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SHORT COMMUNICATION

Repeatability of between-group differences in collective foraging is shaped by group composition in social spiders

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Abstract. Stable between-group variation in collective behavior has been observed in a variety of taxa. We examine here whether climate of origin (arid/wet), colony personality composition (shy/bold/mixed), and group size determine the repeatability of collective foraging behavior in *Stegodyphus dumicola* Pocock, 1898 (Eresidae). Experimental colonies were created with contrasting ratios of bold/shy group members and run through 20 simulated prey capture events in a greenhouse. We found that (i) larger colonies and colonies composed of bold spiders were more repeatable in how many attackers they deployed to prey stimuli, (ii) colonies composed of shy spiders were more repeatable in their latency of attack, and (iii) climate of origin had no effect on the repeatability of colony behavior. Colony bold/shy composition had no effect on within-group variation in foraging behavior. Thus, differences in repeatability were the result of increases in between-group differences in foraging behavior, and not shifts in the behavioral flexibility of individual colonies. These results indicate that changes to colony composition and group size can alter the extent to which colonies exhibit characteristic behavioral differences.

Keywords: Behavioral consistency, collective personality, temperament, behavioral syndromes

Stable between-group differences in collective behavior are often referred to as "collective" or "colony-level" personality (Jandt et al. 2014). For spider societies, the collective personality type of a colony (average level of collective behavior) can determine its performance and success (Pruitt & Keiser 2014; Pruitt et al. 2016, 2017). For instance, social spider colonies that attack prey quickly with numerous spiders are more likely to survive to reproduce in arid but not wet environments (Pruitt et al. 2017). Like differences in individual-level traits, between-group behavioral differences must be at least somewhat repeatable to have a long-term impact on colony performance. Collective behavior repeatability is decreased by increasing within-group behavioral variation, and increased by increasing between-group variation (Nakagawa & Schielzeth 2013). Despite many studies demonstrating the importance of average levels of collective behavior in dictating colony success, the factors promoting within- and between-colony behavioral variation remain relatively unexplored (but see Marting et al. 2017; Wright et al. 2017).

We tested whether three factors would determine the repeatability of collective foraging in the social spider *Stegodyphus dumicola* Pocock, 1898 (Eresidae): local adaptation to climate, individual personality composition, and group size. These spiders persist in harsh conditions by collectively capturing large prey (Henschel 1998), conferring a survival advantage upon aggressive colonies in especially arid areas, but no advantage in wet sites (Pruitt et al. 2017). We therefore predicted that (i) colonies adapted to arid locations will be less repeatable in their foraging responses compared to wet site colonies, because selection should act to reduce between-colony variation at these sites. The presence of bold spiders increases colonies' collective aggressiveness (Pruitt et al. 2013; Pruitt & Keiser 2014; Lichtenstein et al. 2017b), and their presence is therefore predicted to increase between-colony variation in foraging behavior. We consequently predicted that (ii) the presence of bold spiders will increase the repeatability of collective behavior by increasing between-colony variation. Finally, because group size often increases the accuracy of collective decision-making (Sumpter et al. 2008; Couzin 2009), we predicted (iii) that larger colonies would deploy more precise and repeatable foraging responses.

We collected *Stegodyphus dumicola* colonies from the wet site Rundu, Namibia (18.2992° S, 19.4076° E), and the arid sites Mariental, Namibia (24.5998° S, 17.9413° E), Groblershoop SA (28.8796° S, 21.9284° E), and Upington, South Africa (28.4034° S 21.0712° E) along roadsides in February 2017. Upon transport back to the University of California at Santa Barbara, we kept each colony in 30 cm x 30 cm x 30 cm steel and mesh (lumite) containers (Bioquip 1450BSV). These colonies were kept at 28° C and fed adult crickets *ad libitum* twice a week. After two months, we separated these colonies' individuals into 100ml plastic containers, where they were kept in isolation before we measured each mature spider's boldness, prosoma width, and mass within a week. These measurements were taken only once per spider.

We began spider boldness assays by placing individual spiders in circular plastic arenas (15 cm diameter, 3.5 cm tall) and giving them 30s to acclimate. After acclimation, we puffed each spider's anterior end from 2 cm with two soft jets of air from a rubber squeeze-bulb. These jets of air mimic the approach of an aerial predator, causing spiders to curl into a ball and cease movement (Riechert & Hedrick 1993). Spider boldness was estimated as their latency to emerge from this crouching posture and move one full body length, with bold spiders exhibiting lower latency to resume movement. Tests were terminated after 600s. We deemed spiders that moved within 1–200s to be bold and those that moved within 401s–600s to be shy, after Pruitt et al. (2016). Spiders that moved between 201s and 400s were not used in the study. This metric of boldness is highly repeatable in this species and many other spider species (Riechert & Hedrick 1993; Kralj-Fišer & Schneider 2012; Grinsted et al. 2013; Pruitt & Keiser 2014; Wright et al. 2015; Lichtenstein et al. 2016a).

After measuring spiders' boldness, mass, and prosoma width, we separated them haphazardly into groups ($n_{wet} = 9$, $n_{arid} = 26$). Each experimental group was composed of a set of spiders taken from the same source colony. Colonies varied in size from 4 to 40 spiders, and were composed of entirely bold ($n = 9$), entirely shy ($n = 16$), or half

Table 1.—The repeatability (R), 95% CI, and 84% CI of collective foraging response in *Stegodyphus dumicola* colonies of different climates of origin and boldness compositions.

Behavioral trait	Colony subset	R	Lower 95% confidence interval	Upper 95% confidence interval	Lower 84% confidence interval	Upper 84% confidence interval
Number of attackers						
	All colonies	0.245	0.162	0.310	0.049	0.308
	Wet colonies	0.146	0.000	0.271	0.018	0.232
	Arid colonies	0.273	0.132	0.388	0.159	0.344
	Shy colonies	0.007	0.000	0.051	0.000	0.034
	Mixed colonies	0.138	0.000	0.261	0.023	0.213
	Bold colonies	0.227	0.020	0.371	0.059	0.335
	Large colonies	0.260	0.061	0.435	0.110	0.363
	Medium colonies	0.258	0.075	0.406	0.110	0.349
	Small colonies	0.040	0.000	0.114	0.000	0.084
Latency to attack						
	All colonies	0.644	0.495	0.737	0.538	0.714
	Wet colonies	0.713	0.365	0.842	0.447	0.809
	Arid colonies	0.596	0.418	0.702	0.474	0.682
	Shy colonies	0.724	0.476	0.826	0.565	0.798
	Mixed colonies	0.455	0.150	0.628	0.221	0.582
	Bold colonies	0.337	0.078	0.514	0.128	0.460
	Large colonies	0.276	0.074	0.442	0.112	0.380
	Medium colonies	0.430	0.184	0.603	0.243	0.538
	Small colonies	0.796	0.493	0.884	0.597	0.859

bold and half shy spiders ($n = 10$). The groups were added to 500ml plastic containers to construct a silken nest. After remaining in the plastic containers for a week and being fed crickets *ad libitum*, we moved each colony to a potted *Acacia* plant. Colonies' plastic containers were fastened to host *Acacia* using plastic clothespins. We allowed the newly formed colonies another week to build their webs before evaluating their collective foraging behavior.

To assess collective foraging behavior, we presented colonies with a simulated prey stimulus. During each assay, we recorded colonies' latency to attack and how many attackers responded to prey by leaving the nest to attack. To simulate prey, we placed 1 cm pieces of paper in the colonies' capture webs and vibrated this paper with a handheld vibratory device on a pulse setting. This elicits aggressive foraging responses from social *Stegodyphus* (Grinsted et al. 2013; Pruitt & Keiser 2014). We repeated these tests twice a day Monday to Friday for two consecutive weeks, making 20 tests in total across two weeks. Assays conducted on the same day were separated by 30–60 minutes.

We used these 20 assays per colony across 10 days to estimate the repeatability of spider colony behavior from wet versus arid sites, in colonies with contrasting boldness compositions, and large, medium and small colonies. We categorized colonies as large (13–40 spiders; $n = 12$), medium (8–12 spiders; $n = 13$), and small (4–6 spiders, $n = 10$), because one cannot assess repeatability across non-discrete variables. The group size boundaries were chosen to maximize evenness across categories. We estimated the repeatability of these behaviors using the rptR package (Nakagawa & Schielzeth 2013) in R version 3.4.1 (R development team). We used rptR to fit generalized linear mixed models (GLMMs) fit with Poisson distributions, using either "latency to attack" or "attackers sent" as the response variable, "test iteration" as a predictor variable, "colony ID" as a random effect. The package estimates repeatability as the proportion of variance explained by "colony ID" with 95% bootstrap confidence intervals. Significant repeatability estimates have 95% confidence estimates that do not overlap zero. We compared the repeatability estimates of categories of colonies by seeing whether their 84% confidence intervals overlapped each other. We used 84% confidence intervals because they approximate significant differences at a 95% confidence level (Payton et al. 2003; Modlmeier et al. 2014).

Repeatability estimates are affected by both within- and between-colony variation (Lessells & Boag 1987; Nakagawa & Schielzeth 2010). To gauge whether differences in within-colony variation drives our repeatability estimates, we calculated the intra-colony variability (ICV) of each colony's foraging behavior across twenty trials, and tested whether colony size, composition, and origin climate predicts ICV. Intra-colony variability is analogous to intra-individual variability (IIV) but with colonies instead of individuals. It is an estimate of within-colony behavioral variation. Details on IIV/ICV calculations can be found in Stamps et al. (2012) and Lichtenstein et al. (2017a), which we performed in R version 3.4.1 (R development team). Then, we fit two GLMs using Poisson distributions with "Climate of origin", "Boldness composition", and "Colony size" as fixed predictor variables using JMP pro 13. One model had "Number of attackers ICV" as the response variable, whereas the other had "Latency to attack ICV" as the response variable. These models' residuals followed normal distributions as determined by quantile-quantile (q-q) plots, suggesting they are good fits for the data.

Our colonies were significantly repeatable in how many attackers they sent out and their latency to attack (Table 1) for the pooled data set, confirming that these traits are examples of collective personality. Colonies from wet and dry sites did not differ in the repeatability of these collective behaviors (Table 1; Fig. 1). This similarity in repeatability is surprising, because collective foraging is organized differently in arid and wet sites. Variation in collective foraging behavior is driven by leadership by bold spiders and following by shy spiders at arid sites, whereas the boldness of leaders does not influence the collective foraging of wet site colonies (Pruitt et al. 2017). This means that the relationship between colony personality composition and collective foraging behavior differs between wet and arid colonies. In spite of contrasting organization schemes, colonies from both kinds of sites appear roughly equivalent in how consistently they execute their behaviors.

The personality composition of colonies had a large effect on the repeatability of collective foraging behaviors. Colonies composed of

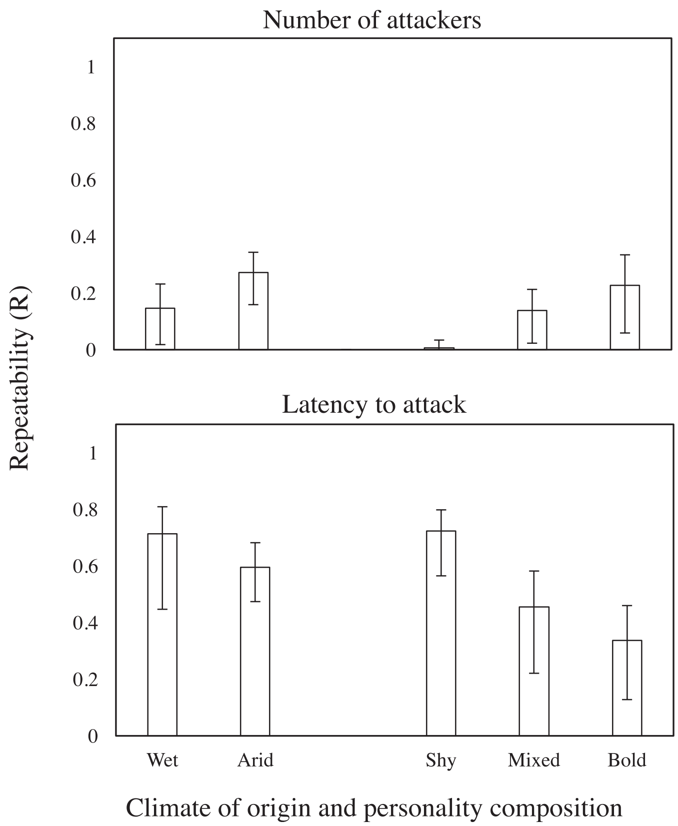

Figure 1.—The repeatability of colonies' number of attackers and latency to attack across different climates of origin and personality compositions. Shy colonies were composed of all shy spiders, bold colonies we composed of bold spiders, and mixed colonies were composed half of each. Error bars represent 84% confidence intervals of the repeatability estimates, because they approximate significant differences at a 95% confidence level. Repeatability estimates with differing letters differ significantly at an $\alpha = 0.05$ level.

bold spiders were more repeatable in the number of attackers they deployed compared to shy colonies, whereas colonies' latency to attack appears less repeatable in colonies composed of bold spiders compared to shy colonies (Table 1; Fig. 1). Also, small colonies were less repeatable in how many attackers they sent out but more repeatable in their latency to attack (Table 1). With these results alone, it is difficult to interpret the effects on repeatability, because the changes in the repeatability of colony behavior could be attributed to differences in within-colony variation (i.e., colony flexibility or behavioral noisiness) or between-colony variation in these behaviors (i.e., how much colonies differ from each other). We therefore tested whether colony composition affected within-colony variation using intra-colony variability (ICV).

The climate of our colonies' collection sites, their size, and the boldness composition of their members were unrelated to both number of attackers ICV (GLM: L-R $\chi^2_4 = 0.014$, $P = 1.000$) and latency to attack ICV (GLM: L-R $\chi^2_4 = 0.008$, $P = 1.000$). Because spider colonies with different boldness compositions and group sizes were indistinguishable in their within-colony variation, one can infer that the differences in repeatability observed above were due to differences in between-colony variation. In other words, larger colonies and colonies composed of bold spiders exhibited greater between-colony variation in the number of attackers they deployed: some colonies of bold individuals attacked with relatively few attackers and others deployed more aggressive assaults. The same was true for small colonies and shy colonies but in terms of their speed of attack: some colonies of shy individuals attacked rapidly and some more slowly. This is likely because small colonies and shy colonies send few attackers, creating little variation in number of attackers, and larger colonies and bold colonies attack very quickly, creating little variation in attack speed (Pruitt & Keiser 2014).

Among the factors that we predicted could affect the repeatability of collective foraging behavior of spider colonies, boldness compositions and colony size appeared to affect the repeatability of these behaviors. These findings stress the importance of distinguishing between the effects of behavioral averages, within- and between-colony variation in behavior when evaluating intraspecific variation in collective traits. It is the ratio of within- versus between colony/individual variation that determines behavioral repeatability (Lessells & Boag 1987; Nakagawa & Schielzeth 2010) but shifts in either component of this ratio and average behavioral expression have different interpretations. Average levels of collective behavior can determine how groups deal with challenges (Pamminger et al. 2012; Lichtenstein et al. 2016b) and as a result whether they survive those challenges (Pruitt et al. 2017). Greater within-colony or within-individual variation can imply greater behavioral plasticity (Pruitt et al. 2011; Dirienzo & Montiglio 2016; Ioannou & Dall 2016; Chang et al. 2017; Lichtenstein et al. 2017a), whereas between-colony or between-individual variation can increase the intensity of species interactions (Royauté & Pruitt 2015; Lichtenstein et al. 2017c) and the efficacy of selection (Dingemanse & Réale 2005). We found that the personality composition of social spider colonies alters between-colony diversity in a key functional behavior that determines *S. dumicola* survival in the wild (Pruitt et al. 2017c). These shifts, in turn, could alter species interactions (e.g., host-inquiline) and selection on these collective traits.

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