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Long-term behavioural consistency in prey capture but not in web maintenance in a social spider

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Abstract Behavioural differences between individuals that are consistent over time or across context are termed behavioural types or personalities. Social spiders are an emerging model for studying animal personality in social systems and our study was motivated by the lack of work examining the persistence of personality in the long-term and under changed conditions. We examined consistency and plasticity in two key behaviours, prey capture and web maintenance, and tested for the presence of a behavioural syndrome between them in the social spider, *Stegodyphus sarasinorum*. Our experiments over a large part of the adult life span show that not all spiders capture prey, suggesting behavioural consistency with implications for task differentiation. Through prey manipulation experiments, we further probed the role of hunger, proximity to prey, body weight and number of days into the experiment on individual propensity to capture prey. Our results demonstrate that under altered prey availability, responses of individuals are plastic and influenced by hunger. These results suggest that behavioural consistency can be modulated significantly by extrinsic factors. In contrast, we did not find consistent differences between individuals in their participation during web maintenance. Additionally, we did not find a behavioural syndrome. Together, these results suggest a scenario of quasi-specialisation in which there is no strict partitioning of tasks. For the first time, our results demonstrate behavioural consistency over extended periods of time in social spiders and have implications for colony efficiency and survival. We argue that studies spanning ecologically relevant time periods and environmental variation can reveal the full extent of behavioural consistency and flexibility.

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Introduction

Individual behavioural differences in a population or a social group that are consistent across time or context are referred to as behavioural type, behavioural consistency or personality (Dall et al. 2004; Sih et al. 2004; Réale et al. 2007; Pruitt et al. 2013; Jandt et al. 2014), and these terms have been used interchangeably in the literature. Studies examining animal personalities have spanned a range of social and asocial vertebrate and invertebrate species (Bell et al. 2009; Dingemanse et al. 2010), and have investigated behaviours such as aggression, boldness, neophobia, foraging, habitat selection, startle response, dispersal, courtship and explorative tendencies (Gosling 2001). Such inter-individual differences in group-living species are considered adaptive at the individual and at the population level (Dingemanse et al. 2010; Dall et al. 2012), because mixed groups show greater reproductive success, feeding efficiency and productivity than homogeneous groups (Pruitt and Riechert 2011a, b; Modlmeier et al. 2012; Pruitt et al. 2012; Wright et al. 2014). Mechanisms responsible for the stability of behavioural types in a population may include genetic, neurological or physiological responses, as well

as positive feedbacks between the behaviour and the state of the individual. At the group level, benefits might accrue from predictable responses of individuals in social behaviours (Wolf et al. 2011; Wolf and Weissing 2012).

Traditionally, the focus of animal personality studies has largely been the examination of consistent behavioural differences *between* individuals, implying that these have evolved to local optima, while treating any variation as noise (Wilson 1998; Wolf and Weissing 2012). Early studies presumed that animal personality implied limited or no behavioural plasticity and undermined the role of behavioural plasticity *within* individuals (intra-individual variation) (Francis 1990; Mather and Anderson 1993). However, this notion has changed considerably, and it is now widely accepted that individuals show behavioural plasticity, making it possible to respond to immediate changes in the environment (Dingemanse et al. 2010; Carter et al. 2012; Stamps et al. 2012), though individuals may vary in the degree of plasticity (Dingemanse et al. 2010). It has been hypothesised that behaviours under morphological and physiological constraints (e.g. mating) are less plastic, while those that are responses to environmental changes (e.g. foraging) are more plastic (Bell et al. 2009). Therefore, both plasticity and personality can be considered complementary aspects of an individual's behavioural phenotype. In fact, recent studies have incorporated personality and plasticity into an integrated framework, while examining the response of individuals over environmental gradients or behavioural contexts (van de Pol and Wright 2009; Dingemanse et al. 2010, 2012). Another paradigm shift in animal personality research has been the concept of behavioural syndromes. The response of individuals in the context of one behaviour may be correlated to their response in the context of another, and constitutes a behavioural syndrome (Sih et al. 2004; Bell and Sih 2007; Jandt et al. 2014). In social species, a negative correlation between behaviours may indicate greater task differentiation amongst individuals, while a positive correlation may suggest a disproportionate contribution of key individuals in performing tasks, as shown in colonies of social insects such as ants (Dornhaus 2008; Robson and Traniello 1999; Pinter-Wollman 2012; Jandt et al. 2014). Some examples of behavioural syndromes include positive correlations between territorial defense and foraging in spiders (Riechert and Hedrick 1993), exploration and dispersal in birds (Dingemanse et al. 2003) or foraging aggressiveness and boldness in spiders (Sweeney et al. 2013). Such linking of behaviours into a syndrome has been attributed to developmental, neuronal, hormonal, phylogenetic, and genetic factors (Bell and Sih 2007; Dingemanse et al. 2007).

Social insects have for long been a popular topic of research in task differentiation, which is a kind of stable individual variation in behaviour. The propensity of individuals to perform certain tasks have been attributed to age polyethism, morphological polyethism and experience in social insects (Beshers and Fewell 2001; Agrahari and Gadagkar 2003; Ravary et al. 2007; Jeanson and Weidenmüller 2013). In social spiders on the other hand, females were considered totipotent because of the absence of apparent polymorphy (Lubin and Bilde 2007). Indeed, most earlier studies on social spiders concluded an absence of task differentiation in foraging and web maintenance (Avilés 1997; Ainsworth et al. 2002; Lubin and Bilde 2007; but see Lubin 1995). Yet, there has been a recent surge of interest in understanding the role of personalities in shaping task specialisation in social spider colonies (Pruitt and Riechert 2011a, b; Grinsted et al. 2013; Pruitt et al. 2013; Settepani et al. 2013; Keiser et al. 2014; Wright et al. 2014).

Social spider colonies consist of highly inbred, similar-aged individuals, with no morphological castes and little overlap of generations (Avilés 1997; Lubin and Bilde 2007). This suite of traits make them highly amenable to investigating inter-individual differences in behavioural consistency, since the confounding effects of genetic variation and age are naturally controlled in these colonies. Additionally, social spiders being sit and wait predators, permit easy observation, and their life spans of up to a year facilitate the investigation of behavioural consistency in individuals across different conditions and for extended periods of time. Recent studies on social spider species have examined behavioural consistency and task differentiation largely in prey capture (Grinsted et al. 2013; Jandt et al. 2014; Pruitt et al. 2013; Settepani et al. 2013; Keiser et al. 2014) and to a lesser extent in web building (Settepani et al. 2013; Grinsted et al. 2013; Keiser et al. 2014). In these studies, individual spiders were assigned to discrete behavioural types (bold vs. shy; aggressive vs. docile) in assays that simulated predator presence or disturbance and behavioural types were examined in experiments conducted over 3–10 days. However, studying personalities over relevant time scales and environmental conditions is important for robust sampling of inter- and intra-individual variation (Bell et al. 2009), and to increase the likelihood of sampling a larger set of participating individuals. Since many social spider species are relatively long lived with life spans up to a year, it is essential to investigate the stability of behavioural consistency in individuals over time frames relevant to their biology and under conditions that they are likely to experience in nature. In spite of this, the persistence of behavioural types over the long term and under changed ecological conditions has not been addressed till now.

In the Indian social spider *Stegodyphus sarasinorum* Karsch (Eresidae), we examined behavioural consistency in two key behaviours, namely, prey capture and web maintenance, over a time frame comprising a large part of the adulthood of individuals, which typically lasts about 2 months in this species that lives for approximately a year. Social spiders can show an increase in their behavioural repertoires as they mature (Lubin 1995) and studying later instars ensure that the

full range of behaviours is captured. Furthermore, we investigated the existence of a behavioural syndrome between these two behaviours to unravel the extent of task differentiation in the colony. To study behavioural consistency under changed conditions, we manipulated prey availability in laboratory experiments to examine the consequence of hunger on participation and plasticity in prey capture behaviour. We hypothesise that under conditions of food scarcity, interindividual differences diminish and individuals will participate in prey capture more equally. There is ample evidence that under natural conditions, spiders can experience periods of low prey availability (Nentwig 1987; Wilder 2011). Our experiments in the laboratory mimic this natural variation in food availability and its consequences for task differentiation and behavioural consistency.

Specifically, we addressed the following questions: (a) Does individuals' participation in prey capture and web maintenance behaviours differ consistently over the long term? (b) Are these behaviours correlated, forming a behavioural syndrome? And (c) does prey scarcity alter individuals' participation in prey capture, suggesting that individuals are plastic and modulated by hunger?

Methods

Biology of *S. sarasinorum*

S. sarasinorum Karsch 1891 (Eresidae), is one of three permanently social spiders found in dry and shrubby habitats in India, Sri Lanka and parts of Myanmar (Jambunathan 1905; Jacson and Joseph 1973; Kraus and Kraus 1988; Miller et al. 2012). Individuals within a colony reside in compact nest-like retreats. Attached to a retreat is a capture web which is connected to nearby support structures. *Stegodyphus* colonies are largely female-biased and inhabited by tens to hundreds of individuals. Female spiders exhibit collective behaviour in prey capture, web maintenance and brood care, while adult males rarely take part in these tasks in *S. sarasinorum*, as in other species of social spiders (Lubin and Bilde 2007). Spiders remain inside their retreat during the day and appear outside only to capture prey intercepted on the web. Webs are built, extended and repaired by females at dusk.

We maintained spiders in compliance with the laws of the country and released them into their natural habitat at the end of our study.

Prey capture

We collected nine spider colonies (21–51 final instar and adult females per colony; 265 spiders in total) from two distinct regions which were 600 km apart in southern India, namely, Kuppam in Andhra Pradesh (12.75° N, 78.37° E; *n*=6

colonies) and Villukuri in Tamil Nadu (8.22°N, 77.37°E; *n*= 3 colonies). Spiders collected from Villukuri were transported to the Indian Institute of Science Education and Research Thiruvananthapuram campus, where we carried out short-term experiments over 10 days in December 2012. The spiders collected in Kuppam were housed in the campus of the Agastya International Foundation, Kuppam where long-term experiments were carried out over 3 to 4 weeks in March and April 2013. The two populations were asynchronous in their reproductive schedules. The same protocol was followed in both experimental locations. Spiders of both sexes were individually weighed to the nearest milligram, and uniquely marked with non-toxic acrylic paint (Fig. 1). Each colony was placed on a frame, housed within a netted enclosure (1×1×1 m), and was allowed to build an extensive capture web (~15 cm radius) before experiments commenced.

We used honey bees (*Apis cerana*) as prey to examine spiders' participation in prey capture. Bee colonies obtained from a commercial bee keeper were maintained during the study period. Bees are a natural prey of spiders, and permitted us to standardise prey size and nutrition. Each trial commenced when we gently placed a live bee on the web, approximately 10–15 cm from the retreat, using a pair of forceps. The trial ended when spiders dragged the immobilised bee into the retreat, or when 20 min elapsed, whichever occurred first. Spiders that contacted, seized or pulled the bee were given a score of one if they showed at least one of these behaviours, while those that did not participate in a given trial were scored zero. We performed two such trials during the day, with a 3–5 h interval between trials. After the first trial of the day, we gently removed the bee, once spiders had transported it close to the retreat. This allowed us to keep the feeding status and motivation of spiders to capture prey comparable across the two trials each day. Each colony was fed on a diet of 12 bees based on our experience with maintaining spider colonies in the laboratory. For each individual, we calculated a

Fig. 1 Marked individuals of the social spider, *Stegodyphus sarasinorum* attacking a honeybee prey during a trial

participation score, given by the total number of trials in which an individual participated. A small number of spiders (<5 % of total spiders over the course of the experiments) moved out of the retreat and settled in the corners of the cage. These individuals were not included in the day's trials and were put back into the retreat at the end of the day.

Web maintenance

Observations of web maintenance behaviours were made in March and April 2013 using the same colonies used in the prey capture experiments at the Kuppam site (n=234 spiders for 5 colonies; the sixth colony was excluded since the data were sparse). Two-minute scan sampling was performed at 4-min intervals during peak web maintenance activity from 1830 to 2000 h. Spiders performed web maintenance continuously without frequent shifts to other activities; hence, we chose a scan duration that captured this continuity. Spiders that did not perform web maintenance on a particular day or remained within the retreat were given a score of zero. For each day, the number of scans in which a spider participated in web maintenance was recorded and used to calculate a participation score.

Hunger manipulation

By performing manipulative experiments in the laboratory, we examined whether hunger, proximity to prey and number of days into the experiment influenced propensity to attack. Spider colonies were collected from the Villukuri site in June 2013. Fourteen late instar females per experimental colony and nine colonies in total (n=126 spiders) were used in this experiment. Similar-sized spiders were uniquely marked, weighed to the nearest milligram and each colony was housed separately in a Petri dish (9 cm diameter, 1.5 cm deep) with a 1×1cm grid. We started experiments 2 days later, by which time the spiders had built a web inside the Petri dish. Each 3-min trial started when a partially wing-cut bee was introduced inside the dish; one of its wings was clipped to curtail movement. The bee was randomly placed on a grid, such that there were no other spiders within 1 cm of that grid. In each trial, we recorded the identities of spiders that responded by approaching and attacking the bee. Prior to the addition of the bee, we noted the position of each spider in the gridded dish. At the end of each trial, all colonies were fed two bees each. We performed one such feeding trial every day for 9 days (feeding treatment). Weights of spiders were obtained on the 10th day and spiders were subjected to hunger (starvation treatment) over the next 10 days, during which we removed the bee at the end of each 3-min trial, and no additional bees were provided when a trial ended.

Statistical analyses

For both prey capture and web maintenance, only females that retained markings until the end of the experiments were included in the analyses. We excluded spiders that lost their markings due to molting, chipping or fading of paint. In some trials, one or two spiders emerged from the retreat but went back inside without contacting the prey, these spiders as well as spiders that dispersed overnight were excluded from a given trial.

Prey capture We used a total of 108 spiders from 9 colonies that retained markings until the end to examine participation in prey capture. The total number of trials over the experiment ranged from 23–63 for the Kuppam colonies (mean±SD= 39.6±17.4 trials/spider) and 6–10 for the Villukuri population (mean±SD=7±2 trials/spider). To determine the variation between and within individuals during prey capture, we performed Generalised Linear Mixed Model (GLMM) logistic regressions with a logit link in MLwiN version 2.28 (Rasbash et al. 2013). Participation by individuals in each trial was coded as a binary response. A significant variation in the random intercept indicates inter-individual variation in their consistency in participation, while a significant variation in the random slope indicates variation in plasticity (intra-individual variation) across individuals (Dingemanse et al. 2009). Colony identity, spider identity and trial number (number of days into the experiment) were included as three levels in the model. Weight of spiders, study site and trial number were included as fixed effects in the model and the significance of fixed effects was calculated using the Wald Z test. A random intercept and random slope model was built by incorporating colony identity and spider identity as random effects. The significance of random effects was assessed by comparing models with and without them using the likelihood ratio test. Overall model selection was performed by the sequential addition of variables. Different models were compared using the likelihood ratio test and the model with the lowest likelihood was chosen. Repeatability was calculated to measure consistent participation by individuals using the 'rptR' package (Schielzeth and Nakagawa 2011) in R (R Core Team 2009).

Web maintenance To determine inter- and intra-individual variation in web maintenance behaviours, we performed a GLMM with a negative binomial response using a log link in MLwiN version 2.28 (Rasbash et al. 2013). Only spiders that lasted all through the experiments were included (n=87 spiders; 5 colonies). We measured participation in web maintenance as count data; since these data were overdispersed, we used a negative binomial instead of a Poisson response. As with prey capture, we used days and spider weight as fixed effects in the model, and their significance was tested using

Wald Z test. The significance of random effects (colony and spider identity) was assessed by comparing models with and without them using the likelihood ratio test. Overall model selection was performed by the sequential addition of variables. Different models were compared using the likelihood ratio test and the model with the lowest likelihood was chosen. Repeatability tests for participation in web maintenance were performed.

The predictions of both the prey capture and web maintenance GLMM models were visualised through the 'ggplot2' package (Wickham 2009) in R 3.01 (R Core Team 2013).

Behavioural associations between prey capture and web maintenance To test for the presence of a behavioural syndrome, we performed Spearman rank correlations between propensities to participate in prey capture and web maintenance using the random intercept values of individuals obtained from the above GLMMs. We also performed correlations using the mean number of times individuals participated in the two behaviours.

Hunger manipulation We performed GLMMs to determine the effect of hunger, distance to prey, spider weight and number of days into the experiment (trial number) on propensity of spiders to attack prey. We included only spiders that retained markings for the entire duration of the experiment in these analyses ($n=4$–6 spiders per colony; 9 colonies). Trial number, distance to prey, spider weight, and treatment (fed or starved) were fixed effects in the model, and their significance was tested using the Wald Z test. We tested the significance of random effects (colony and spider identity) using a likelihood ratio to test models with and without these random effects. Overall model selection was performed by the sequential

addition of variables. We did not include the interaction between spider weight and treatment since these variables were highly correlated. Different models were compared using the likelihood ratio test and the model with the lowest likelihood was chosen. As with the field experiments above, repeatability tests were performed to examine consistent participation by individuals.

Results

Individuals exhibit personality in prey capture but not in web maintenance

Approximately 50 % of total spiders participated in prey capture (mean±SD=50.7±16.23 % total spiders, $n=9$ colonies) and 70 % of total spiders participated in web maintenance (mean±SD=69.03±16.4 % total spiders, $n=5$ colonies). Individuals exhibited consistent differences in prey capture in all colonies, as evidenced by significant variation at the random intercept between individuals (Fig. 2, Table 1). In contrast to prey capture, spiders did not exhibit consistency in web maintenance (Fig. 3, Table 1). Repeatability in individuals' participation in prey capture was low though significant ($R=0.107$, $p=0.005$). Though low repeatability is typical of foraging behaviour (Bell et al. 2009), it was higher than in web building ($R=0.016$, $p=0.01$). Colony identity did not contribute significantly to variation in the random intercept, indicating that colonies responded similarly in both prey capture and web maintenance behaviours (Table 1). Weight of spiders also did not contribute significantly to either behaviour (Table 1).

Fig. 2 Individuals vary in their behavioural consistency in prey capture. In the experimental colonies (only the long-term colonies are presented here ($n=6$)), each *line* represents the slope for a single spider. The random intercepts show significant variation across individuals suggesting personality. Similar slopes suggest low variation in plasticity within and across individuals
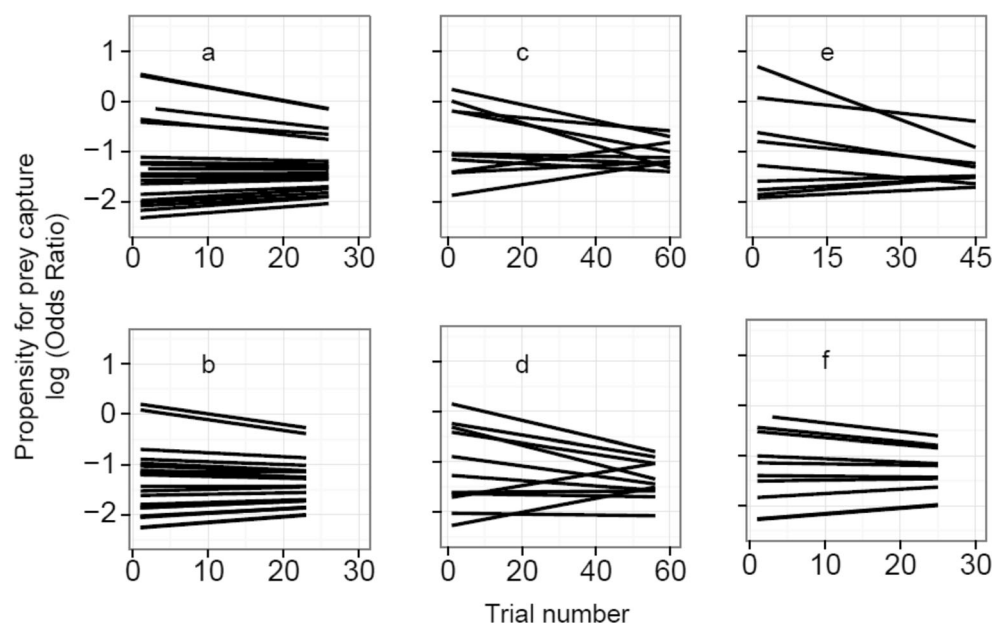
Table. 1 Generalised linear mixed models explaining propensity of individuals for prey capture and web maintenance

	Prey capture		Web maintenance	
	Wald Z	p	Wald Z	p
Trial number/no. of days as a fixed effect	0.25	0.8	0.28	0.78
Spider weight as a fixed effect	0.0	1	0.51	0.61
Site as a fixed effect	1.85	0.06	–	–
Colony ID as a random intercept	0.00	0.50	0.91	0.17
Spider ID as a random intercept	4.60	0.02	1.47	0.11
	χ^2 (df=1)			
Trial number as a random slope at colony level	0.00	0.50	1.00	0.16
Trial number as a random slope at spider level	0.00	0.50	0.50	0.24

Absence of a behavioural syndrome between prey capture and web maintenance

There was no correlation between individual propensity to participate in prey capture and web maintenance, when the average participation of individuals in both behaviours was considered (Spearman rank correlation, rho=-0.03, p=0.78, n=73 spiders from 5 colonies), and even when the individual GLMM intercept values were considered (Spearman rank correlation, rho=0.03, p=0.79, n=73 spiders from 5 colonies).

Individuals fail to show behavioural consistency when hungry

A lack of consistency in participation amongst spiders was observed when prey availability was manipulated, as shown by the non-significant variation in random intercepts

(Table 2). As with the field experiments, repeatability in the lab experiments was low (R=0.072, p=0.01). Moreover, during the feeding treatment, only a few spiders attacked prey, while in the starvation treatment most spiders participated in prey capture (Fig. 4). This indicates that hunger had a significant effect on the propensity of individuals to attack. In addition, individual slopes across spiders were similar and showed non-significant variation, demonstrating a homogenous response amongst spiders to starvation (Table 2). Distance to prey, weight of spiders and trial number did not significantly explain the propensity to participate in prey capture.

Discussion

By definition, behavioural types or personality refers to consistency in behaviour over time and/or context (Jandt et al.
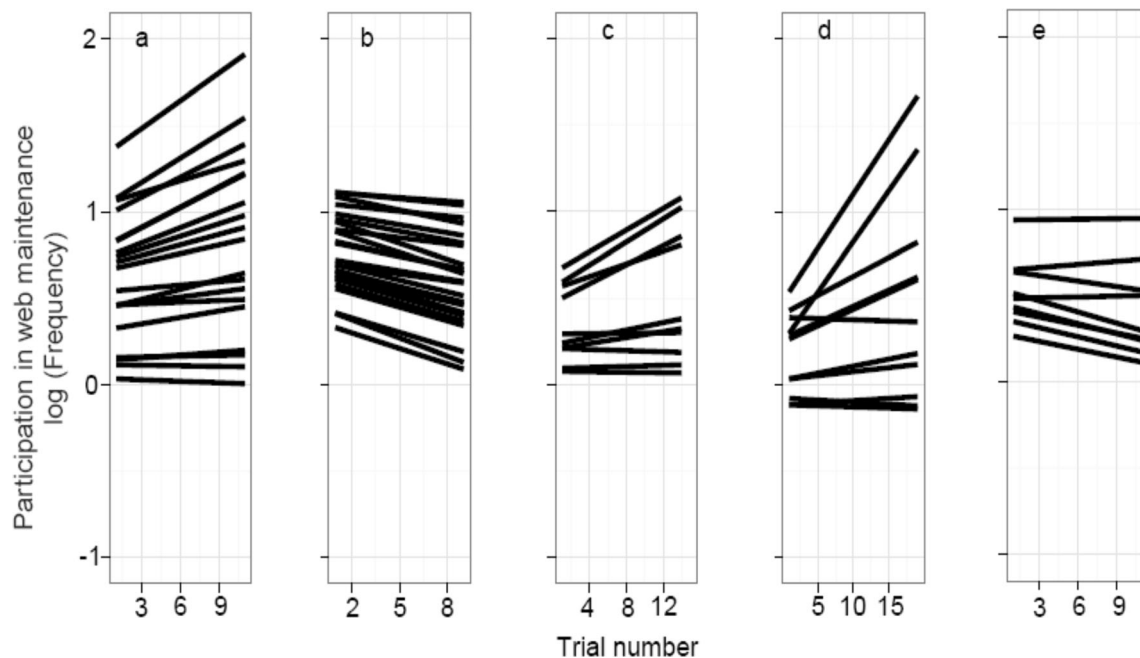

Fig. 3 Spiders do not exhibit behavioural consistency in web maintenance. In experimental colonies (*n*=5), each *line* represents the slope for a single spider. Similar slopes show low variation in plasticity within and between individuals

Table 2 Generalised linear mixed models explaining propensity for prey capture in hunger manipulation experiments. Only treatment (feeding or starvation) was significant in explaining the propensity to capture prey

	Wald Z	p
Trial number as fixed effect	1.81	0.07
Spider weight as fixed effect	0.11	0.91
Distance to prey as fixed effect	0.57	0.57
Treatment	1.71	0.01
Colony ID as a random intercept	1.29	0.13
Spider ID as a random intercept	0.00	0.50
	χ^2 (df=1)	
Trial number as a random slope at colony level	1.5	0.11
Trial number as a random slope at spider level	0	0.50

2014), and is hence more meaningfully addressed in studies that examine its persistence over ecologically relevant time scales and conditions. This is important for the following reasons: (1) Robust sampling of inter- and intra-individual variation (Bell et al. 2009) and (2) Increased likelihood of sampling a larger set of participating individuals. However, previous studies on personality in social spiders have been conducted over the short term (3–10 days; Grinsted et al. 2013; Pruitt et al. 2013; Settepani et al. 2013; Keiser et al. 2014). Our study has incorporated both of the above through experiments that encompassed a large part of the adult life span of females in the social spider *S. sarasinorum*, as well as examined the consequence of hunger on behavioural consistency. The results of our long-term prey capture indicates that there is behavioural consistency in prey capture and agrees with other short-term studies on prey capture in social spiders (Grinsted et al. 2013; Settepani et al. 2013; Keiser et al. 2014). On the other hand, our study did not detect long-term inter-individual

Fig 4 Effect of hunger on participation in prey capture. Starved spiders participate more frequently than satiated spiders (*n*=9 colonies)

behavioural differences in web building, while earlier shorter-term studies have yielded equivocal conclusions (for e.g. Lubin 1995; Settepani et al. 2013; Wright et al. 2014).

Long-term behavioural consistency in prey capture

In our long-term experiments, colonies were maintained under controlled and stable feeding conditions. Under these conditions, some spiders consistently participated more in prey capture than others in the colony. The results from our statistical model show that when food is regular and sufficient, the multi-step process of prey capture, which includes restraining, immobilising and transporting the prey into the retreat, is accomplished by consistent participants. Such consistency in prey capture has been reported earlier in *S. sarasinorum* over the short duration of 3–10 days when feeding was adequate or ad libitum (Grinsted et al. 2013; Settepani et al. 2013). Here, we show that behavioural consistency seen in prey capture over the short term also persists over a considerable part of the adulthood of spiders. The model for prey capture indicated behavioural consistency, while repeatability scores for individual participation were low. This may be explained by the wide range of repeatability scores associated with different behaviours. For instance, aggression and mating behaviours are highly repeatable compared to the low repeatability associated with foraging behaviour (Bell et al. 2009). Our repeatability scores are comparable to other foraging studies in insects such as scorpionflies and water striders (Blackenhorn and Perner 1994; Missoweit et al. 2007).

In our study, while individuals displayed consistency, they also showed low plasticity in prey capture under conditions of constant and adequate prey availability (Fig. 2, Table 1). Prey capture is a collective behaviour, requiring a swift and coordinated response amongst spiders to subdue a prey that can even be potentially risky. Therefore, under such conditions, low plasticity could be advantageous in achieving predictable responses in collective behaviours such as prey capture. The capacity for plasticity is generally thought to insure against unfavourable or changing environmental conditions (Briffa et al. 2008; Bell et al. 2009; Dingemanse et al. 2010), while a lack of plasticity may be explained by the costs incurred in producing or maintaining plasticity (Sih et al. 2004).

Role of prey scarcity on behavioural consistency

When we increased the contrast between experimental conditions, i.e. prey availability, we observed that starvation induced a higher response from individuals (Fig. 4). When prey are scarce, competition for feeding is likely and consequently a greater proportion of spiders scramble to participate in the prey capture process, perhaps to benefit from early access to prey (Willey and Jackson 1993; Whitehouse and Lubin 1999). Thus, though behavioural consistency in individuals'
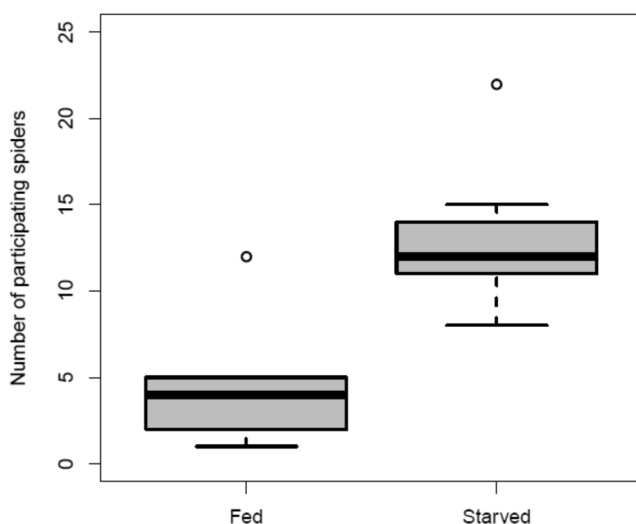
responses can contribute to task specialisation in prey capture, spiders remain conditionally plastic and alter their participation depending on hunger. Such latent plasticity can benefit the individual and the colony under changed ecological conditions such as resource availability, predation pressure, and parasite load; these factors are known to play a role in modulating personalities even in vertebrates (Dingemanse et al. 2004; Réale et al. 2010). In regions with pronounced wet monsoonal and dry months, such as our study sites, prey availability can be seasonally variable (Majer et al. 2013), which in turn is likely to affect the rate of prey interception on webs and food availability for spiders. Our laboratory experiments mirror the natural dynamics in prey abundance and its consequences for modulating individual behavioural consistency. Therefore, we argue that studying behavioural consistency over longer periods is critical as it captures environmental fluctuations that individuals may face over their lifetime. The increased participation of individuals during the starvation treatment can be potentially explained by a gain in experience as trials progressed, irrespective of individual feeding histories. However, we believe that our results are the outcome of the feeding/starvation treatments, because individuals' participation in the laboratory and field experiments did not show an effect of trial number. This implies that spiders neither systematically increased nor decreased their participation with time, in contrast to what would be predicted by individuals gaining experience.

When considered together, the results of the field and laboratory experiments show that participation in prey capture is perhaps driven by behavioural consistency when food is adequate. When prey is scarce, hunger overrides the effect of consistent behavioural differences between individuals, possibly leading to a reduced degree of task differentiation in the colony. In a recent study, Keiser et al. (2014) reported that body condition was more important in foraging than personality attributes in *S. dumicola*, a congeneric African species. Despite the different experimental paradigms, both our study and the study by Keiser et al. (2014) show that individuals' 'body status' can interact with and diminish the role of individual personalities or behavioural types.

Absence of behavioural consistency in web maintenance

Studies of web maintenance behaviour in various social spider species have produced contrasting conclusions with respect to the presence of behavioural types or personalities. While some studies have reported inter-individual differences in participation in web building (Lubin 1995; Keiser et al. 2014; Wright et al. 2014), our study and another (Settepani et al. 2013) did not find such differences. These contrasting findings may be explained by the vastly different measures of participation in web building across these studies. In general, web building behaviour is understudied compared to prey capture; a closer

look at the sub-tasks involved in web construction may reveal differences in the degree of collective participation and coordination between these two behaviours. This remains to be tested empirically.

What might be the reason for finding consistency in one behaviour and not in the other? When contrasted with prey capture behaviour, which requires a swift and coordinated response from multiple individuals, a predictable and timely response is likely to be less crucial in web maintenance, perhaps requiring lesser specialisation in this behaviour amongst individuals in the colony. A broad consensus that participation in prey capture is largely guided by behavioural types or personalities is seemingly emerging in over half a dozen species of social spiders belonging to the Old world genus (*Stegodyphus*) and the New World genus (*Anelosimus*) (Keiser et al. 2014). On a cautionary note, studies so far have not investigated temporal consistency relative to life stages. The temporal salience of behavioural types as well as its interaction with environmental conditions that we have shown in *S. sarasinorum* is the first attempt to understand the dynamics in behavioural consistency and needs to be explored in other social spider lineages.

Absence of a behavioural syndrome between prey capture and web maintenance

An individual's participation in prey capture was not correlated to its participation in web maintenance, indicating the absence of a behavioural syndrome. A negative correlation between these behaviours would point towards a high degree of exclusivity in task differentiation, while a positive correlation would imply the presence of individuals with high propensity for both tasks. The lack of a behavioural syndrome is likely due to the differing levels of risk and energetic investment associated with these behaviours. Prey capture is risky as dangerous prey can inflict fatal injuries, while web maintenance involves comparatively lower risk, especially since it is performed at night when predation is generally presumed to be lower (Cloudsley-Thompson 1995). The absence of a correlation points to behavioural flexibility as shown in task partitioning in multivoltine social insects (Dornhaus 2008; Gordon 1989; Robinson et al. 2009; Jandt et al. 2014), thus ensuring that the colony is buffered against changing conditions. Behavioural flexibility in social spiders is likely to be even more salient since they have univoltine life cycles with slow growth and extended time to reproduction, as a result of which individuals are more likely to experience greater environmental fluctuations over their life spans. Hence, a greater redundancy in task specialisation could buffer against unfavourable conditions.

In sum, we demonstrate that behavioural consistency in foraging is plastic and strongly affected by extrinsic factors such as prey availability, emphasising the importance of

studies that encompass multiple contexts and relevant durations. Consistent individual differences in prey capture, a more equitable participation in web maintenance and the lack of a syndrome between the two behaviours, together suggest a form of quasi-specialisation in *S. sarasinorum* with ample scope for redundancy in task structuring, and with potential implications for colony efficiency and survival.

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