milieu of trait variants within groups shapes emergent group-level phenotypes. In this study, we tested in spiders whether individual differences in behaviour, morphology, or both shape individuals' participation in foraging. We then tested which aspects of group composition (e.g. morphological composition, personality composition, group size) predict colony-level foraging and escape behaviour. We performed these studies both under (1) standardized laboratory conditions, where colonies' ability to build webs was constrained, and (2) under more free-living conditions in the field. Regardless of the laboratory/field distinction, we found that individual task participation was regulated by individuals' body size and group size: larger individuals and individuals in smaller groups tended to participate more in foraging tasks. At the colony level, colonies composed of bolder spiders attacked prey with a larger number of attackers regardless of the laboratory/field distinction. However, our field assessments of colony foraging revealed that the speed with which colonies responded to prey was determined by their group size, morphological composition and personality composition; none of these effects were detected under laboratory conditions. Finally, we found that colonies took longer to retreat from aversive stimuli when more spiders were outside the nest. Taken together, our results suggest that colonies' social organization and collective behaviour are determined by spiders' morphology, behavioural tendencies and colony demographics.

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It is widely believed that sociality has been integral to the success and diversification of some of Earth's most conspicuous animals (Wilson, 1987). Being part of a group means individuals have the opportunity to specialize on different tasks and/or switch tasks less frequently, which can result in heightened vigilance and a more efficient use of time and energy (Arnold, 1988; Jeanson, Fewell, Gorelick, & Bertram, 2007; Zhongqiu & Zhigang, 2008). This, in turn, is predicted to enhance fitness for individuals who otherwise might not perform as well on their own. For example, nest parasitism rates decrease dramatically in many bees and wasps when queens and workers remain on the nest and care for young (Lin & Michener, 1972), and the ability to successfully capture and subdue large prey is often higher as group size increases in cooperative

hunters (Guevara, Gonzaga, Vasconcellos-Neto, & Aviles, 2011; Yip, Powers, & Aviles, 2008).

The manner in which animal societies are organized can augment both individual and colony-level performance (e.g. humans: Smith, 1776). For instance, groups can achieve higher levels of efficiency through task partitioning (Ratnieks & Anderson, 1999), task allocation (Robinson, Feinerman, & Franks, 2009) and division of labour (Duarte, Weissing, Pen, & Keller, 2011), and these behavioural traits are often aligned with age demographics (Seeley, 1982; Wilson, 1971) or specialized morphology (Holldobler & Wilson, 1990; Oster & Wilson, 1978). Most societies, however, lack morphological specialization, and instead, consistent behavioural variation between individuals (i.e. animal personality; Sih, Bell, & Johnson, 2004) has been found to govern division of labour in such systems (Wright, Holbrook, & Pruitt, 2014). These organizational traits are predicted to generate adaptive colony-level phenotypes that further feedback on the performance of the group (Jandt et al., 2014; Jeanne, 1986; Pruitt & Goodnight, 2014).

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Here we consider how consistent individual differences in behaviour (hereafter ‘personality’) and morphology combine to shape task participation and collective behaviour in a social spider. Social and subsocial spiders have emerged as model systems for the study of how animal personality shapes social organization (Grinsted, Pruitt, Settepani, & Bilde, 2013; Settepani, Grinsted, Granfeldt, Jensen, & Bilde, 2013; Wright et al., 2014), collective behaviour (Keiser, Jones, Modlmeier, & Pruitt, 2014), multilevel selection (Aviles, 1986, 1993; Pruitt, 2013) and colony-level adaptation (Pruitt & Goodnight, 2014). The preponderance of available evidence suggests that, similar to the castes of social insects, spider societies enjoy enhanced reproductive output and survival when they are composed of a diverse set of personality types (Pruitt, Oufiero, Aviles, & Riechert, 2012), likely as a consequence of adaptive division of labour (Wright et al., 2014). Yet, this literature also suffers from a series of notable biases, for instance, the tendency for investigations to emphasize personality variation in shaping individuals’ task participation at the cost of ignoring other aspects of functional diversity (Pruitt & Goodnight, 2014; Pruitt & Riechert, 2011). We argue that this is a mistake, since a small but growing number of studies have demonstrated an equally important role for morphological diversity in structuring task participation (Ebert, 1998; Grinsted et al., 2013; Keiser et al., 2014). Yet, how the morphological composition of groups influences collective phenotypes remains unknown. This is in contrast to the social insect literature, which has tended to focus on the role of morphological variation and body size distributions in shaping colony organization (Jandt & Dornhaus, 2014; Oster & Wilson, 1978). In this paper we address some of these biases, in the hopes to build upon this rapidly developing literature (Grinsted et al., 2013; Settepani et al., 2013).

We performed our studies using the African desert social spider, *Stegodyphus dumicola* (Araneae, Eresidae). These spiders build a complex silken retreat permeated by an elaborate series of tunnels that can house hundreds of spiders. Often radiating outwards from the retreat are one or more two-dimensional capture webs. Spiders are recruited to the capture web from the retreat in response to vibratory cues indicative of struggling prey. Importantly, these spiders also exhibit consistent individual variation in their boldness–shyness personality, which is defined here as the latency to resume activity after an aversive stimulus (Sloan Wilson, Clark, Coleman, & Dearstyne, 1994). In laboratory studies, boldness and aggressiveness have been shown to be linked with participation in foraging tasks in *S. dumicola* (Keiser et al., 2014), and extremely bold individuals appear to have the ability to catalyse otherwise sedentary nestmates into aggressive foraging behaviour (Pruitt & Keiser, 2014). Similar results have been obtained in studies of *Stegodyphus sarasinorum*, which hails from an independent origin of sociality within the genus (Grinsted et al., 2013; Johannesen, Lubin, Smith, Bilde, & Schneider, 2007; Settepani et al., 2013). In the present study, we created colonies of different sizes and personality compositions in the laboratory and field in order to uncover how colony-level behaviour and individual task participation is influenced by personality composition, colony size and morphological composition in situ.

We address the following two questions. (1) To what degree can colonies’ collective foraging and escape behaviour be explained by aspects of colonies’ morphological composition, such as colony members’ body size, mass and body condition? This is in contrast to recent studies suggesting that colony-level behaviour is largely determined by personality composition in social spiders and some social insects (Hui & Pinter-Wollman, 2014; Keiser & Pruitt, 2014; Modlmeier, Keiser, Shearer, & Pruitt, 2014). (2) What traits predict the propensity for individuals to participate in collective foraging behaviour in the wild? At present, our understanding of the latter question comes from mostly short-term studies performed on a

small number of colonies in laboratory (Keiser et al., 2014; Pruitt & Riechert, 2011). In our view, interest in such laboratory studies is based on the notion that the patterns observed in laboratory do, to some extent, reflect what occurs in the field. We address this link here by performing a more comprehensive field study on more than 60 colonies and comparing results obtained when colony architecture is constrained within a small arena (i.e. standard laboratory conditions) and under more naturalistic conditions (i.e. where colonies can build freely).

## METHODS

### Natural History

The spider *S. dumicola* lives in multifemale societies containing one to several hundred spiders throughout southwestern Africa (Henschel, 1998). This species exhibits a highly female-biased sex ratio and serial inbreeding behaviour (Aviles, Varas, & Dyreson, 1999; Henschel, Lubin, & Schneider, 1995). Like all social spiders, female *S. dumicola* cooperate together in web maintenance, prey capture and alloparental care (Bilde & Lubin, 2007). The web of this species exhibits two discrete parts, a dense two-dimensional labyrinthine nest retreat where spiders reside most of the time and one or more two-dimensional capture webs, which are used to intercept prey and are repaired by spiders nightly (Keiser et al., 2014).

### Collection and Maintenance

We collected 40 large colonies (80–627 individuals) of *S. dumicola* along roadsides in the southern Kalahari Desert, South Africa in January 2014. We then transported these colonies to our field site in Griekwastad, Northern Cape, South Africa. We isolated each individual and measured their body mass with a digital scale and their prosoma width with digital callipers. Body condition is estimated by taking the residuals from a linear regression of mass versus body size for all spiders in our study (Jakob, Marshall, & Uetz, 1996). We used individuals’ prosoma width as our measure of body size. Positive values indicate spiders that are heavier for any given prosoma width, and negative values indicate individuals that are relatively lighter for their prosoma width.

All of the procedures described herein adhere to the ethics and animal welfare requirements for invertebrate studies in the United States of America and the Republic of South Africa (FAUNA 1060/2012, FAUNA 1072, 2013). After our studies, spiders were transported back to our laboratory at the University of Pittsburgh where they were maintained on a maintenance ad libitum feeding and watering regime until they expired naturally.

### Boldness Assays

We identified the boldness of each individual by assessing their response to two rapid puffs of air using an infant nose-cleaning bulb, an aversive stimulus that is designed to mimic the rapid approach of many flying predators (Pruitt, Iturralde, Aviles, & Riechert, 2011; Riechert & Hedrick, 1993). Boldness is quantified as individuals’ latency to resume movement following the stimulus, and this personality metric is highly repeatable in *S. dumicola* (repeatability = 0.63; Keiser et al., 2014). Furthermore, boldness and body size are associated with the propensity for individuals to participate in foraging and web-building tasks under laboratory conditions (Keiser et al., 2014), suggesting boldness is an informative metric of individuals’ role within their society. To assess the boldness of individuals, spiders were provided a 60 s acclimation time in a black plastic arena (diameter = 12 cm, height = 4 cm). We then administered two rapid puffs of air to the spider’s prosoma

anteriorly and measured the time until the spider moved one full body length. Spiders were allowed 600 s before the trial was terminated. For experimental manipulations of groups' personality compositions, we sorted spiders into nominal personality categories as follows: individuals with long latencies to resume movement (400–600 s) were classified as 'shy', while individuals that resumed activity within 1–200 s were classified as 'bold'. Individuals that resumed activity between 200 and 400 s after the stimulus were classified as 'median'. We then gave each individual spider a unique three-colour ID mark with acrylic paint on their posterior abdomen. The boldness of each spider was measured once and individuals were used in only one experimental colony and then discharged from the experiment. Using a fully factorial design, we constructed colonies of 10 or 30 individuals composed of one of four personality compositions: all bold, all shy, 50:50 bold and shy, or all individuals of 'median' boldness ( $N = 64$  experimental colonies): 10 bold ( $N = 6$ ), 10 shy ( $N = 13$ ), 10 mixed ( $N = 7$ ), 10 median ( $N = 11$ ), 30 bold ( $N = 6$ ), 30 shy ( $N = 8$ ), 30 mixed ( $N = 7$ ), 30 median ( $N = 6$ ). Throughout our study, spiders were checked every 6–8 h for instances of moulting; spiders that moulted during the course of the study were remarked and placed back within the colony retreat.

### Collective Behaviour Assays

#### Collective foraging

We allowed each colony 24 h to produce a silken retreat in 240 ml clear plastic parfait cups. Once daily for the following 3 days, we tested the collective foraging of each colony inside these containers (laboratory condition, foraging web absent). In this set of assays, each colony foraged on a web of identical volume (i.e. the area of their retreat inside the parfait cup). Colony architecture was constrained to a standardized container, similar to the conditions of most laboratory studies and the foraging web was absent. We performed collective foraging assays by placing a 1.5 cm<sup>2</sup> piece of white paper in the centre of the retreat silk. After a 20 s acclimation period, we used a hand-held vibrator (GoVibe) to shake the piece of paper in a manner that simulates a prey item struggling in the silk. We then recorded (1) the latency for the first spider to emerge from the retreat, (2) the latency for the first spider to attack the paper and (3) the number of individuals that participated in the attack. We also recorded the identity of each individual that performed/participated in each of these tasks. After our laboratory measurements, we fastened each colony to the branch of a hookbush acacia (*Acacia mellifera*) in the field with two wooden clothespins. We placed colonies in the acacia trees at 2000 hours to allow web building overnight. At 0600 and 1800 hours each day following placement in the field, we again tested the collective foraging of each colony, but in these instances with a capture web present (field condition, foraging web present). Although previous studies suggest that the distance of the prey stimulus from the retreat does not impact colony foraging behaviour (Pruitt et al., 2013), we always placed the prey stimulus 10 cm away from the entrance to the retreat in our field measurements of colony foraging behaviour. Although the two-dimensional capture web area differed across experimental colonies of 10 versus 30 individuals (Keiser & Pruitt, 2014), their retreat volumes remained identical (i.e. 240 ml, the area within the parfait cup).

#### Escape behaviour

Directly following the collective foraging assay, we tested how quickly spiders evacuated into the retreat after an aversive stimulus (i.e. striking the branch to which the colony was attached with a blunt probe). These abrupt vibrations travel throughout the capture web and universally cause spiders to evacuate back into the retreat.

After this stimulus, we measured the latency for the first and last individual to enter their silken retreat. We failed to record the identity of the first and last individuals to enter the retreat, thus prohibiting our ability to assess how individual traits shaped participation in this context.

### Statistical Analyses

In our models predicting individual task participation during foraging, we included the following independent variables: boldness (latency to resume movement), group size, body condition, prosoma width, personality composition (composition), boldness\*group size, boldness\*composition, prosoma width\*group size and prosoma width\*composition. The response variables for our models predicting task participation were (1) the number of times each individual was the first to emerge in response to prey, (2) the number of times each individual was the first to attack prey and (3) the number of times each individual participated in prey capture. For all three of these models we used GLMMs with a Poisson error distribution. In our models predicting colony-level foraging behaviour responses (latency to emerge, latency to attack and number of individuals to attack), we included the following independent variables: capture web area (in cm<sup>2</sup>) (field colonies only), group size, personality composition and the mean  $\pm$  SD boldness, prosoma width and body condition of colony members. Based on previous studies on ants (Hui & Pinter-Wollman, 2014; Modlmeier, Keiser, et al., 2014) and social spiders (Pruitt et al., 2013), we predicted that larger colonies and colonies composed of bolder individuals would tend to behave more aggressively during prey capture. The distributions of the residuals from our models predicting colony-level foraging behaviour were all roughly normally distributed. We performed an independent set of analyses for when colonies were permitted to build webbing freely (field condition) and when they were constrained (laboratory condition). For our model predicting colony escape behaviour, we included the following independent variables: capture web area (in cm<sup>2</sup>), group size, personality composition, distance of the nearest individual from the retreat (distance from retreat) and the number of individuals outside of the nest at the time of the aversive stimulus (number outside). Unstandardized regression coefficients ( $\beta$ ) and SEs are reported in the Results.

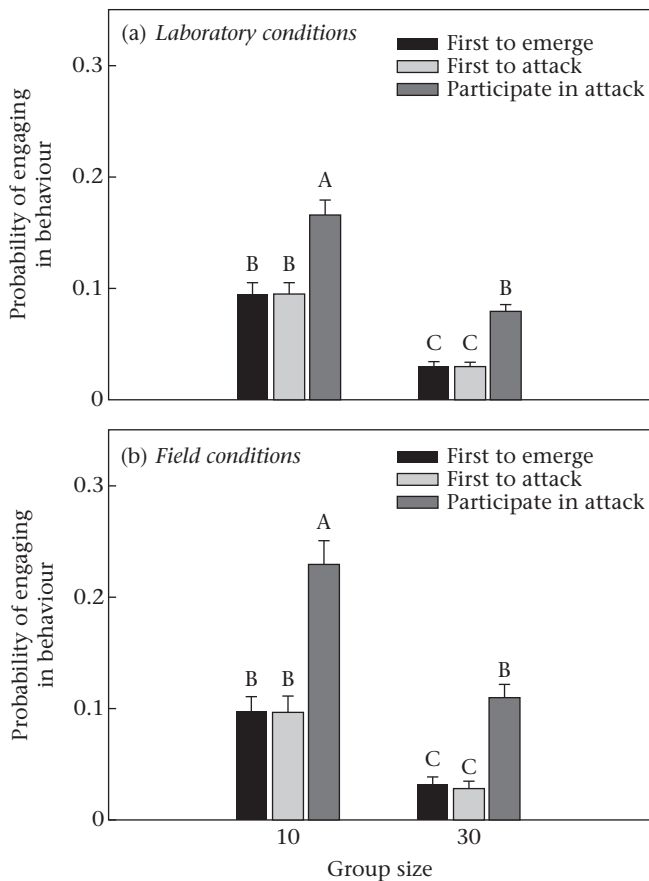
To decipher the degree to which *S. dumicola* personality is state dependent, we ran multiple regressions with prosoma width, body mass and body condition as independent variables, and boldness as our response variable. For all of our analyses we designated experimental colony ID and source colony ID as random effects in our models. Post hoc pairwise comparisons were conducted with Tukey's HSD. All statistics were performed in JMP 10.

## RESULTS

### Task Participation

Regardless of the laboratory/field distinction, we detected strong associations between group size and individuals' tendency to participate in all aspects of foraging (Fig. 1, Table 1, Supplementary Table S1). Individuals' probability of being the first to emerge in response to prey, the first to attack prey, or the first to participate in an attack were 200–300% greater in smaller colonies than in larger colonies (laboratory:  $F_{1,99.72} = 51.18$ ,  $\beta \pm SE = 0.04 \pm 0.01$ ,  $P < 0.0001$ ; field:  $F_{1,36.3} = 18.67$ ,  $\beta \pm SE = 0.06 \pm 0.01$ ,  $P = 0.0001$ ). Larger colonies were three times as large as smaller colonies.

We also detected an association between individuals' body size (prosoma width) and their probability of participating in attacks (Table 1), where very large individuals (top decile) were 15% more likely to participate in prey capture than very small individuals



**Figure 1.** Individuals' mean  $\pm$  SE probability of engaging in various aspects of cooperative foraging depending on colony size (10 versus 30 spiders) and whether they were observed under (a) laboratory or (b) field conditions. Groups not sharing the same letter differed significantly according to post hoc Tukey HSD groupings.

(bottom decile) (laboratory:  $F_{1,222.3} = 12.05$ ,  $\beta \pm SE = 0.05 \pm 0.02$ ,  $P = 0.0006$ ; field:  $F_{1,88.15} = 5.70$ ,  $\beta \pm SE = 0.05 \pm 0.02$ ,  $P = 0.019$ ). Here again, the association between body size and tendency to participate in prey capture was robust to whether we observed colonies in standardized laboratory or field conditions. We failed to detect associations between individuals' personality types and their tendency to engage in any aspect of foraging regardless of the laboratory/field distinction.

#### State-dependent Personality

We found that individual boldness score depended significantly on body condition and body mass: individuals with lower body conditions and mass tended to behave more boldly (body condition:  $F_{1,213.7} = 11.8$ ,  $\beta \pm SE = 0.14 \pm 0.06$ ,  $P = 0.0006$ ; mass:  $F_{1,238.4} = 13.8$ ,  $\beta \pm SE = 0.11 \pm 0.04$ ,  $P = 0.0002$ ). Boldness, however, was not significantly associated with individuals' prosoma width ( $F_{1,217.4} = 3.58$ ,  $\beta \pm SE = 0.08 \pm 0.08$ ,  $P = 0.08$ ). The correlation between mass and boldness, and body condition and boldness, however, were both quite weak (both  $r < 0.12$ ).

#### Collective Foraging Behaviour

Our models predicting colonies' collective foraging behaviour differed subtly based on whether we assayed colonies' behaviour in laboratory or field conditions. Regardless of the laboratory/field distinction, we found that colonies' personality composition was a

determinant of the number of attackers that responded to prey (Table 2, Supplementary Table S2). In particular, colonies composed of bolder spiders attacked with more than 200% as many spiders as colonies bearing other personality compositions (laboratory:  $F_{1,46} = 21.79$ ,  $\beta \pm SE = 4.39 \pm 0.62$ ;  $P < 0.0001$ ; field:  $F_{1,52} = 15.22$ ,  $\beta \pm SE = 3.12 \pm 0.53$ ,  $P < 0.0001$ ; Fig. 2). Under laboratory conditions we failed to detect an association between colonies' response times and any aspects of their phenotypic compositions. In contrast, we detected subtle effects of colony size and within-group trait variation on colonies' speed of response in situ. Smaller colonies were faster to emerge and to attack prey than larger colonies in the field ( $F_{1,46} = 7.81$ ,  $\beta \pm SE = -9.14 \pm 3.27$ ,  $P = 0.008$ ; Fig. 3). Colonies harbouring a more behaviourally diverse set of individuals in terms of their boldness emerged in response to prey in 45% less time than colonies composed of a more homogenous set of individuals ( $F_{1,47} = 4.14$ ,  $\beta \pm SE = -0.19 \pm 0.09$ ,  $P = 0.048$ ). Likewise, colonies composed of a more diverse set of individuals, in terms of their body sizes (prosoma widths), attacked prey in 40% less time than more homogenous colonies ( $F_{1,45} = 4.36$ ,  $\beta \pm SE = -264.6 \pm 126.79$ ,  $P = 0.042$ ).

#### Collective Escape Behaviour

We failed to detect an association between the latency for the first spider to enter the nest in response to an aversive stimulus and any of our independent variables (all  $P > 0.31$ ). However, colonies with more spiders present on the capture web at the time of the aversive stimulus took longer to fully evacuate the capture web ( $F_{1,42} = 8.99$ ,  $\beta \pm SE = 13.09 \pm 4.37$ ,  $P = 0.006$ ).

## DISCUSSION

#### Task Participation

Colony size was associated with individuals' participation in foraging tasks. Perhaps unsurprisingly, individuals in smaller colonies were more likely to be the first to emerge and attack during a foraging event. This is almost certainly a reflection of the fact that in smaller colonies, all else being equal, individual spiders have a higher likelihood of being the first to emerge and attack by sheer chance alone, given the colony's smaller size (expected probabilities: 1/10 versus 1/30). Identical patterns of significance were detected regardless of the laboratory/field distinction (Table 1). We do not think that living in smaller groups actually changes individuals' foraging/initiation tendencies in any way; this result instead implies equal task sharing among group members. Group size was also important in predicting individuals' tendency to join in an attack, where individuals in smaller colonies were more likely to join. This means that a higher proportion of spiders in smaller colonies foraged than did spiders in larger colonies. This is perhaps because, in smaller colonies, there are merely fewer individuals with which to share or divide the brunt of a task. Thus, a relatively larger proportion of individuals must engage in a task in order to successfully complete it in small colonies. Taken together, this could mean that individuals in smaller colonies need to spend more time/energy engaged in foraging behaviour. This, in turn, likely increases their energy costs and increases their chance of risky encounters with dangerous prey or cryptic predators while foraging. Notably, the willingness of others to join in an attack is actually vital in these societies, since the ability to subdue large and more profitable prey is a major contributor to foraging success (Guevara & Aviles, 2011; Harwood & Aviles, 2013) and the maintenance of sociality in cooperative hunters (Purcell & Aviles, 2008; Whitehouse & Lubin, 2005; Yip et al., 2008). Thus, individuals in larger colonies could obtain at least two benefits: (1) each individual is required to participate in foraging less than if it occupied a smaller colony, as a

**Table 1**

Effects tests from a GLMM analysis testing for associations between individuals' traits and their tendency to participate in various aspects of collective foraging under laboratory and field conditions

|                            | Laboratory |     |       |         |                   | Field |     |       |         |                   |
|----------------------------|------------|-----|-------|---------|-------------------|-------|-----|-------|---------|-------------------|
|                            | $N_p$      | ndf | ddf   | F ratio | Prob > F          | $N_p$ | ndf | ddf   | F ratio | Prob > F          |
| First to emerge            |            |     |       |         |                   |       |     |       |         |                   |
| Boldness                   | 1          | 1   | 410.2 | 0.44    | 0.51              | 1     | 1   | 845   | 0.04    | 0.85              |
| Group size                 | 1          | 1   | 992.1 | 100.91  | <b>&lt;0.0001</b> | 1     | 1   | 406.8 | 42.84   | <b>&lt;0.0001</b> |
| Body condition             | 1          | 1   | 54.77 | 1.35    | 0.25              | 1     | 1   | 32.84 | 1.57    | 0.22              |
| Prosoma (mm)               | 1          | 1   | 979.9 | 0.66    | 0.42              | 1     | 1   | 71.07 | 0.00    | 0.94              |
| Personality composition    | 3          | 3   | 202.5 | 0.12    | 0.95              | 3     | 3   | 199.9 | 0.03    | 0.99              |
| Group size * boldness      | 1          | 1   | 1026  | 0.24    | 0.62              | 1     | 1   | 573.1 | 0.00    | 0.99              |
| Composition * boldness     | 3          | 3   | 406   | 0.07    | 0.97              | 3     | 3   | 844.4 | 0.10    | 0.96              |
| Group size * prosoma (mm)  | 1          | 1   | 943.2 | 0.07    | 0.79              | 1     | 1   | 445.9 | 0.52    | 0.47              |
| Composition * prosoma (mm) | 3          | 3   | 28.85 | 1.08    | 0.37              | 3     | 3   | 26.03 | 1.05    | 0.39              |
| First to attack            |            |     |       |         |                   |       |     |       |         |                   |
| Boldness                   | 1          | 1   | 530.9 | 0.68    | 0.41              | 1     | 1   | 781   | 0.06    | 0.81              |
| Group size                 | 1          | 1   | 873.6 | 103.65  | <b>&lt;0.0001</b> | 1     | 1   | 420.8 | 53.54   | <b>&lt;0.0001</b> |
| Body condition             | 1          | 1   | 53.01 | 0.56    | 0.46              | 1     | 1   | 28.77 | 0.89    | 0.35              |
| Prosoma (mm)               | 1          | 1   | 875.1 | 0.52    | 0.47              | 1     | 1   | 76.4  | 0.56    | 0.45              |
| Personality composition    | 3          | 3   | 198   | 0.32    | 0.81              | 3     | 3   | 181.3 | 0.27    | 0.85              |
| Group size * boldness      | 1          | 1   | 958   | 0.07    | 0.79              | 1     | 1   | 581.8 | 0.11    | 0.75              |
| Composition * boldness     | 3          | 3   | 523.9 | 0.09    | 0.97              | 3     | 3   | 777.4 | 0.10    | 0.96              |
| Group size * prosoma (mm)  | 1          | 1   | 844.8 | 0.00    | 0.95              | 1     | 1   | 437.5 | 0.29    | 0.59              |
| Composition * prosoma (mm) | 3          | 3   | 26.34 | 0.18    | 0.91              | 3     | 3   | 21.48 | 0.34    | 0.79              |
| Participate in attack      |            |     |       |         |                   |       |     |       |         |                   |
| Boldness                   | 1          | 1   | 1094  | 1.66    | 0.20              | 1     | 1   | 956.9 | 3.39    | 0.07              |
| Group size                 | 1          | 1   | 99.72 | 51.18   | <b>&lt;0.0001</b> | 1     | 1   | 36.3  | 18.67   | <b>0.0001</b>     |
| Body condition             | 1          | 1   | 272.7 | 3.49    | 0.06              | 1     | 1   | 257.6 | 2.96    | 0.09              |
| Prosoma (mm)               | 1          | 1   | 222.3 | 12.05   | <b>0.0006</b>     | 1     | 1   | 88.15 | 5.70    | <b>0.0191</b>     |
| Personality composition    | 3          | 3   | 160   | 0.49    | 0.69              | 3     | 3   | 94.77 | 0.49    | 0.69              |
| Group size * boldness      | 1          | 1   | 214.8 | 2.12    | 0.15              | 1     | 1   | 135.6 | 1.49    | 0.22              |
| Composition * boldness     | 3          | 3   | 1120  | 0.66    | 0.58              | 3     | 3   | 971.4 | 0.36    | 0.78              |
| Group size * prosoma (mm)  | 1          | 1   | 270.3 | 2.65    | 0.10              | 1     | 1   | 200   | 2.11    | 0.15              |
| Composition * prosoma (mm) | 3          | 3   | 63.98 | 0.79    | 0.50              | 3     | 3   | 112.2 | 0.67    | 0.57              |

 $N_p$ : number of parameters associated with the effect. Significant outcomes are shown in bold.

consequence of task sharing, and (2) the absolute number of spiders that respond to prey is greater in large colonies, which means colonies potentially subdue prey faster and are more likely to capture particularly large, profitable prey.

As seen in field studies on the congener *S. sarasinorum* and a laboratory study on *S. dumicola* (Grinsted et al., 2013; Keiser et al., 2014; Settepani et al., 2013), we found that larger spiders were more likely to join in cooperative prey capture. This raises the question of whether allocating larger individuals to prey capture has any particular advantage for the colony and/or whether it just serves the individual interests of larger individuals. We reason that larger individuals may be more individually efficient/effective at subduing prey, given their larger size. Therefore, colonies could be allocating their most efficient workers to foraging, which may help small individuals obtain food (Yip & Rayor, 2013). Larger individuals might also enjoy lower risk of injury or death when subduing large or dangerous prey (argued in Ainsworth, Slotow, Crouch, & Lubin, 2002). Alternatively, some data suggest that individuals that subdue prey and initiate feeding earlier also feed for longer and gain more mass (Amir, Whitehouse, & Lubin, 2000; Willey & Jackson, 1993). Thus, it may be in the interests of larger individuals to attack and initiate feeding earlier. In fact, larger individuals might be larger for this very reason (i.e. their tendency to attack and initiate feeding begets their larger size). Larger individuals are also more likely to reproduce (Bilde et al., 2007), and this could further enhance the profitability of arriving early to prey.

#### Colony-level Behaviour

Colonies' collective foraging behaviour was determined by a combination of their group size, morphological composition and

behavioural composition. Small colonies emerged more rapidly in response to prey and were also faster to attack prey than larger colonies (Fig. 3). Although the precise cause of this pattern is unknown, we reason that smaller colonies may rely on rapid response times in order to subdue prey quickly because their webs are smaller and potentially less effective at prey retention (Keiser & Pruitt, 2014), or because they merely have fewer individual with which to overwhelm their prey. One may reason that variation in web size or the distance of the prey stimulus from colony retreats may underlie this pattern. However, we held the distance of the prey stimulus from the retreat constant across colony sizes and capture web area was not significantly associated with any aspect of colony-level foraging that we measured (Table 2).

The extent of morphological and behavioural variation within colonies was also associated with their speed of emergence and attack, but only in field conditions. Colonies composed of a more behaviourally diverse set of individuals, in terms of their boldness, were faster to emerge in response to prey. Whereas, colonies composed of more morphologically diverse individuals, in terms of their prosoma width, were faster to attack. Although, again, the reasons for these effects are unknown, we propose that trait complementarity and catalytic interactions between unlike individuals may cause changes in colonies' collective behaviour. For instance, across many animal societies, individuals may change their behaviour based on the behavioural tendencies (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Holbrook, Wright, & Pruitt, 2014; King, Williams, & Mettke-Hofmann, 2015) or the body sizes (Amir et al., 2000) of their fellow group members which, in turn, could impact the collective behaviour of the group (Jandt et al., 2014; Modlmeier, Keiser, et al., 2014). Finally, as seen in other studies (Dyer, Croft, Morrell, & Krause, 2009; Hui & Pinter-

**Table 2**  
Effects tests from a multiple regression testing for associations between colonies' collective foraging behaviour and various aspects of colony composition under laboratory and field conditions

|                                     | Laboratory |     |     |         |                   | Field |     |       |         |                   |
|-------------------------------------|------------|-----|-----|---------|-------------------|-------|-----|-------|---------|-------------------|
|                                     | $N_p$      | ndf | ddf | F ratio | Prob > F          | $N_p$ | ndf | ddf   | F ratio | Prob > F          |
| Colony latency to emerge            |            |     |     |         |                   |       |     |       |         |                   |
| Capture web area (cm <sup>2</sup> ) | –          | –   | –   | –       | –                 | 1     | 1   | 46    | 0.25    | 0.62              |
| Group size                          | 1          | 1   | 52  | 0.15    | 0.70              | 1     | 1   | 46    | 7.81    | <b>0.0075</b>     |
| Personality composition             | 3          | 3   | 52  | 1.46    | 0.24              | 3     | 3   | 46    | 1.97    | 0.13              |
| Mean(mass (g))                      | 1          | 1   | 52  | 0.00    | 0.98              | 1     | 1   | 46    | 2.37    | 0.13              |
| Mean(prosoma (mm))                  | 1          | 1   | 52  | 0.00    | 0.98              | 1     | 1   | 46    | 2.32    | 0.13              |
| Mean(body condition)                | 1          | 1   | 52  | 0.00    | 0.98              | 1     | 1   | 46    | 2.35    | 0.13              |
| SD(mass (g))                        | 1          | 1   | 52  | 0.71    | 0.40              | 1     | 1   | 46    | 0.51    | 0.48              |
| SD(prosoma (mm))                    | 1          | 1   | 52  | 1.32    | 0.26              | 1     | 1   | 46    | 1.63    | 0.21              |
| SD(body condition)                  | 1          | 1   | 52  | 0.00    | 0.95              | 1     | 1   | 46    | 0.02    | 0.90              |
| SD(boldness)                        | 1          | 1   | 52  | 1.89    | 0.17              | 1     | 1   | 46    | 4.10    | <b>0.0485</b>     |
| Colony latency to attack            |            |     |     |         |                   |       |     |       |         |                   |
| Capture web area (cm <sup>2</sup> ) | –          | –   | –   | –       | –                 | 1     | 1   | 44    | 0.19    | 0.66              |
| Group size                          | 1          | 1   | 52  | 0.08    | 0.77              | 1     | 1   | 44    | 6.70    | <b>0.0130</b>     |
| Personality composition             | 3          | 3   | 52  | 2.38    | 0.08              | 3     | 3   | 44    | 0.52    | 0.67              |
| Mean(mass (g))                      | 1          | 1   | 52  | 0.01    | 0.93              | 1     | 1   | 44    | 0.17    | 0.68              |
| Mean(prosoma (mm))                  | 1          | 1   | 52  | 0.01    | 0.94              | 1     | 1   | 44    | 0.16    | 0.69              |
| Mean(body condition)                | 1          | 1   | 52  | 0.01    | 0.94              | 1     | 1   | 44    | 0.19    | 0.67              |
| SD(mass (g))                        | 1          | 1   | 52  | 0.42    | 0.52              | 1     | 1   | 44    | 2.18    | 0.15              |
| SD(prosoma (mm))                    | 1          | 1   | 52  | 1.02    | 0.32              | 1     | 1   | 44    | 4.36    | <b>0.0426</b>     |
| SD(body condition)                  | 1          | 1   | 52  | 0.00    | 0.98              | 1     | 1   | 44    | 1.04    | 0.31              |
| SD(boldness)                        | 1          | 1   | 52  | 2.07    | 0.16              | 1     | 1   | 44    | 1.45    | 0.24              |
| Number of attackers                 |            |     |     |         |                   |       |     |       |         |                   |
| Capture web area (cm <sup>2</sup> ) | –          | –   | –   | –       | –                 | 1     | 1   | 47.12 | 0.67    | 0.42              |
| Group size                          | 1          | 1   | 52  | 2.55    | 0.12              | 1     | 1   | 47.08 | 2.85    | 0.10              |
| Composition                         | 3          | 3   | 52  | 15.22   | <b>&lt;0.0001</b> | 3     | 3   | 47    | 21.79   | <b>&lt;0.0001</b> |
| Mean(mass (g))                      | 1          | 1   | 52  | 0.17    | 0.68              | 1     | 1   | 47.34 | 0.71    | 0.40              |
| Mean(prosoma (mm))                  | 1          | 1   | 52  | 0.17    | 0.68              | 1     | 1   | 47.33 | 0.67    | 0.42              |
| Mean(body condition)                | 1          | 1   | 52  | 0.18    | 0.67              | 1     | 1   | 46.98 | 0.68    | 0.42              |
| SD(mass (g))                        | 1          | 1   | 52  | 0.30    | 0.59              | 1     | 1   | 47.04 | 0.28    | 0.60              |
| SD(prosoma (mm))                    | 1          | 1   | 52  | 0.01    | 0.92              | 1     | 1   | 46.99 | 0.03    | 0.87              |
| SD(body condition)                  | 1          | 1   | 52  | 0.06    | 0.81              | 1     | 1   | 46.97 | 0.04    | 0.84              |
| SD(boldness)                        | 1          | 1   | 52  | 0.21    | 0.65              | 1     | 1   | 46.98 | 0.63    | 0.43              |

$N_p$ : number of parameters associated with the effect. Significant outcomes are shown in bold.

Wollman, 2014; Keiser & Pruitt, 2014), creating colonies of contrasting personality compositions had impacts on collective behaviour. In this study, colonies composed of bold individuals responded to prey with twice as many attackers.

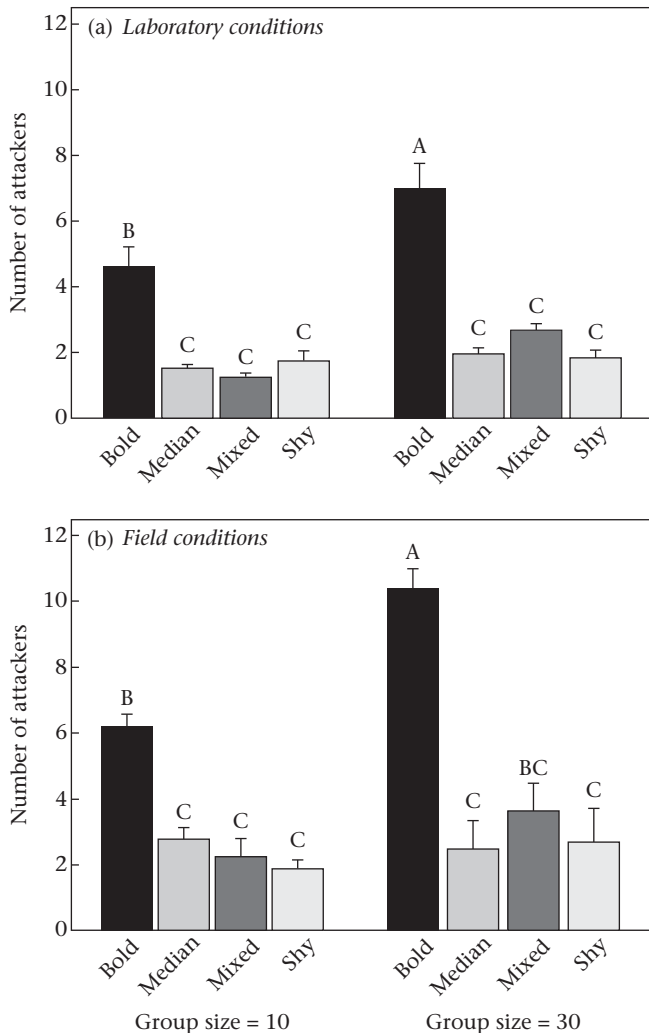
Interestingly, almost all of these subtle effects were detected under field conditions only (Table 2). We argue that this provides evidence that laboratory conditions constrain colonies' ability to express their full (collective) behavioural repertoires. We reason that variation in the web architecture of laboratory versus field colonies may underlie these differences. Previous studies on social spiders (Modlmeier, Forrester, & Pruitt, 2014) and other social arthropods (Pinter-Wollman, Gordon, & Holmes, 2012) have shown that variation in nest architecture can cause shifts in collective behaviour. While we failed to detect an association between capture web area and collective behaviour here, we reason that the mere presence of the capture web may allow for the more subtle expression of variation in colonies' collective foraging behaviour. This could be a consequence of differences in the biomechanical properties of the flexible capture web or perhaps how the web is placed within the environment. Although spiders will forage readily on either their capture web or the retreat, there may also be subtle differences in the way that spiders behave on either structure. Additional studies are needed to address these possibilities.

In terms of colonies' escape behaviour, we found that the only significant predictor of colonies' escape speed was the number of spiders outside of the nest at the time the aversive stimulus was applied. Colonies with many spiders outside the nest took longer to flee back into the nest. This is a fairly intuitive result. However, it

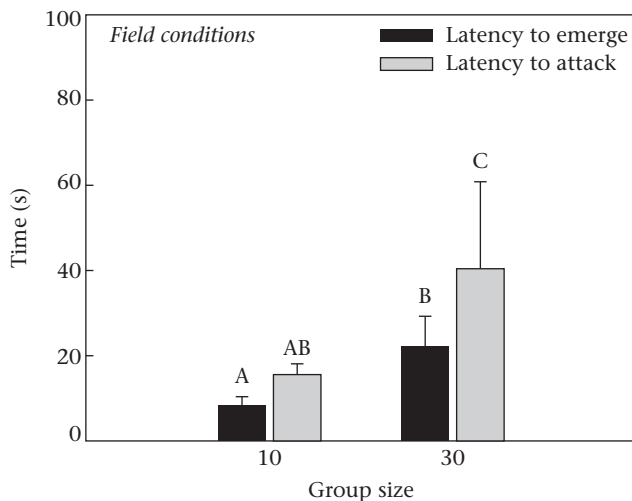
may still have some functional consequences, because it suggests that colonies that mount an aggressive assault (e.g. bolder colonies) on prey may also be slower to flee when and if the scenario becomes dangerous. We reason that this could result in reduced escape efficiency and higher mortality costs for colonies that forage more aggressively.

### Conclusions

A large number of recent papers have explored the interplay between group composition, social organization, collective behaviour and group success (Aplin, Farine, Mann, & Sheldon, 2014; Burns & Dyer, 2008; Dyer et al., 2009; Farine, Aplin, Garroway, Mann, & Sheldon, 2014; Modlmeier, Liebmann, & Foitzik, 2012; Wright et al., 2014). Here we found that individuals' propensity to engage in various aspects of collective foraging was determined by group size and individual body size, and appears to be unrelated to individuals' personality types. This result is in contrast to previous studies on spiders (Wright et al., 2014). The patterns observed here more closely resemble those of social insect societies, where group size and morphology are often important drivers of social roles (Oster & Wilson, 1978, 1980, 1983). Although personality appears to be unrelated to individuals' tendency to participate in various aspects of foraging, personality composition did still impact colonies' collective foraging behaviour. Like several previous studies on spiders and other taxa, our results suggest that groups' average personality type (boldness) and their degree of within-group



**Figure 2.** Mean  $\pm$  SE number of attackers that emerged in response to prey relative to colony size (10 versus 30 spiders), personality composition (all bold, moderate/median boldness, mixed 50% bold and 50% shy, or all shy) and whether they were observed under (a) laboratory or (b) field conditions. Groups not sharing the same letter differed significantly according to post hoc Tukey HSD groupings.



**Figure 3.** Mean  $\pm$  SE latency to emerge and to attack for colonies of different sizes (10 versus 30 spiders) while observed under field conditions. Groups not sharing the same letter differed significantly according to post hoc Tukey HSD groupings.

variation (in boldness and body size) shaped colonies' speed and intensity of attack.

We argue that the next difficult step for our studies on *Stegodyphus*, and perhaps the literature in general, is to determine how variation in social organization (e.g. task participation patterns) and colony-level behaviour impacts performance in the wild, and to determine whether different environments favour different collective phenotypes. This, in turn, could yield deeper insights into (1) how trait variation is maintained in these systems, (2) why selection might favour different group membership rules and (3) why systems favour different patterns in social preferences and behavioural plasticity (e.g. conformity versus trait divergence and complementarity).

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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.2015.04.001>.

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