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Individual differences in personality and behavioural plasticity facilitate division of labour in social spider colonies

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Among factors hypothesized to favour consistent individual differences in behaviour (i.e. personality or behavioural types), the social environment has received relatively little attention. Within-group variation in personality may facilitate the emergence of division of labour, if individuals with different personalities tend to specialize on different tasks. In turn, functional benefits derived from division of labour may promote the coexistence of alternative behavioural types. We investigated how intracolonial variation in personality influences individual and collective patterns of task performance in the social spider *Anelosimus studiosus*. Colonies composed of a mixture of aggressive and docile females showed greater nonreproductive division of labour than monotypic colonies of either behavioural type. Within mixed-personality colonies, aggressive individuals tended to perform more prey capture, colony defence and/or web repair, while docile individuals became brood care specialists. Task differentiation was shaped by social dynamics, but behavioural plasticity varied with personality type: docile individuals were more socially responsive, shifting their task allocation in the presence of aggressive colonymates. Efficiency gains from personality-linked division of labour may help to explain the superior performance of diverse colonies and to maintain individual behavioural variation in *A. studiosus* and other social species.

While it has long been recognized that individuals vary in traits including behaviour, burgeoning research seeks to explain the causes and consequences of consistent individual differences in behaviour across time and contexts, a phenomenon known as animal personality (Gosling, 2001), behavioural types/syndromes (Sih, Bell, Johnson, & Ziemba, 2004), or temperament (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). A fundamental evolutionary question is how within-population variation in personality is maintained in the face of selection for optimal behavioural phenotypes or high plasticity (Krebs & Davies, 1997; Sih et al., 2004). Theoretical models have proposed a variety of mechanisms for the persistence of alternative behavioural types (Dall, Houston, & McNamara, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2010), but empirical tests are scarce (but see Laskowski & Pruitt, 2014; Nicolaus et al., 2012). An important but understudied factor in the ecology and evolution of individual differences is the social environment, which may influence both the expression and fitness outcomes of behavioural variation and consistency (Bergmüller & Taborsky, 2010; Jandt et al., 2014; Sih & Bell, 2008; Webster & Ward, 2011). In animals ranging from guppies to ants, social groups composed of a mix of personality types (e.g. bold–shy, aggressive–docile) have been shown to outperform relatively homogenous groups, as measured by colony productivity (Modlmeier & Foitzik, 2011; Modlmeier, Liebmann, & Foitzik, 2012) and individual foraging (Dyer, Croft, Morrell, & Krause, 2009) and reproductive success (Pruitt & Riechert, 2011a). A possible benefit of diverse social composition is that group members with different personalities specialize on different roles or tasks, facilitating division of labour at the group level (Fewell, Schmidt, & Taylor, 2009; Michener, 1974). Division of labour is thought to be a key adaptation in social insects, where it has been studied most intensely (Hölldobler & Wilson, 1990; Jeanson & Weidenmüller, 2014; Wilson, 1971), but it occurs in a variety of taxa including other arthropods (Duffy, Morrison, & Macdonald, 2002; Tizo-Pedroso & Del-Claro, 2011) and cooperative vertebrates (Arnold, Owens, & Goldizen, 2005; Bruintjes & Taborsky, 2010; Hurtado, Fénéron, & Gouat, 2013). Here we ask, what is the role of the social environment, particularly a group's personality composition, in structuring division of labour and maintaining individual behavioural variation in a social spider?

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Although sociality is rare in spiders, a phylogenetically diverse array of species live in multifemale colonies with members cooperating in web maintenance, foraging and brood care (Avilés, 1997; Lubin & Bilde, 2007). The temperate-zone spider *Anelosimus studiosus* (Araneae, Theridiidae) is facultatively social, with females occurring either as solitary individuals or in colonies containing up to 40 adults (Riechert & Jones, 2008). Females feed their early-instar offspring during the summer, then die; offspring overwinter as juveniles and mature in spring the following year. Males contribute little to colony function. In addition, *A. studiosus* expresses a heritable behavioural polymorphism whereby females consistently show one of two discrete personality types: aggressive or docile (Pruitt & Riechert, 2009a). Aggressive individuals are more aggressive towards predators, parasites, prey, mates and other females (Pruitt & Riechert, 2009b; Pruitt, Riechert, & Jones, 2008). Natural colonies vary tremendously in the relative proportion of aggressive and docile members (Pruitt & Riechert, 2009a), and this personality composition can have strong effects on colony function and individual fitness. Under certain conditions, individuals in mixed-personality colonies enjoy higher survivorship and reproductive success than those in monotypic colonies of either behavioural type (Pruitt & Ferrari, 2011; Pruitt & Riechert, 2011a). However, the underlying explanation for this advantage remains unresolved. One hypothesis is that docile colony members provide a passive benefit by dampening social conflict and agonistic interactions, which may limit the success of colonies with high proportions of aggressive individuals. Alternatively, co-occurring aggressive and docile colonymates may serve different, but complementary, social roles. Aggressive individuals appear to be predisposed to specialize on prey capture (Pruitt & Riechert, 2011a) and colony defence (Pruitt & Riechert, 2011b), but their overall pattern of task allocation has not been quantified, nor has the behavioural repertoire of docile individuals. By tracking participation by all colony members across a full range of colony maintenance tasks, we can address whether docile individuals contribute disproportionately to other tasks such as brood care, thereby enhancing division of labour and possibly ergonomic efficiency in mixed-personality colonies.

While personality is defined by within-individual behavioural consistency, it does not preclude behavioural plasticity; evidence suggests that individuals with different personality types can vary in their responsiveness to environmental cues, including social cues (Koolhaas et al., 1999; Sih & Bell, 2008). The social insect literature provides a rich theoretical foundation for evaluating how social dynamics influence individual and collective patterns of behaviour. In the context of division of labour, intrinsic variation in individuals' behavioural tendencies may be amplified by feedback between group members and their shared social environment, causing further task differentiation via self-organization (Beshers & Fewell, 2001; Jeanson & Weidenmüller, 2014). Given the large colony sizes, complex nests and long life cycles of many social insects, it is difficult to experimentally test for relationships between individual variation, division of labour and colony performance. The relatively small, short-lived and easily observable colonies of *A. studiosus* present a tractable system for investigating how the social environment impacts individual and collective behaviours and their functional outcomes (Pruitt & Riechert, 2011a). Specifically, in the present study, we sought to determine whether and how individuals with different personalities alter their task allocation as a function of colony composition and what the consequences are for the emergence of division of labour across colony maintenance tasks.

To address the questions outlined above, we established three colony compositions in *A. studiosus*: pure, monotypic colonies of either all aggressive or all docile individuals, and heterogeneous colonies containing an even mixture of aggressive and docile personality types. We then observed task participation across four major tasks (colony defence, prey capture, web repair and brood care) and quantified individual- and colony-level patterns of behavioural organization.

METHODS

Collection and Laboratory Maintenance

Late-instar *A. studiosus* were collected along a river in eastern Tennessee, U.S.A. (35°59′32″N, 84°11′34″W) in March 2011. Multifemale colonies were collected by placing a pillowcase over the colony and trimming off the supporting branches. Spiders were then transported to the laboratory at the University of Pittsburgh, where their colonies were hand-sorted and individuals were housed communally with their colonymates in 1.5-litre plastic cups containing poultry wiring to facilitate web construction. Throughout their time in the laboratory, spiders were kept on an ad libitum diet of size-matched crickets provided once each week. Water was provided by spraying colonies with a mist of tap water.

Interindividual Distance Test

Upon reaching maturity, females were run through interindividual distance trials to assess their behavioural types (docile or aggressive). Two females of unknown tendency were individually marked with fluorescent powder and placed in the centre of a clear plastic container ($13 \times 13.5 \times 2.5$ cm). After 24 h of settling time, we measured the distance between them. All females that showed an interindividual distance greater than zero (i.e. they were not in direct contact) were run through a second confirmatory test with a known docile female (i.e. one that previously showed an interindividual distance score of zero). This test is necessary to distinguish the two types of females, because aggressive females demand space and chase away docile females. Females that showed an interindividual distance of less than 7 cm in the second confirmatory test were categorized as 'docile' and females that showed an interindividual distance of more than 7 cm were categorized as 'aggressive'. Seven centimetres corresponds with a natural break in the distribution of interindividual distance measures between the two phenotypes (Pruitt & Riechert, 2009a). Interindividual distance scores are repeatable over individuals' lifetimes, heritable and highly correlated with other several aggressiveness and boldness measures (Pruitt et al., 2008).

Colony Establishment

In May 2011, after their behavioural types had been determined, each female ($N = 180$, 90 aggressive and 90 docile) was randomly mated with a male taken from a different source colony, and then assigned to an experimental colony with three other females of known behavioural type taken from the same source colony. To avoid statistical issues of nonindependence among experimental colonies, only one experimental colony was created from each source colony ($N = 45$). Colonies were composed of one of three personality compositions: four aggressive females (hereafter referred to as 'pure aggressive'), four docile females ('pure docile'), or two aggressive and two docile females ('mixed'). We established 15 colonies of each composition, but one pure docile colony was excluded from data analysis because an individual died during the experiment. A colony size of four is frequently observed at our collection site, with an average of 5.89 females (Riechert & Jones, 2008). Colonymates were marked individually using fast-drying acrylic paint and placed in a 1.5-litre plastic cup containing a