



Temporarily social spiders do not show personality-based task differentiation



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Task differentiation in cooperative groups can arise through a wide range of mechanisms. A recent hypothesis, supported by empirical studies of social spiders, suggests that a variation in individual personalities might be one such mechanism. Personality-based task differentiation can either arise as an emergent property of group living based on inherent behavioural variation among individuals, or alternatively it could be an adaptation to permanent sociality favoured by individual fitness benefits arising from increased group efficiency and productivity. We tested whether personality-based task differentiation is present in the temporarily social spider *Stegodyphus tentoriicola* which represents the ancestral state from which permanent sociality in spiders has evolved. This species is closely related to the permanently social *Stegodyphus sarasinorum* in which personality-based task differentiation has been documented. We measured individual boldness and investigated individual participation in simulated prey capture events twice per day on 5 consecutive days. We found no evidence for personality-based task differentiation: *S. tentoriicola* spiders did not exhibit consistent personalities in boldness or consistent task differentiation in prey attack. Our results lend support for the hypothesis that personality-based task differentiation is an adaptation to permanently social living in spiders as their ancestral representative lacks this trait.

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Animals that live in groups, irrespective of their degree of cooperation, face the cost of sharing common resources such as feeding or mating opportunities. Competition for resources invariably promotes conflict within the group which threatens stability and reduces benefits of cooperation. These types of conflict can be resolved through task specialization, which in its most extreme form, as seen in eusocial species, can result in reproductive skew, sterile workers, and behavioural and morphological polymorphisms among worker types (Wilson, 1971). Within-group individual differences in task participation, i.e. task differentiation or task specialization, should be associated with improved performance of the associated task resulting in increased group efficiency and productivity (Oster & Wilson, 1978; Wallace, 1982; Wilson, 1975). Whether task specialization evolves as an adaptive trait once permanent groups have formed or arises spontaneously as an emergent property of group formation (Holbrook et al., 2009; Jeanson & Weidenmüller, 2014), for example founded in

differences between individuals in their propensity to adopt certain roles (Reale & Dingemans, 2010), remains poorly understood. Task specialization has been shown to arise spontaneously in forced associations of otherwise solitary organisms. As an example, Jeanson et al. (2008) showed that solitary halictine bees alter their behaviour in experimental nesting associations: previously unspecialized bees are able to instantaneously specialize in either excavation or nest guarding in a forced social context. This and similar studies suggest that task differentiation can emerge in a social context through differences in state (plastic or condition dependent) or behavioural type (i.e. personality) between individuals (Reale & Dingemans, 2010). Such emergent behavioural differentiation may come under strong selection if it benefits individuals in the group during or following the transition to permanent sociality and may underlie the evolution of irreversible division of labour.

Individual behavioural specialization can arise through a variety of mechanisms: environmental and genetic factors can play a role (Schwander, Lo, Beekman, Oldroyd, & Keller, 2010) as can age, sex or body size (Schwander, Rosset, & Chapuisat, 2005; Seeley & Kolmes, 1991), and differentiation can be accompanied by discrete polymorphism (Holldobler & Wilson, 1990; O'Riain,

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Jarvis, Alexander, Buffenstein, & Peeters, 2000). Furthermore, task specialization can occur in species in which group members are morphologically similar and belong to the same age class and sex (Gordon, 1996). An intriguing hypothesis suggests that variation in personalities among group members, i.e. consistent and repeatable interindividual differences in behaviour across time and context (Reale, Reader, Sol, McDougall, & Dingemanse, 2007), can lead to task differentiation (Reale & Dingemanse, 2010). Empirical studies testing this hypothesis are rare, despite the fact that individual personalities have been documented in a large number of both social and nonsocial animals including birds, fish, mammals, insects and spiders (Bell, Hankison, & Laskowski, 2009). One study documented the role of personality (boldness) in task differentiation in the social spider *Stegodyphus sarasinorum*. In this species, colony members differed consistently in their boldness scores and bolder individuals were shown to specialize in prey attack (Grinsted, Pruitt, Settepani, & Bilde, 2013). Similarly, a study by Bergmuller and Taborsky (2007) on the cichlid fish *Neolamprologus pulcher* showed that helpers that invest more time in territory defence are more aggressive and explorative than helpers that spend more time in territory maintenance. Another recent study by Wright, Holbrook, and Pruitt (2014) on the facultatively social spider *Anelosimus studiosus* showed that more aggressive individuals specialized in prey capture, web building and colony defence while more docile individuals specialized in brood care.

Here we asked whether personality-based task differentiation in social species might be founded in pre-existing personality differences in subsocial or temporarily social ancestors. More specifically, we investigated whether personality-based task differentiation occurs in groups of a temporarily social species. This would support the hypothesis that personality-based task differentiation emerges simply by having individuals with inherent behavioural differences in groups. In contrast, if personality-based task differentiation is absent in ancestral temporarily social species, it would suggest that task specialization evolves as an adaptation to group living once permanent sociality has evolved. We performed our study in a subsocial spider that represents the ancestral state to permanent social spiders (Lubin & Bilde, 2007). Subsocial spiders are characterized by an extended communal and cooperative juvenile stage after which spiders disperse to live solitarily as adults. Sociality in spiders has evolved repeatedly from subsocial congeners through loss of premating dispersal and a prolonging of their cooperative stage (Agnarsson, Aviles, Coddington, & Maddison, 2006; Johannesen, Lubin, Smith, Bilde, & Schneider, 2007; Kraus & Kraus, 1988; Kullmann, 1972). We have previously documented personality-based task differentiation in prey attack behaviour in the social spider *S. sarasinorum* (Grinsted et al., 2013). Therefore, in this study, we used the closely related subsocial congener *Stegodyphus tentoriicola* (for a phylogeny of the genus see Settepani, Bechsgaard, & Bilde, 2015) to investigate whether task differentiation based on variation in personalities may have arisen prior to permanent sociality.

We investigated whether *S. tentoriicola* showed repeatable variation in individual personality (boldness) and consistent individual variation in prey attack (i.e. task differentiation), and whether boldness could predict participation in prey attack (i.e. personality-based task differentiation). If personality-based task differentiation is an emergent property of group living we would expect to detect it in a subsocial species that represents the ancestral state of permanent sociality. If personality-based task differentiation is instead an adaptation to permanent social living in spiders that evolved only after or at the transition to sociality we would not expect to find evidence of it in this study of a subsocial species.

METHODS

Study Organism

Stegodyphus tentoriicola is a subsocial spider species of the family Eresidae that occurs in arid and semiarid habitats in South Africa (Kraus & Kraus, 1990; World Spider Catalog, 2014). It is an annual and semelparous species that shows extended maternal care followed by a stage of offspring cooperation prior to their dispersal (Avilés, 1997; Lubin & Bilde, 2007). Males and females live solitarily as adults and during the mating season males wander around in search of a female (Ruch, Heinrich, Bilde, & Schneider, 2009). After mating, females produce a single egg sac from which spiderlings emerge. The mother feeds her offspring via regurgitation of digested fluids for a few weeks after which the young consume their mother's body (known as matrophagy; Lubin & Bilde, 2007). The spiderlings stay in their natal nest where they live communally and cooperate for up to a couple of months before they disperse to build solitary nests. The genus *Stegodyphus* contains three independently evolved social species while the remaining species are subsocial. Social species are characterized by permanent group living and life-long cooperation within their natal nest, lack of premating dispersal and an intranest mating system (Lubin & Bilde, 2007). Both morphological and phylogenetic evidence suggests that social spiders evolved from subsocial congeners (Agnarsson et al., 2006; Johannesen et al., 2007; Kraus & Kraus, 1988; Kullmann, 1972; Settepani et al., 2015).

Experimental Set-up

Eleven colonies (i.e. nests) of *S. tentoriicola* were collected between Kimberley and Colesberg (South Africa) in November 2013. At the time of collection colonies were composed of juveniles in their cooperative, social stage, postmatrophagy and pre-dispersal. Colonies were fed wild-caught termites, *Hodotermes mossambicus*, ad libitum before handling. Colonies were then dissected and individuals counted. Colonies were composed of an average of 82 spiders (range 31–148).

Twenty spiders per colony were randomly selected and their prosoma width and body length measured to the nearest 0.01 mm with a digital calliper. Prosoma width is a reliable measure of body size in spiders as it represents a sclerotized body part that is not affected by satiation state (Hagstrum, 1971). Spiders were marked on their abdomen with a unique colour combination of water-based acrylic paint. Marked individuals were placed in the centre of a petri dish (9 × 1.5 cm, one spider per dish) and left undisturbed for approximately 1 h. Thereafter, each spider ($N = 220$) was tested individually in boldness assays (see below) before construction of experimental colonies (see below). To test for repeatability of boldness scores, boldness was assayed twice with a 20–30 min interval between measurements during which the spiders were left undisturbed. This interval allowed the spiders to settle down and resume their crawling/exploring behaviour. Immediately after the boldness assays, marked spiders from the same source colony were placed together in plastic containers (10 × 10 cm and 6 cm high, 20 spiders per container) with mesh lids and a few twigs for structural support where they were left for 39–65 h to build a web. Thereafter, we performed prey capture participation assays twice per day for 5 consecutive days ($N_{\text{trials}} = 10$). At the end of the 5 experimental days we repeated the two boldness assays and measured prosoma width and body length again. Prosoma width was not expected to differ between the first and second measure, but using an average of two measurements reduces potential measurement error.

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