



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



Colin M. Wright^{*}, Carl N. Keiser, Jonathan N. Pruitt

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, U.S.A.

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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 &

^{*} Correspondence: C. M. Wright, Department of Biological Sciences, University of Pittsburgh, 4249 Fifth Avenue, Pittsburgh, PA 15260, U.S.A.

E-mail address: cmw132@pitt.edu (C. M. Wright).

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,

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