



## 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 & Dingemanse, 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 & Dingemanse, 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.

One of the 11 experimental colonies experienced significant mortality (eight of 20 spiders had died) and was excluded from further analysis. Hence, for the analyses we used 10 colonies from which a total of 191 spiders had survived (a maximum of two spiders had died from each of these colonies).

The two prosoma width measures were highly correlated (Pearson correlation:  $r_{188} = 0.87$ ,  $t = 24.4$ ,  $P < 0.0001$ ), as were the two body length measures (Pearson correlation:  $r_{188} = 0.93$ ,  $t = 35.1$ ,  $P < 0.0001$ ), and prosoma width and body size were also highly correlated (Pearson correlation:  $r_{189} = 0.88$ ,  $t = 25.3$ ,  $P < 0.0001$ ; first set of measurements). Hence, for all analyses we used the average of the two prosoma width measures as a measure of spider body size.

#### *Individual Boldness Assays*

Boldness was measured with puff tests designed to mimic the approach of an avian predator as described by [Riechert and Hedrick \(1993\)](#) and [Pruitt, Grinsted, and Settepani \(2013\)](#). Each spider was placed in the centre of a petri dish ( $9 \times 1.5$  cm) and left undisturbed for 20–30 min to acclimatize. During this time the spider started behaving normally, crawling around exploring the dish. The lid of the petri dish was then removed and the spider was left undisturbed for another minimum of 2 min in case removal of the lid had caused disturbance. Most spiders continued or resumed crawling/ exploring during this time. Then the spider received two rapid jets of air from an infant's ear-cleaning bulb ([Grinsted et al., 2013](#)). All spiders reacted by huddling and remaining motionless for a period of time. We measured the time (s) that it took the spider to resume movement after receiving the stimulus. Individuals with short latencies were deemed bolder than individuals with longer latencies. Hence, small values indicate high levels of boldness, whereas high values indicate shyness. If a spider did not resume movements within 10 min it was classified as 'no response' and this response (on average 18.2% of spiders in each round of boldness assays) was left out of analyses. Frequency histograms of boldness measures are shown in [Appendix Fig. A1](#). Petri dishes were cleaned with ethanol after each individual boldness test to avoid interference by chemical cues.

#### *Prey Capture Participation Assays*

We investigated individual participation in simulated prey capture events twice per day on 5 consecutive days for a total of 10 trials. Trials were carried out in the mornings (between 0800 and 1100 hours) and in the afternoons (between 1500 and 1800 hours) outdoors in shade. To minimize the effect that variation in hunger state among individual spiders may have on individual behaviours, spiders were fed ad libitum with wild-caught termites half-way through the experiment (after trial 5). We recorded which individuals did not participate in feeding (one to five spiders in each colony did not feed) in order to test whether this had an effect in the following prey capture assays.

Prior to each simulated prey capture event the lids were removed from the boxes and colonies were left undisturbed for a minimum of 20 min (maximum 60 min) as it often took the spiders several minutes to settle down after this disturbance. During this time we checked for moults and deaths. Moulded spiders (zero to four spiders per colony over the course of the experiment) were repainted before each assay and dead ones were removed. When a spider was repainted we waited for the paint to dry and for the spider to settle down before starting the assay. The order in which the colonies were tested was randomized.

We used standardized simulated prey capture assays to record individual participation in prey attack as described by [Grinsted](#)

[et al. \(2013\)](#). To simulate a prey item getting caught in the capture web we created vibrations with a handheld, waterproof vibratory device (Minivibe Bubbles, FunFactory GmbH, Bremen, Germany) with multiple vibration frequency settings. A grass stem was attached to a piece of metal thread (10 cm) attached to the vibrator. This procedure was used to avoid any confounding effects of prey phenotype on spider attack behaviour. The vibrating tip of the stem was put in contact with a centrally placed area of capture web within the plastic container. Vibrations were stopped when the first spider attacked and bit the stem or after a maximum of 10 min if spiders had not attacked within that timeframe (spiders failed to attack in 17 of 100 trials). In each trial we recorded (1) the identity of the first spider to bite the stem (First to Attack) and (2) the identity of the spider(s) that had reacted by moving towards the stimulus by the time of attack (React at Time of Attack; spiders failed to react in six of 100 trials).

Several distinct clusters of individuals often formed at different locations within each container rather than a single cluster containing all individuals. Clusters situated closer to the source of vibrations might have received a stronger stimulus than clusters further away. To account for this, prior to the start of vibrations we recorded which individuals were sitting 'close' (Sitting Close to Stimulus) as opposed to 'not close' to the stimulus and tested whether this influenced participation propensity. Sometimes spiders were scattered all over the container, i.e. most individuals were not sitting in close contact with others, but rather sat alone and all at roughly equal distance to the point of vibration. In these cases it was not possible to identify individuals that were sitting close and these data were not obtained.

#### *Statistics*

All analyses were performed in R, version 3.1.0 ([R Development Core Team, 2011](#)).

#### *Repeatability of boldness*

We calculated the intraclass correlation coefficient (ICC) using the ICC package ([Wolak, Fairbairn, & Paulsen, 2012](#)) and used this as a measure of the repeatability of individual boldness measures. The ICC estimates the proportion of the variation in the data that can be attributed to variation among individuals (as opposed to within-individual variation). If the ICC is high then variation among individuals is high while individual trait values vary very little deeming them repeatable. We calculated the ICC for the two initial boldness measures (before trials), for the two latter measures (after trials), as well as for all four boldness measures together.

#### *Task differentiation*

We investigated task differentiation (i.e. consistent unequal task participation) with a permutation test ([Adams & Anthony, 1996](#); [Manly, 1997](#)) conducted on each separate colony as described by [Grinsted et al. \(2013\)](#). For each spider we calculated the proportion of trials in which the spider had participated in prey attack. Then we took the standard deviation of the proportions per colony and used that as a test statistic. A high standard deviation would indicate high variation among individuals in the proportion of trials in which they participated, and, hence, would suggest task differentiation as opposed to a low standard deviation which would indicate that all spiders participated equally in prey attack. Then we randomized the binary participation of individuals within colonies and within trials to obtain the expected distribution of standard deviations per colony, i.e. keeping the number of participants constant within trials. We ran 1000 permutations and determined the  $P$  value for each colony as the number of permutations revealing a standard deviation at least as large as that of the original data.

**Table 1**

Results from a GLMM of various predictor variables on the response variable First to Attack representing a binary response ( $N = 352$ ) of individual spiders during simulated prey attack events before the feeding event

Predictor variables	<i>df</i>	$\chi$	<i>P</i>
Sitting close	5, 4	9.26	<b>0.002</b>
Prosoma width	6, 5	0	1
Boldness before trials	7, 6	0	1

Significant *P* value is indicated in bold.

**Table 2**

Results from a GLMM of various predictor variables on the response variable React at Time of Attack representing a binary response ( $N = 352$ ) of individual spiders during simulated prey attack events before the feeding event

Predictor variables	<i>df</i>	$\chi$	<i>P</i>
Sitting close	5, 4	32.8	<b>&lt;0.001</b>
Prosoma width	6, 5	0.15	0.70
Boldness before trials	7, 6	0.17	0.68

Significant *P* value is indicated in bold.

Then we used Fisher's omnibus test (Haccou & Meelis, 1994) to combine all *P* values into one. We performed permutation tests on the binary response variables First to Attack (10 colonies, 10 trials), React at Time of Attack (10 colonies, 10 trials) and Sitting Close to Stimulus (five colonies, seven trials; we had to exclude five colonies and three trials because of extensive scattering of spiders within the box; see Methods).

#### Prey capture participation

We used Bayesian linear mixed models to investigate the effect of various predictor variables on the binary response variables First to Attack and React at Time of Attack using the *bglmr* function from the *blme* package (Dorie, 2014). We ran separate models for trials performed before and after feeding, as the feeding event after trial 5 could influence task participation. In the models run on observations before feeding we included the following predictor variables: average prosoma width (mm), average boldness before trials (*s*) and sitting close to the stimulus (binary). In the models run on observations after feeding we included the same predictors, although we replaced average boldness before trials with average boldness after trials and added whether individuals had fed during the feeding event (binary). In all models we included the following random effects: colony ID,

spider ID and trial ID (unique to each colony for each trial). The error structure was set to binomial.

We also constructed a similar binomial model to test whether boldness or body size could predict whether spiders fed during the feeding event after trial 5. The binary Fed was the response variable, and average boldness before and after feeding and average prosoma width were included as main effects. Colony ID was a random effect.

For each model we tested to ensure there were no over-dispersion or collinearity issues and that the full model was significantly different from a null model before proceeding to significance testing of the predictor variables. Significance testing of main effects was done by comparing full models with reduced models in which the variable in question had been removed, using likelihood ratio tests ( $\chi^2$ ). Variables that showed no significant trend ( $P > 0.10$ ) were removed from the full model before testing the remaining effects.

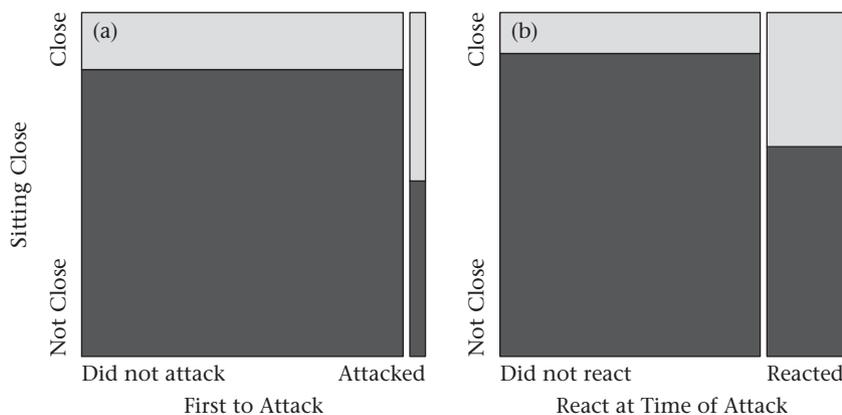
#### Ethical Note

The species used in this study is not subject to ethical laws in the country in which the experiments were performed. Collecting, marking and experimental procedures were performed in November 2013 under licence from the Province of the Northern Cape (FAUNA 1072/2013), Province of the Eastern Cape (CRO 63/12CR, CRO 64/12CR) and the South African Parks (BILDT1008). The experiments were noninvasive and based on behavioural observations. Distress to the animals was minimized as much as possible: spiders used in the experiment were kept in plastic containers under natural conditions and they were provided with water and food ad libitum before, during and after the experiment. After the study the spiders were transported to Aarhus University (Denmark) where they were kept in a climate chamber (25 °C) with a light:dark period of 13:11 h with abundant food.

## RESULTS

#### Repeatability of Boldness

Individual boldness scores showed low to moderate repeatability when boldness assays were performed 20–30 min apart: ICC before trials = 0.28 (lower and upper CI: 0.10–0.44; Fig. A2a), ICC after trials = 0.37 (lower and upper CI: 0.23–0.50; Fig. A2b). This means that 28–37% of the variation in boldness scores could be attributed to variation among individuals. However, boldness



**Figure 1.** The effect of sitting close to the vibration stimulus on whether spiders (a) attacked and (b) reacted to it. The binary 'Sitting Close' (light grey) versus 'Not Close' (dark grey) is plotted against binary measures of prey attack participation: (a) First to Attack and (b) React at Time of Attack. Graphs depict pooled repeated measures of individual spiders during 10 trials across 5 days and hence do not directly reflect the results of the statistical analyses.

**Table 3**

Results from a GLMM of various predictor variables on the response variable First to Attack representing a binary response ( $N = 537$ ) of individual spiders during simulated prey attack events after the feeding event

Predictor variables	df	$\chi$	<i>P</i>
Sitting close	8, 7	6.64	<b>0.010</b>
Prosoma width	8, 7	2.87	0.090
Boldness after trials	8, 7	6.48	<b>0.011</b>
Having fed	8, 7	2.84	0.092

Significant *P* values are indicated in bold.

**Table 4**

Results from a GLMM of various predictor variables on the response variable React at Time of Attack representing a binary response ( $N = 537$ ) of individual spiders during simulated prey attack events after the feeding event

Predictor variables	df	$\chi$	<i>P</i>
Sitting close	7, 6	44.4	<b>&lt;0.001</b>
Prosoma width	8, 7	2.58	0.11
Boldness after trials	7, 6	6.40	<b>0.011</b>
Having fed	7, 6	5.21	<b>0.022</b>

Significant *P* values are indicated in bold.

measures across time and context (four assays conducted across approximately 7 days that included feeding and prey capture assays) showed no repeatability: ICC = 0.086 (lower and upper CI: 0.0009–0.19; Fig. A2c).

*Task Differentiation*

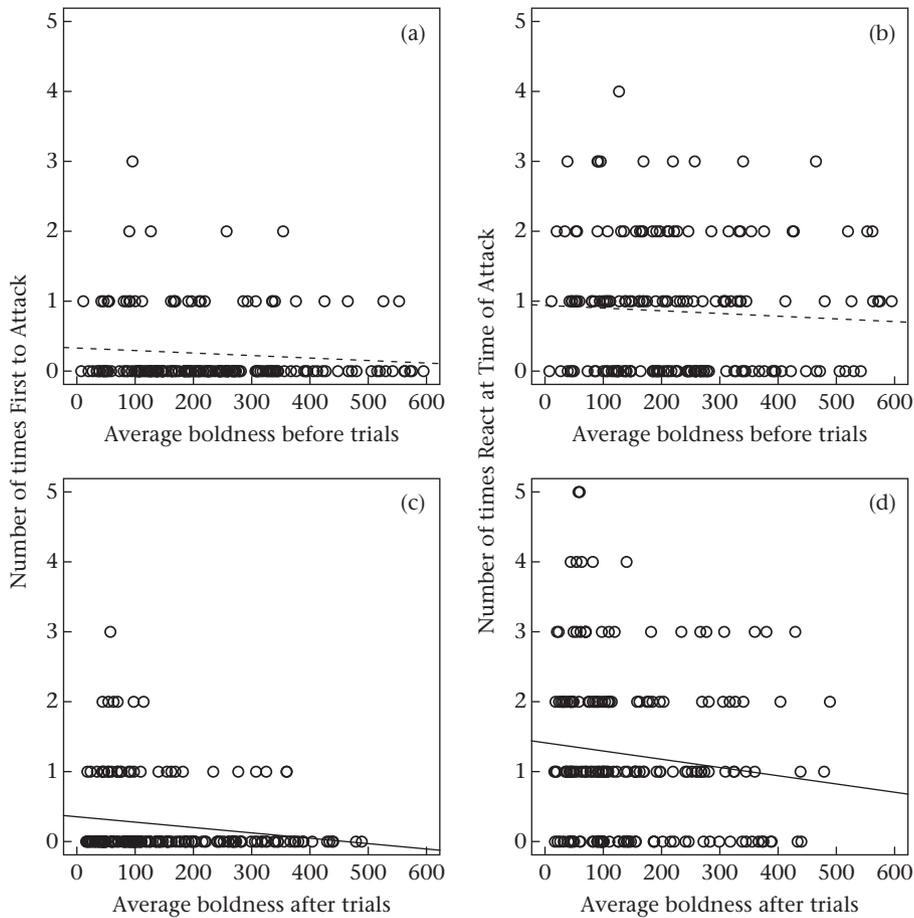
We found significant differences between individuals both in First to Attack (combined *P* value = 0.017) and in React at Time of Attack (combined *P* value < 0.001) as well as in Sitting Close to Stimulus (combined *P* value = 0.025).

*Predictors of Prey Capture Participation*

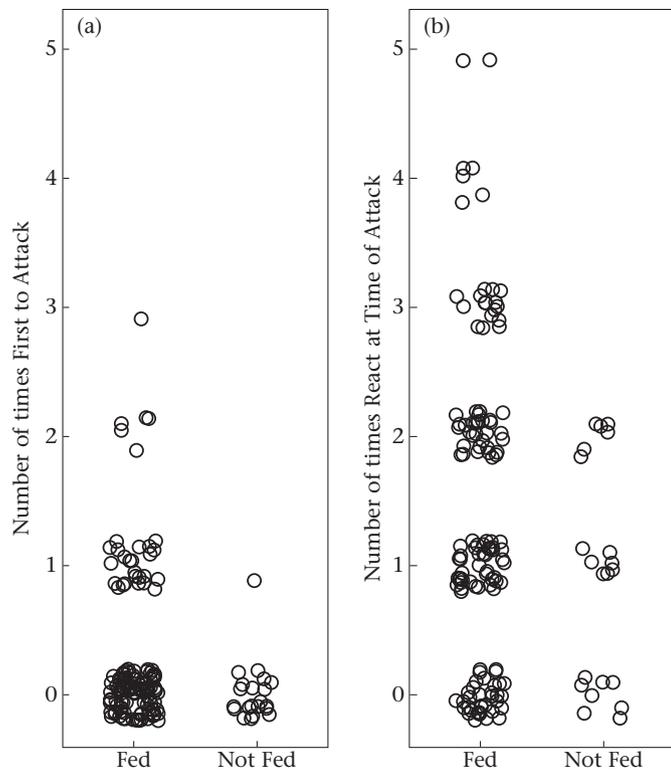
Before the feeding event the only significant predictor for First to Attack or React at Time of Attack was whether spiders were sitting close to the stimulus (Tables 1 and 2), with spiders being more likely to participate in prey capture if they sat close (Fig. 1). Neither prosoma width nor boldness before trials had an effect on either of these behavioural responses before feeding (Tables 1 and 2).

After the feeding event, sitting close to the stimulus was still a highly significant predictor of both First to Attack and React at Time of Attack; however, boldness after trials now also had a significant effect on both responses (Tables 3 and 4), with bolder spiders (with shorter latencies to resume movement) being more likely to participate in prey capture (Fig. 2). Furthermore, spiders that had fed were more likely to react to the stimulus (Table 4, Fig. 3) but feeding did not predict First to Attack (Table 3, Fig. 3).

Neither boldness nor body size could predict whether spiders fed during the feeding event (full model including average boldness



**Figure 2.** The number of times individual spiders (a, c) were the first to attack or (b, d) had reacted at the time of the attack during five prey attack events either (a, b) before or (c, d) after feeding plotted against individual boldness scores. Boldness scores in (a) and (b) are averages of the first and second boldness assays while scores in (c) and (d) are averages of the third and fourth boldness assays. Lines show a simple linear regression and do not directly reflect the results from the statistical analyses which were performed on binomial data. Full lines indicate a statistically significant association whereas dotted lines indicate a nonsignificant association.



**Figure 3.** The number of times individual spiders (a) were the first to attack or (b) had reacted at the time of the attack during the five trials after feeding plotted against whether individuals had fed or not fed during the feeding event.

before, average boldness after and average prosoma width:  $\chi^2_{2, 2} = 3.99, P = 0.26$ ).

## DISCUSSION

We found that subsocial *S. tentoriicola* spiders in their juvenile, cooperative stage did not exhibit consistent personalities in boldness measures. That is, a trait that has been found to be repeatable over time in permanently social congeneric spiders (Pruitt et al. 2013) was not repeatable in this temporarily social species. Therefore, we propose that boldness in this species is shaped by a spider's inconsistent physiological state, e.g. its feeding state, and does not represent a consistent personality trait. Furthermore, although we did find significant differences between individuals in their propensity to participate in prey attack, these differences could be explained mainly by their spatial position in the nest and their physiological state, factors that are inherently not consistent among individuals. Spiders that were sitting close to the simulated prey were more likely to attack, as were spiders that had fed and were in a physiological state that resulted in a more bold behavioural type at the end of experiments. Hence, we found no evidence of consistent personality-based task differentiation in *S. tentoriicola*, because the only significant predictors of task participation that we identified were all inconsistent factors. The observed differences in propensity to participate in prey attack suggests that if task differentiation does exist, it is either not personality driven or is shaped by personality traits other than boldness.

Our results are in contrast to empirical data from several permanently social spider species. Task differentiation in the social spider *S. sarasinorum* was found to be shaped by personality: boldness scores were repeatable over several days and

bold individuals specialized in prey attack (Grinsted et al., 2013; Pruitt et al., 2013). Colonies of *S. sarasinorum* were mostly composed of juveniles and subadults and no effect of developmental stage was found on personality or prey attack participation in this species (Grinsted et al., 2013; Pruitt et al., 2013). Additionally, individual differences in boldness scores are consistent across developmental stages and time (from juveniles to adults) in the social *Stegodyphus dumicola* (Klauge, 2014). Also in the facultatively social spider *A. studiosus* personality measures are heritable and consistent over time and aggressive and docile individuals perform different tasks (Wright et al., 2014). The lack of both consistent task differentiation in prey attack and consistent individual personalities in a subsocial spider provide support for the hypothesis that personality-based task differentiation has evolved as an adaptation to permanent social living. Social spiders evolved from subsocial congeners, so the absence of a trait in a subsocial spider could indicate that this trait evolved either at or after the transition to permanent sociality in spiders (Lubin & Bilde, 2007). Personality-based task differentiation might therefore be an adaptation to a permanent social lifestyle selected through individual fitness benefits associated with task efficiency through specialization (Wilson, 1975, 1987; Wright et al., 2014) although thorough studies are now needed to confirm this. We did not find support for the hypothesis that personality-based task differentiation is simply a nonselected emergent property of group living in spiders.

It is interesting in itself that we did not detect consistent interindividual personality in *S. tentoriicola* as personalities have been documented in a wealth of both social and nonsocial vertebrates and invertebrates (Bell et al., 2009). While boldness was moderately repeatable when measured twice within 30 min, we did not detect consistency in boldness measures over the course of the experimental period (across 7 days). We cannot exclude the presence of other personality traits that may vary consistently among individuals in this species. However, this may be unlikely, as boldness in spiders is often part of a behavioural syndrome when documented: boldness usually correlates with other personality traits such as aggressiveness, prey consumption or sexual cannibalism (e.g. solitary fishing spiders, *Dolomedes triton*: Johnson & Sih, 2007; solitary American grass spiders, *Agelenopsis aperta*: Riechert & Hedrick, 1993; social velvet spiders: Klauge, 2014; Pruitt et al., 2013; social tangle web spiders: Pruitt, Iturralde, Avilés, & Riechert, 2011). Whether the lack of consistent personalities is a result of selection for behavioural plasticity or insufficient selection for consistency in *S. tentoriicola* may be an intriguing focus for future studies.

Contest competition for limited resources during the cooperative stage may occur in *S. tentoriicola* groups and so it might be beneficial for an individual to attack a prey first. First feeders might have the advantages of choosing a feeding spot on the prey that maximizes prey extraction (Ward & Enders, 1985) and a longer feeding time than other individuals in the group. It has previously been shown that first feeders in social spider groups are the only individuals whose feeding is not shortened by conspecifics (Willey & Jackson, 1993).

The reason why individuals showed significant variation in propensity to engage in prey attack was probably because some clusters of spiders were consistently positioned closer to the vibration stimulus than others, resulting in the same spiders repeatedly feeling the vibration more strongly than others and reacting faster. When we applied the vibration stimulus of the simulated prey we were limited to positioning it in a spot where the silk was strong and from where silk was connected with all spider clusters in the box. Random factors and positive feedback can also play a role in determining first feeders. Individuals in a nest might

differ in physiological state or in exposure to random environmental effects at different life stages such as food intake or microhabitat. Individual experience resulting in positive feedback might result in a higher propensity of certain individuals to attack consecutively. This is supported by our result that spiders that fed successfully had a higher propensity to attack in the following trials. Experience has previously been shown to influence the decision of an individual to execute a task. Ravary, Lecoutey, Kaminski, Chaline, and Jaisson (2007) showed that when workers of the ant *Cerapachys biroi* were exposed to successful feeding experiences they showed a higher propensity for food exploration than workers that failed to feed.

Our results suggest that the temporarily social *S. tentoriicola* in its cooperative stage does not show consistent personalities or consistent task differentiation in prey attack behaviour. These results cannot directly address the selective advantage of task differentiation in social spiders; however, they do provide support for the hypothesis that personality-based task differentiation documented in social spiders is an adaptation to permanently social living.

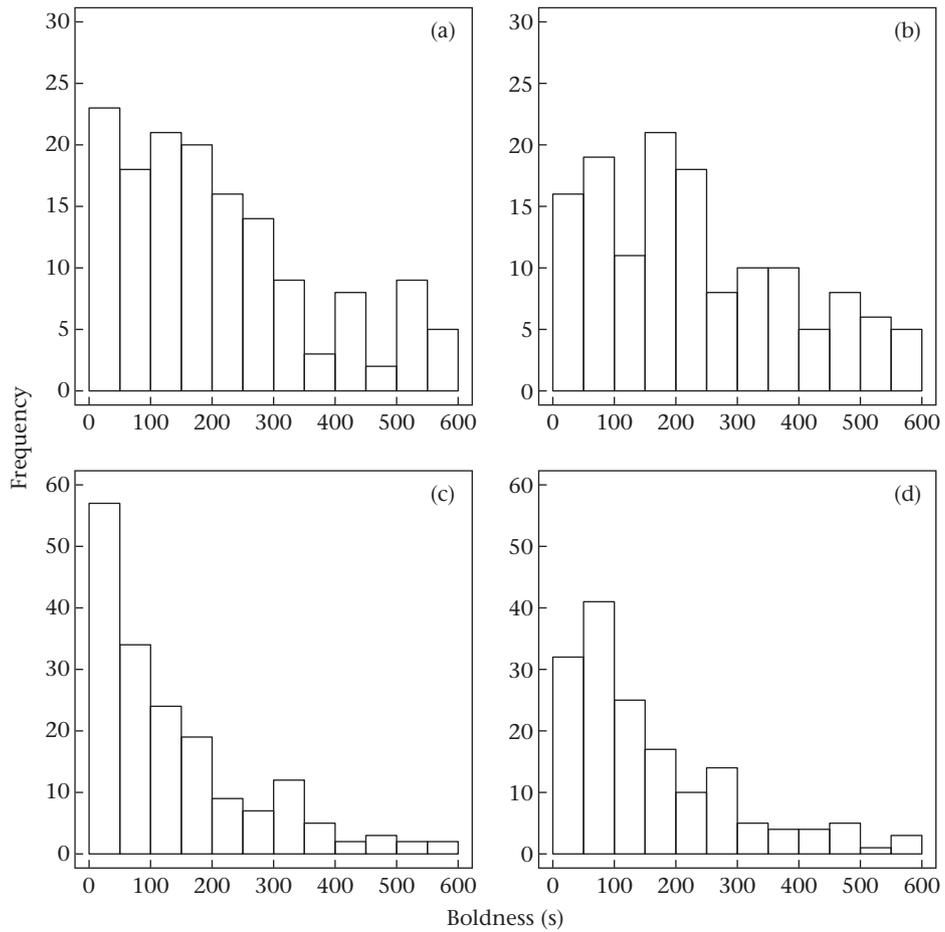
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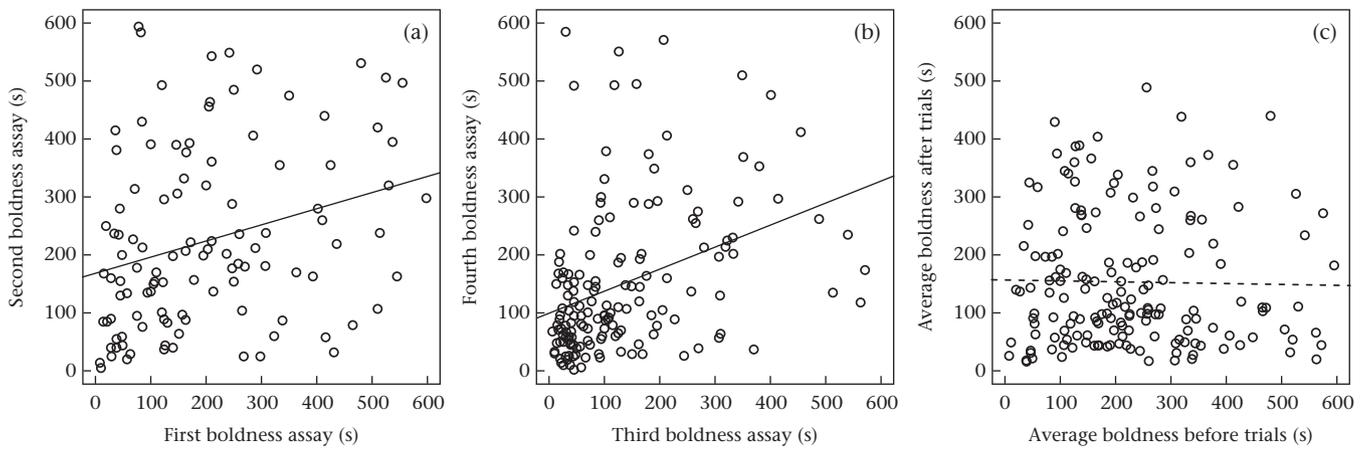
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Appendix



**Figure A1.** Histograms depicting the observed frequency of boldness measures in each of the four boldness assays (boldness assays were performed twice before and twice after the prey capture participation trials): (a) first assay (before trials); (b) second assay (before trials); (c) third assay (after trials); (d) fourth assay (after trials). Boldness was measured as the latency to resume movement after a disturbance. Hence, short latencies correspond to high levels of boldness.



**Figure A2.** Correlations between boldness measures from different boldness assays. (a) Assays before prey capture participation trials, (b) assays after the trials and (c) average boldness before and after trials.