

## Individual and Group Performance Suffers from Social Niche Disruption

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**ABSTRACT:** The social niche specialization hypothesis predicts that animal personalities emerge as a result of individuals occupying different social niches within a group. Here we track individual personality and performance and collective performance among groups of social spiders where we manipulated the familiarity of the group members. We show that individual personalities, as measured by consistent individual differences in boldness behavior, strengthen with increasing familiarity and that these personalities can be disrupted by a change in group membership. Changing group membership negatively impacted both individual and group performance. Individuals in unfamiliar groups lost weight, and these groups were less successful at performing vital collective tasks. These results provide a mechanism for the evolution of stable social groups by demonstrating that social niche reestablishment carries a steep cost for both individuals and groups. Social niche specialization may therefore provide a potential first step on the path toward more organized social systems.

**Keywords:** animal personality, social niches, individual specialization, *Stegodyphus dumicola*, familiarity, group living.

### Introduction

Consistent individual differences in behavior or personality are present across a range of taxa (Bell et al. 2009) and are often related to fitness parameters (Smith and Blumstein 2009), making their widespread presence difficult to explain from an adaptive perspective. Recent theoretical work predicts that personalities are a result of adaptive evolution (Bergmüller and Wolf 2010; Wolf and Weissing 2010). In particular, the social niche specialization hypothesis predicts that repeated social interactions among individuals within a group may play a key role in promoting consistent individual differences in behavior (Bergmüller and Taborsky 2010; Montiglio et al. 2013), an especially

compelling hypothesis given that nearly all animal species are required to interact with conspecifics at least occasionally (e.g., mating encounters and territorial interactions). The hypothesis predicts that personalities are a result of individuals maintaining a certain social role or niche within the group. These social niches develop within groups because when individuals repeatedly interact, it may benefit the individual to behave (*a*) in a predictable way and (*b*) differently from each other. This is because these stable behavioral differences among individuals could help reduce competition among group members. Repeated interactions with the same members could then reinforce these initial behavioral differences if individuals are able to increase their efficiency at a given behavior or task (i.e., specialization), eventually leading to the development of an individual's social niche (Bergmüller and Taborsky 2010; Montiglio et al. 2013). In other words, the set of behaviors and/or tasks that an individual reliably performs within a social context can be considered to represent their social niche. In support of this hypothesis, individual spiders in colonies that are more familiar with each other (i.e., have repeatedly interacted for longer periods of time) exhibit greater consistent individual variation in task-related behaviors indicative of maintaining a social niche (Laskowski and Pruitt 2014; Modlmeier et al. 2014; but see Carter et al. 2014; Laskowski and Bell 2014). Social niches should be especially advantageous to individuals in stable groups, where the individuals' predictable roles could help the group coordinate more quickly or efficiently to achieve mutual goals. If maintaining a social niche is beneficial, then conversely, switching social niches might be costly if individuals need to learn new behaviors or tasks or if this causes increased competition, for example. While there is support that consistent individual differences in behavior will emerge as a result of maintaining a social niche (Favati et al. 2014), thus far, it is unknown whether and how the establishment of these social niches impacts individual and group success. This is a crucial prediction because for social niche specialization to be a viable

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mechanism for generating and maintaining consistent individual differences in behavior, individuals must benefit somehow from maintaining their social niche; put another way, there should be a cost when individuals are forced to establish new social niches following a group perturbation.

Thus, the goal of this article is simple: to investigate the influence of social niches on individual and group success. We test this hypothesis by manipulating familiarity among individuals in colonies of the social spider *Stegodyphus dumicola* and assessing the consequences on individual- and colony-level performance. Social spiders are an excellent system for investigating the interplay between social interactions and consistent individual differences in behavior. Social spiders are multifemale societies that exhibit highly female-biased primary sex ratios and perennial inbreeding, which results in very high relatedness among colony constituents (Avilés 1986, 1997). Colonies lack morphological castes, and members repeatedly cooperate in communal tasks such as nest defense, prey capture, web maintenance, and brood care over their lifetimes (Avilés 1997; Lubin and Bilde 2007). Despite this colony-level cooperation in vital collective tasks, individuals within colonies tend to specialize on only a subset of tasks (Gordon 1996). Importantly, there is growing evidence that individual participation in communal tasks in social spiders is linked to an individual's personality, particularly measures of boldness (Grinsted et al. 2013; Settepani et al. 2013; Holbrook et al. 2014; Wright et al. 2014, 2015). Bolder individuals are more likely to participate in riskier tasks such as prey capture or nest defense (Grinsted et al. 2013; Settepani et al. 2013), whereas shyer individuals perform more nest care (Holbrook et al. 2014; Wright et al. 2014). Additionally, variation in boldness is linked with other behaviors such as aggression in a behavioral syndrome in this genus of spiders (Grinsted et al. 2013; Pruitt et al. 2013), and laboratory measures of boldness predict task participation in the field (Grinsted et al. 2013; Wright et al. 2015). All this suggests that an individual spider's level of boldness could be a good indicator of their social niche within a colony. Indeed, previous work has shown that these consistent individual differences in boldness strengthen with time spent in the colony (i.e., familiarity; Laskowski and Pruitt 2014; Modlmeier et al. 2014), suggesting strengthening of individual specializations or social niches. At present, how the presence of these social niches impacts individuals' or colonies' success is unknown. Importantly, all females within the colony have the opportunity to reproduce (Avilés 1997; Lubin and Bilde 2007), and body size is closely linked to reproductive potential, with larger females being able to invest more into their egg case (Vollrath and Rohde-Arndt 1983; Rypstra 1993; Salomon et al. 2008).

In accordance with previous findings (Laskowski and Pruitt 2014; Modlmeier et al. 2014), we predicted that more

familiar colonies would exhibit greater consistent individual differences in behavior indicative of more established social niches. We predicted that, on one hand, the presence of stronger consistent individual variation in behavior in more familiar colonies would benefit individuals in terms of weight gain and colonies in terms of performance at collective tasks, and that on the other hand, experiencing a social disturbance would disrupt the established social niches, with an associated cost to both individual and colony success. Finally, we predicted that the costs of reestablishing social niches after the social disturbance would be ephemeral and dissipate as individuals become more familiar with each other.

## Methods

### Overview

In this experiment, we generated colonies composed of familiar and unfamiliar individuals that lived together for variable amounts of time. We repeatedly assessed individual boldness in response to a simulated predator attack and individual weight gain as an indicator of individual success before and after the familiarity manipulation. Collective task trials (defense against intruder and prey capture) were performed immediately after the completion of the familiarity manipulation.

### Animal Collection and Maintenance

Colonies of mature *Stegodyphus dumicola* were collected along the southern Kalahari Desert Basin in February 2014. Colonies were collected along roadside fences and hook-bush acacia (*Acacia mellifera*) by placing the colony within a fabric pillowcase and trimming its supporting branches. Whole colonies were shipped to a laboratory at the University of Pittsburgh. Colonies were hand-sorted, and spiders were isolated in 59-mL plastic condiment containers for 6 weeks prior to the start of our experiment. All experimental spiders were mature females and were individually identified using a two-color identity code painted on the cephalothorax. Spiders were assigned to experimental colonies randomly; however, individuals used to create experimental colonies came from the same source colony to maintain natural levels of within-group relatedness, which is high for social spiders (Avilés 1997; Lubin and Bilde 2007). The same source colony was used to generate one complete replicate of our familiarity manipulation (see below), allowing us to control for any differences in relatedness among source colonies.

### Familiarity Manipulation

We generated experimental spider colonies ( $N = 6$  individuals each) following the methods of Laskowski and Pruitt

(2014). Each colony was placed into a 1.5-L plastic container with a small piece of poultry wire to facilitate web construction. All colonies built and maintained capture webs within the container throughout the experiment and cooperated to capture their prey (6-week-old crickets) during weekly feedings. When not active, social spiders will huddle together within retreats in the web. Thus, all members of a colony had the opportunity to repeatedly interact with each other over the course of the experiment in ecologically relevant tasks. All colonies were generated at the same time, and the entire familiarity manipulation lasted for a total of 5 weeks. Each colony experienced a single social disturbance that occurred after either 1, 2, 3, or 4 weeks. This social disturbance involved all individuals being removed from the colony's webbing and placed in a new, clean container with a new and unfamiliar set of individuals that came from the same source colony and had been treated in the same way (mixed colonies). Thus, a colony that experienced a social disturbance 4 weeks previously would be more familiar with their group mates than a colony that experienced the social disturbance only 1 week previously. Then, to control for the potential confounding effects of the actual physical disturbance, we created a second set of control colonies. These colonies were treated in the exact same way as mixed colonies, but when they experienced the social disturbance after either 1, 2, 3, or 4 weeks, they were instead placed in a new, clean container with the exact same set of individuals as before. Therefore, individuals in the control and mixed colonies both experienced the same physical disturbance, but only the identity of the individuals in the two colonies was altered, allowing us to isolate the effects of familiarity per se on behavior and performance. Altogether, one replicate of our familiarity manipulation contained eight treatment combinations in a factorial design where we manipulated whether group membership changed during the experiment (control vs. mixed colonies) and when that change in membership occurred (time since social disturbance being 1, 2, 3, or 4 weeks), with a total of 64 experimental colonies (eight replicates × eight replicates).

#### *Individual and Collective Assessment*

We assessed all experimental (i.e., control and mixed) individuals' morphology and behavior before and after the familiarity manipulation. We weighed each spider using a digital microbalance and assayed the boldness of all individuals (as in Laskowski and Pruitt 2014) prior to its assignment to an experimental colony. The boldness assay was designed to measure how an individual responds to a simulated potential predator attack; boldness behavior is a good predictor of individual task preferences and, therefore, we argue, their social niche (Grinsted et al. 2013; Settepani et al. 2013; Wright et al. 2014, 2015). To do this, we placed a single in-

dividual in a rectangular enclosure (13.5 cm × 13 cm × 3.5 cm) and allowed it 60 s to settle. We then applied two rapid bursts of air to the anterior, dorsal side of the spider from ~6 cm away using an infant nose-cleaning bulb. This universally elicited a huddle response by all individuals, where they drew their legs into their bodies, which is a common death-feigning response to an avian predator attack (Riechert and Hedrick 1990). As our measure of boldness, we recorded the amount of time in seconds for the spider to recover and begin moving one body length (up to a maximum of 10 min). In this way, we interpreted spiders that recovered more quickly from a simulated risk of predator attack as bolder. This assay was repeated once per day for 5 days. Twenty-four hours after completion of the boldness assays, the spiders were placed in the familiarity manipulation. Then, 24 h after completion of the familiarity manipulation, individuals were again isolated, weighed, and assayed for boldness once more (once per day for 5 days).

We also assessed group performance at collective tasks after completion of the familiarity manipulation and after individuals had been measured for their boldness postmanipulation. Twenty-four hours after the final individual boldness assay, colonies were reformed and assessed for their ability to complete two collective tasks: prey capture and colony defense against an intruder. Prey capture assays were performed once per week, and colony defense tasks were then performed 24 h after prey capture to standardize hunger levels among the colonies. We performed three prey capture tasks and two colony defense tasks. For the prey capture assays, we removed a rubber stopper from the top and bottom of a colony's container and dropped a domestic cricket in the center of the web. We then observed the colony during the prey capture sequence and recorded whether the colony was successful in subduing the cricket or whether the cricket escaped out of the bottom of the colony. For our colony defense assay, we again removed the two rubber stoppers and then placed a common inquiline of *S. dumicola* colonies (Wickler and Seibt 1993), a foreign spider of genus *Cheiracanthium*, centrally within the colony. We then recorded whether individuals in the experimental colony were successful at expelling the intruder over the next 24 h.

#### *Statistical Analyses*

The latency of a spider to recover from the simulated predator attack was inverted (maximum latency of 600 s minus spider latency) to ease interpretation. In this way, higher boldness scores represent bolder behavior (faster to recover activity). Our collective behavior assessments were coded as successful versus unsuccessful, so each colony received a score for their proportion of successful collective task completion (three prey capture attempts and two colony defense attempts).

We first tested how familiarity and length of familiarity influenced the strength of consistent individual differences in boldness behavior. To do this, we estimated the between- and within-individual variance components of boldness behavior within each treatment combination. We then used these variance components to estimate repeatability, which is the proportion of between-individual variation to total variation (Nakagawa and Schielzeth 2010). A significant repeatability is interpreted as evidence of consistent individual differences in behavior, and significantly larger repeatability estimates would indicate greater consistent individual variation in a particular treatment combination. We ran a separate linear mixed model for each treatment combination (control vs. mixed at 1, 2, 3, and 4 weeks since social disturbance), with boldness after the familiarity manipulation as the response variable. We included experimental colony and individual (nested within experimental colony) as random effects.

We then tested whether an individual's boldness behavior changed from the beginning to the end of the familiarity manipulation. To test this, we estimated the correlation in individual boldness before and after the experiment using a bivariate mixed model, with individual boldness before and after the familiarity manipulation (five measures each) as the response variables. We ran a separate mixed model for each treatment combination and included individual and experimental colony as random effects. We then standardized the resulting among-individual covariance estimates to achieve (unitless) correlation coefficients, which are directly comparable across models (Dingemanse and Danchin 2013). A significant correlation would indicate that individuals in that treatment combination maintained their boldness behavior over the 5-week familiarity manipulation.

Finally, we tested how variation in boldness behavior influenced individual and group performance. To assess the effect on individual performance, we estimated each individual's mass change at the end of the experiment as the percent of mass gained or lost compared to their initial mass prior to being placed in their experimental colony. We ran a mixed model with percent mass change as the response variable and included treatment (mixed or control), time since social disturbance (1, 2, 3, or 4 weeks), and their interaction as fixed effects. We additionally included an individual's average boldness before and after the experiment and their interaction as fixed effects to test how an individual's behavior influenced mass change. Boldness scores before and after the experiment were standardized to a mean of 0 and a variance of 1 prior to analysis. Experimental colony was included as a random effect.

We then tested the effect of the experimental familiarity manipulation on collective performance. To do this, we ran a generalized linear model with a colony's overall probability of defending or capturing prey as the response variable

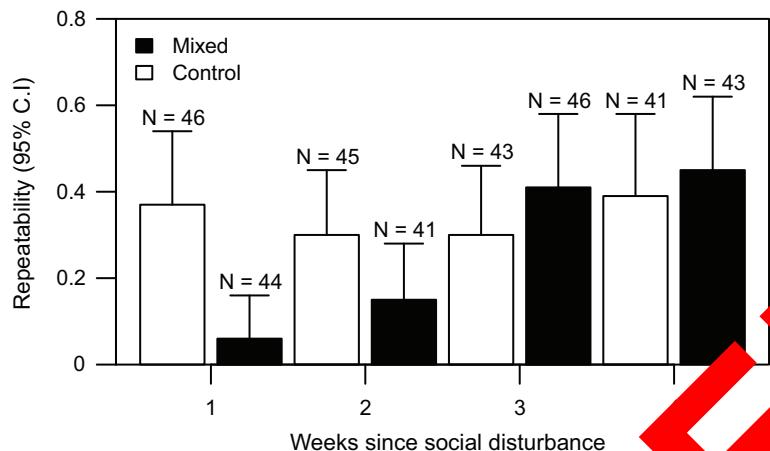
and included treatment, weeks since disturbance, and their interaction as fixed effects. A separate model was run for defense and prey capture. We also wished to characterize the strength of consistent individual variation within each experimental colony to test whether this influenced the colony's collective performance. To do this, we estimated an average colony flexibility score in boldness behavior. This was estimated as the average of the variances of each individual spider's boldness behavior after a familiarity manipulation. Thus, a colony with a high flexibility score would be composed of individuals that had high variance (i.e., were inconsistent) in their boldness behavior. We tested whether average colony flexibility was predicted by the familiarity manipulation. To do this, we ran a linear model with average colony flexibility as the response variable and included treatment and time since social disturbance and their interaction as fixed effects. Finally, we tested whether average flexibility score predicted collective success at either task.

We used general(ized) linear (mixed) models throughout (using restricted maximum likelihood estimation [REML]), assuming a Gaussian error distribution when boldness behavior was the response variable and a binary error when collective behavior was the response variable. We used the 95% confidence interval (CI) to assess the significance of all effects: if the 95% CI did not overlap 0, then we interpreted this as a significant effect of the fixed effect. We tested for the significance of the random effects by comparing the log likelihood of a model including the random effect (i.e., individual) to a model without it. For the bivariate mixed model, to estimate the individual correlation between behavior before and after the familiarity manipulation, we instead used Markov chain Monte Carlo (MCMC) estimation because REML estimation did not allow an accurate assessment of the error around the correlation estimate. All data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.33f0n> (Laskowski et al. 2016).

## Results

### *Familiarity Disturbance Disrupts Social Niches*

Replicating previous results (Laskowski and Pruitt 2014; Modlmeier et al. 2014), we found that increasing familiarity within a colony increased the strength of consistent individual variation in boldness behavior. Individuals in control colonies that remained with their familiar group mates for the entirety of the experiment exhibited significant repeatability in boldness behavior after the familiarity manipulation, regardless of when the social disturbance occurred (fig. 1; table A1; tables A1–A4 are available online). In contrast, the familiarity manipulation among the mixed colonies was effective at disrupting this consistent individual var-



**Figure 1:** Estimates of the repeatability of boldness after the familiarity manipulation among the familiarity treatment groups. Individuals in control colonies exhibited significantly repeatable behavior regardless of when the social disturbance occurred, whereas the repeatability of boldness increased the more time had passed since the social disturbance in mixed colonies. N = the number of individuals within each treatment group (nested within experimental colony).

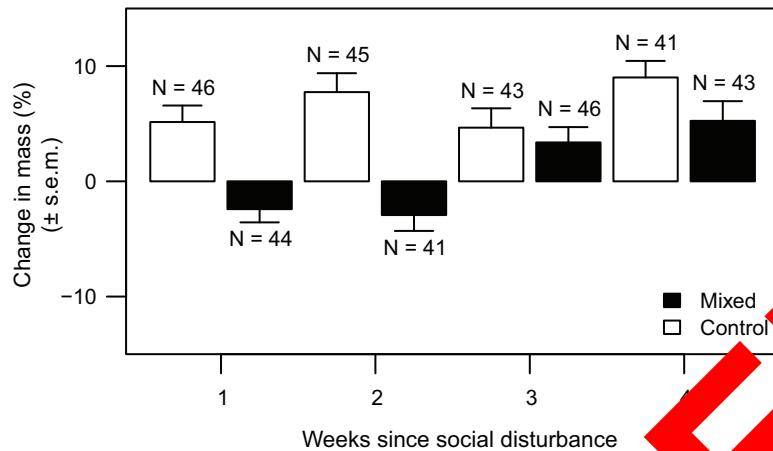
iation in behavior: repeatability in these colonies was lower the more recently the social disturbance transpired (fig. 1; table A1). Importantly, increasing familiarity among group mates after the disturbance allowed the reestablishment of individual differences in behavior: mixed colonies that had not been disturbed for longer than 2 weeks regained similar patterns of behavioral variation to those found in the control colonies (fig. 1).

Individual behavior before being placed in a new colony or familiarity manipulation was predictive of individual behavior after the manipulation but only in colonies that were more familiar with each other. In control colonies, regardless of when the physical disturbance occurred, there was a significant positive correlation between individual boldness behavior before being placed in the familiarity manipulation and individual boldness behavior after the familiarity manipulation (1 week: correlation coefficient: 0.32, 95% CI [0.16, 0.5]; 2 weeks: 0.34 [0.19, 0.40]; 3 weeks: 0.34 [0.16, 0.55]; 4 weeks: 0.31 [0.12, 0.42]), suggesting that familiarity with their group mates allowed control individuals to maintain a similar behavioral strategy over the whole manipulation. In contrast, in mixed colonies that had been recently disturbed, there was no evidence of any correlation between individual behavior before and after the manipulation (1 week: 0.01 [-0.09, 0.11]; 2 weeks: 0.02 [-0.11, 0.16]). With increasing familiarity, however, a positive correlation reappeared in mixed colonies that were disturbed 3 or 4 weeks previously (3 weeks: 0.31 [0.12, 0.48]; 4 weeks: 0.21 [0.06, 0.37]). Taken together, our results suggest that social stability within a colony exaggerated initial personality differences in boldness behavior, whereas a changeover in group membership forced individuals to immediately alter their be-

havior to a point at which predictable and consistent differences among individuals disappear. However, after several weeks together with their group mates, individuals were able to return to the behavioral tendencies they exhibited prior to the familiarity manipulation; in other words, the characteristic differences in individuals' behavior reappeared.

#### *Disrupting Social Niches Has Negative Consequences for Individual and Colony Performance*

Changeover in group membership resulted in significant negative impacts on both individual and colony performance. At the individual level, both the colony's familiarity treatment and an individual's own behavior affected individual mass gain. Individuals from control colonies always enjoyed positive mass gain over the course of the experiment ( $6.60\% \pm 0.78\%$  mass change, mean  $\pm$  SE); however, individuals in mixed colonies that had recently been disturbed actually suffered mass loss (mixed colonies disturbed at 1 week:  $-2.41\% \pm 1.14\%$ ; 2 weeks:  $-2.92\% \pm 1.38\%$ ; fig. 2; table A2). Increasing familiarity in the mixed colonies was able to rescue this effect, as individuals in mixed colonies that were disturbed longer than 2 weeks previously gained mass at similar levels to those in control colonies (3 weeks:  $3.37\% \pm 1.33\%$ ; 4 weeks:  $5.24\% \pm 1.71\%$ ; fig. 2; table A2). Interestingly, an individual's boldness behavior before and after the manipulation interacted to influence individual mass gain (table A2). Individuals that were initially fairly shy at the beginning of the experiment exhibited increased mass gain if they increased their boldness by the end of the experiment; in contrast, individuals that were initially the boldest at the beginning of the experiment gained



**Figure 2:** Change in body mass (as a percentage of the starting weight) within each familiarity treatment. All mixed colonies that were disturbed more recently experienced mass loss over the course of the experiment, whereas control colonies always gained weight regardless of when the social disturbance occurred. N = the number of individuals within each treatment group (nested within experimental colony).

more mass if they actually reduced their boldness at the end of the experiment (fig. 3).

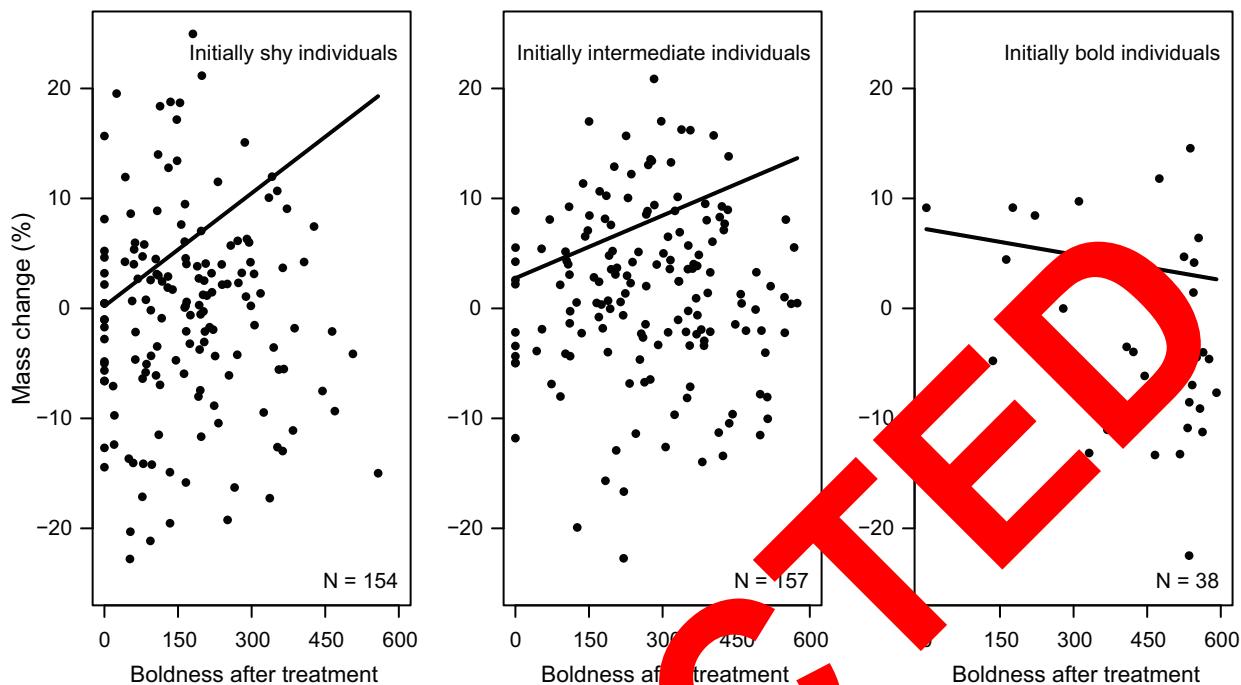
At the colony level, the familiarity manipulation influenced the colony's ability to perform collective tasks such as colony defense and prey capture. Mixed colonies were less likely to successfully capture their prey or defend their nest against intrusion by a lethal intruder (prey capture: estimate of mixed treatment effect =  $-0.510 (-0.588, -0.058)$ ,  $t = -2.25$ ,  $P = .028$ ; nest defense: estimate of mixed treatment effect =  $-0.435 (-0.793, -0.058)$ ,  $t = -1.08$ ,  $P = .018$ ; table A3). This negative impact on colony performance appears to be driven by the presence of highly flexible and inconsistent individuals. We first confirmed that average colony flexibility was significantly predicted by the interaction between colony treatment and time since social disturbance, such that more recently disturbed colonies were composed of more variable (i.e., inconsistent) individuals (treatment  $\times$  time since social disturbance estimate =  $-0.477 (-0.545, -0.210)$ ,  $t = -2.68$ ,  $P = .009$ ; table A4). This average colony flexibility was then a good predictor of colony's overall probability of successful performance at the collective tasks: colonies that were most successful at defending their nest or capturing prey were composed of individuals with lower individual flexibility (prey capture: estimate of average flexibility effect =  $-0.239 (-0.405, -0.073)$ ,  $t = -2.88$ ,  $P = .005$ ; nest defense: estimate of average flexibility effect =  $-0.172 (-0.291, -0.054)$ ,  $t = -2.91$ ,  $P = .005$ ; fig. 4).

### Discussion

Replicating previous results, we demonstrate that increasing familiarity among the same individuals in a cooperat-

tive group is sufficient to strengthen consistent individual differences in behavior indicative of social niches. Importantly, imposing social disturbance by manipulating group membership appeared to force individuals out of their predictable behavioral patterns, thus disrupting their social niches. This disruption caused individual spiders to lose weight and colonies to perform more poorly at vital collective tasks such as prey capture and colony defense. Altogether, our results strongly support the hypothesis that repeated social interactions can generate and/or strengthen social niches, which are beneficial to both individuals and colonies as a whole, and conversely, that establishing new social niches with unfamiliar individuals comes at a potentially steep cost.

Individual behavior (and boldness in particular) is known to influence task specialization and performance in *Stegodyphus* spiders (Grinsted et al. 2013; Settepani et al. 2013; Wright et al. 2014, 2015), and recent articles have indicated that bolder individuals may have a particularly strong influence on the collective behavior of their colony (Pruitt and Keiser 2014; Pruitt and Pinter-Wollman 2015). During the course of the familiarity manipulation, our experimental colonies had the opportunity to repeatedly interact at important collective tasks such as web building and prey capture and therefore generate social niches. By disrupting the group composition of some of the colonies, our experimental treatment was effective at manipulating social niches in these spiders. The reduced repeatability of boldness behavior exhibited by recently disturbed mixed colonies indicates that these individuals left their established social niches as a result of our manipulation. Importantly, this disruption of social niches caused individuals in the mixed colonies to actually lose weight, weighing about 10% less than their control



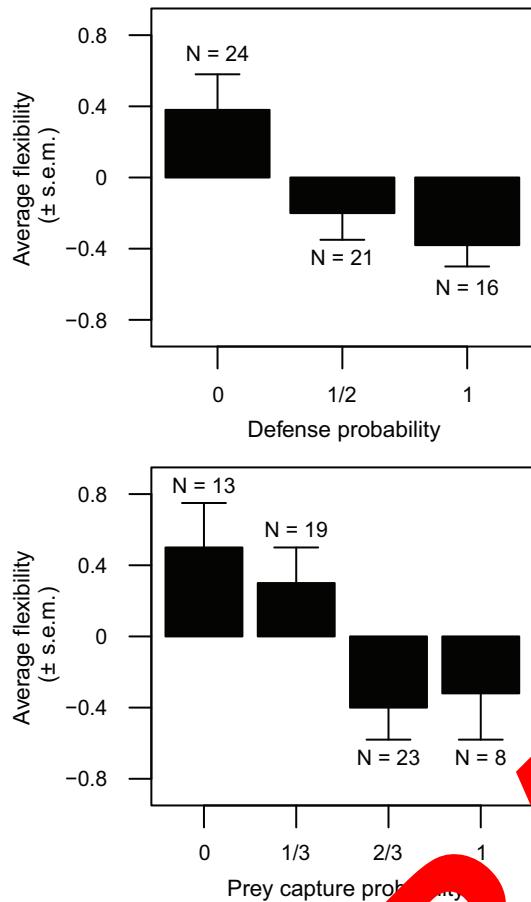
**Figure 3:** Change in body mass (as a percentage of the starting weight) based on the average boldness before and after being placed in the familiarity manipulation. For ease of presentation, individuals were separated into groups based on their average boldness score prior to the familiarity treatment (individuals with boldness scores <200 in the left panel, individuals with boldness scores >200 and <400 in the middle panel, and individuals with boldness scores >400 in the right panel). Increasing boldness after the treatment resulted in positive weight gain for spiders that were initially shy and intermediate; however, initially bold spiders gained more weight if they reduced their boldness by the end of the experiment. Dots represent individual spider's boldness scores and mass change (corrected for differences among treatment groups); lines indicate the predicted relations from the model.

colony counterparts by the end of the experiment. In contrast, individuals in control colonies gained on average 7% (and sometimes as high as 50%) of their initial starting mass, regardless of when the physical disturbance occurred. Notably, all females in social spider colonies are capable of reproduction (Avilés 1997; Lubin and Bilde 2007), and given that body size strongly determines the size of a potential egg case (Vollrath and Jordan 2003; Rypstra 1993; Salomon et al. 2013), the weight reduction in the recently disturbed mixed colonies was likely detrimental.

Interestingly, while our familiarity manipulation had strong impacts on individual weight gain, the individual spider's behavior did as well. Bolder behavior at the beginning of the experiment generally had a positive impact on individual weight gain, except in the individuals that were initially the boldest; these individuals were most successful when they actually reduced their boldness by the end of the experiment. This pattern of decreasing propensity to take risks with increasing assets (i.e., weight) is in line with the hypothesis of asset protection (Clark 1994). While we were unable to determine whether weight gain or a behavioral change occurred first, it seems plausible that they are both

involved in a dynamic feedback loop (Sih et al. 2015). One hypothetical pathway might be that these bold individuals were best able to exploit foraging opportunities, giving them the resources to rapidly amass weight early on, but once some weight threshold is reached, this encourages the individuals to reduce their exposure to risk.

In addition to impacting individual performance, the disruption of social niches negatively influenced the colony's ability to perform vital tasks. The social niche specialization hypothesis assumes that one of the major benefits of social niches is that they allow individuals to more quickly align themselves for cooperative tasks because individuals can be relied on to behave in a certain way. Colonies that were composed of inconsistent and highly flexible individuals performed worse at collective tasks compared to colonies composed of consistent, specialized individuals. This is especially interesting given that behavioral flexibility is often considered advantageous if it allows individuals to rapidly adjust to external conditions, and a key question in the animal personality literature has been to understand when and why behavioral consistency is favored (Dingemanse and Wolf 2010). These data suggest that the costs and benefits



**Figure 4:** Colonies that were more successful at performing collective tasks had lower average flexibility. Flexibility estimates were mean centered, and variance was scaled to 1 prior to analysis. N = the number of colonies within each probability category.

of behavioral flexibility may operate at different levels of organization (Farine et al. 2015). Thus, at least in animals that live in stable social groups, accounting for differences in group performance may be a promising area for future research to better understand the evolution of behavioral consistency and flexibility.

Our findings are also consistent with classic hypotheses regarding division of labor, where colonies composed of behaviorally stable and specialized individuals are predicted to outperform undifferentiated societies because of enhanced individual task specialization and task efficiency (Oster and Wilson 1978; Wilson 1987). Consistent with this theory, there is now ample evidence of personality-based task differentiation in spider societies, and these patterns are consistently associated with performance advantages at both the individual and the colony level (Pruitt et al. 2008; Grinstead et al. 2013; Settepani et al. 2013; Pruitt and Goodnight 2014;

Wright et al. 2014, 2015). Our results importantly add to this literature by suggesting that social stability may be a key element in the formation and exaggeration of individual differences to the betterment of the society. From an evolutionary perspective, one wonders the degree to which personality-based task differentiation acts as a precursor to even more highly differentiated societies (e.g., eusocial societies). For spiders, this question is difficult to address because there is little evidence of morphological castes in any species (but see Avilés et al. 2006). In social insects, division of labor based on behavioral differences such as personality seems to emerge spontaneously with the transition to group living, suggesting that personality-based division of labor could emerge immediately with the transition to sociality (Jeanson and Fewell 2008; Jeanson et al. 2008), and further morphological specialization might occur only after. Taken together, positive associations between group living, repeatable behavioral variation, and colony success have now been documented in eight species of social spider, representing at least five independent origins of sociality (summarized in table 1 in Keiser et al. 2014). It therefore appears that consistent individual differences in behavior may be a general phenomenon structuring the organization of social spiders (and potentially other societies like them), with effects similar to those seen in the morphologically differentiated societies of ants. We therefore posit that social stability may itself be an underappreciated driver behind such patterns for these and other kinds of animal societies.

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#### Literature Cited

- Avilés, L. 1986. Sex-ratio bias and possible group selection in the social spider *Anelosimus eximius*. *American Naturalist* 128:1–12.
- . 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pages 476–498 in J. C. Choe and

- B. J. Crespi, eds. The evolution of social behaviour in insects and arachnids. Cambridge University Press, Cambridge.
- Avilés, L., W. P. Maddison, and I. Agnarsson. 2006. A new independently derived social spider with explosive colony proliferation and a female size dimorphism. *Biotropica* 38:743–753.
- Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour* 77:771–783.
- Bergmüller, R., and M. Taborsky. 2010. Animal personality due to social niche specialisation. *Trends in Ecology and Evolution* 25:504–511.
- Carter, A. J., S. English, and T. H. Clutton-Brock. 2014. Cooperative personalities and social niche specialization in female meerkats. *Journal of Evolutionary Biology* 27:815–825.
- Clark, C. W. 1994. Antipredator behavior and the asset-protection principle. *Behavioral Ecology* 5:159–170.
- Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* 82:39–54.
- Dingemanse, N. J., and M. Wolf. 2010. Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3947–3958.
- Farine, D., P.-O. Montiglio, and O. Spiegel. 2015. From individuals to groups and back: the evolutionary implications of group phenotypic composition. *Trends in Ecology and Evolution* 30:609–621.
- Favati, A., O. Leimar, T. Radesäter, and H. Lövlie. 2014. Social status and personality: stability in social state can promote consistency of behavioural responses. *Proceedings of the Royal Society Biological Sciences* 281:20132531.
- Gordon, D. M. 1996. The organization of work in social insect colonies. *Nature* 380:121–124.
- Grinsted, L., J. N. Pruitt, V. Settepani, and T. Bilde. 2013. Individual personalities shape task differentiation in a social spider. *Proceedings of the Royal Society B: Biological Sciences* 280:20131110.
- Holbrook, C. T., C. M. Wright, and J. N. Pruitt. 2014. Individual differences in personality and behavioral plasticity facilitate division of labour in social spider colonies. *Animal Behaviour* 97:177–183.
- Jeanson, R., R. M. Clark, C. T. Holbrook, K. Bertram, J. H. Fewell, and P. F. Kukuk. 2008. Division of labor and socially induced changes in response thresholds in associations of solitary halictine bees. *Animal Behaviour* 76:603–602.
- Jeanson, R., and J. H. Fewell. 2008. Influence of the social context on division of labor in associations of eusocial insects. *Behavioral Ecology* 19:567–574.
- Keiser, J., D. Jones, A. Modlmeier, and J. Pruitt. 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.
- Laskowski, K. L., and A. Bell. 2014. Strong personalities, not social niches, drive individual differences in social behaviour in sticklebacks. *Animal Behaviour* 90:287–295.
- Laskowski, K. L., P.-O. Montiglio, and J. N. Pruitt. 2016. Data from: Individual and group performance suffers from social niche disruption. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.33f0n>.
- Laskowski, K. L., and J. N. Pruitt. 2014. Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society B: Biological Sciences* 281:20133166.
- Lubin, Y., and T. Bilde. 2007. The evolution of sociality in spiders. *Advances in the Study of Behaviour* 37:83–145.
- Modlmeier, A. P., K. L. Laskowski, A. E. DeMarco, A. Coleman, K. Zhao, H. A. Brittingham, D. R. McDermott, et al. 2014. Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. *Biology Letters* 10:20140419.
- Montiglio, P.-O., C. Ferrari, and D. Réale. 2013. Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368:201203.
- Nakagawa, S., and H. Schielzeth. 2010. Repeatability analysis: Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* 85:935–956.
- Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in the social insects. Princeton University Press, Princeton.
- Pruitt, J. N., and C. J. Goettl. 2014. Site-specific group selection drives locally adapted group positions in nature. *Nature* 514:359–362.
- Pruitt, J. N., L. Grinsted, and V. Settepani. 2014. Linking levels of personality: personality types of the “average” and “most extreme” group members predict colony-level personality. *Animal Behaviour* 86:391–399.
- Pruitt, J. N., and C. N. Keiser. 2014. The personality types of key catalyst individuals shape colonies’ collective behaviour and success. *Animal Behaviour* 93:87–95.
- Pruitt, J. N., and M. Winter-Wollman. 2015. The legacy effects of key catalyst individuals on collective behaviour scale to how long they remain within their group. *Proceedings of the Royal Society B: Biological Sciences* 282:20151766.
- Pruitt, J. N., S. E. Riechert, and T. C. Jones. 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour* 76:871–879.
- Riechert, S. E., and A. V. Hedrick. 1990. Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta*. *Animal Behaviour* 40:679–687.
- 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.
- Salomon, M., D. Mayntz, and Y. Lubin. 2008. Colony nutrition skews reproduction in a social spider. *Behavioral Ecology* 19:605–611.
- Settepani, V., L. Grinsted, J. Granfeldt, J. L. Jensen, and T. Bilde. 2013. Task specialization in two social spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae). *Journal of Evolutionary Biology* 26:51–62.
- Sih, A., K. J. Mathot, M. Moirón, P.-O. Montiglio, M. Wolf, and N. J. Dingemanse. 2015. Animal personality and state-behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology and Evolution* 30:50–60.
- Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19:448–455.
- Vollrath, F., and D. Rohde-Arndt. 1983. Prey capture and feeding in the social spider *Anelosimus eximius*. *Zeitschrift für Tierpsychologie* 61:334–340.
- Wickler, W., and U. Seibt. 1993. Pedogenetic sociogenesis via the “sibling-route” and some consequences for *Stegodyphus* spiders. *Ethology* 95:1–18.
- Wilson, E. O. 1987. Causes of ecological success: the case of the ants. *Journal of Animal Ecology* 56:1–9.
- Wolf, M., and F. J. Weissing. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3959–3968.

Wright, C. M., C. T. Holbrook, and J. N. Pruitt. 2014. Animal personality aligns task specialization and task proficiency in a spider society. *Proceedings of the National Academy of Sciences of the USA* 111:9533–9537.

Wright, C. M., C. N. Keiser, and J. N. Pruitt. 2015. Personality and morphology shape task participation, collective foraging and es-

cape behaviour in the social spider *Stegodyphus dumicola*. *Animal Behaviour* 105:47–54.

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*Top left:* A portrait of the social spider species, *Stegodyphus dumicola*. *Top right:* a group of individually marked spiders huddling together. The abdominal markings have been painted to keep track of individuals' identities in the experiments. *Bottom:* two *S. dumicola* cooperating to subdue a potential intruder (Hemiptera: Reduviidae), an important collective task measured in the study. Photo credit: Graham Montgomery.

**RETRACTED**