Research

CrossMark
click for updates

Author for correspondence:
Lena Grinsted
e-mail: lena.grinsted@biology.au.dk

Royal Society **Publishing**
Informing the science of the future

Individual personalities shape task differentiation in a social spider

Lena Grinsted[1], Jonathan N. Pruitt[2], Virginia Settepani[1] and Trine Bilde[1]

[1]Department of Bioscience, Aarhus University, Ny Munkegade 116, Building 1540, 8000 Aarhus C, Denmark
[2]Department of Biological Sciences, University of Pittsburgh, 213 Clapp Hall, 4249 Fifth Avenue, Pittsburgh, PA 15260, USA

Deciphering the mechanisms involved in shaping social structure is key to a deeper understanding of the evolutionary processes leading to sociality. Individual specialization within groups can increase colony efficiency and consequently productivity. Here, we test the hypothesis that within-group variation in individual personalities (i.e. boldness and aggression) can shape task differentiation. The social spider *Stegodyphus sarasinorum* (Eresidae) showed task differentiation (significant unequal participation) in simulated prey capture events across 10-day behavioural assays in the field, independent of developmental stage (level of maturation), eliminating age polyethism. Participation in prey capture was positively associated with level of boldness but not with aggression. Body size positively correlated with being the first spider to emerge from the colony as a response to prey capture but not with being the first to attack, and dispersal distance from experimental colonies correlated with attacking but not with emerging. This suggests that different behavioural responses to prey capture result from a complex set of individual characteristics. Boldness and aggression correlated positively, but neither was associated with body size, developmental stage or dispersal distance. Hence, we show that personalities shape task differentiation in a social spider independent of age and maturation. Our results suggest that personality measures obtained in solitary, standardized laboratory settings can be reliable predictors of behaviour in a social context in the field. Given the wealth of organisms that show consistent individual behavioural differences, animal personality could play a role in social organization in a diversity of animals.

1. Introduction

Task differentiation is considered to be a major cause for the ecological success of social insects [1,2]. As individual colony members specialize on specific tasks necessary for colony survival, such as egg laying, foraging or nursing, colony-level efficiency and productivity are expected to increase [3]. Task specialization among workers is accompanied by morphological polymorphism in some species, but is more commonly expressed as differences in individual predispositions or propensities to perform certain tasks among morphologically similar individuals [4]. While allocation into reproductive versus worker caste is typically permanent in eusocial insects, and can result from environmental factors, genotype or a mix of both [5], individuals within worker castes rarely specialize permanently on a single task [4]. In species with age polyethism, individual workers switch tasks according to age. Task differentiation is achieved in these species, because workers of different ages are present in the colony concurrently [6]. In social animals where all group members are of approximately equal age, task differentiation might not result from age polyethism. This is the case in social spiders of the genus *Stegodyphus*, where all group members are of the same age cohort, although some variation in body size and developmental stage within colonies can still be found [7].

An interesting possibility is that task differentiation may emerge as a result of stable variations in individual personalities within colonies [8–10]. Behavioural type, or personality, is defined as behavioural differences among individuals that are consistent across time and context [11,12]. For example, an individual

can be more or less bold, or more or less aggressive, and although age, context and state may influence its specific behavioural trait value, the difference between one individual and another will generally be maintained. Repeatable individual behavioural types have been documented in a wealth of both vertebrate and invertebrate organisms (including birds, fish, mammals, insects and spiders) [13]. Hence, animal personality has the potential to play an organizing role in the social structures of an impressive diversity of group-living animals. Consistent individual behavioural differences might provide a general mechanism by which task differentiation is achieved in societies that lack strict functional or morphological castes.

Individual behavioural types can have heritable components, or be partly or purely shaped by extrinsic factors (e.g. social interactions or nutrition), and, importantly, have proved to be adaptive on both the individual and group level [14–16]. For example, colonies of the ant *Temnothorax longispinosus* were more productive in both the laboratory and in the field when they consisted of individuals with a higher variation in behavioural types [17,18]. Similarly, compared with behaviourally homogeneous groups, mixed-personality groups of the facultative social spider *Anelosimus studiosus* enjoyed higher reproductive success [19], and behaviourally polymorphic groups of several permanently social *Anelosimus* species showed higher prey capture and feeding efficiency [20]. One possibility is that variation in personality increases colony fitness in these species because it leads to task differentiation that enhances colony-level efficiency. Consistent with this hypothesis, a number of laboratory studies on social spiders of the genus *Anelosimus* suggest that variation in personalities has the potential to structure task participation (e.g. prey capture [19]; colony defence [21]). However, these studies have the limitation that they were performed under highly controlled laboratory conditions and with uncharacteristically small group sizes: two to six spiders in species that can exhibit group sizes in the thousands.

In this study, we tested the hypothesis that individuals' behavioural types predispose them to take on certain functions within their group, resulting in task differentiation (i.e. significant unequal participation in a certain task). Most importantly, we tested for this association in field settings using colony sizes that resemble those commonly found in nature. In doing so, our study builds upon the proof of concept studies performed on social *Anelosimus* spiders [19,21] and various social insects [22,23]. Our model, *Stegodyphus sarasinorum*, is characterized by a lack of distinct castes and no overlapping generations. Group members are highly related and approximately of the same age, and recent studies have documented consistent, repeatable behavioural types [24] and a tendency for task differentiation in prey capture [25].

A common problem with studies on personalities of group-living animals, in particular, is that obtaining comparable and repeatable behavioural trait values requires standardized laboratory tests that remove variation in social context [15]. Hence, behavioural types are usually assessed under conditions where the animals' natural social surroundings have been eliminated, and hence may not directly reflect the behavioural decisions of animals in their natural social context. In our study, we carefully investigated the association between behavioural types assayed in the laboratory, outside of a natural social context, and individual performance in natural group settings in the field.

We tested for a link between personalities and task differentiation within colonies of the social spider *S. sarasinorum*. Specifically, we tested the following hypotheses:

— variation in individual personality trait values can predict task differentiation in prey capture, defined as consistently unequal participation in prey attack during simulated prey capture events;

— body size or developmental stage does not predict task participation or personality trait values; and

— standardized personality assays, devoid of social context, can be used as predictors of individual behaviours in natural group settings in the field.

2. Methods

(a) Study organism

Stegodyphus sarasinorum Karsh (Eresidae) is one of three permanently social species in its genus, and is found in India and some adjacent countries [26,27]. Social *Stegodyphus* spiders are well suited for the study of behavioural adaptations associated with the transition to permanent sociality in spiders, as all three species are independently derived from subsocial congeners, and the remaining species within the genus all exhibit subsocial behaviour (i.e. cooperation among spiderlings in the maternal nest prior to dispersal) [28,29]. *Stegodyphus* spiders inhabit dry, shrubby, open bush land in seasonal habitats [30]. Females perform extended and suicidal maternal care by regurgitation of food and later by letting the spiderlings feed directly on their body. In social *Stegodyphus* species, less than half of the females reproduce [31], although all females (reproducers and helpers) provide suicidal allomaternal care to the colony offspring [32,33]. Social spiders lack a pre-mating dispersal stage and reproduce with their colony members. Hence, colonies can persist for several generations and colony members are highly inbred [28]. As their life cycles are seasonal and annual, colony members are of approximately the same age and developmental stage at any time of the year [34,35]. Females cooperate in all colony tasks. For example, prey capture and web maintenance involve extending their maternal nest (a dense, silken structure built primarily around branches of spiny bushes) and building and repairing their capture web (two-dimensional structures extending from one or many sides of the nest, attached to surrounding vegetation). Spiders usually hide inside their nests, except during web maintenance and prey capture. Web maintenance is performed during dusk and dawn [27], and prey capture and feeding occurs at any time of the day or night when prey gets caught in the capture web. When a prey item lands in the capture web, a few spiders emerge from the nest, attack the prey and drag it back to the nest, where they will share the prey with many other colony members.

(b) Construction of experimental colonies

Sixteen colonies of *S. sarasinorum* were collected near Kuppam, Andhra Pradesh, southern India (78°15′24″ E, 12°49′35″ N) in January 2012. Larger colonies were preferentially collected to ensure large group sizes. Each colony was dissected, and spiders were counted. Colony sizes ranged from 51 to 277 spiders, and most colonies consisted of juveniles and subadults (one moult from the adult stage). Two colonies contained only juveniles, six contained only subadults, five had a mix of juveniles and subadults, whereas three consisted of a mix between juvenile, subadult and adult spiders.

Forty spiders from each colony were randomly chosen and each individual had its abdomen marked with a unique three-colour code of water-based acrylic paint. Adult males of *S. sarasinorum* rarely participate in prey capture and were therefore preferentially

avoided, although males of *Stegodyphus* spiders can only be recognized visually when subadult and adult. Colour-coded colony members were placed together in plastic containers ($10 \times 10 \times 6$ cm) with perforated lids and provided a few twigs for structural support in web building. The following day, each spider was tested individually in boldness and aggression assays (see below). Afterwards, spiders were returned to their container with their colony members and left overnight for constructing a nest. The following day (day 0 of the experiment; D_0), colonies were placed in the field in preparation for prey capture participation assays (see below). All data recorded have been made available online on Dryad at http://dx.doi.org/10.5061/dryad.nd779.

(c) Individual behavioural assays

We assessed two different behavioural traits of all spiders used in the experimental colonies prior to the prey capture participation assays: (i) boldness and (ii) aggression. Both traits represent repeatable personality traits in *S. sarasinorum* [24]. Spiders were housed individually in 59 ml plastic cups for 2–4 h prior to testing and allowed a minimum of 2 h between behavioural assays.

(i) Boldness: response to puff of air

Boldness was assessed with puff tests designed to mimic the approach of an avian predator according to Riechert & Hedrick [36]. A spider was placed in the centre of a square plastic enclosure ($13.5 \times 13 \times 3.5$ cm) and given approximately 60 s to acclimatize before receiving two rapid jets of air from an infant ear-cleaning bulb. Spiders reacted to air puffs by huddling and remained motionless for a period of time. We measured the time, in seconds, that it took the spider to resume movement after receiving the stimulus. Individuals with short latencies were deemed more 'bold' than individuals with longer latencies, as resuming movement quickly after perceiving a threat can be interpreted as a bold behaviour. Boldness was therefore measured in seconds, and *low* values indicate *high* levels of boldness, whereas *high* values indicate shyness.

(ii) Aggression: response to prod stimulus

Aggression levels were assessed with prod tests designed to mimic the approach of an unknown arthropod according to Riechert & Johns [37]. A spider was placed in the centre of a square plastic enclosure and given approximately 60 s to acclimatize before receiving a gentle prod stimulus with the blunt, wooden end of a dissecting teasing needle (DR Instruments). We recorded and ranked the spider's response as follows: (0) huddle: the spider pulled its legs against its body; (1) run: the spider ran away from the stimulus; (2) walk: the spider walked away; (3) lurch: the spider shifted forward but did not initiate locomotion; (4) no response: the spider did not exhibit any movement; and (5) raise: the spider lifted one or more of its anterior legs (a threatening posture). Higher values indicate higher levels of aggression. The ranking of these behaviours was adopted from work by Riechert and co-workers [37,38], and modified to suit the responses recorded from *S. sarasinorum*. Response (4) ('no response') is not a flight response (such as walking, turning or running), and not an escalatory display behaviour (such as raised legs). Thus, it lies intermediate along the axis of fearful versus aggressive behaviour. To explore whether the ranking of 'no response' as the second highest level of aggression had a disproportionately large influence on our findings, we re-ran the analyses with all 'no response' individuals removed.

(d) Prey capture participation assays
(i) Preparation

On D_0, each experimental colony was placed outdoors in their original habitat in the afternoon before dusk. After removing the lid, each plastic container with its nest of 40 spiders inside was attached carefully to a branch of a bush with a plastic clothes peg. The same type of thorny bushes on which *S. sarasinorum* frequently nests in this area were chosen. Spiders hid motionless within their nests in the boxes during the attachment. On the following day (D_1) colonies had built small capture webs extending from their nests in the boxes, and some individuals had dispersed. If a large group of dispersers (about half of the colony members) had settled as a group together on nearby vegetation, the original colony was considered as split and from D_1 treated as two separate colonies. Budding by subgroups dispersing together is a common way of forming new colonies in social spiders, and the hypothesis that the composition of personalities in a group can predict task differentiation within this group could still be tested within each of the physically separated subgroups. Two colonies split in this way, and hence we had a total of 18 experimental colonies. When only a few individuals had dispersed, as for the remaining colonies, dispersers were returned to their original nest. On each day of the experiment, the bushes surrounding each colony were carefully inspected, and dispersers were returned to their nests at least 15 min prior to the start of the behavioural assays. We measured the straight-line dispersal distance to the nearest centimetre for each dispersing spider, as dispersal behaviour could be associated with personality or participation in prey capture. On average, 10.1 spiders per colony dispersed and were returned to their colony over the course of the 10 days, and less than 1 (0.63 spiders) of these dispersed twice. The two dispersal distances of the spiders that dispersed twice were added for use in statistical analyses. We investigated individual participation in simulated prey capture events once per day on 10 consecutive days, D_1–D_{10} (10 trials performed in total per colony). Previous studies suggest that individual propensity to engage in prey attack is independent of hunger state [25]. However, in order to minimize a potential subtle effect of a constant variation in hunger state among group members through the 10 days, all colonies were fed two grasshoppers (medium-sized according to available prey items in the field) on D_5, after assaying the colonies. This amount of food was estimated to satiate all colony members, minimizing variation in hunger state among individuals. To examine whether feeding the spiders affected their participation in prey attack, we compared individuals' participation through D_0–D_5 with participation through D_6–D_{10} (see electronic supplementary material for more detail).

(ii) Procedure

We used standardized simulated prey capture events to record individual participation in prey attack. By simulating and standardizing the prey capture events, we made each event directly comparable and eliminated the variance that is inevitable when using live prey (e.g. variance in prey size and prey movement in the web). In order to simulate a prey item getting caught in the capture web, a piece of dry leaf (approx. 2 cm^2) was placed and vibrated in the capture web. To create vibrations, we used a handheld, waterproof vibratory device (FunFactory, Minivibe Bubbles) with multiple vibration frequency settings (see electronic supplementary material, figure S1). A piece of metal thread (10 cm) was attached to the vibrator, and the tip of the metal thread was touching the leaf. Vibrations were ceased when the first spider attacked and bit the leaf (see electronic supplementary material, figure S1) or after a maximum of 10 min. We recorded (i) the identity of the first spider to emerge from the nest as a reaction to the simulated prey capture (first spider to emerge); (ii) the identity of the first spider to bite the leaf (first spider to attack); and (iii) all spiders that were outside of the nest at the time of attack, including the one that had attacked (out at time of attack). Occasionally, two spiders simultaneously attacked and both were then considered as *first to attack*. The total number of spiders out at time of attack varied from 1 to 10, with

a mean of 2.3 spiders. Each colony was tested once per day on $D_1–D_{10}$, in the afternoon before dusk.

(iii) Final handling of colonies

After the last assay had been performed on D_{10}, the colonies were collected and dissected. On average, 35 of the original 40 spiders were recovered alive, of which an average of 28 had retained their individual colour codes. Only individuals that were alive upon collection, or had been observed in the colony up until D_9 and had retained their colour ID (not moulted), were used in statistical analyses. We obtained measures of body size and developmental stage to test for their influence on behavioural type and prey capture participation. Prosoma (head) width was measured to the nearest 0.01 mm with digital callipers. Prosoma width is generally recognized as a reliable measure of body size in spiders as it represents a sclerotized body part that is not affected by satiation state [39,40]. Reproductive organs (epigynes and pedipalps) were examined using a stereo microscope, and spiders were categorized as one of three developmental stages that were coded on an ordinal scale (1–3) for statistical analyses: juvenile (1), subadult (2) or adult (3).

(e) Statistics
(i) Task differentiation

We tested for unequal task participation using a permutation test [41,42] conducted separately per colony by randomizing the participation in prey attacks among individuals within attack events (see electronic supplementary material for more detail). As a test statistic, we used the standard deviation of the proportions of days where individual spiders had participated in a simulated prey capture event. We ran a total of 1000 permutations and determined the p-value per colony as the number of permutations revealing a standard deviation at least as large as that of the original data (see electronic supplementary material for more detail). We finally used Fisher's omnibus test [43] to combine the 18 p-values into one. Permutation tests were performed on each of three different binary response variables: (i) first to emerge, (ii) first to attack and (iii) out at time of attack.

(ii) Determinants of participation in prey attack

We used linear mixed models to investigate the effect of behavioural traits and body size on individuals' propensity to engage in simulated prey capture events, using the lmer function from the lme4 package [44] in R [45]. We constructed three different models, one for each of the three response variables: (i) first to emerge, (ii) first to attack and (iii) out at time of attack. In each model, we used the following predictors: (i) boldness, (ii) aggression, (iii) prosoma width and (iv) dispersal distance. We used colony ID, spider ID and day as random factors, and implemented an offset term with the log of colony size (see electronic supplementary material for more detail on model construction, check of assumptions and significance testing). As prosoma width and developmental stage were highly correlated (Pearson's $r = 0.71$), additional similar models were constructed where prosoma width was excluded and developmental stage included as a predictor, as well as any predictors that showed a significant association with the response variable in the original models (see electronic supplementary material for more detail).

Only one spider (of 412 recovered after 10 days) had an aggression score of 2 (i.e. walking as a response to prodding). As this spider could represent an influential case with disproportionate effect on the model outcomes, it was left out of the analyses. Hence, sample size was 411 spiders from 18 colonies each. Supplementary analyses were performed where the one spider with an aggression score of 2 was included to test whether excluding it significantly changed our findings (see electronic supplementary material for more detail).

(iii) Determinants of personality

We tested whether each of the two personality measures (i) boldness and (ii) aggression was associated with prosoma width and dispersal distance. In each of the two models, the other personality measure was also included as a predictor, and colony ID as a random effect. Boldness, as a response variable, was log-transformed. Additional tests were performed where prosoma width was excluded and developmental stage, as well as any significant predictors from the main models, were included. The MCMCglmm function from the MCMCGLMM package [46] with a specified ordinal error structure was used in models where aggression was the response variable, as aggression was measured at an ordinal scale (see electronic supplementary material for more detail).

3. Results
(a) Task differentiation

Spiders showed unequal participation in simulated prey capture events (table 1). Unequal participation in being the first spider to attack was significant (combined p-value $= 0.022$) and in being out at the time of attack was highly significant (combined p-value < 0.001). However, participation was not unequal in being the first to emerge from the nest (table 1). Individual participation was not affected by feeding on D_5 (i.e. individuals participated to similar extends during $D_1–D_5$ as they did during $D_6–D_{10}$; see electronic supplementary material, figure S2).

The average colony size was 31.4 spiders upon collection on D_{10} and on average 18.9 spiders had been out at time of attack through the 10 trials in each colony. Hence, each spider had a probability of participating of less than one $(18.9/31.4 = 0.60)$. However, a total of 71 of 450 spiders were out at the time of attack more than once across the 10 trials (see electronic supplementary material, figure S3) and thereby contributed to significant unequal task participation.

(b) Determinants of participation in prey attack

All three measures of participation in simulated prey capture events were significantly associated with boldness (figure 1) but not with aggression or developmental stage. Bolder individuals (i.e. with short latencies to resume movement) were significantly more likely to emerge from the nest, to attack as the first spider and to be out at the time of attack (all three tests: $\chi^2 > 8$, $p < 0.01$; table 1). Larger spiders were also more likely to emerge as the first spider and to be out at the time of attack (both tests: $\chi^2 > 3$, $p < 0.05$; figure 1), whereas body size had no effect on being the first to attack $(\chi^2 = 1.56, p = 0.21;$ table 1).

Supplementary analyses revealed no difference in these findings whether or not the individual with an aggression score of (2), walking, was included, and whether or not aggression score (4), no response, was included (see electronic supplementary material, table S1 for details).

(c) Determinants of personality

Bolder individuals were generally more aggressive, and vice versa, independent of body size and developmental stage,

Table 1. Results from simulated prey capture events in the field repeated 10 times in each of 18 spider colonies for the three binary response variables. The unequal participation row shows the combined p-values from simulation tests within each colony, testing whether individual spiders participate unequally in prey capture reflecting task differentiation. The bottom five rows show the test values obtained from GLMMs describing the effect of five predictor variables on each of the three response variables. Significant p-values are shown in italics.

	first spider to emerge			first spider to attack			out at time of attack		
unequal participation	combined p-value		0.25	combined p-value		0.022	combined p-value		*< 0.001*
test values	χ^2	**d.f.**	p	χ^2	**d.f.**	p	χ^2	**d.f.**	p
boldness	8.85	6,5	*0.0029*	11.2	6,5	*0.00082*	16.2	7,6	*<0.0001*
aggression	0.13	8,7	0.72	0.21	8,7	0.65	0.03	8,7	0.86
dispersal distance	3.48	7,6	0.062	16.1	6,5	*<0.0001*	10.8	7,6	*0.0010*
prosoma width	3.90	6,5	*0.048*	1.56	7,6	0.21	5.20	7,6	*0.023*
developmental stage[a]	0.0011	6,5	0.97	0.055	7,6	0.81	0.32	7,6	0.57

[a]Additional tests: these models do not include prosoma width as a predictor and only include the predictors that were significant in the main models.
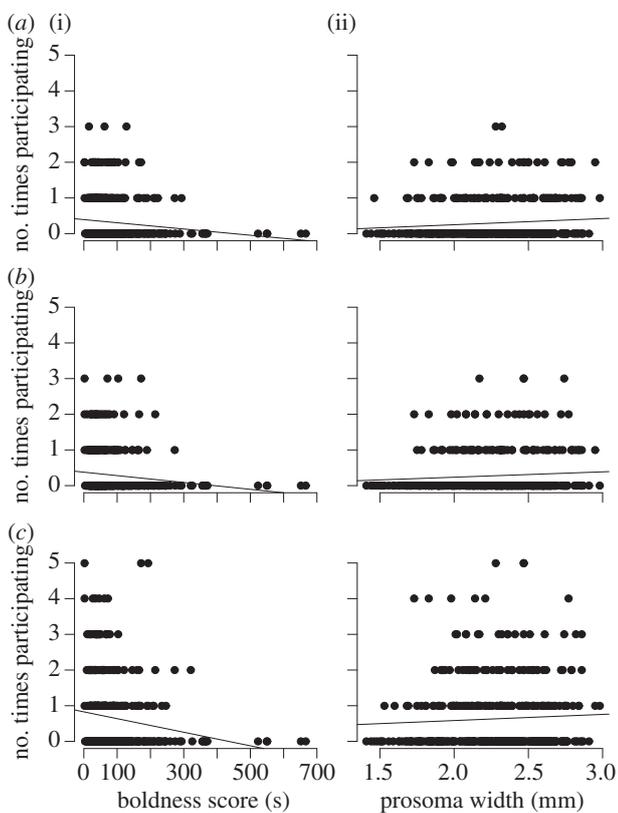

Figure 1. Graphs depicting the number of times spiders participated in 10 simulated prey capture events plotted against (i) boldness (measured as latency to resume movement after air puffs, hence *low* values reflect *high* levels of boldness) and (ii) prosoma width (reflecting body size). Prey capture participation was measured in three ways: as (*a*) the first spider to emerge from the colony, (*b*) the first spider to attack and (*c*) whether spiders were out at the time of attack. Note that the plots and trend lines do not directly reflect the results from the statistical models where random effects were taken into account.

reflecting the behavioural syndrome reported by Pruitt *et al.* [24]. Aggression was the only significant predictor of boldness ($\chi^2 = 48.4$, d.f. $= 5.4$, $p < 0.001$). Prosoma width, dispersal distance and developmental stage were not significantly associated with boldness (prosoma width: $\chi^2 = 0.039$, d.f. $= 5.4$, $p = 0.84$; dispersal distance: $\chi^2 = 0.34$, d.f. $= 6.5$, $p = 0.56$; developmental stage: $\chi^2 = 0.021$, d.f. $= 5.4$, $p = 0.88$). Similarly, boldness was the only significant predictor of aggression (boldness: MCMC $p < 0.001$, prosoma width: MCMC $p = 0.72$; dispersal distance: MCMC $p = 0.10$; developmental stage: MCMC $p = 0.10$). See an overview of associations between different variables in table 2.

4. Discussion

We found that the boldness personality trait was a strong predictor of individual participation in the cooperative task of prey attack in the social spider *S. sarasinorum*, irrespective of age and maturation. This suggests that variation in personalities within groups may be a main driver of task differentiation in this species. We showed a strong association between behaviours assessed in standardized laboratory settings devoid of social context and individuals' behaviour in natural group settings in the field. This confirms that individual-based personality assays can be informative predictors of cooperative behaviour in a natural social setting.

First, we found consistent differentiation in prey attack behaviour in *S. sarasinorum*, as individuals showed significant unequal participation in simulated prey capture events across 10 days. Second, we showed that boldness strongly predicted all three measures of participation in prey capture: first spider to emerge from the nest, first spider to attack and having emerged at the time of attack. However, our second personality measure, aggressiveness, which is highly correlated with boldness [24], was not associated with any of the three measures of participation in prey capture. Perhaps aggressiveness towards predators, as our 'response to prod stimulus' indicates [37], does not correlate with aggressiveness towards prey in this species. Third, body size was positively associated with emerging from the nest but not with attacking, whereas dispersal was positively correlated with tendency to attack but not with being the first to emerge (table 2). Together, this suggests that responding to stimuli from a prey caught in the web elicits different responses according to a set of individual characteristics. Simply responding by emerging from the

Table 2. Overview of associations between variables. First column lists five different predictor variables. Columns 2–4: models using three different response variables from prey attack participation. Columns 5 and 6: models using the two different personality traits as response variable. Asterisks represent level of significance; n.s. refers to non-significant associations and dashes indicate meaningless associations.

	first spider to emerge	first spider to attack	out at time of attack	boldness	aggression
boldness	**	***	***	—	***
aggression	n.s.	n.s.	n.s.	***	—
dispersal distance	n.s.	***	***	n.s.	n.s.
prosoma width	*	n.s.	*	n.s.	n.s.
developmental stage	n.s.	n.s.	n.s.	n.s.	n.s.

nest seems to be affected not only by personality traits but also by internal state, such as higher food intake rate with a larger body size. This may explain why we did not find consistent unequal participation in being the first spider to emerge. Conversely, the act of attacking the prey was unaffected by body size, and potentially driven merely by personality traits: boldness combined with another trait, yet unidentified, that also drives tendency to disperse. Clearly, the set of behavioural traits measured here cannot solely be attributed to a single factor (e.g. high activity levels), as neither boldness nor aggressiveness were correlated with dispersal, and only boldness, and not aggression, predicted prey capture participation (table 2). Fourth, neither body size nor developmental stage predicted boldness, aggression or propensity to attack prey, eliminating both age polyethism as a mechanism behind task differentiation and the possibility of personality being purely a product of age or maturation. Together, these findings highlight the complexity of the underlying mechanisms behind individuals' behaviours in social groups, while establishing that personality traits are solid components of these mechanisms.

Task differentiation among workers is expected to increase colony fitness in social insects [2,3]. Social spiders differ from social insects in the lack of strict division of labour and caste formation. Hence, spider societies are often considered to be egalitarian, where all individuals can and do perform all colony tasks approximately equally [28,47]. However, reproduction is skewed, as less than half of the females in colonies usually reproduce, whereas both reproducers and non-reproducers provide allomaternal care [31,33,48,49]. Recent studies have suggested that reproductive roles may be allocated at an early developmental stage in the social spider *Stegodyphus dumicola* [7], and that *S. sarasinorum* show task differentiation in prey attack, independent of hunger state, in field experiments across 3 days [25]. Here, we confirm the consistency of this task differentiation across 10 days and identify one of the mechanisms behind it: variation in personality. The composition of individual personalities within *S. sarasinorum* colonies was also found to influence *colony-level* personality: colony-level responsiveness in prey capture was repeatable over time and was predicted by the boldness of colony members, indicating that individual personalities can influence colony-level fitness traits [24]. Additionally, in the behaviourally polymorphic facultative social spider *A. studiosus* [38], bolder, more aggressive individuals participate disproportionally more in prey capture and nest defence [19,21]. Our study documents how differences in personality shape task differentiation in *S. sarasinorum* colonies in field settings. These novel findings show that the link between individual personality and task performance in

groups, previously observed only in laboratory experiments on social *Anelosimus* spiders of artificially low colony sizes, maintains a robust signature under field conditions in colonies of a natural size. Thus, these data move beyond proof-of-principle studies and add to the growing body of evidence undermining the view of social spider colonies as egalitarian societies where all individuals are functionally equivalent. Like in many other cooperative animals, spider societies have a more complex social organization than previously anticipated, suggesting that advanced forms of social structure might be an emergent property of social living [50]. Furthermore, our study forges another substantive link between two major subjects within animal behaviour literature—personality and task differentiation—suggesting that task differentiation studies could benefit from considering individual personalities [51].

Social spiders are characterized by extraordinarily high relatedness among colony members due to a within-colony mating system causing inbreeding [28,52]. Hence, genetic diversity and heterozygosity is extremely low in social spiders [53,54], and any genetic basis for variation in behaviour may be highly constrained [55]. However, task specialization and personality can be determined purely by extrinsic factors such as nutrition, social encounters or previous foraging success [4,56,57]. For example, task differentiation was induced in the ant *Cerapachys biroi* purely by manipulating foraging success in same-sized, similar-aged and genetically closely related workers [58]. Workers that were allowed to be successful in foraging foraged more and spent less time with brood, showing that experience alone can create variation in foraging propensity. A simple reinforcement mechanism of modifying an internal response threshold may in this case be enough to facilitate task specialization [58]. We hypothesize that similar simple mechanisms of positive reinforcements and threshold modulations due to experience (e.g. previous experience in prey capture events or nutritional levels at critical points during development) may underlie the behavioural variation observed within inbred spider societies [3,59].

To conclude, we found that variation in personality may drive task differentiation in social groups in field conditions. We document an association between personalities measured in standardized, solitary laboratory settings and individual behaviours in natural social settings, deeming standardized tests of behavioural type as informative predictors of natural behaviour in groups in *S. sarasinorum*. The next step will be to examine whether variation in behavioural types presents a fitness advantage for colonies of this species compared with behaviourally homogeneous colonies, and whether individuals specializing in prey attack are more or less likely to reproduce. Such relationships have already been established

in other social insects and facultatively social spiders [17–19,60,61]. This study provides an important link between task differentiation and individual personality under naturalistic conditions, traits that are expected to affect both individual and colony-level fitness. Further long-term studies on different social organisms are now required to determine the generality and robustness of the link between animal personality and social organization.

References

1. Wilson EO. 1975 *Sociobiology*. Cambridge, MA: Belknap.

2. Wilson EO. 1987 Causes of ecological success: the case of the ants. The 6th tansley lecture. *J. Anim. Ecol.* **56**, 1–9. (doi:10.2307/4795)

3. Beshers SN, Fewell JH. 2001 Models of division of labor in social insects. *Annu. Rev. Entomol.* **46**, 413–440. (doi:10.1146/annurev.ento.46.1.413)

4. Gordon DM. 1996 The organization of work in social insect colonies. *Nature* **380**, 121–124. (doi:10. 1038/380121a0)

5. Schwander T, Lo N, Beekman M, Oldroyd BP, Keller L. 2010 Nature versus nurture in social insect caste differentiation. *Trends Ecol. Evol.* **25**, 275–282. (doi:10.1016/j.tree.2009.12.001)

6. Michener CD. 1974 *The social behavior of the bees*. Cambridge, MA: Belknap Press.

7. Grinsted L, Bilde T. 2013 Effects of within-colony competition on body size asymmetries and reproductive skew in a social spider. *J. Evol. Biol.* **26**, 553–561. (doi:10.1111/jeb.12072)

8. Réale D, Dingemanse NJ. 2010 Personality and individual social specialisation. In *Social behaviour: genes, ecology and evolution* (eds T Székely, AJ Moore, J Komdeur), pp. 417–441. Cambridge, UK: Cambridge University Press.

9. Arnold KE, Owens IPF, Goldizen AW. 2005 Division of labour within cooperatively breeding groups. *Behaviour* **142**, 1577–1590. (doi:10.1163/156853905774831927)

10. Bergmuller R, Taborsky M. 2007 Adaptive behavioural syndromes due to strategic niche specialization. *BMC Ecol.* **7**, 12. (doi:10.1186/1472-6785-7-12)

11. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)

12. Sih A, Bell A, Johnson JC. 2004 Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378. (doi:10.1016/j.tree.2004.04.009)

13. Bell AM, Hankison SJ, Laskowski KL. 2009 The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**, 771–783. (doi:10.1016/j.anbehav.2008.12.022)

14. Dall SRX, Houston AI, McNamara JM. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739. (doi:10.1111/j.1461-0248.2004.00618.x)

15. Bergmuller R, Schurch R, Hamilton IM. 2010 Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. *Phil. Trans. R. Soc. B* **365**, 2751–2764. (doi:10.1098/rstb.2010.0124)

16. Bergmuller R, Taborsky M. 2010 Animal personality due to social niche specialisation. *Trends Ecol. Evol.* **25**, 504–511. (doi:10.1016/j.tree.2010.06.012)

17. Modlmeier AP, Foitzik S. 2011 Productivity increases with variation in aggression among group members in *Temnothorax* ants. *Behav. Ecol.* **22**, 1026–1032. (doi:10.1093/beheco/arr086)

18. Modlmeier AP, Liebmann JE, Foitzik S. 2012 Diverse societies are more productive: a lesson from ants. *Proc. R. Soc. B* **279**, 2142–2150. (doi:10.1098/rspb.2011.2376)

19. Pruitt JN, Riechert SE. 2011 How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proc. R. Soc. B* **278**, 1209–1215. (doi:10.1098/rspb.2010.1700)

20. Pruitt JN, Oufiero CE, Aviles L, Riechert SE. 2012 Iterative evolution of increased behavioral variation characterizes the transition to sociality in spiders and proves advantageous. *Am. Nat.* **180**, 496–510. (doi:10.1086/667576)

21. Pruitt JN, Riechert SE. 2011 Within-group behavioral variation promotes biased task performance and the emergence of a defensive caste in a social spider. *Behav. Ecol. Sociobiol.* **65**, 1055–1060. (doi:10.1007/s00265-010-1112-z)

22. Chapman BB, Thain H, Coughlin J, Hughes WOH. 2011 Behavioural syndromes at multiple scales in *Myrmica* ants. *Anim. Behav.* **82**, 391–397. (doi:10.1016/j.anbehav.2011.05.019)

23. Jeanne RL. 1988 *Interindividual behavioral variability in social insects*. Boulder, CO: Westview Press.

24. Pruitt JN, Grinsted L, Settepani V. In press. Linking levels of personality: personalities of average and extreme group members shape colony-level personality. *Anim. Behav.* (doi:10.1016/j.anbehav.2013.05.030)

25. Settepani V, Grinsted L, Granfeldt J, Jensen JL, Bilde T. 2013 Task specialization in two social spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae). *J. Evol. Biol.* **26**, 51–62. (doi:10.1111/jeb.12024)

26. Platnick NI. 2012 *The world spider catalog*, version 12.5. See http://research.amnh.org/iz/spiders/catalog.

27. Jacson CC, Joseph KJ. 1973 Life-history, bionomics and behavior of social spider *Stegodyphus sarasinorum* Karsch. *Insect. Soc.* **20**, 189–203. (doi:10.1007/BF02223347)

28. Lubin Y, Bilde T. 2007 The evolution of sociality in spiders. *Adv. Study Behav.* **37**, 83–145.

29. Kullmann EJ. 1972 Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). *Am. Zool.* **12**, 419–426.

30. Kraus O, Kraus M. 1988 The genus *Stegodyphus* (Arachnida, Araneae): sibling species, species groups, and parallel origin of social living. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)* **30**, 151–254.

31. Salomon M, Mayntz D, Lubin Y. 2008 Colony nutrition skews reproduction in a social spider. *Behav. Ecol.* **19**, 605–611. (doi:10.1093/beheco/arn008)

32. Seibt U, Wickler W. 1987 Gerontophagy versus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. *Anim. Behav.* **35**, 1903–1905. (doi:10.1016/S0003-3472(87)80087-8)

33. Salomon M, Lubin Y. 2007 Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (Araneae, Eresidae). *Behav. Ecol. Sociobiol.* **61**, 1743–1750. (doi:10.1007/s00265-007-0406-2)

34. Crouch TE, Lubin Y. 2000 Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae). *J. Arachnol.* **28**, 158–168. (doi:10.1636/0161-8202(2000)028[0158:EOCAPA]2.0.CO;2)

35. Lubin Y, Birkhofer K, Berger-Tal R, Bilde T. 2009 Limited male dispersal in a social spider with extreme inbreeding. *Biol. J. Linn. Soc.* **97**, 227–234. (doi:10.1111/j.1095-8312.2009.01190.x)

36. Riechert SE, Hedrick AV. 1993 A test for correlations among fitness-linked behavioral traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Anim. Behav.* **46**, 669–675. (doi:10.1006/anbe.1993.1243)

37. Riechert SE, Johns PM. 2003 Do female spiders select heavier males for the genes for behavioral aggressiveness they offer their offspring? *Evolution* **57**, 1367–1373. (doi:10.1554/02-677)

38. Pruitt JN, Riechert SE, Jones TC. 2008 Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*.

Anim. Behav. **76**, 871–879. (doi:10.1016/j.anbehav. 2008.05.009)

39. Hagstrum DW. 1971 Carapace width as a tool for evaluating rate of development of spiders in laboratory and field. *Ann. Entomol. Soc. Am.* **64**, 757–760.

40. Jakob EM, Marshall SD, Uetz GW. 1996 Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61–67. (doi:10.2307/3545585)

41. Adams DC, Anthony CD. 1996 Using randomization techniques to analyse behavioural data. *Anim. Behav.* **51**, 733–738. (doi:10.1006/anbe.1996.0077)

42. Manly BFJ. 1997 *Randomization, bootstrap and Monte Carlo methods in biology*. New York, NY: Chapman and Hall.

43. Haccou P, Meelis E. 1994 *Statistical analysis of behavioural data*. Oxford. UK: Oxford University Press.

44. Bates D, Maechler M, Bolker B. 2011 lme4: linear mixed-effects models using S4 classes. See http:// CRAN.R-project.org/package=lme4.

45. R Development Core Team. 2012 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.

46. Hadfield JD. 2010 MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. *J. Stat. Software* **33**, 1–22.

47. Avilés L. 1997 Causes and consequences of cooperation and permanent-sociality in spiders. In *The evolution of social behavior in insects and arachnids* (eds JC Choe, BJ Crespi), pp. 476–498. Cambridge, UK: Cambridge University Press.

48. Vollrath F. 1986 Eusociality and extraordinary sex-ratios in the spider *Anelosimus eximius* (Araneae, Theridiidae). *Behav. Ecol. Sociobiol.* **18**, 283–287. (doi:10.1007/BF00300005)

49. Vollrath F, Rohde-Arndt D. 1983 Prey capture and feeding in the social spider *Anelosimus eximius*. *J. Comp. Ethol.* **61**, 334–340.

50. Jeanson R, Kukuk PF, Fewell JH. 2005 Emergence of division of labour in halictine bees: contributions of social interactions and behavioural variance. *Anim. Behav.* **70**, 1183–1193. (doi:10.1016/j.anbehav. 2005.03.004)

51. Dall SRX, Bell AM, Bolnick DI, Ratnieks FLW. 2012 An evolutionary ecology of individual differences. *Ecol. Lett.* **15**, 1189–1198. (doi:10.1111/j.1461-0248.2012.01846.x)

52. Johannesen J, Hennig A, Dommermuth B, Schneider JM. 2002 Mitochondrial DNA distributions indicate colony propagation by single matri-lineages in the social spider *Stegodyphus dumicola* (Eresidae). *Biol. J. Linn. Soc.* **76**, 591–600. (doi:10.1046/j. 1095-8312.2002.00082.x)

53. Roeloffs R, Riechert SE. 1988 Dispersal and population-genetic structure of the cooperative spider, *Agelena consociata*, in West African rainforest. *Evolution* **42**, 173–183. (doi:10.2307/ 2409125)

54. Smith DRR. 1986 Population genetics of *Anelosimus eximius* (Araneae, Theridiidae). *J. Arachnol.* **14**, 201–217.

55. Lubin Y. 1995 Is there division of labour in the social spider *Achaearanea wau* (Theridiidae)? *Anim. Behav.* **49**, 1315–1323. (doi:10.1006/anbe. 1995.0163)

56. Pinter-Wollman N. 2012 Personality in social insects: how does worker personality determine colony personality? *Curr. Zool.* **58**, 580–588.

57. Keller L. 2009 Adaptation and the genetics of social behaviour. *Phil. Trans. R. Soc. B* **364**, 3209–3216. (doi:10.1098/rstb.2009.0108)

58. Ravary F, Lecoutey E, Kaminski G, Chaline N, Jaisson P. 2007 Individual experience alone can generate lasting division of labor in ants. *Curr. Biol.* **17**, 1308–1312. (doi:10.1016/j.cub. 2007.06.047)

59. Theraulaz G, Bonabeau E, Deneubourg JL. 1998 Response threshold reinforcement and division of labour in insect societies. *Proc. R. Soc. B* **265**, 327–332. (doi:10.1098/rspb.1998.0299)

60. Pruitt JN, Ferrari MCO. 2011 Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species. *Ecology* **92**, 1902–1908. (doi:10.1890/11-0701.1)

61. Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A. In press. Behavioural syndromes and social insects: personality at multiple levels. *Biol. Rev.* (doi:10.1111/brv.12042)