Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider

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While there are now a number of theoretical models predicting how consistent individual differences in behaviour may be generated and maintained, so far, there are few empirical tests. The social niche specialization hypothesis predicts that repeated social interactions among individuals may generate among-individual differences and reinforce within-individual consistency through positive feedback mechanisms. Here, we test this hypothesis using groups of the social spider Stegodyphus mimosarum that differ in their level of familiarity. In support of the social niche specialization hypothesis, individuals in groups of spiders that were more familiar with each other showed greater repeatable among-individual variation in behaviour. Additionally, individuals that were more familiar with each other exhibited lower within-individual variation in behaviour, providing one of the first examples of how the social environment can influence behavioural consistency. Our study demonstrates the potential for the social environment to generate and reinforce consistent individual differences in behaviour and provides a potentially general mechanism to explain this type of behavioural variation in animals with stable social groups.

1. Introduction

A fundamental goal in the field of the animal personality literature is to understand the mechanisms responsible for generating and maintaining consistent individual differences in behaviour. While there are now a number of well-developed theoretical models predicting potential causal mechanisms (reviewed in [1–3]), thus far empirical tests of these predictions are extraordinarily few (but see [4–6]). In order to fully explain the presence of consistent individual differences in behaviour, or personalities, a potential mechanism would need to address the two key aspects of personality: among-individual variation in behaviour and within-individual consistency over time. A recent hypothesis, termed the social niche specialization hypothesis, predicts that the social environment may play a key role in both promoting individual differentiation and individual consistency [7,8].

The social niche specialization hypothesis predicts that when a group of individuals interacts repeatedly, it can be beneficial for them to develop ‘social niches’ [7,8]. These social niches provide a way to reduce competition among individuals and increase individual pay-offs. First, by differentiating their behaviour from each other, individuals can reduce direct competition with group mates [6,9]. This type of niche specialization has been well established in ecology, where the presence of competing conspecifics can generate diet specializations among individuals [10,11], and the social niche specialization hypothesis expands this concept beyond the foraging context. The presence of among-individual variation in behaviour can increase colony productivity [12] and individual reproduction.
[13] within social groups, supporting the prediction that social niches can enhance individual fitness and colony success.

Once among-individual differences in behaviour are established, the social niche specialization hypothesis predicts that they will be reinforced, thereby generating within-individual consistency in behaviour [7,8]. Predictability in behaviour might increase successful interactions among individuals, which can be especially important in stable social groups [1,14]. Within-individual consistency could also be generated if changing behaviour is too costly or if positive feedback mechanisms, for example learning, reinforce an individual’s likelihood to repeat the behaviour [15,16]. Therefore, the social niche specialization hypothesis addresses both aspects of animal personality by predicting that groups of individuals that have repeatedly interacted should exhibit greater among-individual variation and lower within-individual variation in behaviour. Stated another way, familiar groups of individuals should exhibit stronger personalities.

While the development of social niches is theoretically possible in any group of repeatedly interacting individuals, these niches will probably be strongest when group membership is stable. When group turnover is low, individuals can more easily maintain the same social niche. For example, several studies have shown that individual birds will maintain consistent foraging behaviours when in the same social group [17,18]. However, when the social context changes, frequently so will individual behaviour [17,19]. In particular, a recent study demonstrated that social interactions did not strengthen personalities in three-spined sticklebacks, even when group membership was experimentally maintained [20]. However, in the wild, sticklebacks maintain fairly fluid groups with high turnover [21,22]. Therefore, it seems likely that social niche specialization holds the potential to be a more powerful mechanism in groups with stable membership where repeated interactions among individuals are frequent.

Here, we test the key prediction of the social niche specialization hypothesis that familiarity among group members should generate individual personalities, using the social spider Stegodyphus mimosarum. Social spiders of the genus Stegodyphus offer a superb model to evaluate the social niche specialization hypothesis because the dispersal tendency of this species is extraordinarily low, and thus persistent social interactions among colony members are a common feature in this species. Specifically, we compared the strength of consistent individual differences in behaviour in groups of spiders that had lived together for differing amounts of time (i.e. were more or less familiar with each other). We measured two ecologically relevant differences in behaviour in groups of spiders that had lived together for differing amounts of time (i.e. were more or less familiar with each other). We measured two ecologically relevant differences in behaviour in groups of spiders that had lived together for differing amounts of time (i.e. were more or less familiar with each other). We measured two ecologically relevant differences in behaviour in groups of spiders that had lived together for differing amounts of time (i.e. were more or less familiar with each other).

2. Material and methods

(a) Collection and laboratory maintenance

Stegodyphus mimosarum live in multi-female colonies ranging from 1 to 2000 members throughout eastern Africa [25,26]. Their webs are composed of two structures: a two-dimensional capture web and a dense three-dimensional retreat composed of a series of silken tunnels. Spiders reside within their retreat for the majority of the day, and only emerge in response to prey or at night in order to repair their capture web. Females cooperate together in colony maintenance tasks including collective web maintenance and defence, cooperative prey capture and alloparental care [27].

Ten colonies of S. mimosarum were collected in the town of Bela-Bela (24°53’S 28°17’E) in Limpopo, South Africa in November 2012. Colonies were collected by knocking down their capture webs, trimming off colonies’ supporting foliage and placing the colony in a cloth pillow case. Colonies were then transported to laboratory at the University of Pittsburgh, USA. Colonies were sorted in the laboratory and their colony size (1–700 spiders) was determined. Eight of the largest colonies (400–600 individuals) were selected for use in our study. From each of these colonies, we haphazardly selected 48 females for inclusion in our studies. Assignment of females to different treatment groups was determined randomly using a random number generator in Excel (Microsoft). Prior to being assigned to a treatment, females were housed individually in 2 oz deli cups that contained a dome of poultry wiring to facilitate web construction. Females were maintained in isolation for four weeks prior to the start of our experiment and sustained on an ad libitum diet of size-matched two-week-old crickets.

(b) Manipulation of familiarity

In order to observe how repeated social interactions influenced among- and within-individual behavioural variation, we manipulated the amount of time groups of spiders lived together. We generated 64 experimental colonies of six individuals and each colony was assigned to one of two familiarity treatments: control colonies (n = 32 colonies), where familiarity was maintained throughout the experiment, and mixed colonies, where familiarity changed over the experiment. Altogether, the familiarity treatment ran for five weeks, and within each treatment, each colony was exposed to a social disturbance after either one, two, three or four weeks (n = 8 groups per social disturbance per treatment). So, for example, colonies that experienced a social disturbance after one week were then left undisturbed for four weeks and would have longer to become familiar with each other than colonies that were disturbed after four weeks. By varying the time of the social disturbance, we could investigate how the length of social familiarity influenced individual behavioural variation. The social disturbance involved all of the members being removed from the colony and then being placed into a new container with all the same individuals (control treatment) or with new and unfamiliar individuals (mixed treatment). Colonies in the mixed treatment were reassembled using individuals from the same source colony that had not previously interacted. Therefore, individuals in the control and mixed colonies both experienced the same disturbance, but only the identity of the individuals in the mixed colonies was altered; any differences between the control and mixed colonies could be attributed to differences in familiarity among colony members.

We used a split design where each of our eight source colonies was used to establish one replicate of each of our eight treatment combinations (mixed and control colonies at one, two, three and four weeks since social disturbance). Relatedness among individuals is known to influence social spider behaviour [28,29], and this design ensured that all source colonies equally contributed to all treatment groups. Therefore, if relatedness among individuals was more influential on behaviour than familiarity, we would expect to see no differences between the control and mixed colonies. All experimental colonies were housed in 1.5 l clear, plastic deli cups that contained a concave-up dome of poultry wiring to facilitate web construction. Lids were covered with a 1 × 1 mm screen, which allowed ample airflow and low
humidity levels. Colonies were kept on a maintenance diet of ad libitum six-week-old crickets once weekly. To ensure successful prey capture, crickets were immobilized prior to being placed in colonies’ capture webs. After the social disturbance, all individuals were housed within a new 1.5 l container with chicken wire. All colonies resumed normal feeding behaviour within 3 days of the social disturbance. At the end of our five-week experiment, all colonies were disassembled, individuals were isolated back into 2 oz deli cups and their personality types were repeatedly assayed daily for the next 10 days in two ecological contexts.

(c) Personality assay: boldness towards predators
This assay was designed to measure how quickly an individual recovered from a potential predator attack. Variation among individuals in this behaviour could be influential in determining individual specializations within the nest on tasks such as colony defence [12,23,24], and is a known determinant of division of labour and collective behaviour in this species. Boldness–shyness assays were initiated by removing spiders from their home containers and placing them within a rectangular enclosure (13.5 x 13 x 3.5 cm). Spiders were permitted 60 s to acclimate before applying two rapid jets of air to the dorsal, anterior part of the animal from approximately 10 cm away, using an infant ear-cleaning bulb. This stimulus universally elicited a huddle response from S. mimosarum and resembles the rapid approach of an avian predator [23,30]. As our measure of boldness, we recorded the individual’s latency to resume movement following the huddle response. Five boldness assays (one per day) were completed on each spider beginning 24 h after the end of the familiarity treatments. After completing their assays, spiders were returned to their home containers.

(d) Personality assay: tendency to attack prey
This assay was designed to measure how quickly an individual attacked a simulated prey item, a behaviour that is probably important in determining foraging task specializations within a colony [12,23,24]. We staged prey capture events in spiders’ home containers and noted whether they attacked a prey stimulus or not. Using a simulated prey item allowed us to standardize the prey escape cues each spider was exposed to. Trials were initiated by removing the lid to the spider’s container and placing a 1.5 x 1.5 cm piece of printer paper in the spider’s capture web. We then allowed spiders 2 min acclimation time before administering a vibratory stimulus. We subsequently vibrated the paper using a portable, handheld vibratory device (FunFactory, Minivibe Bubbles). A thin aluminium wire extended from the end of the vibrator and made contact with the paper, which resulted in the paper flittering back and forth within the capture web, similar to lepidopteran prey. We vibrated the paper for a total of 10 min, or until the spiders emerged and bit the paper. For this behavioural assay, we recorded a binary response of whether the spider approached and attacked the stimulus within the 10 min time frame or not. Prey capture assays started 24 h after individuals had completed their boldness assays. This ensured that individuals had enough time to construct rudimentary capture webs and retreats within their home containers. Prey capture assays were implemented daily for 5 days.

(e) Data analysis
In order to ease analysis and interpretation of our data, we first inverted our measure of boldness: latency to resume movement after a huddle response. To do this, we subtracted each individual’s latency from the maximum time of 10 min (600 s). Therefore, individuals with higher boldness scores were considered more ‘bold’ (i.e. they resumed movement more quickly after the huddle response), compared with individuals with lower boldness scores which were considered more ‘shy’. The resulting boldness scores were non-Gaussian distributed and best approximated a Poisson error distribution which we used for all further analyses. Attack tendency was a binary variable and we used a categorical (yes/no) error distribution for all analyses.

We first tested for the main effects of familiarity treatment (mixed versus control) and time since social disturbance (one, two, three and four weeks) on each of our behavioural measures. We ran a separate generalized linear mixed model for each behaviour including familiarity treatment, time since social disturbance and their interaction as fixed effects. We also included individual, experimental colony and source colony as random effects to account for the non-independence of our behavioural measures. There was no significant variation among experimental or source colonies and so we subsequently removed these effects from further analyses.

Our primary research question was to determine whether increasing familiarity among colony mates increased consistent individual differences in behaviour. To test this, we compared the among- and within-individual variation components of each behaviour in each of our treatment combinations. However, it is important to note that because of its binary nature, it is impossible to directly estimate the within-individual (residual) variance in attack tendency. We ran a separate model for each behaviour in each familiarity treatment (control versus mixed) at each time point (weeks since social disturbance) including individual as a random effect. We then used these variance components to estimate repeatability as the proportion of total variation attributable to among-individual variation. We corrected all repeatability estimates as appropriate for each behaviour’s distribution (Poisson with additive overdispersion for boldness, binary for attack tendency [31]). We did not include any other fixed or random effects, such as experimental colony, source colony or body size, as these factors only varied between, not within, individuals, and any variance attributable to these factors would remain in the within-individual (residual) variance, providing a conservative repeatability estimate [32]. Additionally, in preliminary analyses, we found that these effects had no significant or consistent effect on either behaviour nor accounted for any significant portion of behavioural variation (data not shown). Therefore, all repeatability estimates reported here can be considered ‘non-adjusted’ and should be more broadly generalizable [31]. We used generalized linear mixed models with Markov chain Monte Carlo (MCMC) estimation for all analyses. MCMC is a Bayesian statistical method that is powerful for fitting non-Gaussian distributions and partitioning variance among random effects [32,33]. We used MCMCglmm [33] in R v. 2.15 (http://www.r-project.org), which returns 95% credibility intervals for both fixed and random effects. If the 95% CIs of two variance estimates did not overlap, we interpreted this as evidence that the estimates are significantly different from each other. Throughout, we used non-informative proper priors [33] appropriate for the relative error distributions (Poisson for boldness; categorical for attack latency) and preliminary analyses indicated that our results were not sensitive to changes in prior settings (data not shown). We ensured convergence and adequate chain mixing by comparing the posterior distributions and auto-correlation plots of five independent chains with 500,000 iterations, a 1000 burn-in period and thinning every 100 iterations for each model. The complete dataset can be found in the electronic supplementary material.

3. Results
The average boldness score across all individuals was 216 ± 5.3 (± s.e.), meaning that individuals resumed moving after the huddle response after 383 s. While there was no main
effect of familiarity treatment (treatment effect: $-0.97$, 95% CI: ($-2.99$, 1.16)), there was a significant effect of time since social disturbance (time effect: $-0.56$ ($-1.16$, $-0.03$)). Groups that had been together longer tended to be shyer than groups that had recently been disturbed (figure 1a). This effect did not differ between the two colony types (colony $\times$ time interaction: $-0.31$ ($-0.56$, 1.02)).

Across both treatments and all time periods, attacks on a simulated prey item occurred in 25% of all trials; this proportion did not differ between colony types (colony effect: $0.008$ ($-1.13$, 1.25)) or across time (time effect: $-0.11$ ($-0.42$, 0.22); colony $\times$ time interaction: 0.15 ($-0.30$, 0.58); figure 1b).

We found evidence for consistent individual differences in both boldness and attack tendency in both familiarity treatments (figure 2 and table 1). In support of the social niche specialization hypothesis, the repeatability of boldness was significantly higher in the control colonies compared with the mixed colonies at all time points, except when the colonies had not been disturbed for four weeks. Importantly, this increase in repeatability was driven by lower within-individual variation in boldness in the control colonies compared with the mixed colonies. This means that individuals in the control colonies exhibited more consistent behaviour at all time points compared with individuals in the mixed colonies. Additionally, the among-individual variation (and therefore repeatability of boldness) significantly increased the longer a group had been together regardless of whether it was a control or mixed colony. After not being disturbed for four weeks, individuals in the mixed colonies achieved similar among- and within-individual variation to those in the control colonies. By contrast, the repeatability of attack tendency remained at a similar level in both familiarity treatments across all time periods (table 1).

### 4. Discussion

The field of animal personality currently seeks potentially generalizable mechanisms that can generate and maintain consistent individual differences in behaviour. The social niche specialization hypothesis offers one such mechanism. The social niche specialization hypothesis posits that individuals will develop social niches as a result of living within a stable social group. In support of this view, we demonstrated here that consistent individual differences in boldness
behaviour increased in the social spider *S. mimosarum* the longer that individuals remained in a stable social group.

We recovered evidence that social niches for boldness behaviour developed as a result of familiarity among colony mates. Control colonies all experienced a social disturbance but were placed back with their original familiar colony mates. If social group familiarity is a key driver of repeatability, we would expect to see stronger personalities in these individuals as compared with the mixed colonies, regardless of when the social disturbance occurred. As predicted, the repeatability estimates of boldness were significantly higher in the control colonies than mixed colonies at all time points, except when the colonies had not been disturbed for four weeks. This increase in repeatability was driven by lower within-individual variation in the control colonies. Individuals became more consistent in their behaviour the longer they had spent with a social group, supporting the hypothesis that repeated social interactions can increase the benefits of predictable behaviour [7,8]. Our data suggest that, at least in this species, four weeks of repeated social interactions are needed to fully establish social niches. While several studies have now investigated how different ecological factors influence among-individual variation in behaviour [4–6,11], fewer have investigated how these factors generate individual consistency in behaviour (but see [19,34]). Our study demonstrates that the stability of the social environment may be especially influential in generating and even reinforcing individual differences once they appear. A promising next step will be to test whether colonies composed of behaviourally consistent (predictable) members perform better than colonies of unpredictable individuals.

While we found evidence for increased social niches in boldness with longer group fidelity, we found no such pattern for individuals' tendency to attack. Repeatabilities in attack tendency were similar regardless of the familiarity treatment or the time since the social disturbance. The overall low attack rates (attacks only occurred in approx. 25% of all trials) and distribution of the data (it is impossible to directly estimate the within-individual variance in a binary variable) probably reduced our ability to partition the behavioural variance. Granted, it is possible that our simulated prey was not as realistic as we hoped; however, this interpretation is at odds with the findings of other studies on other social *Stegodyphus* that used identical methods [23]. Another explanation may be that attack tendency is more strongly influenced by genetic or unchanging (or slowly changing) state variables, for example body size [35,36]. While we found no evidence that body size influenced attack tendency in *S. mimosarum* (data not shown), it remains that some other unmeasured state variable may influence this particular behaviour. It is also possible that among-individual variation in this particular behaviour is not as important as variation in boldness in familiar groups; other studies have found relatedness to be the most influential determinant of foraging efficiency in some social spiders [28,29]. Consistent with this view, Modlmeier et al. [12] found that colony productivity increased with within-colony variation in some aspects of behaviour (brood care and exploration) but not others (aggressiveness). Boldness has already been implicated as an important determinant of task differentiation in other *Stegodyphus* species [23,24] and our data support the finding that among-individual differences in boldness are a particularly important element of social organization in social *Stegodyphus*.

Social niche specialization may be a particularly powerful mechanism for generating social organization in societies where individuals exhibit group fidelity, such as our spiders. By contrast, it may be difficult for evolutionary processes to

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**Table 1.** Variance component (among- and within-individual) and repeatability estimates of boldness and attack behaviours in control and mixed colonies that experienced a social disturbance one, two, three or four weeks ago. The within-individual variance could not be estimated for the binary variable of attack tendency (see Material and methods for details). Numbers in parentheses indicate 95% credibility intervals.

<table>
<thead>
<tr>
<th>time since social disturbance</th>
<th>one week</th>
<th>two weeks</th>
<th>three weeks</th>
<th>four weeks</th>
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<tbody>
<tr>
<td><strong>boldness</strong></td>
<td></td>
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<tr>
<td>among control colonies</td>
<td>6.87 (3.94, 11.49)</td>
<td>21.80 (11.90, 36.32)</td>
<td>15.11 (9.12, 29.53)</td>
<td>23.41 (13.03, 46.33)</td>
</tr>
<tr>
<td>within control colonies</td>
<td>4.45 (3.51, 6.06)</td>
<td>3.52 (2.64, 4.79)</td>
<td>2.61 (2.00, 3.64)</td>
<td>4.95 (3.61, 7.22)</td>
</tr>
<tr>
<td>R</td>
<td>0.62 (0.47, 0.73)</td>
<td>0.86 (0.78, 0.92)</td>
<td>0.86 (0.79, 0.93)</td>
<td>0.83 (0.73, 0.91)</td>
</tr>
<tr>
<td>among mixed colonies</td>
<td>4.12 (0.78, 10.30)</td>
<td>0.05 (0, 7.05)</td>
<td>11.93 (6.24, 21.52)</td>
<td>21.75 (11.22, 42.17)</td>
</tr>
<tr>
<td>within mixed colonies</td>
<td>19.31 (14.47, 27.03)</td>
<td>23.58 (16.68, 33.20)</td>
<td>12.01 (8.82, 16.33)</td>
<td>9.91 (7.12, 13.69)</td>
</tr>
<tr>
<td>R</td>
<td>0.16 (0.05, 0.36)</td>
<td>0.002 (0, 0.24)</td>
<td>0.54 (0.35, 0.66)</td>
<td>0.74 (0.56, 0.82)</td>
</tr>
<tr>
<td><strong>attack tendency</strong></td>
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<tr>
<td>among control colonies</td>
<td>1.40 (0.39, 4.85)</td>
<td>1.73 (0.32, 5.00)</td>
<td>6.26 (2.16, 18.37)</td>
<td>2.02 (0.21, 6.24)</td>
</tr>
<tr>
<td>within control colonies</td>
<td>0.32 (0.12, 0.56)</td>
<td>0.35 (0.12, 0.56)</td>
<td>0.70 (0.42, 0.85)</td>
<td>0.32 (0.11, 0.62)</td>
</tr>
<tr>
<td>R</td>
<td>2.88 (0.84, 7.45)</td>
<td>3.14 (0.94, 8.73)</td>
<td>4.30 (1.46, 13.15)</td>
<td>3.31 (1.23, 8.68)</td>
</tr>
<tr>
<td>mixed colonies</td>
<td>0.45 (0.22, 0.66)</td>
<td>0.50 (0.23, 0.70)</td>
<td>0.55 (0.34, 0.78)</td>
<td>0.50 (0.26, 0.70)</td>
</tr>
</tbody>
</table>

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select for the proper mix of personalities in groups where membership changes with each generation. This may help to explain why a previous study on sticklebacks recovered no evidence that repeated social interactions increased among-individual variation or within-individual consistency in behaviour [20]. Because sticklebacks form large schools in the wild, and while certain pairs are found together more often than chance would predict [21], school membership is generally fluid [21,22]. We argue that in these types of groups, the formation of social niches will be difficult because individuals are constantly interacting with new individuals [37]. Instead, we expect that more plastic behaviour would be beneficial. By contrast, repeated social interactions in more stable societies may provide a mechanism by which individuals sense gaps in their societies’ workforce and fill them (i.e. via shifts in personality). In other words, simple mechanisms such as positive feedback loops throughout development may, over time, permit the adaptive differentiation of individuals’ personalities and (perhaps) their social roles. Such simple feedback loops have been implicated in numerous studies on social insect societies and manifest behaviourally as individual differences in task performance thresholds [38,39] (but see [40]). Here, we studied how repeated social interactions among individuals in a social group influences behavioural variation, but another potential scenario where social niches might be important is in species with long-term mating partnerships [14]. An exciting area for future research would be to investigate how the number of stable social partners influences the development of social niches.

5. Conclusion

The presence of consistent individual differences in behaviour has sparked so much interest in part because they have the potential to impact any number of evolutionary and ecological processes. While studies documenting the presence of personalities in animals continue to grow, we still know little about the factors responsible for their existence. Here, we show that living in stable social groups has the potential to generate and maintain consistent individual differences in behaviour. Individuals that were from groups that were more familiar with each other exhibited greater among-individual variation and within-individual consistency in behaviour. Many species form social groups, suggesting that the development of social niches may allow individuals to increase their own fitness by enhancing their fit with their (social) environment. However, stability of group membership can vary dramatically among species and populations, and we urge that more studies explore the potency of group fidelity to drive the generation and maintenance of individual differences in key functional traits, such as behaviour.

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References

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