Behavioral Ecology and Sociobiology (2019) 73: 35
https://doi.org/10.1007/s00265-019-2645-4

ORIGINAL ARTICLE

Early ontogenic emergence of personality and its long-term persistence in a social spider

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Received: 20 September 2018 / Revised: 29 January 2019 / Accepted: 7 February 2019 / Published online: 21 February 2019

Abstract

Recent studies increasingly show that personality types in animals can vary with time. Personality types including boldness and aggression have been recently reported as important determinants of collective task performance, task specialisation and task proficiency in social spiders. These studies were performed in subadult and adult spiders and over the short term (3–15 days). Therefore, the ontogeny of these personality types and its persistence over timescales relevant to the lifespan of any social spider species remains unknown. In the social spider *Stegodyphus sarasinorum*, we investigated 1) if early instar juveniles exhibited consistent and repeatable personality types, 2) if personality types persisted over the long term in subadults and 3) if personality types are influenced by subadult body condition. Juveniles (3rd and 4th instars) showed consistent inter-individual differences and repeatability in boldness and aggression (across 21 days). Subadults showed consistency in boldness and aggression over a duration of 51 days, which covers a significant part of the subadult stage. However, repeatability of these traits declined over the long term. Moreover, boldness and aggression were not influenced by body condition (nutritional state) of subadults. Thus, we hypothesise that the early ontogeny of personality and its long-term persistence can influence behavioural propensities and task partitioning through later life stages in social spider colonies.

Significance statement

Personalities have been demonstrated in a number of animal species. In animal societies, individuals with different personality types are known to engage in different activities within the group, leading to overall efficiency. Personalities have recently been shown to exist in social spiders. For example, aggressive spiders have a greater tendency to hunt prey than less aggressive individuals. However, for most animals, it remains unknown whether personality types manifest in very young individuals. Here, we show for the first time in social spiders that juveniles have personalities just as in adults. We also show that personality types persist over significant portions of individuals' life spans. These findings show that stable personality types can be important in collective tasks such as capturing prey.

Keywords Ontogeny · Personality · Repeatability · Social spiders · *Stegodyphus sarasinorum*

Introduction

Animals within a population may exhibit stable and consistent inter-individual differences in personality traits such as boldness, aggression, exploration, neophobia and sociability (Dall et al. 2004; Sih et al. 2004a; Réale et al. 2007; Dall and Griffith 2014). Even invertebrates with relatively simple nervous systems may exhibit consistent personality types (Briffa and Weiss 2010; Kralj-Fiser and Schuett 2014). Though individuals can be categorised into personality types depending on the average level of their behavioural response, variation across time and context in such responses has been noted in several animal taxa (Dingemanse et al. 2010a). For example, an aggressive individual may also exhibit high boldness (due to a positive correlation between boldness and aggression) only in the presence of a predator (predator as context; Bell and Sih 2007; Dingemanse et al. 2010b). Thus, individuals show plasticity in personality traits depending on extrinsic

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Communicated by J. Pruitt

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(e.g. environment) and/or intrinsic (such as body condition, sex, ontogeny, and maternal effects) factors (Dall et al. 2004; Nussey et al. 2005; van Oers et al. 2005; Stamps and Groothuis 2010; Sih et al. 2015).

Inter-individual differences in personality types and its repeatability may not persist over time, especially if personality traits are confounded by a rapidly changing internal state of the animal (Sih et al. 2015). Previous studies have shown that repeatability in personality traits is generally high when observed over short intervals, as the animal is more likely to be in the same internal state (Bell et al. 2009; Dingemanse et al. 2012). Long term personality studies in different species have also shown that repeatability varies depending on the type of personality trait and the animal species being studied (for example, see David et al. 2012; Niemelä et al. 2012; Wilson and Krause 2012; Herde and Eccard 2013). Therefore, there is mixed empirical support regarding the consistency of personality over longer durations. For example, firebugs (Gyuris et al. 2012) and frogs (Wilson and Krause 2012) showed consistency in personality traits over the long term, while fishes (Bell and Stamps 2004) and marmots (Petelle et al. 2013) did not. Thus, consistent behavioural responses to stimuli over the short term cannot be assumed to be stable and repeatable over an individual's life-span. In fact, there is evidence that short term personality studies may even misclassify personality traits of recently captured wild animals in laboratory studies (Biro 2012).

Inter-individual consistency in personality, if stable across time, is thought to have important biological consequences for persistence of the group during unfavourable conditions (Sih et al. 2004b), in speciation (Wilson 1998), and can favour cooperation in social animals (McNamara et al. 2004). In social animals, including ants and social spiders, consistent inter-individual variation in personality is implicated in efficient task specialisation, and colonies composed of mixed personalities were more successful than colonies that were relatively homogenous (Modlmeier and Foitzik 2011; Pruitt and Riechert 2011; Modlmeier et al., 2012).

Social spiders have recently received a lot of attention in animal personality studies. In the absence of age polyethism and morphological castes in social spiders (Avilés 1997; Lubin and Bilde 2007), personality types are thought to lead to task specialisation, division of labour (Grinsted et al. 2013; Holbrook et al. 2014; Wright et al. 2015) and task proficiency (Wright et al. 2014). Personality types (bold/shy and aggressive/docile) are known to exist within colonies (Pruitt et al. 2008; Grinsted et al. 2013; Keiser and Pruitt 2014) and intercolony variation in personality traits have been reported (Pruitt et al. 2013; Keiser et al. 2014). Collective behaviours in social spiders such as prey capture and allomaternal brood care are performed by individuals with specific personality types. For example, some individuals within colonies of *Stegodyphus sarasinorum* and *Stegodyphus dumicola* attacked prey more consistently than others (Grinsted et al. 2013; Pruitt et al. 2013; Keiser et al. 2014). In *Anelosimus studiosus*, consistent prey capture was linked to aggressive personality types, while docile individuals participated disproportionally in brood care (Holbrook et al. 2014). All these studies have examined personality only over the short term (3–15 days) in late instar subadults and adults.

Since social spiders have a lifespan of ~ 1 year (Lubin and Bilde 2007), it is unclear if personality types persist over longer durations, or if they are confounded by the current state of the individual. Therefore, it remains unknown if within-individual personality traits persist over time, which can be captured only when spiders are repeatedly observed over longer timescales. If individuals show substantial within-individual variation in personality over time, then the loss of or a reduction in inter-individual consistency and its repeatability maybe expected. There is some evidence that consistent inter-individual differences in behaviour/personality depends on the spider's internal state. For instance, in well-fed *S. sarasinorum*, consistent inter-individual differences in prey capture behaviour were observed, while hungry spiders showed more equal participation (Beleyur et al. 2015). Similarly, repeatability in aggression reduced in *Anelosimus studiosus* when feeding levels were low (Lichtenstein et al. 2016). It is therefore essential to understand if within-individual personality types persist over timescales commensurate to the lifespan of social spiders, since personalities are implicated in collective task participation and task proficiency. Often the mechanisms contributing to long-term personalities in animals are heritable (Dochtermann et al. 2015) and in this context, it would be interesting to understand how personality types are inherited in social spider colonies in which individuals are highly related due to inbreeding with natal siblings (Smith and Engel 1994; Lubin and Bilde 2007). Alternatively, personality types in social spiders may also emerge gradually over ontogeny due to prior experience (Gordon 1996; Grinsted and Bacon 2014). If so, then repeatability in personalities is expected to be lower in the early growing instars when compared to later instar stages and personality-mediated task partitioning should develop with age in social spiders.

Theoretical models predict two mutually independent ways by which the internal state (such as body condition) of an animal influences its personality. Animals in higher body condition are likely to be less bold and less aggressive in order to guard their acquired nutritional state or resources (Clark 1994; Wolf et al. 2007). On the other hand, animals in higher body condition can be bolder and more aggressive in order to sustain their state (see McElreath et al. 2007; Sih and Bell 2008; Sih et al. 2015). However, these predictions have received mixed empirical support in social spiders. For instance, more aggressive *Anelosimus studiosus* individuals (a new world social spider) have higher body condition (Pruitt et al. 2011), while bolder *Stegodyphus dumicola* individuals (an old world social spider) have lower body condition (Wright et al. 2015).

Therefore, the influence of body condition on personality types can follow different trajectories in new and old world social spider species and thus merits further empirical investigation.

In this study, we asked if bold and aggressive personality traits manifest during the early growing instars in individuals of the social spider *Stegodyphus sarasinorum*. Since spiderlings (hereafter referred to as juveniles) engage in collective prey capture and web building without help from adult spiders after gerantophagy (a phenomenon wherein adults are consumed by juveniles) in their 2nd instar (Jacson and Joseph 1973), we asked: 1) Do juveniles (3rd and 4th instars) show consistency in these two personality traits which are known to be associated in task partitioning and task proficiency? 2) Are bold and aggressive individuals consistent and repeatable in these traits over the long term (51 days) during later instars? *S. sarasinorum*, like most other social spiders, is a slow-growing species with a lifespan of ~ 12 months. The subadult stage in *S. sarasinorum* lasts approximately 70 days (Jacson and Joseph 1973), so a test for consistency over a 50-day period would sufficiently reflect the persistence of within-individual personality during most of the subadult stage. 3) Does short-term repeatability in these personality traits corroborate with long-term repeatability in subadults? 4) Are personality types in subadults linked to their body condition? Separate colonies were used for personality assays of juveniles, and later instar subadults, since the same individuals could not be assayed from early to later instars due to frequent moulting resulting in us being unable to ascertain identities of painted individuals.

Methods

Study species

Stegodyphus sarasinorum Karsch (Eresidae) is an inbred social spider (Smith and Engel 1994) found in arid and semi-arid parts of the Indian subcontinent (Jacson and Joseph 1973; Platnick 2017). Colonies are female-biased (Avilés 1997; Lubin and Bilde 2007), and individuals live within dense silken retreats. Females engage in cooperative behaviours such as prey capture, web maintenance and brood care without exhibiting any apparent morphological castes (Jacson and Joseph 1973; Avilés 1997; Lubin and Bilde 2007; Settepani et al. 2013). Individuals moult 12 times in their lifespan, before reaching the ultimate instar (Jacson and Joseph 1973). Females are semelparous (but can produce a second egg sac if the first is removed) and care for the young by regurgitation. Subsequently, mothers and other adult females within the colony are consumed by 2nd instar juveniles, after which the juveniles independently engage in collective behaviours such prey capture and web building/maintenance (Jacson and Joseph 1973). Adult spiders show an association between boldness and prey capture (Grinsted et al. 2013; Settepani et al. 2013).

Spider collection and construction of experimental colonies

We collected 13 colonies consisting of juveniles in the 3rd and 4th instars from Kuppam (12.75° N, 78.37° E), Andhra Pradesh, India, in October 2017. We also collected 14 colonies consisting of subadults (2 instars before the final instar) from Kuppam in January 2015, and subjected them to personality tests over the long term. We collected seven colonies consisting of subadults (2 instars before the final instar) from Krishnagiri (12.51° N, 78.21° E), Tamil Nadu, India, in May 2018 for short term personality tests. Colonies were brought back to the lab in well-ventilated plastic boxes (25 × 18 × 10 cm) within 15 h. Thirty juveniles/subadult spiders were randomly picked from each colony to construct the corresponding experimental colonies. Two colonies which were used for long term experiments had only 19 and 11 females respectively, so the entire colony was used to build experimental colonies in these cases. Individual juveniles/spiders were then uniquely marked using acrylic non-toxic water colours (with remarking of moulted spiders) and maintained inside rectangular well-ventilated plastic boxes (juveniles in 8.5 cm × 5 cm × 4 cm boxes; subadults in 20 × 13 × 3.5 cm boxes). Juveniles/spiders were given 3 days to acclimatise and build capture webs. Juvenile colonies were fed with one honeybee (*Apis cerana*) each and then were subsequently fed a day before each assay (1 bee once every 4 days). Subadult colonies subjected to long term tests were fed with one honeybee a day before each assay and with 2 honeybees after completing the assay. Subadult colonies subjected to short term tests were fed with 2 honeybees before the start of the assays. On this diet, we ensured that juveniles/spiders were neither overfed nor starved, as hunger levels are known to play an important role in behavioural consistency with respect to prey capture (Beleyur et al. 2015; Lichtenstein et al. 2016). One subadult colony subjected to long term tests suffered heavy mortality for unknown reasons and was later excluded from the analyses. Juvenile individuals were subjected to six trials of boldness and aggression tests.

Boldness and aggression assays

Boldness and aggression assays were repeatedly performed once every 4 days over 21 days (six trials) as described in Grinsted et al. (2013) with minor modifications. Juveniles took longer to build capture webs inside boxes after each assay because of which we were unable to perform trials on consecutive days. Juveniles were isolated individually in 150 ml plastic cups for 2 h before performing boldness assays as follows: Individual juveniles were placed in the centre of a rectangular plastic dish (12.5 × 8.5 × 2 cm) and given 1 min to acclimatise, following which a rapid jet of air was delivered to the spider using a 5-ml plastic medical syringe without a needle. Most juveniles reacted to the air-puff by huddling, and the time to resume movement in seconds (s) was noted. Juveniles that did not huddle were given a score of 0 s. Thus, low scores indicated greater boldness. The assay ended if a juvenile did not resume movement within 20 min of delivering the air-puff. After the boldness assays, juveniles were again kept in isolation for 2 h as mentioned above, and then aggression assays were performed by prodding the abdomen of the juvenile with the blunt end of a tooth-pick and assigning an aggression score to each spider (1–6 ranging from low to high) depending on the response: huddle (1), run (2), walk (3), lurch (4), no response (5) or leg raise in a threat stance (6). Higher scores indicated greater aggression. On completion of the aggression assays, juveniles were returned to their respective experimental colonies.

Subadult spiders

Test for personality over the long term (51 days) Boldness and aggression assays were repeatedly performed once every 10 days (January–March 2015) over 51 days (six trials) as described above.

Test for personality over the short term To see if repeatability in personality types declined over the long term, we subjected subadults to short term personality tests over four consecutive days as described above.

Estimation of body condition Body condition is a good predictor of nutritional status in spiders and other animals (Schulte-Hostedde et al. 2001; Parthasarathy and Somanathan 2018). Before subjecting subadults to long term personality assays, individuals were weighed to the closest 0.1 mg using a digital weighing balance (Mettler Toledo JB1603–C/Fact) and were photographed alive at × 1 magnification under a dissection microscope (Leica, EC 3). Cephalothorax widths (CW; distance between the last posterior pair of eyes) were obtained from these images. Body condition was estimated by regressing body weight against CW, after log transformations of both these variables. From the slope (b_{OLS}) and Pearson's R, we calculated body condition by the scaled mass index method (SMI), as described by Peig and Green (2009):

$$\mathrm{SMI} = \text{body weight}\,(\text{average CW within a population}/\text{Individual CW})^{\mathrm{bOLS}/R}$$

Statistical analyses

All statistical analyses were performed in *R* (V 3.5.1, R Core Team 2018). Only individuals that survived the entire duration of the experiment were included in the analyses (191 out of 390 juveniles; 246 out of 390 subadults subjected to long term assays; 203 out of 210 subadults subjected to short term assays). To check for inter-individual differences in boldness, we built three separate general linear mixed models (GLMM) using the *lme4* package in *R* (Bates et al. 2015) for juveniles, subadults subjected to long term as well as to short term personality tests. In < 10% of observations spiders did not huddle (boldness score of 0 s) or took > 20 min to resume movement; these cases were excluded from the analyses. Boldness scores were Box-Cox transformed to meet the assumptions of the linear model. In these models, the transformed boldness score (latency to resume movement in s) was the continuous response variable, trial number was the fixed effect, and spider ID nested within colonies was the random effect. Model assumptions were diagnosed by inspecting the residual QQ plots and plots of predicted vs. fitted values. Addition of random slopes (trial number) at the level of individuals did not improve the model fit (as evident from the non-significant deviance value, χ^2), but did so at the level of colonies (except for juveniles which resulted in an over-fitted model). Therefore, the final model we present here includes random slopes at the colony level for subadults subjected to short and long term personality tests. In the case of juveniles, we present the model with only random intercepts.

To test for inter-individual variation in aggression, we built three separate cumulative link mixed models (CLMM) using the *ordinal* package in *R* (Christensen 2018) for: juveniles/subadults subjected to long term and short term personality tests. CLMM was used in this case because aggression scores were in the ordinal scale. Here, ordinal aggression score (1–6) was the response variable, trial number was the fixed effect, and juvenile/subadult ID nested within colonies was the random effect. Inclusion of random slopes (trial number) at the level of colonies did not improve the model fit, but did so at the level of individuals for subadults (but not for juveniles). Therefore, the final model is a multilevel model with random slopes for subadult individuals, while we present the intercept-only model for juveniles. To estimate variation in boldness and aggression explained by individuals (juvenile ID/spider ID), we compared the above random intercepts GLMM and CLMM models consisting of only colony ID as the random effect (null model), with models including juvenile ID/subadult ID nested within colonies as random effects. Significant deviance values (χ^2) from the null model were considered an indicator of inter-individual variation in boldness and aggression.

Next, we checked if boldness varied between- and within-spiders across time (trials). Box plots depict this variation, but does not show the direction of variation (though it is still useful for visualisation; Fig. 1). We built random intercept random slope models for individuals and colonies to better depict this variation. Since the frequentist linear mixed model approach resulted in over-fitted models, we used a Bayesian approach to fit the multilevel mixed model using the *rstanarm* package in R (Goodrich et al. 2018). The fixed and random effects were similar to the models described above, except that trial numbers were included as random slopes at the level of both individuals and colonies. The weakly informative priors available by default in the package were used, and the model was run with 2000 iterations and 6 chains (8 chains for subadults subjected to short term personality tests) such that all effective sample sizes were at least > 1000. Model diagnostics were checked using the *shinystan* app of *rstanarm*. From these models, reaction norm plots (also known as random slope random intercept plots) were built using the *sjPlot* package in R (Luedecke 2018). In these plots, the y-intercepts depict inter-individual variation while the slopes of lines depict consistency through trials (Dingemanse et al. 2010a). Since aggression scores were in the ordinal scale, we were unable to generate reaction norm plots for this personality measure.

Repeatability estimates are a qualitative descriptor of consistency in personality traits over time (de Villemereuil et al. 2018). Repeatability in boldness was calculated by the rptR method in R as described by Nakagawa and Schielzeth (2010), with boldness scores as the continuous response variable, trial as fixed effect and juvenile/spider ID as random effect. The model was run with 5000 bootstrap runs, and the variance explained by the fixed effect (marginal R^2 of trials) was determined following Nakagawa and Schielzeth (2013). Since aggression scores were in the ordinal scale, its repeatability was determined by MCMC linear mixed models with ordinal error structure using the *MCMCglmm* package (Hadfield 2010) in *R*. We used a parameter extended prior with the residual variance fixed to 1, and with $V = 1$, nu = 1000, α.mu = 0 and α.V = 1 for the random effects. These models were run with aggression score (1–6) as the ordinal response variable, trial number as fixed effect and subadult/juvenile ID as random effect. Further specifications of the model are as follows: iterations = 50,000–700,000, thinning interval = 50 and sample size = 13,000.

Finally, we examined the effect of body condition on boldness and aggression of subadults subjected to long term personality tests only, by building GLMM or CLMM models with log transformed boldness scores (to meet the assumptions of the model) or aggression ranks of individuals from the first trial as the response variable, body condition as fixed effect and colony ID as random effect. Since we measured the body weight and CW of spiders only once, 3 days before the first personality trials, these variables may have changed unequally for individuals during the course of the experiment (51 days). Therefore, we included boldness or aggression scores from the first trial alone in the model.

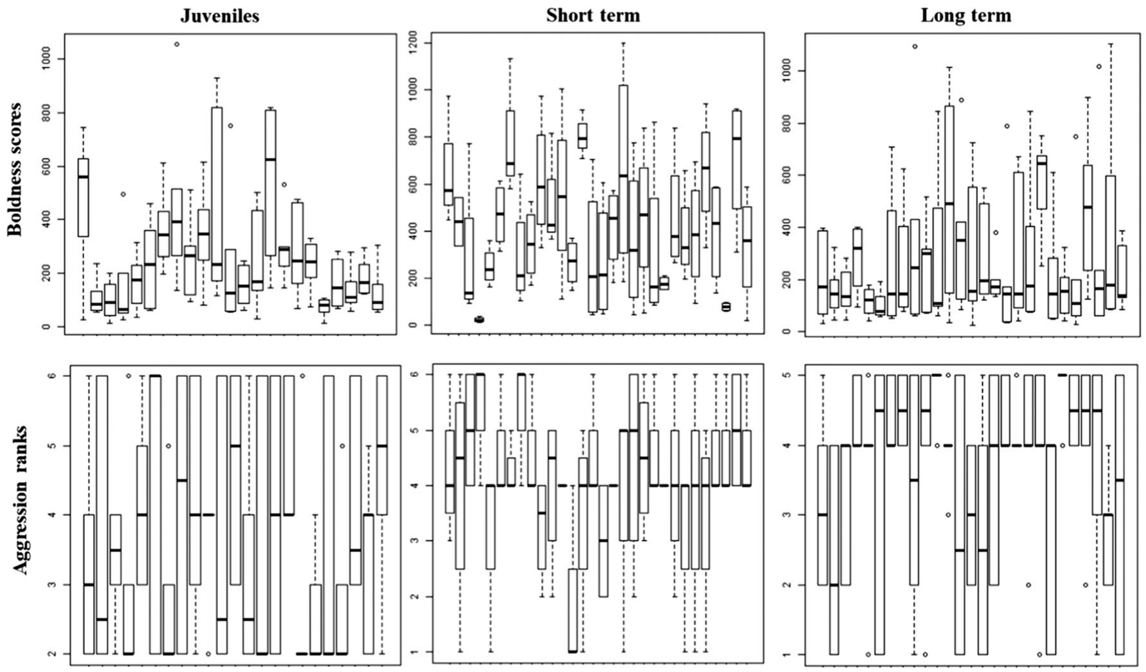

Fig. 1 Boxplots showing variation in boldness scores and aggression levels of individuals from three representative colonies. The top panel represents boldness while the bottom panel represents aggression. Left panel represents a juvenile colony, middle panel represents a colony from short term tests while the right panel represents a colony subjected to long term personality tests. Each bar represents an individual within a colony. Open circles indicate outliers. Individuals that show less variation in boldness and aggression exhibit greater consistency in these personality traits

Data availability The datasets used in the current study are available upon request to the corresponding author.

Results

Personality in juveniles

Juveniles exhibited significant inter-individual differences in boldness and aggression as evidenced by the significant variation explained by juvenile ID as random effect, after comparison with null model (Table 1, Fig. 2). Aggression, on an average, increased as trials progressed (Table 1), though the variance attributed to trials was only 0.6% (R^2 values, Table 2). Inter-individual differences in personality types were repeatable, although repeatability in aggression was lower than boldness (Table 2).

Short term personality in subadults

Spiders exhibited significant inter-individual differences in boldness and aggression over the short term (4 days) as evidenced by the significant variation explained by the random effect (spider ID) when compared to the null model (Table 1, Fig. 3). Repeatability in boldness was similar to juveniles subjected to short term personality tests (Table 2). For boldness, significant random slopes at the level of colonies ($\chi 2 = 38.36$, $P < 0.01$) suggests that some colonies showed greater variation (or lower consistency) over time (Fig. 3). For aggression, significant random slopes at the level of individuals (likelihood ratio = 6.51, $P < 0.05$) suggested that individuals differed in their within-individual variation (consistency) in aggression rank over time.

Long term personality in subadults

Individuals showed significant inter-individual differences in boldness and aggression over the long term (51 days, Table 1, Fig. 3). However, repeatability declined relative to short term estimates, suggesting that spiders are less consistent in personality traits over longer durations (Table 2, Fig. 3). Trials were a significant predictor of aggression, but not of boldness (Table 1). Aggression, on an average, reduced as trials progressed. However, the variance associated with trials (R^2) in influencing aggression was only 0.2% (Table 2). Significant random slopes for boldness at the level of colonies ($\chi^2 = 28.09$, $P < 0.01$) showed unequal within-colony variation (consistency) in boldness over time (Fig. 2). Significant random slopes for aggression at the level of individuals (likelihood ratio = 15.0, $P < 0.01$) suggested that some individuals varied more than others (unequal consistency) in aggression ranks over time.

Table 1 Inter-individual variation in boldness and aggression in juveniles (over 21 days) and subadults over the short (4 days) and long term (51 days) in *S. sarasinorum*. Models with random effect (subadult/juvenile ID) explained significant variation in boldness and aggression scores when compared to the null models (as evidenced by the significant χ^2 or likelihood ratio test (LRT) values), indicating inter-individual differences in personality. Aggression increased as trials progressed for juveniles, but decreased for subadults subjected to long term tests. $(e)^{\beta}$ refers to odds. Global intercepts are unavailable for ordinal regressions. β coefficients and their 95% CI for boldness are in the Box-Cox transformed scale. *Indicates significance at $P < 0.05$

Model	Boldness in juveniles (21 days)			Aggression in juveniles (21 days)		
Random effects	χ^2	*df*		LRT	*df*	
Juvenile ID	95.13*	1		27.20*	1	
Fixed effects	β	95% CI	*t*	$(e)^{\beta}$	95% CI	*z*
Intercept	4.89	4.66–5.13	41.81*		NA	
Trial number	−0.01	−0.04-0.01	−1.06	1.16	1.09–1.23	4.71*
Model	Boldness in spiders over the short term (4 days)			Aggression in spiders over the short term (4 days)		
Random effects	χ^2	*df*		LRT	*df*	
Spider ID	51.65*	1		15.47*	1	
Fixed effects	β	95% CI	*t*	$(e)^{\beta}$	95% CI	*z*
Intercept	11.15	9.02–13.29	10.91*		NA	
Trial number	0.41	−0.34–1.17	1.13	0.97	0.86–1.11	−0.31
Model	Boldness in spiders over the long term (51 days)			Aggression in spiders over the long term (51 days)		
Random Effects	χ^2	*df*		LRT	*df*	
Spider ID	6.21*	1		43.23*	1	
Fixed Effects	β	95% CI	*t*	$(e)^{\beta}$	95% CI	*z*
Intercept	8.97	7.95–9.97	18.08*		NA	
Trial number	−0.07	−0.27-0.12	−0.78	0.92	0.87–0.97	−2.67*

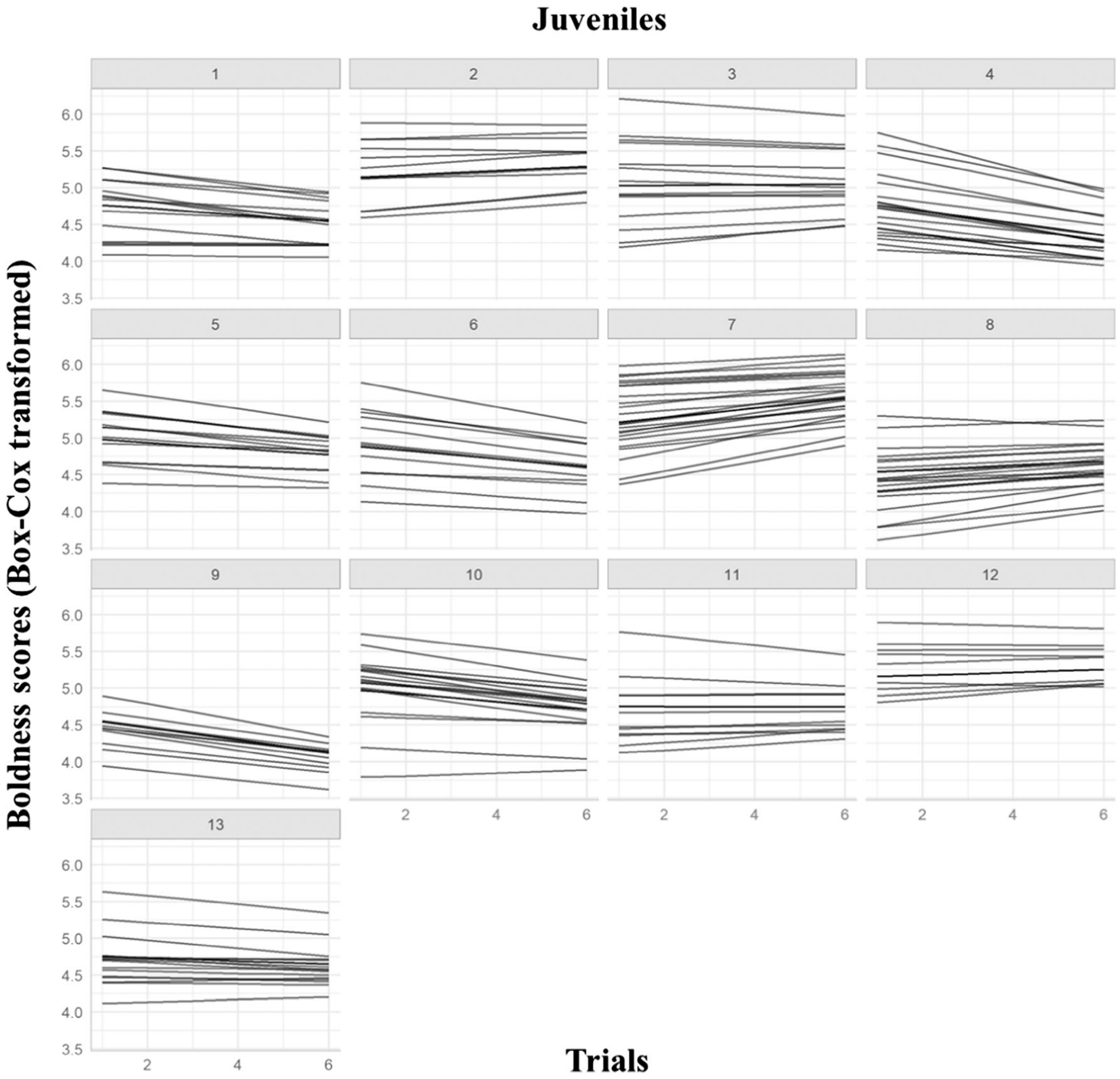

Fig. 2 Reaction norm plots (Random intercept random slopes) depicting within-and between-juvenile variation in boldness across trials. Numbered boxes (1–13) represent juvenile colonies. X-axis represents trial numbers while Y-axis depicts Box-Cox transformed boldness scores. Each line represents an individual within a colony. Lines with similar slopes within colonies indicate similar within-individual variation (consistency) within colonies. Variation in the intercept indicates inter-individual differences in boldness within colonies

Table 2 Repeatability in boldness and aggression in juveniles (over 21 days), subadults over the short term (4 days) and long term (51 days) in *S. sarasinorum*. Repeatability in personality (R) declines over the long term. *$P < 0.001$; # indicates marginal R^2 for boldness and McFadden's R^2 for aggression. Trials explained very little variance in boldness and aggression. 95% CI for McFadden's R^2 and P values for repeatability in aggression determined by MCMC GLMM are unavailable

		Boldness		Aggression	
Juveniles (over 21 days)	Repeatability	R	95% CI	R	95% CI
	Juvenile ID	0.32*	0.25–0.38	0.13	0.08–0.20
	Trials	0.001#	0.0–0.006	0.006#	NA
Subadults over the short term (4 days)	Subadult ID	0.32*	0.24–0.40	0.21	0.14–0.30
	Trials	0.01#	0.003–0.03	0#	NA
Subadults over the long term (51 days)	Subadult ID	0.10*	0.05–0.14	0.14	0.09–0.19
	Trials	0.005#	0.001–0.01	0.002#	NA

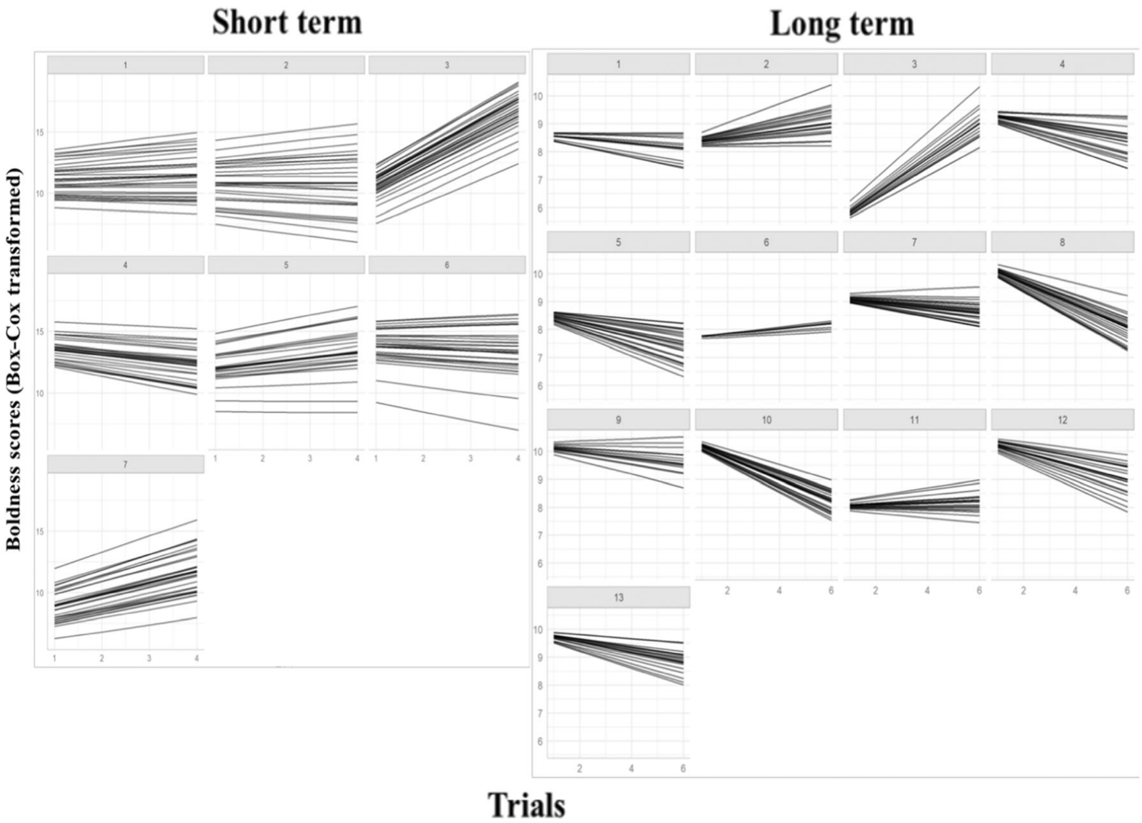

Fig. 3 Reaction norm plots (Random intercept random slopes) showing between- and within-individual variation in boldness across trials in subadults. Plots on the left panel represent colonies subjected to short term personality tests (over 4 days), while plots on the right panel represent colonies subjected to long term tests (over 51 days). Each numbered square represents a colony number. The Y-axis denotes Box-Cox transformed boldness scores while the X-axis denotes trial numbers. Lines represent individuals within colonies. Lines with similar slopes within colonies indicate similar within-individual variation (consistency). Subadults subjected to short term personality tests show greater variation in the intercepts, indicating greater inter-individual differences in boldness. Similarly, subadults subjected to long term personality tests show greater variation in slopes relative to spiders subjected to short term tests, indicating greater within-individual variation (or lower consistency) in boldness over time

Influence of body condition of spiders on boldness and aggression

Body condition was negatively correlated with cephalothorax width (CW) (Spearman's rho = −0.16, $P < 0.01$) but was positively correlated with body weight (Spearman's rho = 0.16, $P < 0.01$). There was substantial variation in body condition between individuals across experimental colonies (range = 33.72–83.88, mean ± SD = 48.78 ± 7.82). Yet, body condition was not a significant predictor of either boldness or aggression (Table 3), suggesting that the current nutritional state did not influence personality types of individuals.

Discussion

In this study, we show that early instar juveniles of the social spider *Stegodyphus sarasinorum* exhibited inter-individual consistency in personality traits. We also show that in subadults these personality traits are stable over the long term (51 days, which covers a large part of the subadult lifespan). However, there was a reduction in the repeatability of personality traits over the long term relative to the short term (4 days), suggesting temporal variation in the personalities of individuals. Moreover, body condition did not influence boldness and aggression, suggesting that personality types are unlinked to the current nutritional status of the individual. Together, our results suggest that inter-individual differences in personality types tend to persist over durations

Table 3 GLMM and CLMM models show that body condition of spiders did not influence boldness and aggression as evidenced by non-significant β and $(e)^{\beta}$ values respectively. $(e)^{\beta}$ represents odds. Estimates of the boldness are in the log scale. Global intercepts are unavailable for ordinal regressions. *Indicates significance at $P < 0.01$

Fixed effect	GLMM (boldness)			CLMM (aggression)		
	β	SE	*t*	$(e)^{\beta}$	SE	*z*
Intercept	5.37	0.53	9.95*		NA	
Body condition	−0.006	0.01	−0.68	0.96	0.01	−1.87

commensurate to the lifespan of spiders. Most importantly, early ontogenic emergence of personality in juveniles is interesting because this can potentially mediate collective task partitioning during later stages of their life history. Additionally, we speculate that the early ontogenic emergence may determine which females reproduce within social spider colonies in which reproductive skew is reported (Salomon et al. 2008).

Though personality mediated task partitioning has been repeatedly implicated in social spiders (Grinsted et al. 2013; Pruitt et al. 2013; Settepani et al. 2013; Keiser et al. 2014; Holbrook et al. 2014; Wright et al. 2014, 2015), the ontogenic emergence of personality types remained obscure. Since social spiders are inbred (Smith and Engel 1994; Lubin and Bilde 2007), with high genetic relatedness between individuals, it has been assumed that consistent inter-individual variation in personality is more likely to arise gradually through prior experience (see Gordon 1996 for social insects; Grinsted and Bacon 2014 for social spiders), and less likely through genetic inheritance. If personalities in social spiders indeed arise by social learning or through gaining experience in collective tasks, then inter-individual consistency in personality and its repeatability during early growing instars should be absent or low relative to older individuals. However, this was not investigated until our study, mainly due to difficulties such as mortality and frequent moulting leading to loss of individual identities over time. Here, we show that juveniles exhibited significant inter-individual consistency in boldness and aggression (Table 1) and repeatability in boldness was similar to short term repeatability in subadults (Table 2). However, repeatability in aggression in juveniles was lower ($R = 0.13$, Table 2) than in subadults over the short term ($R = 0.21$, Table 2). This may be because aggression as a trait is more labile in juveniles, or its repeatability may have reduced during the relatively longer duration of our experiment (21 days). The manifestation of personality traits in early instar juveniles suggest that they may be influenced by the genotype of individuals (despite inbreeding, some genetic variation exists within colonies; see Smith et al. 2009) or may have arisen through prior experience or social learning early in ontogeny such as during the stage when they were cared for by their (allo) mothers (1st and 2nd instars).

The benefits of consistent personality types in juveniles remain enigmatic. In juveniles, personality types may be implicated in maximising feeding by better access to prey and feeding positions for early attackers compared to individuals that scavenge (Whitehouse and Lubin 1999; Amir et al. 2000). Therefore, personality of juveniles and its persistence over time can determine personality-mediated task participation in later instars. We know that less than 50% of the females within the colony reproduce while the rest remain as helpers (Salomon et al. 2008). This reproductive skew is reportedly not because of body size asymmetries due to contest competition within the colony, but is likely to be an adaptation to maximise colony-level benefits through inclusive fitness (Grinsted and Bilde 2013). Therefore, we hypothesise that individual personality types which emerge early may be a group-level adaptation facilitating reproductive skew in adult social spiders. These are interesting questions worthy of investigation in future studies.

We also show that inter-individual differences in personality types persist in *S. sarasinorum* over the long term (51 days). However, repeatability estimates of boldness and aggression were lower over the long term, suggesting within-individual variation over time. Our short term repeatability estimates (for 4 days) for boldness and aggression were higher ($R_{\text{Boldness, Aggression}} = 0.32, 0.21$, Table 2) when compared to long term estimates ($R_{\text{Boldness, Aggression}} = 0.10, 0.14$, Table 2). Though repeatability in behaviour generally tends to decline when measured in the laboratory than in the field in many animals (Bell et al. 2009), short term repeatability estimates of personality in various social spider species was higher when colonies were held in boxes in the laboratory (Pruitt et al. 2013; Keiser et al. 2014), even for durations as long as 9 weeks (Lichtenstein et al. 2016). Therefore, it is likely that the reduction in the repeatability of boldness and aggression is largely because individuals showed relatively greater within-individual variation over the long term. Alternatively, as subadult spiders used for short and long term personality assays were from different populations, differences in repeatability estimates may simply be because of populational level differences in the consistency of personality types. Nevertheless, juveniles, which were collected from the same population as subadults in the long term assays, showed greater repeatability in boldness perhaps suggesting that reduction in repeatability in personalities over longer durations is likely to be due to temporal variation rather than population level differences.

A reduction in repeatability of personality over the long term may also perhaps be attributed to habituation of spiders, as on an average, spiders became less aggressive over the long term (Table 1). Boldness and aggression assays were designed to mimic avian (Riechert and Hedrick 1993) and invertebrate predators (Riechert and Johns 2003) respectively, so it is possible that spiders may have learnt that the assays were not associated with a predatory threat, leading to habituation (sensitization) which affected their responses in assays and caused a reduction in repeatability over the long term. However, this is unlikely as we performed the assays only once in intervals of 10 days. Moreover, the variance explained by trials in influencing aggression over time was low (0.6% for juveniles and 0.2% for subadults subjected to long term assays; R^2 values in Table 2). Besides, since habituation/sensitisation should affect all individuals within the group, this is unlikely to reduce repeatability (Bell et al. 2009). Therefore, the within-individual variation in personality traits maybe an adaptive response or is possibly associated with a slowly changing internal state of the individual (other than nutritional status), as we also show that personality types were not a mere manifestation of the current body condition of spiders.

Interestingly, personality types were not influenced by body condition. In the new world social spider *Anelosimus studiosus*, more aggressive spiders were associated with higher body condition (Pruitt et al. 2011). However, lesser food rather than body condition per se, reduced repeatability in aggression in these spiders (Lichtenstein et al. 2016). Similarly, spiders did not show consistent inter-individual differences in prey capture behaviour in *S. sarasinorum* when starved (Beleyur et al. 2015). As hunger precedes a reduction in body condition, together these results suggest that personality traits can be modulated by prey availability. When prey is abundantly available, spiders within the colony are likely to exhibit consistent inter-individual differences in behaviour/personality, while when prey is scarce such inter-individual differences are likely to reduce or disappear altogether. Besides, other intrinsic factors including biogenic amines have been shown to influence individual behaviour (Price 2010; Jones et al. 2011) and may explain inter-individual differences in personality types.

In conclusion, we show that consistent inter-individual differences in personality types emerge early during ontogeny in social spiders and are likely to persist over the long-term commensurate to their lifespan. The emergence of personalities in early life stages in individuals possibly influences propensities for performing certain behaviours and task partitioning in social spider colonies through later life stages—a proposition we consider worthy of enquiry. The relevance of early emergence and persistence of personalities within the ecological framework is poorly understood in spiders (Keiser et al. 2018) and in other animals. Moreover, the mechanisms leading to early ontogenic emergence of personalities in highly inbred social spiders with high genetic relatedness within colonies remains enigmatic and merits investigation in future studies.

Authors' contribution BP and HS conceptualised the study and designed experiments; CHJ and SK and BP performed experiments; BP analysed data; BP and HS wrote and revised the manuscript.

Funding information This study was financially supported by the Council for Industrial and Scientific Research (CSIR) India.

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