

Research



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Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider

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The *social niche specialization hypothesis* predicts that repeated social interactions will generate social niches within groups, thereby promoting consistent individual differences in behaviour. Current support for this hypothesis is mixed, probably because the importance of social niches is dependent upon the ecology of the species. We test whether repeated interactions among group mates generate consistent individual differences in boldness in the social spider, *Stegodyphus dumicola*. In support of the social niche specialization hypothesis, we found that consistent individual differences in boldness increased with longer group tenure. Interestingly, these differences took longer to appear than in previous work suggesting this species needs more persistent social interactions to shape its behaviour. Recently disturbed colonies were shyer than older colonies, possibly reflecting differences in predation risk. Our study emphasizes the importance of the social environment in generating animal personalities, but also suggests that the pattern of personality development can depend on subtle differences in species' ecologies.

1. Introduction

Consistent individual differences in behaviour, i.e. animal personalities, have been documented in hundreds of species of animals [1]. Yet, the pervasive maintenance of individual variation stands in contrast to the general notion that selection and genetic drift should remove such variation. Classical niche theory argues that inter- and intraspecific variation can reduce competition among individuals, thereby promoting increased trait variation both between and within species [2,3]. Derived from this concept, the *social niche specialization hypothesis* postulates that repeated interactions within a group can lead to a behavioural diversification of its members, i.e. greater among-individual variation, if different social niches are available [4,5]. Subsequently, positive feedback can reinforce these differences generating individual consistency [6]. Social niches within groups are predicted to increase group and individual performance, which has been supported somewhat by empirical work linking behavioural variation and group performance in social arthropods [7–9]. Yet to date, few empirical studies have investigated whether the social environment can indeed generate stronger personalities.

The few studies that have explicitly tested the social niche specialization hypothesis have revealed mixed results. Studies in sticklebacks (*Gasterosteus aculeatus*) and meerkats (*Suricata suricatta*) found no evidence for social niche specialization, regardless of group tenure [10,11]. In contrast, longer group tenure in the social spider *Stegodyphus mimosarum* decreased within-individual

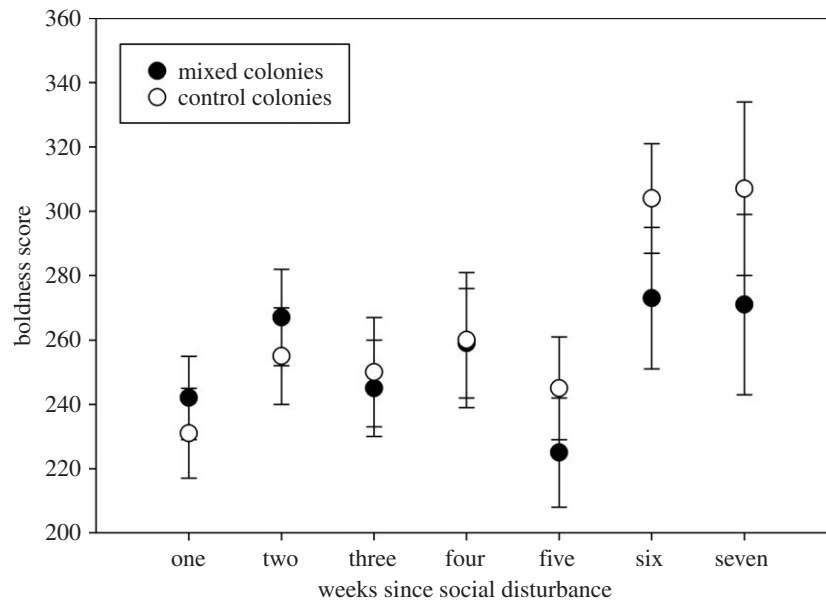


Figure 1. Average boldness scores in mixed and control colonies after one to seven weeks since a social disturbance. Boldness scores are depicted as the raw (inverted) boldness scores with standard errors to ease interpretation.

and increased among-individual variation in boldness, providing support for the hypothesis' key predictions [12]. Thus, more research is needed to determine the pervasiveness of social niches and their relationship with species' ecologies.

Here, we further investigate how repeated interactions among group members influence social niche differentiation in boldness in the social spider *Stegodyphus dumicola*. Although a congener of *S. mimosarum*, *S. dumicola* represents an independent evolutionary transition to social living in this genus [13]. Moreover, *S. dumicola* occupies more arid regions of southwest Africa along the Kalahari Desert, a habitat characterized by lower primary productivity and intense predation by ants [14]. Thus, comparing the effects of social niche specialization hypothesis in related species could yield insights into (i) the generality of the hypothesis and (ii) whether/how differences in species' ecology shape the development of personality. We test one of the key predictions of the social niche specialization hypothesis that repeated interactions among group members generate stronger individual differences in behaviour in groups. We focus on individual differences in boldness; an ecologically relevant trait linked to individual task participation [15], collective aggressiveness [16,17] and colony performance [16].

2. Material and methods

A detailed description of animal collection, boldness assays and group manipulation can be found in the electronic supplementary material. We manipulated both the identity of group members and the amount of time that groups lived together to test how repeated social interactions influenced among- and within-individual behavioural variation. We generated 84 experimental colonies of six spiders each. Each colony was assigned as either a *control* colony ($n = 42$ colonies), where group identity was maintained throughout the experiment, or a *mixed* colony ($n = 42$ colonies), where group identity changed sometime over the course of the experiment. Within each treatment, each colony experienced a social disturbance after one to seven weeks ($n = 6$ groups per social disturbance per treatment). For the social disturbance, we removed all members from a colony and placed them in a new container with all the same

individuals (*control*) or with completely new and unfamiliar individuals (*mixed*). By varying the time of the social disturbance, we could explore how the length of group tenure influenced individual behavioural variation. By comparing control and mixed colonies, we could then test whether any differences between them were due to the effects of repeated interactions among the same members and not the effect of the social disturbance *per se*.

Individuals' boldness after a simulated predator attack was measured five times (once per day) after completion of the group manipulation. Higher boldness scores indicate faster recovery from the simulated attack.

We tested the main effects of group identity treatment (mixed versus control) and time since social disturbance (one to seven weeks) on boldness in a linear mixed model with boldness score as the response variable and group identity treatment, time since social disturbance and their interaction as fixed effects. Individual and colony ID were included as random effects. The resulting treatment effect can be viewed as a contrast estimate that reflects the difference in the score of the mixed colonies compared with the control colonies.

To test whether among- and within-individual variation in behaviour differed between treatment groups, we ran a separate linear mixed model with boldness as the response variable and individual as a random effect for each treatment combination (mixed or control colonies at one to seven weeks). We scaled the variance in boldness to 1 within each treatment combination to enable comparison of variance components across groups. We then estimated the repeatability of boldness in each treatment combination.

Throughout, we used linear mixed models with Gaussian error distribution and Markov Chain Monte Carlo estimation using MCMCglmm [18] in R v. 2.15 (<http://www.r-project.org/>). We used 95% credibility intervals of each effect to test significance. Because random effects are constrained to be positive, we also tested whether the inclusion of the individual effect significantly improved the likelihood of the model. We compared the deviance information criterion (DIC) of the model including the individual effect, to the DIC of a model without it, with lower DIC values indicating better supported models. We initially included prosoma width (body size), experimental and source colony as additional effects in our models, however, these did not influence average behaviour or behavioural variation so they were removed. We used non-informative proper priors with 500 000 iterations, a 1000 burn-in and thinning every 100 iterations for each chain.

Table 1. Variance component and repeatability estimates (95% CI) of boldness scores in each treatment.

| | one | two | three | four | five | six | seven |
|------------------------|---|---|---|---|---|----------------------|----------------------|
| mixed colonies | | | | | | | |
| among | 0.03 (1.7 × 10 ⁻⁴ , 0.07) | 7.5 × 10 ⁻³ (1.3 × 10 ⁻⁴ , 0.02) | 0.02 (1.7 × 10 ⁻⁴ , 0.07) | 0.04 (1.4 × 10 ⁻⁴ , 0.10) | 0.01 (1.7 × 10 ⁻⁴ , 0.04) | 0.33 (0.16, 0.58) | 0.40 (0.11, 0.83) |
| within | 0.38 (0.30, 0.46) | 0.36 (0.28, 0.43) | 0.38 (0.30, 0.47) | 0.36 (0.27, 0.46) | 0.45 (0.34, 0.56) | 0.10 (0.07, 0.13) | 0.02 (0.01, 0.04) |
| R | 0.06 (4.6 × 10 ⁻⁴ , 0.17) | 0.02 (4.0 × 10 ⁻⁴ , 0.07) | 0.05 (3.8 × 10 ⁻⁴ , 0.16) | 0.09 (5.8 × 10 ⁻⁴ , 0.23) | 0.03 (4.5 × 10 ⁻⁴ , 0.09) | 0.76 (0.62, 0.88) | 0.93 (0.87, 0.98) |
| ΔDIC | -2.37 n = 49 | +1.51 n = 45 | -0.72 n = 45 | -2.98 n = 36 | +1.15 n = 33 | -112.45 n = 24 | -107.92 n = 11 |
| reconstituted colonies | | | | | | | |
| among | 0.18 (0.09, 0.28) | 0.06 (2.6 × 10 ⁻⁴ , 0.12) | 0.25 (0.12, 0.40) | 0.17 (0.06, 0.33) | 0.16 (0.06, 0.27) | 0.12 (0.05, 0.21) | 0.17 (0.02, 0.38) |
| within | 0.27 (0.21, 0.34) | 0.33 (0.25, 0.42) | 0.19 (0.14, 0.24) | 0.25 (0.17, 0.33) | 0.24 (0.18, 0.31) | 0.17 (0.12, 0.22) | 0.14 (0.07, 0.21) |
| R | 0.39 (0.24, 0.53) | 0.14 (1.0 × 10 ⁻³ , 0.29) | 0.56 (0.41, 0.72) | 0.40 (0.20, 0.62) | 0.39 (0.22, 0.58) | 0.41 (0.22, 0.59) | 0.51 (0.21, 0.82) |
| ΔDIC | -62.49 n = 51 | -8.93 n = 40 | -88.37 n = 36 | -33.44 n = 26 | -42.27 n = 34 | -41.19 n = 31 | -21.77 n = 11 |

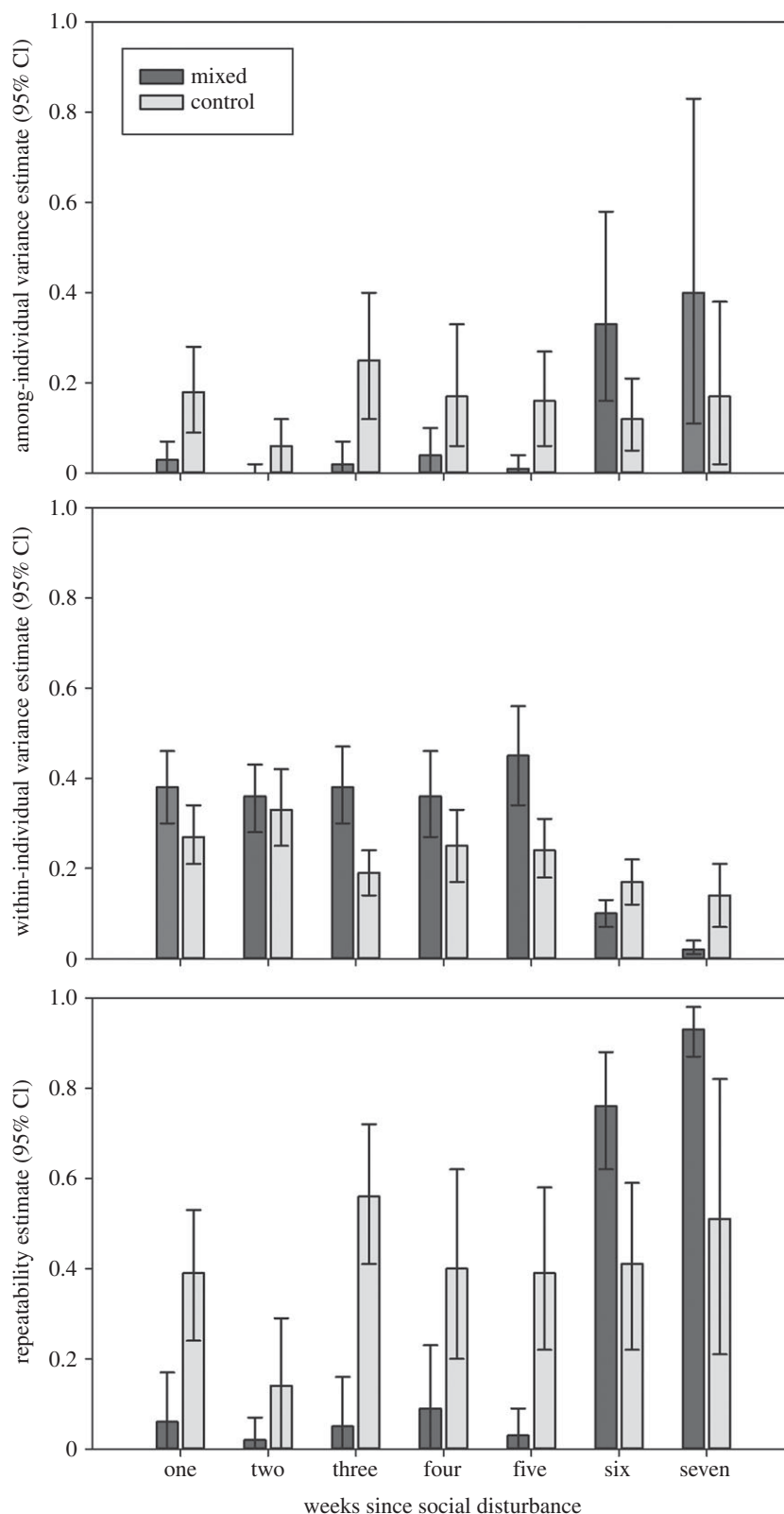


Figure 2. Variance component and repeatability estimates of boldness in mixed and control colonies after one to seven weeks since a social disturbance. Estimates are displayed as the posterior modes and the error bars are the 95% CI limits.

Unless stated otherwise, we report posterior modes and 95% CIs throughout.

3. Results

The average boldness scores between group identity treatments did not differ from one another (mixed colonies:

252.2 ± 6.4 ; control colonies: 257.7 ± 6.7 ; treatment effect: $4.53 [-21.15, 28.13]$). In general, there was a trend for individuals who were left undisturbed for longer to be bolder (effect of time: $5.88 [-0.22, 12.63]$) which was similar across the treatments (treatment \times time interaction: $8.51 [-4.05, 21.01]$; figure 1).

We found evidence that repeated interactions among colony mates increased consistent individual differences in

behaviour. There was a general trend for control colonies to exhibit greater repeatability in boldness when they had been disturbed one to five weeks ago (table 1 and figure 2), though this was not strictly significant across all weeks. This trend was driven both by greater among-individual variation and lower within-individual variation in the control compared to the mixed colonies (table 1). However, after colonies had been left undisturbed for six to seven weeks, we saw similarly high repeatabilities in both treatments.

4. Discussion

The social niche specialization hypothesis predicts that repeated social interactions will lead to greater consistent individual variation in behaviour [4,5]. By manipulating the group identity and length of tenure among group members, we demonstrated that repeated social interactions with the same group members beget more pronounced personalities, i.e. greater among-individual variation and lower within-individual variation, in *S. duminicola*. We also found that longer group tenure increased boldness in these spiders, in contrast to its congener [12]. This further suggests that the developmental impacts of repeated social interactions on personality may be species specific.

In contrast to an earlier study on *S. mimosarum* that detected a decrease in boldness over time after disturbance [12], *S. duminicola* spiders tended to become bolder over time. Hence, the response to social disturbance differs between the two species: *S. mimosarum* groups that were recently disturbed were bolder, whereas recently disturbed groups of *S. duminicola* were shy. We reason that *S. duminicola* might exhibit a more fearful response to disturbance because of the high incidence of predatory ants throughout its range [14]. Field observations have shown that attacks by predatory ants are a major cause of social disturbance (i.e. splitting of groups) for this species in the field. Thus, social disturbance may serve as an indirect measure of recent predation risk in this system.

Only one of three recent tests for social niche specialization has recovered support for social niche specialization: the spider *S. mimosarum* exhibits more pronounced personalities when individuals repeatedly interact with the same set of individuals [12]. Our results on *S. duminicola* corroborate these earlier results and emphasize that a stable social environment can generate more pronounced personalities both via increased among-individual variation and decreased within-individual variation in behaviour. Moreover, the loss of both between-individual variance and repeatability after social disturbance for up to five weeks (table 1 and figure 2) could mean that mixed colonies had to generate new social niches, whereas the control colonies were able to maintain their established social niches. While it is unclear which (if any) aspects of social conflict are reduced via behavioural diversification in *S. duminicola*, our results indirectly support the idea that social niche specialization could be one of the key drivers of personality in social spiders. Interestingly, our results stand in contrast to a study on *S. duminicola* that did not find support for social niche differentiation [19]. However, this could be due to the fact that Keiser *et al.* [19] (i) had a two weeks shorter period of observation, and (ii) did not control for mortality-induced differences in group size. Notably, our mixed colonies required between six and seven weeks to fully establish substantial repeatability (figure 2), which would have gone undetected by a shorter study. From an evolutionary point of view, this is an important finding, because societies are presumed to benefit from a more diverse group composition via avoidance of conflict or social heterosis [20]. Further studies that probe the interrelatedness of group stability, social organization, species ecology and group success will be vital to further assess this hypothesis.

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