



RESEARCH PAPER

Exploring How a Shift in the Physical Environment Shapes Individual and Group Behavior across Two Social Contexts

Carl N. Keiser, Andreas P. Modlmeier, Nishant Singh, Devin K. Jones & Jonathan N. Pruitt

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA

Correspondence

Carl N. Keiser, Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, USA.
E-mail: cnk21@pitt.edu

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Abstract

The presence or absence of social counterparts can be instrumental in shaping both individual and collective behaviors. Furthermore, factors of the social environment may safeguard individuals from environmental stressors. In the study reported here, we tested the effects of moving into a new habitat on the mean, variance, and repeatability of individual behavioral tendencies between two social contexts (isolated vs. in a social group). Using the arid social spider, *Stegodyphus dumicola* (Araneae: Eresidae), we tested whether individuals' boldness was influenced by either (i) their time spent in a social group or (ii) their latency since having moved into a new habitat. We found that the effect of moving into a new habitat on individuals' boldness depended on whether spiders entered the novel environment in isolation or as part of a social group. Spiders that experienced a habitat shift with a social group showed no change in their average boldness, whereas individuals that shifted environments in isolation showed an increase in their mean boldness. Interestingly, neither of these trends was influenced by the time which had elapsed since the habitat shift, suggesting that shifting habitats has a lasting effect on isolated spiders' behavioral tendencies. Finally, we assessed how time spent in a new environment influenced colonies' collective foraging behavior. Here, we found that the longer social groups remained in a new environment, the faster the group responded to prey. Taken together, our data demonstrate that the effects of shifting physical environments on individuals' boldness may depend on individuals' social context, and that group tenure is associated with subtle shifts in colonies' collective foraging behavior.

Introduction

Recent years have seen a growing interest in the causes and consequences of consistent individual differences in behavior—from invertebrates to primates (Gosling 2001; Wolf & Weissing 2012). These advances have revealed far-reaching consequences of between-individual variation in behavior: guiding individual fitness, population dynamics, species interactions, and, potentially, even driving/constraining adaptive evolution (Bell & Stamps 2004; Sinn et al. 2006; Pruitt et al. 2012a; Pruitt 2013). Due to the impressive predictive value of understanding between-individual variation in behavior (reviewed in: Sih et al. 2004; Réale et al. 2007; Sih et al. 2012),

it is important to identify the factors that shape the presence and magnitude of this variation.

A number of recent studies have demonstrated that phenotypic plasticity and experience may be influential in shaping individuals' behavioral types and the structure of behavioral syndromes. Early exposure to social cues, environmental stressors, nutrient limitation, and dissimilar rearing environments have all been shown to influence individuals' behavioral types or behavioral syndrome arrangement (Riechert 1993; Sih 2011; DiRienzo et al. 2012; Tremmel & Müller 2012; Sweeney et al. 2013). One factor that could have a large influence on the expression of individual behavioral differences is environmental instability. Specifically, theory predicts that stable environments

should favor the expression of between-individual variation as individuals can cultivate stable, optimal strategies (however diverse) over time, which will be reflected in their behavioral type (Henrich & Boyd 1998; Niemelä et al. 2013). In contrast, unpredictably stochastic habitats may make it more difficult for individuals to track features like resource availability and social context (Niemelä et al. 2013). This stochasticity is predicted to yield behavioral plasticity because individuals' traits may need to shift dynamically along with environmental cues (Via et al. 1995). We currently lack empirical studies that test how shifting physical and/or social environments influence the development and maintenance of between-individual variation, especially in social animals.

Social experience (i.e., living solitarily or among conspecifics) can be another critical factor in determining future decision-making, learning, brain development, and personality (Engeszer et al. 2004; Maleszka et al. 2009). Theory here predicts that group living should favor the evolution of social niche specialization and thus between-individual variation in behavior (Bergmüller & Taborsky 2010). For instance, in *Drosophila melanogaster*, individuals exhibit characteristic preferences in their tendency to join groups, which produces greater between-individual variation throughout ontogeny via social niche construction: social individuals tend to join groups and, in turn, living in groups increases individuals' sociability (Saltz 2011; Saltz & Foley 2011). Thus, over time, social individuals become more social and asocial individuals become more asocial via positive feedbacks. Consequently, the time that an individual spends in a particular social setting is positively associated with greater repeatability in behavioral tendencies associated with group living. Other evidence suggests that sociality will favor increased between-individual behavioral variation in order to diminish niche overlap among group constituents, generate division of labor (Pruitt & Riechert 2011), and facilitate the evolution of cheater/exploitative behavioral types like scroungers and social parasites (Harkins 1987). Taken together, we predict that group living will generate an increased signature in individuals' personality traits which may persist through shifts in the physical environment.

Moving to a novel environment via dispersal, migration, or accidental displacement carries with it many costs, such as increased risk of encountering predators (Christenson 1984; Sunahara et al. 2002) and difficulty estimating the quality of the new habitat (Stamps & Swaisgood 2007). However, Pinter-Wollman et al. (2009) suggest, via the 'beneficial

sociality in novel environments' (BSNE) hypothesis, that animals experience fewer costs from encountering novel habitats when alongside conspecifics. Thus, in animals that change habitats both individually and in groups, such as social spiders (Lubin & Robinson 1982; Vollrath 1982), the breadth of behavioral consistency and between-individual variation may be contingent on whether or not individuals dispersed alongside conspecifics. After a group dispersal event, one might predict stability in the mean value or variance in behavioral traits most important for group performance in the new habitat, that is, hunting-related traits in foraging societies. Furthermore, the duration of group membership before and after a group-founding event may equally influence the range or consistency in individuals' behavior. McPherson et al. (1992) suggest that group tenure is especially important because extended group membership can reinforce group dynamics without the need for continuous recruitment.

Stegodyphus dumicola (Araneae: Eresidae) is an Old World philopatric social spider that lives in colonies of numerous adults and juveniles who forage communally, exhibit alloparental care, and exhibit limited dispersal capabilities (Bodasing et al. 2002; but see Schneider et al. 2001). Penultimate juveniles and adults will disperse from the natal colony via bridging and ballooning and can found new colony sites solitarily or in groups (Eberhard 1987; Henschel et al. 1995; Schneider et al. 2001; Lubin & Suter 2013). Individuals who disperse solitarily are solely responsible for all tasks related to colony construction, web maintenance, and foraging. Alternatively, individuals who disperse in a group can forage individually or cooperatively, and web maintenance is distributed among colony-mates. Despite the characteristic differences between these lifestyles, we regularly find both singletons and social colonies in the field. Given these divergent strategies, this system is well-suited to explore the effects of environmental stochasticity on between-individual variation across social contexts, because shifts in both the social and physical environment occur regularly to solitary and group-living individuals.

Herein, we test the hypothesis that environmental stability, as estimated by time elapsed since a shift in an individual's physical environment, will be associated with a stronger repeatability in a key personality trait: boldness. Boldness is the latency to resume activity after an aversive predatory stimulus and is associated with foraging traits at both the individual and colony level in two *Stegodyphus* species (Grinsted et al. 2013; Pruitt et al. 2013). In addition, we test

how living in different social contexts (i.e., solitary or among conspecifics) after experiencing a shift in the physical environment can alter the trajectory of individual behavioral traits. Specifically, we aim to test the following questions: (i) Does time spent with conspecifics influence colony foraging traits like latency to attack prey or the number of individuals that attack? (ii) How does a shift in an individual's physical environment (dispersing to a novel enclosure) influence the mean, variance, and repeatability of boldness across two social contexts (solitary or among conspecifics)? (iii) Does time elapsed since a shift in the physical environment influence these behavioral traits? For Question I, we predict that groups that have spent longer together will exhibit reduced latencies to attack prey and greater incidence of cooperative (i.e., multi-individual) prey capture, because older groups will have more elaborate web architectures and established social structures. For Question II, we predict that spiders which experience a shift in the physical environment alongside conspecifics will exhibit greater between-individual variation and repeatability than individuals that experience a stable environment (Fig. 1), because living in a group will beget social niche partitioning, task specialization, and trait differentiation (Dall et al. 2012). In contrast, we predict that spiders which disperse to a novel environment in isolation will exhibit low between-individual variation and repeatability, because isolated individuals must perform every task for themselves and thus should exhibit a high degree of plasticity.

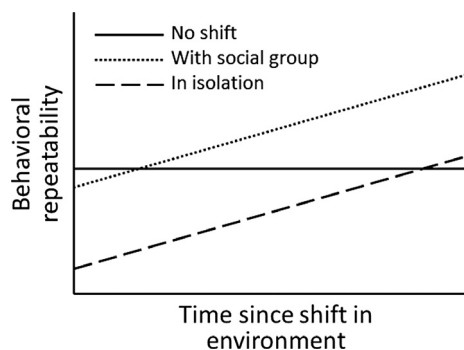


Fig. 1: Theoretical graph predicting the change in individual behavioral consistency (i.e., repeatability) based on the time since a shift in either the physical or the social environment. The bold line represents individuals that do not experience a shift and remain at a constant level of repeatability. Individuals that experience a shift in the physical environment while living in a group exhibit a brief decrease in repeatability, which then increases as individuals reliably specialize on certain tasks (dotted line). Individuals living solitary exhibit a drastic drop in repeatability directly after experiencing an environmental shift, but repeatability increases steadily until returning to baseline value (dashed line).

For Question III, regardless of social context, we predict that time spent in a new environment will be positively associated with behavioral repeatability (Fig. 1).

Methods

Study Organisms

Stegodyphus dumicola is a communal spider that lives in dense three-dimensional webbed retreat structures. Attached to the retreat is a two-dimensional capture web where individuals forage for prey solitary or cooperatively (Whitehouse & Lubin 1999). Spiders used in this study were collected from 6 sites separated by at least 10 km in the Northern Cape of South Africa. Colonies were collected in the Bushveld on roadside fences and in bushes and shrubs, mainly *Acacia* sp. Group size per colony was counted within two days of collection and ranged from 1 to 696 spiders. All subsequent experimentation was performed in the laboratory at the University of Pittsburgh, PA. Spiders were isolated into 30-ml translucent plastic rearing containers with chicken wire as a substrate, maintained at ~25°C under ambient lighting, and fed one immobilized 2-wk-old cricket weekly.

Experimental Design

Once weekly for 5 wk, we constructed six experimental colonies containing 10 individuals from six different source colonies. Therefore, each source colony was used to create one experimental colony per week. Each experimental colony contained 10 individuals chosen randomly from the same source colony. Each individual was removed from its 30-ml rearing container and transferred to a clear plastic 1-liter container with a piece of folded chicken wire together with its conspecifics. These groups were maintained under the laboratory conditions described above and were fed one 6-wk-old cricket during their first week together and three 2-wk-old crickets weekly thereafter. Thus, upon the onset of behavioral assays, we had six colonies for each time treatment (5, 4, 3, 2, and 1 wk). Additionally, singleton colonies were constructed every week where individuals were moved from their 30-ml rearing containers to 1-l plastic enclosures and kept in isolation for the same durations ($n = 64$ individuals). Isolated spiders were fed one two-week-old cricket weekly. This allows us to ascertain if any differences observed in individuals' behavioral tendencies across time were due to a shift in the social environment (i.e., solitary to group

living) or the physical environment (i.e., small to large living area). A separate group of control spiders (negative controls) were set up at the beginning of the experiment and maintained in the same 30-ml plastic cups throughout experimentation and tested at the same time as experimental spiders ($n = 68$ individuals). Thus, in summary, we can compare the behavioral tendencies of spiders that experienced no shift in their environment, a shift in their physical environment only, or a shift in both their social and physical environment and then test whether the time that had elapsed since this transition (1–5 wk prior) influenced these outcomes.

Colony Foraging Assays

To determine how time spent in a social group influences collective foraging behavior, we stage prey-capture events for all 30 colonies of ten spiders. These colonies had been established 1–5 wk prior and were tested at the same time in order to control for the effects of spider age or subtle differences in the laboratory environment.

Trials were initiated by placing a single 2-wk-old cricket in the center of the capture web, which had been constructed in the plastic cup of each colony. We then recorded the latency for the first individual to leave the retreat after prey introduction and the latency for the first individual to attack the prey item. After the prey was attacked, we also recorded the duration of the foraging bout (i.e., the time taken for all individuals to abandon the prey item) and the total number of spiders that joined the foraging group.

Boldness Assays

After assaying colonies' collective foraging behavior, we isolated spiders across all social environments and time durations, measured their mass and prosoma width, and moved them individually into clean 30-ml plastic cups. After 24 h, we determined the behavioral type of each individual by measuring their boldness once a day over four consecutive days (i.e., four measurements per individual).

Boldness assays were performed by placing a spider into a clean square plastic container (12.5 cm \times 13 cm \times 3.5 cm), allowing it a 1-min acclimation period, and then administering two rapid puffs of air to the anterior prosoma with an infant ear cleaning bulb, to simulate the approach of a flying predator (Barth & Höller 1999; Uetz et al. 2002; Lohrey et al. 2009). We then measured the latency for the spider to resume movement after this antagonistic

stimulus. Spiders were allowed 600 s to resume movement before the trial was terminated. Assays in which a spider did not resume movement within 600 s were not included in our estimates of individuals' boldness (654 of 1190 trials), because the artificially truncated value may have unknowingly concealed meaningful variation among individuals that ranged beyond 600 s. Individuals with long latencies to resume movement are termed less bold, whereas individuals that resume movement rapidly are deemed more bold after (Riechert & Hedrick 1993; Pruitt et al. 2008). However, we used the inverse of individuals' latency to resume movement (i.e., 600-latency to resume movement in second) as our 'boldness' metric for statistical analyses and for plotting our data after (Cote et al. 2010). That practice ensures that larger values correspond to greater boldness, which is a more intuitive.

Statistical Analyses

We tested for between-individual differences in boldness (i.e., behavioral types) using a general linear mixed model (GLMM) with individual identity nested within experimental colony ID and experimental colony ID nested within population. We specified individual ID, experimental colony ID, and population as random effects in our model and the boldness values for each consecutive assay as our response variable. We then used this model to partition variance into *within-* vs. *between-*individual components, where our estimate of repeatability is the proportion of variance explained by between-individual differences relative to the total variance (i.e., both within and between; Boake 1989; Falconer & Mackay 1996). We also used linear regression to test whether individual mass and prosoma width were significant predictors of individuals' boldness and included the same random effects in the model.

The colony foraging data were analyzed with repeated-measures MANOVA with group tenure (1–5 wk) and the average boldness of the colony constituents as independent variables and colonies' latency to emerge from retreat, time to first attack, trial duration, and the total number of attackers as dependent variables. As latency to attack prey can be a result of individual hunger state, we tested for differences in hunger state between spiders in different group durations and social contexts by estimating body condition via the residuals of a linear regression of spiders' body mass on body size (Jakob et al. 1996). Then, we used ANOVA with body condition as a dependent variable and treatment as an independent

variable. Population and colony ID were included as random effects. To compare the average boldness of solitary vs. grouped individuals, we used nonparametric Kruskal–Wallis tests with treatment (i.e., social context and group tenure) as independent variables, average between-individual variance for each colony, average within-individual variance for each colony, and mean boldness within each colony as dependent variables. Finally, we compared variation in boldness and repeatability of boldness among treatments using confidence intervals, where non-overlapping confidence intervals signify a significant difference in either measure across treatments.

Results

Collective Foraging Behavior

Group tenure was a significant predictor of colony-level foraging behaviors ($F_{12,35} = 2.18$, $p = 0.04$), though groups' mean boldness score was not a significant factor predicting colony foraging traits ($F_{3,13} = 1.29$, $p = 0.32$). Groups that were together for longer periods of time responded to prey more quickly ($F_{4,18} = 3.11$, $p = 0.04$; Fig. 2). However, group tenure did not affect colonies' latency to attack ($F_{4,16} = 2.58$, $p = 0.08$), duration of the foraging bout ($F_{4,16} = 2.22$, $p = 0.11$), or the number of individual attackers ($F_{4,25} = 1.15$, $p = 0.36$). We also found that, via our estimates from the regression on body mass and prosoma width, there was no difference in the body condition of individual spiders in any treatment ($F_{6,16} = 1.46$, $p = 0.21$). That is, neither the duration of time since the spider(s) moved to a new habitat nor

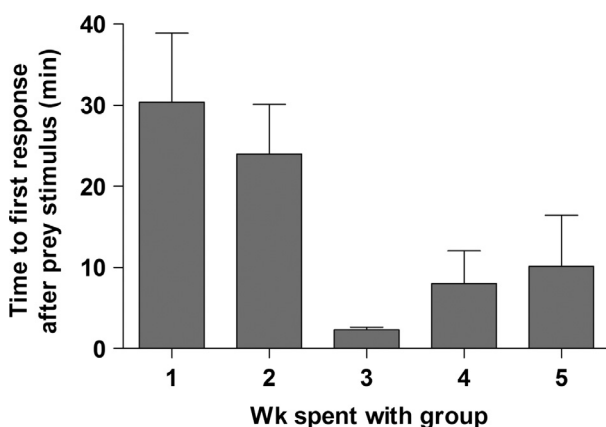


Fig. 2: Social groups that were together for longer responded to prey entrance into the foraging web faster by emerging from the retreat more quickly ($F_{4,18} = 3.11$, $p = 0.04$).

their social context influenced individual spiders' body condition.

Boldness Assays

Individual spiders exhibited between-individual differences in behavior across all social contexts ($F_{279,535} = 1.34$, $p = 0.008$; overall repeatability = 0.77; Table 1). Spider body mass ($F_{1,267} = 0.26$, $p = 0.61$) and prosoma width ($F_{1,192} = 0.48$, $p = 0.49$) were not associated with individual boldness scores. Strongly overlapping 95% confidence intervals demonstrate that the repeatability of boldness scores did not differ between groups which were together for different durations, regardless of social context (Table 1).

We failed to detect an effect of social environment on between-individual behavioral variation ($\chi^2 = 10.8$, $df = 10$, $p = 0.37$). That is, we detected similar levels of between-individual variation regardless of how long individuals had remained in a social group. Moreover, between-individual behavioral variation did not differ across individuals who experienced habitat shifts solitary vs. in a group ($\chi^2 = 6.81$, $df = 2$, $p = 0.34$). Our data also did not support the hypothesis that a longer time spent in a group will increase behavioral consistency ($\chi^2 = 2.66$, $df = 4$, $p = 0.62$), and within-individual variance in boldness was similar across individuals in all time treatments and social contexts ($\chi^2 = 4.47$, $df = 2$, $p = 0.11$). Finally, individuals that moved to a new habitat solitary showed greater mean boldness than those who moved to the same habitat among a social group or those that did not experience a shift in the environment ($\chi^2 = 12.9$, $df = 2$, $p = 0.002$; Fig. 3). This increased boldness was not influenced by time since the solitary habitat shift: solitary spiders that moved to novel habitats remained bolder across 5 wk ($\chi^2 = 4.80$, $df = 4$, $p = 0.31$).

Discussion

Individual behavioral traits are partly a product of current and past social interactions and abiotic habitat stochasticity (Sih et al. 2012). In this manuscript, we sought to test how time since a shift in the physical environment can influence the mean, variance, and repeatability in boldness across two social contexts in a social spider. Additionally, we tested whether time spent with a social group was associated with various aspects of collective foraging behavior. We failed to detect any effect of a shift in individuals' physical environment to our measured traits when in the presence of conspecifics. Furthermore, we failed to detect an effect of time individuals' spent in a social

Table 1: The time since a shift in the physical environment across two social contexts (isolation vs. among conspecifics) did not influence the repeatability of individual behavioral traits. 95% confidence intervals of the mean boldness value are overlapping across all treatment groups. A negative repeatability estimate occurred when there was a large standard error associated with between-individual variance components

	Weeks since habitat shift	n	Repeatability (<i>r</i>)	95% CI	Tukey group	Weeks since habitat shift	n	Repeatability (<i>r</i>)	95% CI	Tukey group	
Solitary shift	1	22	0.30	−0.15,0.63	A	Group Shift	1	6	−0.01	−0.15,0.14	A
	2	12	0.35	−0.16,0.68	A		2	6	0.19	−0.02,0.34	A
	3	10	0.35	−0.20,0.79	A		3	6	0.41	0.09,0.45	A
	4	13	0.67	0.09,0.63	A		4	6	0.31	0.05,0.42	A
	5	11	0.22	−0.21,0.57	A		5	6	0.29	0.02,0.36	A
	Combined	68	0.29	0.02,0.62	A		Combined	30	0.35	0.14,0.41	A
Negative control	N/A		0.45	0.08,0.55	A						
Overall repeatability			0.77		N/A						

setting on the mean, variance, or repeatability of their boldness. This is at odds with our hypothesis that group living and longer group tenure facilitates greater between-individual variation (articulated by Bergmüller & Taborsky 2010; supported in comparative work in social spiders of genus *Anelosimus*, Pruitt et al. 2012a). We did, however, detect an increase in individuals' boldness following a solitary shift to a novel habitat. That is, this increase in boldness was not observed in individuals who experienced a shift in the physical environment alongside a social group. Finally, we found that time spent in a social group was positively associated with response time to prey stimulus. This result was consistent with our hypothesis that time spent in a group would be associated with augmented foraging behavior.

Groups that were together for longer durations may have exhibited faster response times to prey stimuli for a number of non-mutually exclusive reasons: (i) one or a few individuals had specialized on foraging tasks (Dall et al. 2012); (ii) the group as a whole had become more proficient at foraging over time (Lubin 1995); (iii) individuals had more time to familiarize themselves with their habitat (Stamps 1995); or (iv) the physical features of the capture web have improved over time (Blackledge & Wenzel 2001). Although the data presented here are insufficient to rigorously test these hypotheses, we reason that a combination of these phenomena is likely responsible for the observed trend. In particular, we note anecdotally that the general structure and complexity of colonies' architecture appeared to increase over time. Spider foraging webs often change architecture and structure across an individual's lifetime (Witt et al. 1972), and web construction aptitude increases experientially throughout the lives of many spiders (Heiling & Herberstein 1999). Lastly, our data on body condition index indicate that spiders in the solitary

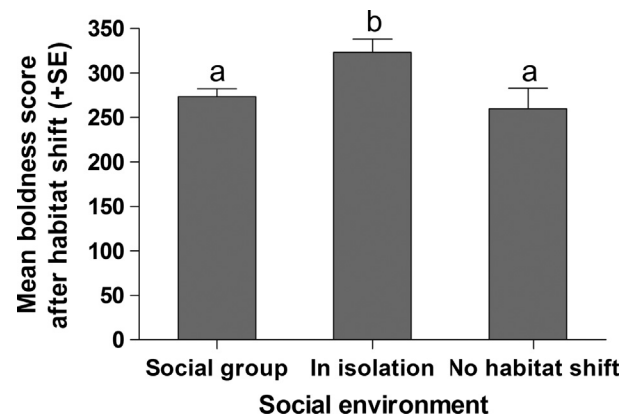


Fig. 3: Individuals that moved to a larger enclosure in isolation showed greater mean boldness than those that moved to an identical environment among a social group or those which stayed in a constant environment ($\chi^2 = 12.9$, $df = 2$, $p = 0.002$). Significant differences are represented by different letters.

social context were no different in body condition, and likely hunger state, than spiders in a social group. Thus, individual hunger state is unlikely to play a significant role in the collective foraging of the group.

Importantly, our data do not support the hypothesis that colonies' collective foraging behavior was driven by the average personality types of their constituents, because we failed to detect an association between any metric of colonies' collective behavior and the average boldness of their constituents. Granted, groups may have shifted their behavioral tendencies along some other personality axis (e.g., aggression); however, at least two other studies on social *Stegodyphus* have independently demonstrated that individuals' boldness is the single best predictor of individuals' foraging behavior and the collective behavior of colonies (Grinsted et al. 2013; Pruitt et al. 2013). Thus, we argue that personality composition is unlikely to

be the driving agent behind colonies' collective foraging behavior in this study.

The only difference observed in behavior between social environments was an increased mean boldness in individuals that dispersed to a novel habitat in isolation. As *S. dumicola* colonies can be genetically monomorphic (through serial inbreeding; Smith et al. 2009), we suspect that our observed differences between social environments represent a behavioral reaction norm where genotypes express a different set of behavioral phenotypes across different environments (Dingemanse et al. 2010). Theory and empirical evidence suggest that differences in the breadth of behavioral plasticity between individuals can indeed arise through differences in past social experience (Dingemanse & Wolf 2013). In this study, when highly related individuals were reared in different social environments, we observed shifts in their average boldness. Thus, we speculate that individuals' personalities appear to be sensitive to their social environment, as has been observed in numerous diverse test systems (e.g., Crickets, DiRienzo et al. 2012; Rainbow Trout, Frost et al. 2007; Great Tits, Carere et al. 2005; House Mice, Benus & Henkelmann 1998).

Finally, we argue that living in a social group may buffer individuals from the need to exhibit shifts in their behavior in response to a change in the physical environment. Social buffering has been suggested as a driving force in the evolution of many collective behaviors, like group foraging (Clark & Mangel 1986), social thermoregulation during overwintering (Arnold 1988), and mass migrations (Guttal & Couzin 2010). In fact, one stressor which many animals regularly experience across a range of social environments is shifts in habitat, from emergence events (e.g., aquatic-terrestrial habitat shifts, Brittain 1982) to natal habitat dispersal (e.g., avian fledging, Yackel Adams et al. 2006). In the case where individuals experience new habitats among conspecifics, an individual can rely on others within the group to accomplish some functional collective tasks (Pinter-Wollman et al. 2009), because an individual's tendency to perform a task can be contingent on the actions of social counterparts (Efferson et al. 2008). In particular, conforming to the behaviors of group members can reduce behavioral heterogeneity and may shift mean response of the group optimally via a skew effect of the most or least responsive individual (Webster & Ward 2011). In this system, we note that individuals failed to increase their boldness when they shifted habitats as part of a social group, and individuals did not exhibit greater behavioral variation or consistency

as a consequence of recent social experience. Thus, behavioral conformity could be a powerful mechanism homogenizing the behavior of individuals in social groups. In contrast, solitary individuals have no group to which they can conform or rely upon, and thus, they must modify their behavior to meet current environmental conditions. In particular, we argue that living alone may require a greater degree of individual responsiveness and boldness, because an individual cannot rely upon the presence of conspecifics to accomplish colony maintenance tasks (e.g., prey capture, colony defense). Consistent with this hypothesis, data from multiple species of social spiders have independently confirmed that greater boldness and aggressiveness are essential for spiders' success in isolation (Jones et al. 2010; Pruitt et al. 2012b; Keiser & Pruitt 2014).

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