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Title

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Permalink

Journal

The American Naturalist, 187(6)

ISSN

Authors

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Publication Date

2016-06-01

DOI

Peer reviewed

Individual and group performance suffers from social niche disruption

Short title: Costs of social niche establishment

Article

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

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 less familiar 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 re-establishment carries a steep cost to both individuals and groups. Social niche specialization may therefore provide a potential first step on the path towards more organized social systems.

INTRODUCTION

Consistent individual differences in behavior, or personalities, are present across a range of taxa (Bell et al. 2009) and are often related to fitness parameters (Smith and Blumstein 2008) making their widespread presence difficult to explain from an adaptive perspective. Recent theoretical work predicts that personalities are a result of adaptive evolution (Dingemanse 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, territorial interactions). The hypothesis predicts that personalities are a result of individuals maintaining a certain social role or niche within their 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. they 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. And, 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 in order for social niche specialization to be a viable mechanism for generating and maintaining consistent individual differences in behavior, individuals must benefit somehow from maintaining their social niche; or, 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 paper 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 multi-female societies that exhibit highly female-biased primary sex ratios and perennial inbreeding, which results in very high relatedness among colony constituents (Aviles 1986; Aviles 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 (Aviles 1997; Lubin and Bilde 2007). Despite this colony-level cooperation in vital collective tasks, individuals within colonies tend to specialize on just 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; Holbrook et al. 2014; Settepani et al. 2013; Wright et al. 2014; Wright et al. 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 brood 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 predicts tasks participation in the field (Grinsted et al. 2013; Wright et al. 2015). All this suggests that an individual spider's level of boldness should 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. But as of yet, 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 (Aviles 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 (Rypstra 1993; Salomon et al. 2008; Vollrath and Rohde-Arndt 1983).

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, on the other hand, that 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 or 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 as an indicator of individual success before and after the familiarity manipulation. Collective task trials (defense against intruder and prey capture) were performed after the completion of the familiarity manipulation.

Animal collection & maintenance

Colonies of mature *S. dumicola* were collected along the southern Kalahari Desert Basin in February 2014. Colonies were collected along roadside fences and hookbush acacia (*Acacia mellifera*) by placing the colony within a fabric pillowcase and trimming its supporting branches. Whole colonies were shipped to the laboratory at the University of Pittsburgh, PA, USA. Colonies were hand-sorted and spiders were isolated in 59ml 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 atop their 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 (Aviles

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 in (Laskowski and Pruitt 2014). Each colony was placed into a

1.5l 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

(six-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 five weeks. Each colony experienced a single social disturbance

that occurred after either one, two, three, or four weeks. This social

disturbance involved all individuals being removed from the colony's webbing

and being placed into 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). So a colony that experienced a social disturbance four weeks previously would be more familiar with their group mates than a colony that only experienced the social disturbance just one 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 at either one, two, three or four weeks, they were instead placed into 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 mixed colonies was altered allowing us to isolate the effects of familiarity *per se* on behaviour and performance. Altogether, one replicate of our familiarity manipulation contained 8 treatment combinations in a factorial design where we manipulated whether group membership changed during the experiment ("control" versus "mixed" colonies) and when that change in membership occurred ("time since social disturbance" – one, two, three, or four weeks) with a total of 64 experimental colonies (8 complete replicates).

Individual and collective assessment

We assessed all experimental (i.e. control and mixed) individuals' mass 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 and 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; Wright et al. 2015). To do this, we placed a single individual into a rectangular enclosure (13.5x13x3.5cm) and allowed it 60s to settle. We then applied two rapid bursts of air to the anterior, dorsal side of the spider from ~6cm away using an infant nose-cleaning bulb. This universally elicited a "huddle" response by all individuals where they draw 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 minutes). In this way, we interpreted spiders that recovered more quickly from a simulated risk of a predator attack as bolder. This assay was repeated once per day for five days. 24 hours after completion of the boldness assays, the spiders were placed in the familiarity manipulation. Then 24 hours after completion of the familiarity manipulation, individuals were again isolated, weighed, and assayed for boldness as before (once per day for five days).

We also assessed group performance at collective tasks after completion of the familiarity manipulation and after individuals had been measured for their boldness post-manipulation. 24 hours after the final individual boldness assay, colonies were reformed and assessed for their

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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 hours 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 it 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 24h.

Statistical analyses

The latency of a spider to recover from the simulated predator attack was inverted (maximum latency of 600 seconds – 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 defenses 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 one, two, three and four 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 Dochtermann 2013). A significant correlation would indicate individuals in that treatment combination maintained their boldness behavior over the five 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 (one, two, three, four 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 zero and a variance of one prior to analysis. Experimental colony was included as a random effect.

Then, we 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 the familiarity manipulation. Thus a colony with a high flexibility score would be composed of individuals that had high variance (i.e. 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 then 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% CI to assess the significance of all fixed effects: if the 95% CI did not overlap zero 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. 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: https://www.doi.org/doi: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 (Figure 1, Table A1). In contrast, the familiarity manipulation among the mixed colonies was effective at disrupting this consistent individual variation in behavior: repeatability in these colonies was lower the more recently the social disturbance transpired (Figure 1, Table A1). Importantly, increasing familiarity among group mates after the disturbance allowed the re-establishment of individual differences in behavior: mixed colonies that had not been disturbed for longer than two weeks regained similar patterns of behavioral variation to those found in the control colonies (Figure 1).

Individual behavior before being placed in the 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 an individual's boldness behavior after the familiarity manipulation (one week correlation coefficient: 0.32, 95% CI: (0.16,0.52); two weeks: 0.23 (0.09,0.40); three weeks: 0.34 (0.16, 0.55); four weeks: 0.31 (0.12,0.52)), 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 (one week: 0.01 (-0.09,0.11); two weeks: 0.02 (-0.11,0.16)). With increasing familiarity, however, a positive correlation re-appeared in mixed colonies that were disturbed three or four weeks previously (three weeks: 0.31 (0.12,0.48; four 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 behavior to a point that 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 reappear.

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±0.78% mass change: mean±s.e.), however individuals in mixed colonies that had recently been disturbed actually suffered mass loss (mixed colonies disturbed at one week: -2.41±1.14%; mixed at two weeks: -2.92±1.38%; Figure 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 two weeks previously gained mass at similar levels to those in control colonies (mixed at three weeks: 3.37±1.33%; mixed at four weeks: 5.24±1.71%; Figure 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 more mass if they actually reduced their boldness at the end of the experiment (Figure 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 (-0.962, -0.058), t = -2.25, p = 0.028; nest defense: estimate of mixed treatment effect = -0.435 (-0.793, -0.078), t = -2.43, p = 0.018; 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 flexible (i.e. inconsistent) individuals (Treatment x time since social disturbance estimate = -0.477 (-0.832, -0.122), t = -2.68, p = 0.009; Table A4). This average colony flexibility was then a good predictor of a 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 = 0.005; nest defense: estimate of average flexibility effect = -0.172 (-0.291, -0.054), t = -2.91, p =0.005; Figure 4).

DISCUSSION

Replicating previous results, we demonstrate that increasing familiarity among the same individuals in a cooperative group is sufficient to strengthen consistent individual differences in behavior indicative of social niches. Importantly, imposing a 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; Wright et al. 2015) and recent papers 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 colony counterparts by the end of the experiment. In contrast, individuals in control colonies gained on average 7% of their initial starting mass and sometimes as high as 30% regardless of when the physical disturbance occurred. Notably, all females in social spider colonies are capable of reproduction (Aviles 1997; Lubin and Bilde 2007) and given that body size strongly determines the size of a potential egg case (Rypstra 1993; Salomon et al. 2008; Vollrath and Rohde-Arndt 1983), this weight reduction in the recently disturbed mixed colonies is likely detrimental.

Interestingly, while our familiarity manipulation had strong impacts on individual weight gain, so did the individual spider's behavior. 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 if 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 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 upon 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 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 colony level (Grinsted et al. 2013; Pruitt and Goodnight 2014; Pruitt et al. 2008; Settepani et al. 2013; Wright et al. 2014; Wright et al. 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). For social insects, division of labor based on behavioral differences like personality seem 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 et al. 2008; Jeanson and Fewell 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 six independent origins of sociality (summarized in table 5 in Keiser et al. 2014). It therefore appears that consistent individual differences in behavior may be a general phenomenon structuring the

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organization of social spiders (and potentially other societies like them) with effects similar to those seen in the morphologically-differentiated societies of social insects. We therefore posit that social stability may itself be an underappreciated driver behind such patterns for these and other kinds of animal societies.

ACKNOWLEDGEMENTS

ONLINE APPENDIX A: Detailed results tables

Table A1. estimates of boldness scores after completion of the familiarity manipulation in each of the treatment groups.

	Time since social disturbance			
	One week	**Two weeks**	**Three weeks**	**Four weeks**
	Control colonies			
among	152.5 (69.0, 249.4)	123.8 (43.3, 206.4)	113.6 (51.9, 196.0)	165.5 (76.3, 271.8)
within	258.2 (201.8, 317.6)	318.2 (260.7, 392.8)	208.7 (162.7, 264.6)	205.1 (167.8, 247.5)
R	0.37 (0.24, 0.54)	0.30 (0.16, 0.45)	0.30 (0.14, 0.46)	0.39 (0.22, 0.58)
LLR	38.73	22.50	32.34	48.55
p-value	<0.0001	<0.0001	<0.0001	<0.0001
N_{indv} (N_{colony})	46 (8)	45 (8)	43 (8)	41 (8)
	Mixed colonies			
among	29.4 (0, 90.2)	83.5 (1.5, 157.6)	198.7 (98.8, 317.1)	206.9 (96.6, 325.9)
within	433.5 (355.9, 519.5)	422.2 (335.2, 508.9)	259.6 (212.0, 311.8)	230.2 (182.2, 289.1)
R	0.06 (0, 0.16)	0.15 (0.03, 0.28)	0.41 (0.28, 0.59)	0.45 (0.29, 0.62)
LLR	1.36	8.14	51.87	57.76
p-value	0.242	0.004	<0.0001	<0.0001
N_{indv} (N_{colony})	44 (8)	41 (8)	46 (8)	43 (8)

Linear mixed models with REML estimation including 'individual' and 'experimental colony' as random effects. 95% confidence intervals are in parentheses; 'LLR' stands for log-likelihood ratio between a model containing the random 'individual' effect and one without. 'N_{indv} (N_{colony})' lists the number of individual in each treatment group (nested within the number of colonies within that treatment group). Boldness scores were not scaled or centered

prior to analysis as we were inherently interested in investigating differences

in total variance.

Table A2. Summary of fixed effects on individual percent mass change over the course of the experiment.

Fixed effect	Estimate	95% CI	t	p-value
Treatment: mixed	-11.85	(-17.03, -6.67)	-4.57	**<0.001**
Weeks since disturbance	0.89	(-0.43, 2.21)	1.33	0.185
Treatment*Weeks	2.29	(0.40, 4.19)	2.42	**0.018**
Pre-boldness	2.12	(0.89, 3.34)	3.41	**<0.001**
Post-boldness	-1.04	(-2.31, 0.21)	-1.64	0.102
Pre*post	-1.89	(-2.94, -0.83)	-3.51	**<0.001**

Linear mixed model with REML estimation including 'experimental colony' as a random effect. Fixed effects whose 95% C.I. does not overlap zero are bolded. All behavioral fixed effects were mean-centered and variance scaled to one prior to analysis.

Table A3. Summary of fixed effects on collective tasks.

Fixed effect	Estimate	95% CI	t	p-value
Average probability of defending (N = 63 colonies, residual s.e.=0.361 on 59 d.f.; R^2=25.8%)				
Treatment: mixed	-0.510	(-0.962, -0.058)	-2.25	**0.028**
Weeks since disturbance	0.104	(-0.013, 0.222)	1.78	0.079
Treatment*Weeks	0.098	(-0.065, 0.262)	1.20	0.233
Average probability of prey attack (N = 63 colonies, residual s.e.=0.285 on 59 d.f., R^2=28.8%)				
Treatment: mixed	-0.435	(-0.793, -0.078)	-2.43	**0.018**
Weeks since disturbance	0.085	(-0.008, 0.178)	1.83	0.072
Treatment*Weeks	0.088	(-0.042, 0.217)	1.35	0.181

Generalized linear model with REML estimation and a binary error distribution. Fixed effects whose 95% C.I. does not overlap zero are bolded.

Table A4. Summary of fixed effects on average colony flexibility estimates.

Fixed effect	Estimate	95% C.I.	t	p
Treatment: mixed	1.907	(0.927, 2.888)	3.89	**< 0.001**
Weeks since disturbance	- 0.167	(-0.422, 0.088)	- 1.31	0.195
Treatment*Weeks	- 0.477	(-0.832, - 0.122)	- 2.69	**0.009**

Linear model with REML estimation. Fixed effects whose 95% C.I. do not overlap zero are bolded.   N = 63 colonies. Residual s.e. = 0.782 on 59 d.f. Adjusted R^2 = 38.77%.

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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 longer since the social disturbance in mixed colonies. 'N' refers to the number of individuals within each treatment group (nested within experimental colony).

Figure 2. Change in body mass (as percentage of starting weight) within each familiarity treatment group. 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' refers to the number of individuals with each treatment group (nested within experimental colony).

Figure 3. Change in body mass (as percentage of starting weight) based on individual 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 left panel, individuals with 200 < boldness scores < 400 in middle panel, individuals with boldness

scores > 400 in 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 a single individual's boldness scores and mass change (corrected for differences among treatment groups); lines indicate the predicted relationship from the model.

Figure 4. Colonies that were more successful at performing collective tasks had lower average flexibility. Flexibility estimates were mean centered and variance scaled to one prior to analysis. 'N' refers to the number of colonies within each probability category.