RESEARCH ARTICLE

ethology *international journal of behavioural biology* **WILEY**

# Long-Term Behavioural Syndrome in Subadult Indian Social Spiders But Not Over the Short-Term or in Juveniles

**Bharat Parthasarathy**[1] | **Hema Somanathan**[2] | **Jonathan Wright**[3]

[1]Indian Institute of Science, Bangalore, India

[2]School of Biology, Indian Institute of Science Education and Research, Thiruvananthapuram, India

[3]Department of Biology, Centre for Biodiversity Dynamics (CBD), Norwegian University of Science and Technology (NTNU), Trondheim, Norway

**Correspondence**
Bharat Parthasarathy, Indian Institute of Science, Bangalore, India.
Email: bharat.parthasarathy@uni-hamburg.de

**Present address**
Bharat Parthasarathy, Institute of Zoology, University of Hamburg, Hamburg, Germany

## Abstract

Animal personalities and behavioural syndromes have overarching implications for individual survival, fitness and cooperative task participation. In social spiders, personality in boldness and aggression, and their association into behavioural syndromes, are thought to play a role in individual participation and task specialisation in collective behaviours, such as prey capture. However, recent retractions of key publications in this field have exposed gaps and uncertainties in our understanding of factors governing task performance in social spider colonies. Here, we analyse an already-published data set on animal personalities in the Indian social spider *Stegodyphus sarasinorum* to investigate whether boldness and aggression form a behavioural syndrome and assess its persistence over the short- and long-term, and across age classes. Boldness and aggression were negatively correlated traits, forming a syndrome, but only over the long-term in subadult spiders, and not over the short-term in subadults or in juveniles. These results provide evidence for the existence of a behavioural syndrome in at least one social spider species. However, more work is now required to fully understand the observed inconsistencies in behavioural syndrome structures and animal personalities, as well as their possible role(s) in mediating task partitioning and collective performance in social spider colonies.

**KEYWORDS**
aggression, boldness, life stages, personality, *Stegodyphus sarasinorum*

## 1 | INTRODUCTION

Across a diverse range of taxa, populations of animals exhibit consistent individual differences (animal personality) in various behaviours, such as boldness, aggression, neophobia and sociability (Dall et al., 2004; Dingemanse, Kazem et al., 2010; Réale et al., 2007; Sih et al., 2004). Personality traits can be decomposed into among- and within-individual variation (Dingemanse & Dochtermann, 2013) in behaviour, which are group- and individual-level characteristics, respectively (Luttbeg & Sih, 2010). Personality traits can be the important determinants of individual and group survival (Bergeron et al., 2013; Dugatkin, 1992; Moiron et al., 2020; Mouchet et al., 2021),

reproductive performance and fitness (Le Coeur et al., 2015; Reaney & Backwell, 2007; Roth et al., 2021; but see Roth et al., 2019).

Such among-individual differences in various behavioural traits can be correlated across time and/or contexts to form behavioural syndromes (Dingemanse et al., 2012; MacKay & Haskell, 2015; Sih et al., 2004). For instance, a bold individual is also likely to be aggressive (see Garamszegi et al., 2012), resulting in the formation of a behavioural syndrome. Behavioural syndromes may constrain the expression of behavioural plasticity in individuals, which might in turn lead to the expression of sub-optimal behaviours in certain contexts (Dochtermann & Dingemanse, 2013; Johnson & Sih, 2007). For instance, funnel web spiders (*Agelenopsis aperta*) that are bolder

in contests against conspecifics are also more aggressive towards predators because of the positive correlation between boldness and aggression (Riechert & Hedrick, 1993). Hence, bolder spiders may also be likely to be inappropriately aggressive against predators, leading to suboptimal anti-predatory responses. Therefore, there has been increasing interest in animal personality studies in the evolution and maintenance of behavioural syndromes and the links with efficacy in task participation in cooperative social contexts.

Social animals often face the challenge of efficiently partitioning essential tasks. Many social animals overcome this challenge by dividing tasks broadly depending upon dominance hierarchies, morphological castes and/or age polyethism (Gordon, 1996; Nunes et al., 2014). However, some primitively eusocial insects and non-eusocial animals also partition work in other ways not involving morphological castes or age polyethism (Gadagkar, 2009; Gordon, 2016; Unnikrishnan & Gadagkar, 2021). Since much of the focus on the manifestation and maintenance of task partitioning has been in eusocial insects, its existence in non-eusocial species is not fully understood.

Social spiders present an intriguing case of task allocation. Individuals within social spider colonies show remarkable collective behaviours in prey capture, web building and allomaternal care. Yet they do not have morphological castes, reproductive division of labour or conspicuous dominance hierarchies (Avilés, 1997; Lubin & Bilde, 2007). However, in some social spider species, some individuals are consistently more likely to attack prey than others, suggesting some degree of task differentiation (Beleyur et al., 2015; Parthasarathy & Somanathan, 2019; Settepani et al., 2013). This begs the important question of what determines task participation in social spiders.

It has been recently suggested that personality traits and behavioural syndromes may determine patterns of task participation in social animals (Loftus et al., 2021). In social spiders, boldness and/or aggression have been linked with participation in prey capture (Keiser & Pruitt, 2014; Keiser et al., 2014; Lichtenstein et al., 2017; Pruitt & Riechert, 2011; Wright et al., 2015;). However, participation in prey capture in social spiders has been shown to be influenced by hunger (Beleyur et al., 2015) and the specific attributes of the prey species (i.e. risky vs. harmless; Parthasarathy & Somanathan, 2019), with such plasticity perhaps working against the role of personality types in determining task participation. Moreover, repeatability of personality traits in these spiders is often measured across relatively short durations (e.g. Keiser et al., 2014, 2016; Keiser & Pruitt, 2014; Lichtenstein et al., 2017; Wright et al., 2015, 2016). Many species of social spiders have lifespans ranging from several months to 1 year, whereas repeatability of personality types has been typically tested over just 3–5 days. Therefore, short-term personality estimates cannot be assumed to be consistent over longer durations commensurate with the lifespan of individual spiders (see Dingemanse & Wright, 2020). Although Parthasarathy et al. (2019) show that among-individual differences in boldness and aggression can persist for up to 51 days in an Indian social spider *Stegodyphus sarasinorum*, the repeatability of such behavioural traits is much reduced when compared with short-term estimates over only 4 days.

Despite the vast body of literature reporting animal personality in boldness and aggression in various species of social spiders, empirical evidence for behavioural syndromes involving these two behavioural traits has only been reported in two studies on *Stegodyphus sarasinorum*, which has now been retracted due to data irregularities (Grinsted et al., 2013; Pruitt et al., 2013). Therefore, it is important to explore whether these two behavioural traits showing animal personality in social spiders are part of a wider behavioural syndrome. If this is the case, then we need to ask how task participation is achieved across different contexts given such a boldness-aggression syndrome. As bold individuals may show higher activity rates and have greater nutritional demands to sustain *that state*, they are, therefore, likely to attack and feed upon prey more frequently (via a positive feedback mechanism; McElreath et al., 2007; Sih et al., 2015). However, participation in prey capture is also likely influenced by the attributes of the prey itself. Social spiders handle and subdue potentially dangerous prey, such as honeybees, with greater care when compared with prey, such as grasshoppers, that pose little or no risk (Parthasarathy & Somanathan, 2019). In this context, if a positive boldness-aggression syndrome exists, then bold individuals may be inappropriately aggressive, while attacking risky and aggressive prey, and such individuals may be exposed to greater risks of mortality over time. Conversely, less bold individuals might be inappropriately cautious and therefore competitively excluded from feeding on less risky prey by bolder and more aggressive colony members. Therefore, behavioural syndromes in social spiders, if present, could represent potentially important determinants of task participation and inter-individual cooperation and/or conflict.

In this study, we re-evaluate whether the boldness-aggression syndrome exists in the social spider *S. sarasinorum*. Using the same dataset of Parthasarathy et al. (2019), we specifically ask if the boldness-aggression syndrome persists across longer durations and different developmental stages of individual spiders by analysing data consisting of: (a) short-term personality assays in subadults; (b) long-term personality assays in subadults and (c) short-term personality assays in juveniles of *S. sarasinorum*.

## 2 | METHODS

### 2.1 | Study species

*Stegodyphus sarasinorum*, commonly known as the Indian social spider, inhabits arid and semi-arid areas of the Indian subcontinent (Platnick, 2017). It lives in dense silken retreats, and the colonies may consist of one to a few hundred individuals. The colonies show seasonality in reproduction and gerantophagy (offspring consume their (allo)mothers), as a result of which there is little overlap of generations within a colony (Jacson & Joseph, 1973). Juveniles are cared for and fed by allomothers during their 1st and 2nd instars (Jacson & Joseph, 1973; Kullmann, 1972). Subsequently, juveniles consume the adults and engage in collective prey capture and web building from the 3rd instar onwards (Jacson & Joseph, 1973). Therefore, any

animal personality would be expected to manifest in behaviours in this juvenile stage if it is to play a role in task participation, given that individuals moult 12 times before reaching adulthood. These spiders are also highly inbred due to their reduced dispersal potential (Settepani et al., 2017; Smith & Engel, 1994), possibly because of which colonies have highly female-biased sex ratios (Avilés, 1997).

## 2.2 | Experimental setup

In this study, we analysed data from a previously published article (Parthasarathy et al., 2019), which investigates among-individual differences and repeatabilities in boldness and aggression in *S. sarasinorum*. The previous study involved colonies consisting of subadults (2 instars before the final instar) or 3rd and 4th instar juveniles. Details on spider collection, feeding regimen and repeatability estimates of boldness and aggression are shown in Table 1. Briefly, the long-term assessments involved 13 colonies, each consisting of 30 uniquely marked spiders. Short-term and juvenile assessments involved 7 and 13 colonies, respectively, also consisting of 30 uniquely marked spiders. We maintained field-collected colonies in well-ventilated plastic containers in the laboratory (juveniles in 8.5 × 5 × 4 cm boxes: subadults in 20 × 13 × 3.5 cm boxes) at 26°C and 60% RH.

## 2.3 | Personality assays

In social spiders, boldness and aggression are the two behavioural traits that have been assessed for individual repeatability or animal personality in the past. We performed boldness and aggression assays as described in Parthasarathy et al. (2019). Previous studies have employed similar protocols to capture one or both of these personality measures in other species of solitary and social spiders (Keiser et al., 2014, 2016; Riechert & Hedrick, 1993; Riechert and Johns, 2003; Wright et al., 2015, 2016). Similar personality tests were also used in the retracted articles involving *S. sarasinorum* (Grinsted et al., 2013; Pruitt et al., 2013). In short, we performed

boldness assays by delivering a puff of air at the spider from a medical syringe, to which individuals responded by withdrawing their legs under the abdomen in a huddle. We recorded the latency to emerge from "huddling." We deemed individuals that took longer to resume movement as less bold. For an intuitive depiction of our results, we, therefore, reversed latency measures such that bolder individuals were represented with higher scores. To reverse latencies we used the formula: (A x B)/C, where A and B are the lowest and highest latency scores available in each of the three assessments (short-term, long-term and juvenile assessments), and C represents the latency score of each individual. This ensured that the range of the reversed scores remained identical to the original unreversed scores.

For aggression assays, we prodded the abdomen of the spider with a toothpick and observing one of the following 6 responses of the individual: 1 = huddle; 2 = run; 3 = walk; 4 = lurch; 5 = no response; and 6 = leg raise. We ordered aggression scores from low (1 = huddle) to high (6 = leg raise) because behavioural ranks 1–4 are threat avoidance behaviours whilst 5 and 6 are not (Kralj-Fišer et al., 2012; Reichert 1978, 1979; Riechert and Johns, 2003; Tolbert, 1975). For long-term assessments, we performed boldness and aggression assays once every 10 days over a period of 51 days (6 trials). In the case of short-term assessments, we subjected spiders to 4 personality assays (4 trials) over 4 consecutive days. We subjected juveniles to personality assays once every 4 days, over a 21-day period (6 trials). We could not subject juveniles for long-term assessments because of the loss of individual identities due to the frequent moulting of marked individuals in this age class.

## 2.4 | Statistical analyses

We determined the presence of behavioural syndromes by partitioning the (co)variances into among- and within-individual variances (Dingemanse, Dochtermann et al., 2010; Dingemanse & Dochtermann, 2013) using a bivariate mixed-effects model. Correlations in among-individual personality traits constitute a behavioural syndrome, and therefore, correlations across behavioural

**TABLE 1** Collection sites, feeding regimes and repeatability in boldness and aggression of subadult and juvenile *Stegodyphus sarasinorum* colonies subjected to long-term and short-term personality tests

| Assessment | Feeding regimen | Collection Site | Repeatability$_{Boldness, Aggression}$ |
|---|---|---|---|
| Long-term, in subadults | 1 honeybee before and 2 honeybees after each assay | Kuppam, Southern India (12.75°N, 78.37°E) | 0.10*, 0.14 (0.09–0.19) |
| Short-term, in subadults | 2 honeybees before the first assay | Krishnagiri, Southern India (12.51°N, 78.21°E) | 0.32*, 0.21 (0.14–0.30) |
| Short-term, in juveniles | 1 honeybee before each assay | Kuppam, Southern India (12.75°N, 78.37°E) | 0.32*, 0.13 (0.08–0.20) |

We used the honeybee *Apis cerana* as prey for the spiders. Feeding regimes were adapted according to the developmental stage (size) of spiders and the frequency of personality tests that these spiders were subjected to. For example, colonies subjected to short-term assays were fed only once before the first assay because subsequent assays (4 tests) were performed on four consecutive days. We ensured that spiders were not hungry during the assays with this feeding regimen. Kuppam and Krishnagiri are distinct populations separated by ~35 km. Repeatability estimates of boldness and aggression were determined by linear mixed-effects models. * indicates significance at *p* < .005. 95% credible intervals for repeatability in aggression are presented within parenthesis.

traits arising from within-individual variation across time and/or context have to be excluded. We adopted a Bayesian approach to building the mixed-effects models using the Markov Chain Monte Carlo (MCMC) algorithm from the MCMCglmm package in R (De Villemereuil, 2018; Hadfield, 2010). We used parameter extended priors (Gelman, 2006) with the prior means (alpha.mu) set to 0 and the prior covariance (alpha.V) ranging from 10 to 1000. Reassuringly, the model estimates and covariance did not change significantly with the different priors used. We built three separate bivariate models for (a) long-term tests, (b) short-term tests and (c) tests involving juveniles. In all these bivariate models, the boldness scores and aggression ranks were treated as continuous and ordinal response variables, respectively, trial number (representing experimental time) was the fixed effect and spider ID nested within its corresponding colony ID was the random effect. In order to ensure that the use of rank order scores as continuous interval measures did not affect the results or conclusions, we also built separate bivariate binomial models as described above. However, in these separate models we coded aggression scores as a binary dependent variable (i.e. all aggression scores 1–4 representing "threat avoidance behaviours" were coded as 0 whilst actual "aggression" scores 5 and 6 were coded as 1).

When available, partial data from spiders that died during the course of the experiments (144 out of 360 subadults subjected to long-term tests, 7 out of 210 subadults subjected to short-term tests and 199 out of 390 juveniles) were also included in the analyses. The boldness scores were log-transformed to meet the assumptions of the models concerning linearity and heteroskedasticity of posterior estimates. We removed observations, where the spider did not huddle (boldness score of 0 s) or took >1200 s to resume movement (8.7% of total observations for long-term assays, 10.08% of total observations for short-term assays and 4.3% of total observations for assays involving juveniles). Subsequently, we analysed this subset of boldness data by performing a MCMC bivariate regression, as described above, but with the two extremes of boldness scores coded as a binary variable (0 or 1) and aggression scores as a rank-ordered variable. As with any model involving a nominal, ordinal or a binary response variable, the residual variances of aggression scores in these models were fixed at 0.5, and therefore, within-individual variances of aggression cannot be determined (Hadfield, 2010). However, the among-individual (co)variance, which are used for calculating behavioural syndromes can be determined. We performed model diagnostics by observing the trace and density plots, autocorrelation plots and by Heidelberger's tests. We also built Geweke's diagnostic plots and ensured that most of the data point $Z$ scores lay within $\pm 2$ SDs of 0 (De Villemereuil, 2012). The (a) long-term subadult model involved: iterations = 50,000 to 6,50,000; thinning interval = 200; and sample size = 3000. The (b) short-term subadult model involved: iterations = 50,000–6,50,000; thinning interval = 50; and sample size = 12,000. The (c) short-term juvenile model involved: iterations = 50,000–9,50,000; thinning interval = 100; and sample size = 9000.

Finally, we constructed figures from the above bivariate models using the posterior modes of random effects, also called as best unbiased linear predictors (BLUPS) for random effects (spider ID nested within their respective colonies). BLUPS provide predicted estimates of the random effects independent of other terms in the bivariate model, standardized to a mean of 0 (Kruuk, 2004). According to Houslay and Wilson (2017), BLUPS are not best suited for statistical analyses of behavioural syndromes because they yield anti-conservative results, but they can be used for illustrative purposes. Slopes of the estimated effects presented in the figures were calculated by dividing the covariance in boldness and aggression with the variance in boldness.

## 3 | RESULTS

Boldness and aggression were negatively correlated in subadults over the long-term (model with aggression scores as ordinal ranks: −0.54, 95% credible interval (CI) = −0.91−−0.19; model with aggression as binary scores: −0.66, 95% CI = −0.96−−0.34, Figure 1a, see Table 2 for (co)variances). As mentioned above, we reversed boldness latency scores to provide an intuitive depiction of results, and therefore, a significant negative correlation implies that bolder spiders are less aggressive.

In contrast, we found no evidence for correlations between boldness and aggression in the short-term assays for subadults (model with aggression scores as ordinal ranks: 0.02, 95% CI = −0.31−0.38; model with aggression as binary scores: −0.05, 95% CI = −0.40−0.31, Figure 1b, Table 2 for (co)variances) or juveniles (model with aggression scores as ordinal ranks: 0.02, 95% CI = −0.20−0.26; model with aggression as binary scores: 0.11, 95% CI = −0.18−0.40, Figure 1c, Table 2 for (co)variances). Similar trends were seen with binary logistic regression models involving the two extremes of boldness scores (0 and 1200 s) that were analysed separately (Table 3).

Despite the significant among-individual differences for both boldness and aggression for all three assessments, there was substantial within-individual variation in boldness for all three assessments (Table 2, and see Parthasarathy et al., 2019 for further detail and analyses on this point). Time across the experimental duration (trials) had a significant effect on the overall boldness and aggression of spiders, but the direction of this effect differed across different assessments (Table 2). Subadult spiders became significantly bolder over time in our experiments involving long-term assessments (a 4% increase per 10 days), whilst the opposite was true for short-term assessments (a 10% decrease per day). Juveniles became significantly more aggressive (a 5% increase per 4 days) across the experimental duration of 21 days (Table 2). Subadults in the long-term assessments became more aggressive over time (a 7% increase every 10 days), but this effect was significant only from the binomial model and not from the ordinal model involving rank-ordered aggression scores (Table 2).

## 4 | DISCUSSION

In this study, we show that boldness and aggression are strongly negatively correlated personality traits in the Indian social spider
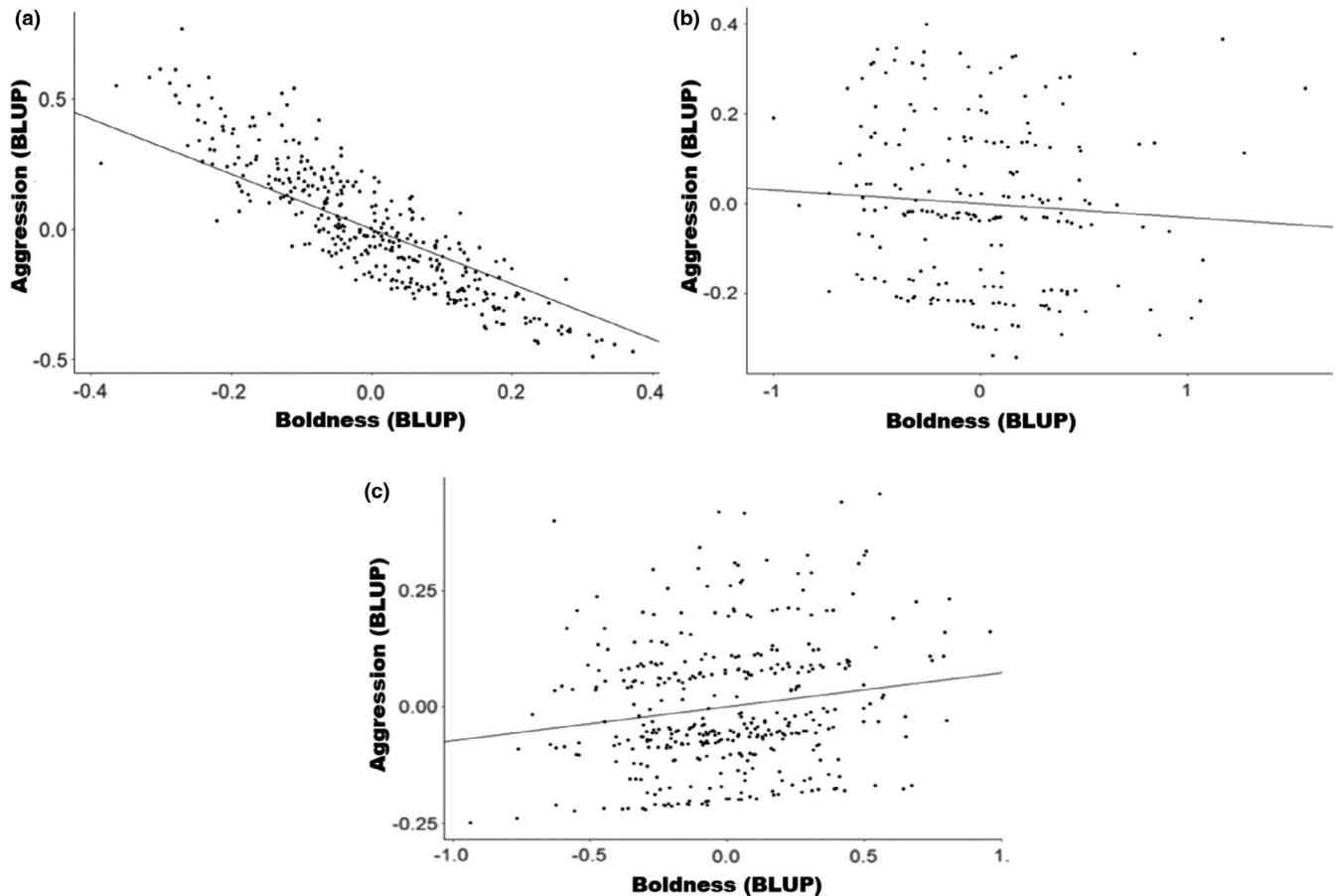
**FIGURE 1** Associations between boldness (*x*-axis) and aggression (*y*-axis) over the long-term (a) and short-term (b) in subadults and in juveniles (c). Straight lines represent model estimates of the covariance. Note, however, that the association between boldness and aggression is significant only over the long-term (a). Boldness scores were reversed such that higher scores depict greater boldness (see Methods for details)

*Stegodyphus sarasinorum*, but only over long-term assessments (spanning 51 days, see Figure 1a and Table 2), which covers a significant proportion of the subadult lifespan in this social spider species (~70 days). In contrast, we find no evidence for a boldness-aggression syndrome in short-term assessments in subadults (spanning 4 days, see Figure 1b and Table 2), and in juveniles (covering 21 days, see Figure 1c and Table 2). Thus, our results contradict those of the retracted papers (Grinsted et al., 2013; Pruitt et al., 2013), which showed a positive correlation between boldness and aggression in *S. sarasinorum*. This difference may possibly be explained by data irregularities in these retracted papers, or because the authors did not partition the variances into among- versus within-individual (co)variances while determining behavioural syndromes (see Dingemanse & Wright, 2020). Nevertheless, our long-term assessments corroborate the short-term findings of Keiser et al. (2014), who also obtained a significant negative association between boldness and aggression in the congeneric African social spider *Stegodyphus dumicola*, although their study also did not partition the variances into among- versus within-individual (co)variances. Here, we partitioned variances into among- and within-individual (co)variances, as well as confirmed our results by running independent statistical models that

showed that our results are consistent irrespective of whether the rank-ordered aggression scores were treated as an interval variable or more correctly reduced to a binary response variable (Table 2).

Why is the strong boldness-aggression syndrome evident only over longer durations in *S. sarasinorum*? Studies on personalities in other taxa show that behavioural syndromes may arise only in certain contexts (Dingemanse et al., 2007; Kralj-Fišer et al., 2017). Hermit crabs (*Pagurus bernhardus*) show a positive correlation between boldness (measured as a latency to emerge, as in these spiders) and aggression against conspecifics *only* when the predation risk was low, but such correlations disappeared when the predation risk was high (Mowles et al., 2012). In zebra finches (*Taeniopygia guttata*), significant negative correlations between boldness and aggression were found *only* during certain developmental stages, but these syndromes were not stable throughout individual lifespans (Wuerz & Krüger, 2015). These results suggest that behavioural syndromes may not necessarily be stable across different contexts and/or time for a given species. It is also likely that short-term tests capture individual variation in behaviour that is influenced to a greater extent by the current state/condition of individual spiders (Dingemanse & Wright, 2020).

**TABLE 2** Estimates, among- and within-individual (co)variances for subadults assayed over the long-term and short-term and for juveniles of *Stegodyphus sarasinorum*

| Variable | Subadults long-term | Subadults short-term | Juveniles short-term |
|---|---|---|---|
| **Fixed effects** | | | |
| Boldness intercept | 2.65 (2.46–2.86) | 3.73 (3.30–4.12) | 3.53 (3.27–3.77) |
| | 2.65 (2.47–2.86) | 3.73 (3.32–4.13) | 3.53 (3.27–3.76) |
| Aggression intercept | −0.64 (−0.77−−0.52) | −0.33 (−0.58−−0.08) | −0.55 (- 0.61−−0.48) |
| | 1.09 (0.98–1.2) | 1.19 (0.89–1.49) | 1.47 (1.36–1.59) |
| Time effect boldness | 0.04 (0.01–0.07) | −0.10 (−0.15−−0.04) | 0.01 (−0.01–0.03) |
| | 0.04 (0.01–0.07) | −0.10 (−0.15−−0.03) | 0.009 (−0.01–0.03) |
| Time effect aggression | 0.07 (0.04–0.1) | −0.01 (−0.07–0.05) | 0.05 (0.02–0.08) |
| | −0.02 (−0.04–0.0004) | −0.02 (−0.07–0.02) | 0.05 (0.03–0.08) |
| **Among-individual (co)variance** | | | |
| $V_{Boldness}$ | 0.06 (0.02–0.11) | 0.32 (0.21–0.44) | 0.19 (0.13–0.24) |
| | 0.06 (0.01–0.11) | 0.31 (0.21–0.43) | 0.19 (0.14–0.24) |
| $V_{Aggression}$ | 0.15 (0.08–0.22) | 0.11 (0.01–0.21) | 0.08 (0.02–0.14) |
| | 0.07 (0.04–0.11) | 0.08 (0.02–0.14) | 0.08 (0.04–0.11) |
| $COV_{Boldness, Aggression}$ | −0.06 (−0.1−−0.02) | −0.009 (−0.07–0.05) | 0.01 (−0.02–0.04) |
| | −0.03 (−0.06−−0.01) | 0.004 (−0.05–0.05) | 0.003 (−0.02–0.03) |
| **Within-individual (co)variance** | | | |
| $V_{Boldness}$ | 1.15 (1.07–1.24) | 0.81 (0.71–0.90) | 0.61 (0.56–0.66) |
| | 1.15 (1.06–1.24) | 0.81 (0.72–0.91) | 0.61 (0.56–0.66) |
| $V_{Aggression}$ | 0.5 (0.5–0.5) | 0.5 (0.5–0.5) | 0.5 (0.5–0.5) |
| | 0.5 (0.5–0.5) | 0.5 (0.5–0.5) | 0.5 (0.5–0.5) |
| $COV_{Boldness, Aggression}$ | −0.008 (−0.07–0.04) | 0.03 (−0.03–0.1) | 0.005 (−0.03–0.04) |
| | −0.03 (−0.07–0.007) | 0.05 (−0.005–0.1) | 0.01 (−0.01–0.04) |

For each row in the table, values presented at the top are from bivariate models where aggression is coded as a binary dependent variable, and the very similar values presented directly below them are from ordinal regression models in which rank-ordered aggression scores were used, confirming the validity of this approach. Significant values are underlined. 95% CI are presented in parenthesis.

**TABLE 3** Among-individual correlation between the two extremes of boldness scores (latencies 0 s and >1200 s) and the corresponding aggression ranks (1–6). 95% CI are presented in the parenthesis

| Assessment | Among-individual correlation |
|---|---|
| Long-term, in subadults | 0.15 (−0.71–0.92) |
| Short-term, in subadults | −0.15 (−0.63–0.3) |
| Short-term, in juveniles | 0.31 (−0.09–0.74) |

No significant correlation between the extreme boldness scores and aggression in all three assessments.

It is also important to emphasize that our long-term assessments involved assaying spiders over much longer intervals (once every 10 days), as opposed to short-term tests in subadults that were performed on four consecutive days. Webs of subadult colonies subjected to short-term tests were inevitably destroyed every day, whenever we removed individual spiders from their respective experimental colonies in preparation for the assays. It is well known that silk is an expensive investment in spiders (Opell, 1997; Vollrath, 1992, 2006), and therefore, subadult colonies that were tested over the short-term had to build new capture webs and retreat shelters overnight, only to be destroyed the following day for subsequent tests. Such repeated assaying of spiders soon after collective web

and retreat (shelter) reconstruction may have introduced additional variation into individual boldness and aggression behavioural scores, which may, thus, have been more a reflection of individual stress levels and/or energetic expenditure due to repeated silk investment in these spiders. This introduction of additional variation into any one or both behavioural scores might explain why we did not detect a boldness-aggression syndrome over the short-term, as compared to the long-term experiments in which webs and retreats were left in place for much longer intervals. In many such systems, performing behavioural assays over different timeframes may necessarily introduce differences in levels of disturbance and energetic investment for individuals.

The change over time (across trials) in boldness scores during our short-term assessments further corroborates this possible confounding effect of repeated disturbance/rebuilding of webs and shelter retreats, especially if our boldness scores also captured some individual variation in activity. Subadult spiders became less bold over the short-term 4-day duration, suggesting that individuals may have become less active, and hence less bold, because of the more frequent disturbance and/or greater energy expenditure associated with frequent web re-construction. However, juveniles were tested only once in 4 days, and thus had 3 days of acclimatization before the next personality assay, and so they are likely to have recovered from the disturbance and/or energetic stress of web rebuilding in

the intervening period. The non-significant effect of time on boldness scores of juveniles substantiates this view. Therefore, it is possible that the presence of a boldness-aggression syndrome in these spiders depends not only on the developmental stage, but also on whether individuals are tested under less disturbed (i.e. stressful and/or energetically costly) and thus more natural conditions.

Alternate plausible explanations for the significant reduction of boldness in colonies over the short-term can be potentially explained by habituation and/or sensitization of spiders to the frequent test stimuli, which in turn might explain why a boldness-aggression syndrome was not detected in these colonies. In contrast, spiders tested less frequently over the long-term may have been less likely to become habituated to the test stimuli. Finally, colonies tested over the short-term were collected from a different source population (see Table 1), and therefore, the presence or absence of behavioural syndromes could be an adaptation to the rearing environment (Sweeney et al., 2013) or local environmental conditions. Such population-specific manifestation of behavioural syndromes is known in other taxa including fishes (i.e. predator presence in *Gasterosteus aculeatus*, Bell & Sih, 2007; Dingemanse et al., 2007; Dingemanse, Dochtermann et al., 2010), skinks (*Lampropholis delicata*, Michelangeli et al., 2019) and spiders (*Eris militaris*, Royauté et al., 2014).

However, the question that remains is: what is the role of the boldness-aggression syndrome in task participation in social spiders? Boldness is associated with collective prey capture (Keiser & Pruitt, 2014; Lichtenstein et al., 2017). However, the functional relevance of such aggressive behaviours quantified in these assays remain currently unclear. Boldness and aggression tests in spiders were designed to mimic those used in encounters with avian (Riechert & Hedrick, 1993) and invertebrate predators (Riechert & Johns, 2003), respectively. These tests were first developed in a desert grass-solitary spider (*Agelenopsis aperta*, Riechert, 1979, Riechert & Hedrick, 1993, Riechert & Johns, 2003) and was later adapted to various species of social spiders (Keiser et al., 2014; Pruitt et al., 2008). If these tests only represent anti-predatory responses of spiders, there should be a positive association between boldness and aggression. However, boldness measured as the latency to emerge after a threat stimulus may also be indicative of activity rates or metabolic states (even hunger) of spiders. Aggression, ranked as threat avoidance or threat confrontational displays may be indicative of the energetic costs incurred in territorial spiders, which can determine contest outcomes with conspecific intruders. However, its relevance is not clear in social spiders which are neither territorial nor aggressive, possibly because of an overall reduction in aggression associated with the evolution of sociality and colony living (Avilés, 1997; Lubin & Bilde, 2007). Nevertheless, individuals might still display certain levels of aggressive behaviours against prey, parasites invading their nests or with their conspecifics when competition for feeding is high (Rypstra, 1993; Whitehouse & Lubin, 1999; BP personal observations). Therefore, boldness and aggression must be negatively correlated in order to maximize individual and collective feeding opportunities, because bold individuals that initiate prey capture must be less aggressive and cautious while handling prey. Inappropriately aggressive behaviours towards risky prey can be fatal for individuals that initiate attacks and subdue prey (Parthasarathy & Somanathan, 2019). The absence of a boldness-aggression syndrome in juveniles suggests that personality-mediated participation in prey capture is likely to manifest only during later developmental stages with learning, experience and proficiency, but this is an interesting proposition worthy of investigation in future studies.

The biological relevance of animal personalities and behavioural syndromes are known in other arachnid species. Bold and voracious female North American fishing spiders (*Dolomedes triton*) indulged in more frequent precopulatory sexual cannibalism (Johnson & Sih, 2005). Boldness and aggression were heritable and uncorrelated in bridge spiders (*Larinioides sclopetarius*), but groups of aggressive spiders gained significantly more body mass and suffered greater mortality than mixed groups composed of aggressive and docile spiders (Kralj-Fišer & Schneider, 2012). Moreover, urban dwelling spiders, such as *L. sclopetarius*, show greater exploration than suburban dwelling species like *Nuctenea umbratica* (Kralj-Fišer et al., 2017). Therefore, animal personality and such trait associations in behavioural syndromes can be important determinants of survival, reproduction and habitat expansion in arachnids.

We conclude by pointing out that the biological significance of behavioural syndromes in social spiders, whether detected or not, is currently unclear because the functional relevance of aggression and boldness, as measured by these personality assays, is not fully understood. Aggression could correlate with contest outcomes against conspecific intruders in territorial species (Kralj-Fišer & Schneider, 2012), whilst conspecific aggression in rarely observed in these heavily inbred social spiders (see Introduction). Boldness and aggression are also likely to reflect temporal variation in individual states, such as hunger, stress levels arising from energy expenditure in web construction or perceived predation threat, and this needs to be understood in order to assess any consistent differences based upon individual tendencies or liabilities. Moreover, personality studies over longer intervals spanning more ecologically relevant timescales may lead to quite different conclusions than experimentally convenient short-term studies. Animal personalities and behavioural syndromes have been considered powerful determinants of task participation in social spiders, but they perhaps reflect more subtle behavioural manifestations of within-and among-individual variation in behaviours whose biological significance is yet to be determined.

## CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

## AUTHOR CONTRIBUTIONS

## ORCID

*Bharat Parthasarathy* https://orcid.org/0000-0001-9829-1317

## REFERENCES

Avilés, L. (1997). Causes and consequences of cooperation and permanent-sociality in spiders. In J. C. Choe, & B. J. Crespi (Eds.), *Social behavior in insects and arachnids* (pp. 476–498). Cambridge University Press.

Beleyur, T., Bellur, D. U., & Somanathan, H. (2015). Long-term behavioural consistency in prey capture but not in web maintenance in a social spider. *Behavioral Ecology and Sociobiology*, 69, 1019–1028. https://doi.org/10.1007/s00265-015-1915-z

Bell, A., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10, 828–834. https://doi.org/10.1111/j.1461-0248.2007.01081.x

Bergeron, P., Montiglio, P. O., Réale, D., Humphries, M. M., Gimenez, O., & Garant, D. (2013). Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. *Journal of Evolutionary Biology*, 26, 766–774. https://doi.org/10.1111/jeb.12081

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, 5, 159–170. https://doi.org/10.1093/beheco/5.2.159

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7, 734–739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

De Villemereuil, P. (2012). Estimation of a biological trait heritability using the animal model. How to use the MCMCglmm R package? Retrieved December 7, 2020, from https://devillemereuil.legtux.org/wp-content/uploads/2012/12/tuto_en.pdf

De Villemereuil, P. (2018). Quantitative genetic methods depending on the nature of the phenotypic trait. *Annals of the New York Academy of Sciences*, 1422, 29–47. https://doi.org/10.1111/nyas.13571

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed- effect modelling approaches. *Journal of Animal Ecology*, 82, 39–54. https://doi.org/10.1111/1365-2656.12013

Dingemanse, N. J., Dochtermann, N. A., & Nakagawa, S. (2012). Defining behavioural syndromes and the role of 'syndrome deviation' in understanding their evolution. *Behavioral Ecology and Sociobiology*, 66, 1543–1548. https://doi.org/10.1007/s00265-012-1416-2

Dingemanse, N. J., Dochtermann, N., & Wright, J. (2010b). A method for exploring the structure of behavioural syndromes to allow formal comparison within and between datasets. *Animal Behavior*, 79, 439–450. https://doi.org/10.1016/j.anbehav.2009.11.024

Dingemanse, N. J., Kazem, A. J. N., Reale, D., & Wright, J. (2010a). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25, 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Dingemanse, N. J., & Wright, J. (2020). Criteria for successful studies of animal personality and behavioural syndromes. *Ethology*, 126, 865–869.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, R. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, 76, 1128–1138. https://doi.org/10.1111/j.1365-2656.2007.01284.x

Dochtermann, N. A., & Dingemanse, N. J. (2013). Behavioral syndromes as evolutionary constraints. *Behavioral Ecology*, 24, 806–811. https://doi.org/10.1093/beheco/art002

Dugatkin, L. A. (1992). Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*). *Behavioral Ecology*, 3, 124–127.

Gadagkar, R. (2009). Interrogating an insect society. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 10407–10414. https://doi.org/10.1073/pnas.0904317106

Garamszegi, L. Z., Marko, G., & Herczeg, G. (2012). A meta-analysis of correlated behaviours with implications for behavioural syndromes: mean effect size, publication bias, phylogenetic effects and the role of mediator variables. *Evolutionary Ecology*, 26, 1213–1235.

Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis*, 1, 515–533.

Gordon, D. (1996). The organization of work in social insect colonies. *Nature*, 380, 121–124. https://doi.org/10.1038/380121a0

Gordon, D. M. (2016). From division of labor to the collective behavior of social insects. *Behavioral Ecology and Sociobiology*, 70, 1101–1108. https://doi.org/10.1007/s00265-015-2045-3

Grinsted, L., Pruitt, J. N., Settepani, V., & Bilde, T. (2013). Individual personalities shape task differentiation in a social spider. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131407. https://doi.org/10.1098/rspb.2013.1407

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22.

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology*, 28, 948–952. https://doi.org/10.1093/beheco/arx023

Jacson, C., & Joseph, K. (1973). Life-history, bionomics and behaviour of the social spider *Stegodyphus sarasinorum* Karsch. *Insectes Sociaux*, 20, 189–204. https://doi.org/10.1007/BF02223347

Johnson, J. C., & Sih, A. (2005). Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, 58, 390–396. https://doi.org/10.1007/s00265-005-0943-5

Johnson, J., & Sih, A. (2007). Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton. Animal Behavior*, 74, 1131–1138. https://doi.org/10.1016/j.anbehav.2007.02.006

Keiser, C. N., Howell, K. A., Pinter-Wollman, N., & Pruitt, J. N. (2016). Personality composition alters the transmission of cuticular bacteria in social groups. *Biology Letters*, 12, 20160297. https://doi.org/10.1098/rsbl.2016.0297

Keiser, C. N., Jones, D. K., Modlmeier, A. P., & Pruitt, J. N. (2014). Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. *Behavioral Ecology and Sociobiology*, 68, 839–850. https://doi.org/10.1007/s00265-014-1696-9

Keiser, C. N., & Pruitt, J. N. (2014). Personality composition is more important than group size in determining collective foraging behaviour in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 281(1796), 20141424.

Kralj-Fišer, S., Hebets, E. A., & Kuntner, M. (2017). Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization. *Behavioral Ecology and Sociobiology*, 71, 1–15. https://doi.org/10.1007/s00265-017-2353-x

Kralj-Fišer, S., & Schneider, J. M. (2012). Individual behavioural consistency and plasticity in an urban spider. *Animal Behavior*, 84, 197–204. https://doi.org/10.1016/j.anbehav.2012.04.032

Kralj-Fišer, S., Schneider, J. M., Justinek, Ž., Kalin, S., Gregorič, M., Pekár, S., & Kuntner, M. (2012). Mate quality, not aggressive spillover, explains sexual cannibalism in a size-dimorphic spider. *Behavioral Ecology and Sociobiology*, 66, 145–151. https://doi.org/10.1007/s00265-011-1262-7

Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the 'animal model'. *Philosophical Transactions of the Royal*

*Society of London. Series B: Biological Sciences*, 359(1446), 873–890. https://doi.org/10.1098/rstb.2003.1437

Kullmann, E. (1972). Evolution of social behavior in spiders (Araneae, Eresidae and Theridiidae). *American Zoologist*, 12, 419–426. https://doi.org/10.1093/icb/12.3.419

Le Coeur, C., Thibault, M., Pisanu, B., Thibault, S., Chapuis, J. L., & Baudry, E. (2015). Temporally fluctuating selection on a personality trait in a wild rodent population. *Behavioral Ecology*, 26, 1285–1291. https://doi.org/10.1093/beheco/arv074

Lichtenstein, J. L. L., Wright, C. M., Luscuskie, L. P., Montgomery, G. A., Pinter-Wollman, N., & Pruitt, J. N. (2017). Participation in cooperative prey capture and the benefits gained from it are associated with individual personality. *Current Zoology*, 63, 561–567.

Loftus, J., Perez, A., & Sih, A. (2021). Task syndromes: linking personality and task allocation in social animal groups. *Behavioral Ecology*, 32, 1–17. https://doi.org/10.1093/beheco/araa083

Lubin, Y., & Bilde, T. (2007). The evolution of sociality in spiders. *Advances in the Study of Behaviour*, 37, 83–145. https://doi.org/10.1016/S0065-3454(07)37003-4

Luttbeg, B., & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3977–3990. https://doi.org/10.1098/rstb.2010.0207

Mackay, J. R. D., & Haskell, M. J. (2015). Consistent individual behavioural variation: the difference between temperament, personality and behavioural syndromes. *Animals (Basel)*, 5, 455–478.

McElreath, R., Luttbeg, B., Fogarty, S. P., Brodin, T., & Sih, A. (2007). Evolution of animal personalities. *Nature*, 450, E5. https://doi.org/10.1038/nature06326

Michelangeli, M., Chapple, D. G., Goulet, C. T., Bertram, M. G., & Wong, B. B. M. (2019). Behavioural syndromes vary among geographically distinct populations in a reptile. *Behavioral Ecology*, 30, 393–401.

Moiron, M., Laskowski, K. L., & Niemelä, P. T. (2020). Individual differences in behaviour explain variation in survival: A meta-analysis. *Ecology Letters*, 23, 399–408. https://doi.org/10.1111/ele.13438

Mouchet, A., Cole, E. F., Matthysen, E., Nicolaus, M., Quinn, J. L., Roth, A. M., Tinbergen, J. M., van Oers, K., van Overveld, T., & Dingemanse, N. J. (2021). Heterogeneous selection on exploration behavior within and among West European populations of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2024994118. https://doi.org/10.1073/pnas.2024994118

Mowles, S. L., Cotton, P. A., & Briffa, M. (2012). Consistent crustaceans: the identification of stable behavioural syndromes in hermit crabs. *Behavioral Ecology and Sociobiology*, 66, 1087–1094. https://doi.org/10.1007/s00265-012-1359-7

Nunes, T. M., Mateus, S., Favaris, A. P., Amaral, M. F. Z. J., von Zuben, L. G., Clososki, G. C., Bento, J. M. S., Oldroyd, B. P., Silva, R., Zucchi, R., Silva, D. B., & Lopes, N. P. (2014). Queen signals in a stingless bee: suppression of worker ovary activation and spatial distribution of active compounds. *Scientific Reports*, 4, 7449. https://doi.org/10.1038/srep07449

Opell, B. D. (1997). The material cost and stickiness of capture threads and the evolution of orb-weaving spiders. *Biological Journal of the Linnean Society*, 62, 443–458. https://doi.org/10.1111/j.1095-8312.1997.tb01635.x

Parthasarathy, B., Joshi, C. H., Kalyadan, S. S., & Somanathan, H. (2019). Early ontogenic emergence of personality and its long-term persistence in a social spider. *Behavioral Ecology and Sociobiology*, 73, 35. https://doi.org/10.1007/s00265-019-2645-4

Parthasarathy, B., & Somanathan, H. (2019). Behavioral responses vary with prey species in the social spider, Stegodyphus sarasinorum. *Behavioral Ecology*, 30(4), 938–947. https://doi.org/10.1093/beheco/arz032

Platnick, N. (2017). The world spider catalog, version 18.5. *Bulletin of the American Museum of Natural History*. [accessed 2017 Jul 11]. http://research.amnh.org/entomology/spiders/catalog/%0Aindex.html

Pruitt, J. N., Grinsted, L., & Settepani, V. (2013). Linking levels of personality: personalities of the 'Average' and 'Most Extreme' group members predict colony-level personality. *Animal Behavior*, 86, 391–399. https://doi.org/10.1016/j.anbehav.2013.05.030

Pruitt, J. N., & Riechert, S. E. (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1209–1215. https://doi.org/10.1098/rspb.2010.1700

Pruitt, J. N., Riechert, S. E., & Jones, T. C. (2008). Behavioural syndromes and their fitness consequences in a socially polymorphic spider Anelosimus studiosus. *Animal Behaviour*, 76, 871–879. https://doi.org/10.1016/j.anbehav.2008.05.009

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Reaney, L. T., & Backwell, P. R. (2007). Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behavioral Ecology*, 18, 521–525. https://doi.org/10.1093/beheco/arm014

Riechert, S. E. (1978). Games spiders play: behavioral variability in territorial disputes. *Behavioral Ecology and Sociobiology*, 162, 135–162. https://doi.org/10.1007/BF00294986

Riechert, S. E. (1979). Games spiders play. II. Resource assessment strategies. *Behavioral Ecology and Sociobiology*, 6, 121–128. https://doi.org/10.1007/BF00292558

Riechert, S. E., & Hedrick, A. V. (1993). A test for correlations among fitness- linked behavioral traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Animal Behavior*, 46, 669–675. https://doi.org/10.1006/anbe.1993.1243

Riechert, S. E., & Johns, P. M. (2003). Do female spiders select heavier males for the genes for behavioral aggressiveness they offer their offspring? *Evolution*, 57, 1367–1373. https://doi.org/10.1111/j.0014-3820.2003.tb00344.x

Roth, A. M., Dingemanse, N. J., Nakagawa, S., McDonald, G. C., Løvlie, H., Robledo-Ruiz, D. A., & Pizzari, T. (2021). Sexual selection and personality: Individual and group-level effects on mating behaviour in red junglefowl. *Journal of Animal Ecology*, 90, 1288–1306. https://doi.org/10.1111/1365-2656.13454

Roth, A. M., Firth, J. A., Patrick, S. C., Cole, E. F., & Sheldon, B. C. (2019). Partner's age, not social environment, predicts extrapair paternity in wild great tits (*Parus major*). *Behavioral Ecology*, 30, 1782–1793. https://doi.org/10.1093/beheco/arz151

Royauté, R., Buddle, C. M., & Vincent, C. (2014). Interpopulation variations in behavioral syndromes of a jumping spider from insecticide-treated and insecticide-free orchards. *Ethology*, 120, 127–139. https://doi.org/10.1111/eth.12185

Rypstra, A. L. (1993). Prey size, social competition, and the development of reproductive division of labor in social spider groups. *American Naturalist*, 142, 868–880. https://doi.org/10.1086/285577

Settepani, V., Grinsted, L., & Bilde, T. (2013). Task specialization in two social spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae). *Journal of Evolutionary Biology*, 26, 51–62. https://doi.org/10.1111/jeb.12024

Settepani, V., Schou, M. F., Greve, M., Grinsted, L., Bechsgaard, J., & Bilde, T. (2017). Evolution of sociality in spiders leads to depleted genomic diversity at both population and species levels. *Molecular Ecology*, 26, 4197–4210. https://doi.org/10.1111/mec.14196

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state-behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, 30, 50–60. https://doi.org/10.1016/j.tree.2014.11.004

Smith, D. R., & Engel, M. S. (1994). Population structure in an Indian co-operative spider, *Stegodyphus sarasinorum* Karsch. *The Journal of Arachnology, 22*, 108–113.

Sweeney, K., Gadd, R. D. H., Hess, Z. L., McDermott, D. R., MacDonald, L., Cotter, P., Armagost, F., Chen, J. Z., Berning, A. W., DiRienzo, N., & Pruitt, J. N. (2013). Assessing the effects of rearing environment, natural selection, and developmental stage on the emergence of a behavioral syndrome. *Ethology, 119*, 436–447. https://doi.org/10.1111/eth.12081

Tolbert, W. W. (1975). Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *Psyche, 82*, 29–52.

Unnikrishnan, S., & Gadagkar, R. (2021). Dominance behaviour and division of labour in the tropical primitively eusocial wasp *Ropalidia cyathiformis. Insectes Sociaux, 68*, 123–132. https://doi.org/10.1007/s00040-020-00803-3

Vollrath, F. (1992). Spider webs and silk. *Scientific American, 266*, 70–77. https://doi.org/10.1038/scientificamerican0392-70

Vollrath, F. (2006). Spider silk: thousands of nano-filaments and dollops of sticky glue. *Current Biology, 16*, 925–927. https://doi.org/10.1016/j.cub.2006.09.050

Whitehouse, M. E., & Lubin, Y. (1999). Competitive foraging in the social spider *Stegodyphus dumicola. Animal Behavior, 58*, 677–688. https://doi.org/10.1006/anbe.1999.1168

Wright, C. M., Keiser, C. N., & Pruitt, J. (2015). Personality and morphology shape task participation, collective foraging and escape behaviour in the social spider *Stegodyphus dumicola. Animal Behavior, 105*, 47–54. https://doi.org/10.1016/j.anbehav.2015.04.001

Wright, C. M., Keiser, C. N., & Pruitt, J. N. (2016). Colony personality composition alters colony-level plasticity and magnitude of defensive behaviour in a social spider. *Animal Behavior, 115*, 175–183. https://doi.org/10.1016/j.anbehav.2016.03.002

Wuerz, Y., & Krüger, O. (2015). Personality over ontogeny in zebra finches: long- term repeatable traits but unstable behavioural syndromes. *Frontiers in Zoology, 12*(Suppl 1), S9. https://doi.org/10.1186/1742-9994-12-S1-S9