

Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider

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Abstract Social animals are extraordinarily diverse and ecologically abundant. In understanding the success of complex animal societies, task differentiation has been identified as a central mechanism underlying the emergence and performance of adaptive collective behaviors. In this study, we explore how individual differences in behavior and body size determine task allocation in the social spider *Stegodyphus dumicola*. We found that individuals with high body condition indices were less likely to participate in prey capture, and individuals' tendency to engage in prey capture was not associated with either their behavioral traits or body size. No traits were associated with individuals' propensity to participate in web repair, but small individuals were more likely to engage in standard web-building. We also discovered consistent differences among colonies in their collective behavior (i.e., colony-level personality). At the colony level, within-colony variation in behavior (aggressiveness) and body size were positively associated with aggressive foraging behavior. Together, our findings reveal a subtly complex relationship between individual variation and collective behavior in this species. We close by comparing the relationship between individual variation and social organization in nine species of social spider. We conclude that intraspecific variation is a major force behind the social organization of multiple independently derived lineages of social spider.

Keywords Animal personality · Collective behavior · Body condition · Social spider · *Stegodyphus* task differentiation

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Carl N. Keiser and Devin K. Jones are the co-first authors.

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Introduction

Social taxa make up some of the most diverse and abundant groups of animal life on the planet. From the most speciose eusocial Hymenoptera to complex primate societies, elucidating the drivers behind the success of social animals has been a pervasive goal of evolutionary and behavioral ecology. Task partitioning, task allocation, division of labor, and behavioral specialization, in particular, have been identified as key mechanisms underlying the collective behavior and success of complex societies (Ratnieks and Anderson 1999; Gordon 2002; Bergmüller and Taborsky 2010). Despite some organizational costs, both the efficiency of collective behaviors and colony-wide performance generally increase as task-sharing and task-switching decrease and individual specialization increases (Ratnieks and Anderson 1999; Gordon 2002). In many cases, behavioral specialization is accompanied by morphological, size, or age class polymorphisms (Ebert 1998; Beshers and Fewell 2001). In others, however, morphologically similar individuals differ consistently in their predispositions or propensities to carry out certain tasks. For example, *Stegodyphus* social spiders live in age-structured colonies, and individuals differ consistently in their propensity to perform foraging tasks (Grinsted et al. 2013).

In *Stegodyphus* and *Anelosimus* social spiders, the propensity to initiate and participate in foraging tasks can be predicted by individual behavioral tendencies, body size indices, or both (Grinsted et al. 2013; Pruitt et al. 2013; Settepani et al. 2013). Social spiders, therefore, represent a fascinating system in which to study the relative importance of morphology and individual behavioral tendencies in task allocation and division of labor, both from the perspective of a cooperative breeder and from spiders (Shear 1970; Kullmann 1972; Riechert 1985).

One of the fundamental characteristics of task allocation and division of labor is the differential tendency of individuals

to perform certain tasks over others and, necessarily, behave differently over time (Beshers and Fewell 2001; Gordon 2002). Consistent individual differences in behavioral traits (i.e., “animal personality,” “behavioral types,” or “behavioral syndromes”) among groups members have proven to be an informative predictor of task participation, collective behaviors, and group productivity across diverse taxa (Le Vin et al. 2011; Pruitt and Riechert 2011a, b; Modlmeier et al. 2012). Thus, the relative abundance of different behavioral types within groups could be a particularly important driver of group performance. This prediction is difficult to assess in the majority of animal social groups (e.g., primate societies, bird flocks, eusocial Hymenoptera, etc.). Yet, in a select number of tractable model systems, experimentally manipulating the personality composition of social groups has had enormous predictive power for understanding collective behavior and group success (e.g., acorn ants, Modlmeier et al. 2012; guppies, Brown and Irving 2013; and social spiders, Pruitt and Riechert 2011a, b).

Social spiders in particular have emerged as a front-running model for understanding how individual personalities shape social group functioning and performance. From these systems, we have established that maintaining behavioral heterogeneity in groups is important for prey capture success (Pruitt and Riechert 2011a), that keystone individuals can differentially shape the collective behavior of groups (Pruitt et al. 2013), and that personality traits have individual-level fitness consequences (Pruitt et al. 2008). Regrettably, at present, the majority of these studies have focused on a very limited number of highly related and recently evolved species of *Anelosimus*, which draws into question the generality of the observed patterns (Agnarsson et al. 2006, 2007). Thus, we reason that the most exciting new discoveries in this field will come by comparing the role of personalities in the social organization of phylogenetically disparate test systems.

In this study, we test how individual behavioral tendencies and body size determine task participation in the social spider *Stegodyphus dumicola* (Araneae, Eresidae). *S. dumicola* lives in foraging societies of up to 2,000 individuals in arid Southwestern Africa and is one of three independently derived social species in the *Stegodyphus* genus (Johannesen et al. 2007). In *Stegodyphus sarasinorum*, individuals differ consistently in their task participation, and this is determined by a combination of behavioral traits and body size (Grinsted et al. 2013; Pruitt et al. 2013; Settepani et al. 2013). In *Stegodyphus mimosarum*, however, individuals appear to lack task differentiation during group foraging (Ainsworth et al. 2002). Although several studies have investigated the collective foraging behavior of *S. dumicola* (e.g., Whitehouse and Lubin 1999; Amir et al. 2000), we have yet to investigate the role of individual personality traits in task participation in this species. Conducting this research is particularly interesting, as comparative data from all three social species in the

Stegodyphus genus will now be available. This, in turn, will allow us to compare and contrast the relationship between individual personalities and social organization across numerous species (i.e., both within and between the *Anelosimus* and *Stegodyphus* genera). Moreover, we include here a series of non-foraging tasks (web repair and web construction) which have, to date, been ignored in this literature. We argue that this will further augment our understanding of how different tasks are correspondingly related to individual behavioral tendencies.

Specifically, we predict that (I) aggressiveness and boldness will be positively linked together in a behavioral syndrome; (II) foraging participation and web repair will be positively associated with boldness, aggression, and body size; (III) an individual’s propensity to participate in one activity will be negatively associated with its propensity to participate in another (i.e., consistent with division of labor); (IV) colonies will exhibit characteristic differences in their collective behavior (i.e., “colony-level personality,” Jandt et al. 2013); and (V) differences in colony-level personality will be explained by their degree of within-colony behavioral variation.

Methods

Study system

S. dumicola builds large webs consisting of a dense communal retreat and a two-dimensional capture web. The spiders used for this experiment were collected along roadway fences and on *Acacia* shrubs in the southern Kalahari Desert in the Northern Cape, South Africa, in January 2013. Colonies were transported to the University of Pittsburgh (Pittsburgh, PA, USA) where colony size was assessed (range, 1–700 individuals). Fifteen female spiders per colony were isolated into 30 ml opaque plastic cups containing a 1×1-cm square piece of poultry wire for substrate. Body mass (range, 0.04–0.21 g) and prosoma width (range, 2.13–3.61 mm) were measured after the 15 spiders were isolated. Spiders were subject to natural light cycles and fed a maintenance diet of one 7 mm cricket weekly.

Spiders remained isolated in the 30-ml opaque plastic cups for the duration of their initial individual-level personality assays (described below). After this time, individuals were given a unique three-color identification pattern atop their abdomen using nontoxic, acrylic paint (Palmer Paint Products, Prism™ Acrylic). Ten individuals were then chosen randomly from each pool of 15 spiders and placed in a 1-l clear plastic container with a 10×10-cm folded piece of wire for substrate. Fifteen artificial colonies were established in this way and these groups were maintained for the remainder of the experiment (32 days). These experimental colonies were

provided 4 days to build a retreat and capture web before being subjected to a series of colony-level behavioral assays. These colony-level behavioral assays were used to (I) test for consistent inter-colony differences in their collective behavior (i.e., prey capture, web repair, web construction), (II) to test for associations between individuals' traits (morphology, behavior) and their participation in different tasks, and (III) to test for associations between colonies' phenotypic composition and their colony-level personality.

Individual-level personality assays

Boldness assays Individual spiders were assayed for boldness by assessing their response to an aversive stimulus. Spiders were placed in an opaque, plastic arena (13 cm×12.5 cm×3.5 cm) and allowed to acclimate for 60 s. To simulate the approach of a predator, two rapid bursts of air were administered to the spider's anterior prosoma using an infant ear-cleaning bulb (see Riechert and Hedrick 1990; Lohrey et al. 2009; Pruitt et al. 2013). Web-building spiders generally have poor eyesight, and thus, rely heavily on air currents, seismic cues, and/or large shadows to detect the approach of predators via (Foelix 1996). This rapid burst of air elicits a huddle response, where the spider draws its legs tightly against its body in a death feign. A stopwatch was used to record the time taken by the spider to resume movement and traverse one full body length. Spiders that failed to move within 10 min were assigned the maximum value of 600 s. To obtain more intuitive values for "boldness," individuals' latencies to resume movement in seconds were subtracted from the maximum value. Thus, a greater latency to resume movement corresponds with a smaller boldness value. Following each boldness assay, the plastic arena was cleaned with isopropanol. Each spider ($n=182$) was assayed four times, once daily for four consecutive days between 900 and 1400 hours. Spiders were fed individually 1 day prior to the onset of personality assays. Multiple tests per individual were used to confirm the repeatability of this assay for *S. dumicola* and to obtain a more precise estimate of each individual's behavioral type.

Aggression assays Spiders were fed again directly after completion of the four consecutive boldness assays, and aggression assays were initiated on the following day. Aggression trials were initiated by placing the spider in a plastic arena (13 cm×12.5 cm×3.5 cm) and providing it 60 s to acclimate. Individuals were then prodded with a blunt probe on their foremost left leg. The immediate response of the individual was then scored and categorized nominally in terms of its aggressiveness. Our nominal scoring system resembles the ordinal ranking of Grinsted et al. (2013) but also resembles the ranking systems used in a variety of other spiders (Riechert and Johns 2003; Pruitt et al. 2008). "Non-aggressive" behaviors included huddle responses, walking away from stimulus,

and lunging away from the stimulus. "Aggressive" behaviors included turning toward the stimulus, raising their anterior legs, shifting their abdomen in place, and walking towards the stimulus with raised front legs. Once the individual's behavior was scored, it was returned to its 30 ml plastic cup and the arena was cleaned with isopropanol. As with boldness assays, each spider ($n=182$) was assayed four times, once daily for four consecutive days between 900 and 1400 hours.

Colony-level personality assays

Colonies were tested multiply for each assay in order to (I) to test for consistent differences in the collective behavior of colonies (i.e., "colony-level personality"), (II) test for associations between individuals traits (body size, personality) and their propensity to participate in each colony maintenance task (Pinter-Wollman 2012; Jandt et al. 2013), and (III) to test for associations between colonies' phenotypic composition and their colony-level personality type.

Prey capture response The prey-capture behavior of each colony was assessed daily for ten consecutive days. Collective prey-capture trials were initiated by placing a small (1×1.5 cm) piece of white printer paper in the capture web of each colony. We then provided 60 s acclimation time before a battery-powered handheld vibratory device (GoVibe) was used to vibrate the piece of paper to simulate a prey item caught in the capture web. To prevent the colony container from moving, it was placed within an identical empty 1-l container which was stabilized in 7 cm of dry sand substrate. A stopwatch was then used to record the time taken for the first spider to emerge from the retreat ("time to emergence") and the subsequent latency for the first spider to attack the paper ("latency of attack"). The trial ended after the first spider attacked the prey item or until the maximum time was reached (600 s). In addition to measuring colonies' latency to emerge and latency to respond during simulated prey capture events, any individuals that had emerged from their retreat by the time of the first attack were identified by their three-color identification pattern. Such individuals were considered to have "joined" in the collective foraging event (Grinsted et al. 2013; Pruitt et al. 2013).

Web repair Web repair trials were initiated on the day following the completion of colonies' ten prey capture assays. To assess the web repair behavior of each colony, we cut all anchor points of the capture web within the 1-l colony container using a clean utility knife blade. Then, over a period of five evenings, web repair activity was observed during dusk using a red headlamp every 30 min between 1900 and 2300 hours. Web-building in *Stegodyphus* spiders occurs primarily at night, so nocturnal observation using a red headlamp is a valuable method to observe natural web-building behavior (Pasquet et al. 1999). Any individuals engaged in web repair during these checks

were identified using their unique three-color identification patterns. In addition, a flashlight with a red filter was used to confirm the silk production of active individuals.

Ambient web building To assess the ambient web building behavior of each colony, we allowed colonies to expand into a larger environment. Colonies' 1-l colony containers were placed in the corner of a square mesocosm (30.4 cm × 30.4 cm × 30.4 cm) consisting of three chiffon sides for ventilation, two clear plastic sides for observation, and an aluminum bottom. A branch containing an ~90° bend was then inserted into the colony and glued to the adjacent corner of the mesocosm. Individuals were allowed to explore the mesocosm, and colonies were observed at dusk during the following five nights using a red headlamp. Colonies were checked every 30 min between 1900 and 2300 hours. Individuals moving outside their webs and engaging in web construction were identified visually using their unique three-color identification pattern. A flashlight was again used to confirm the production of silk.

Statistical analyses

To test for repeatable differences in individual and colony-level personality, we used ANOVA to partition variance into within- versus among-individual components, where repeatability is estimated as the proportion of total variation attributable to between individual differences (Boake 1989; Falconer and Mackay 1996). Colony ID was included as a random effect in these analyses. We used Spearman's rank correlations to identify a syndrome between boldness and aggressiveness. To determine if personality traits were associated with body size and body condition, we used ANOVAs with aggression and boldness as dependent variables and body size (prosoma width) and body condition as dependent variables. Body condition was estimated by the residuals of a linear regression of spiders' body mass on body size (Jakob et al. 1996). To determine whether individuals' traits were associated with their propensity to participate in various tasks, we first performed *z* score normalized principle component analysis on our five observed tasks: number of times each individual joined the attack, number of times first attacker, number of times first to emerge, number of times producing silk during web repair following experimental web destruction, and number of times producing web during standard web-production (cribellate or otherwise). The first principle component (PC1) explained 55.7 % of the variation and was composed of three foraging variables (factor loadings: number of times first to emerge 0.90, number of times first attacker 0.92, number of times joined in attack 0.93), PC2 explained 21.7 % of the variation (factor loadings: number of times producing silk 0.87, number of times repairing the web 0.51), and PC3 explained 15 % of the variation (factor

loadings: number of times producing silk 0.46, number of times engaged in standard web-building 0.70). Thus, values on the PC1 axis denote an individual's propensity to participate in quantify prey capture, values on the PC2 axis denote participation in web repair, and values on the PC3 axis denote participation in web building. To assess whether individuals' traits were associated with task participation, we constructed three separate ANOVA models. The predictor variables in these models were individuals' body condition, body size, aggressiveness, and boldness. The response variables for these three models were PC1, PC2, and PC3. To account for the non-independence of individuals within each test colony, we included colony ID as a random effect in our models. For these analyses, we used Bonferroni-adjusted α values to reduce the experiment-wise type I error rate (Rice 1989). The adjusted level of significance was 0.017 ($\alpha=0.05/3$).

To test whether individuals tended to engage in some colony maintenance tasks over others, or whether some individuals merely performed all colony maintenance tasks, we tested for correlations between individuals' scores along all three PCs. A positive correlation would suggest that some individuals tend to perform many/all colony maintenance tasks (e.g., "elites"), and a negative correlation would be consistent with division of labor.

To determine the drivers of colony-level personality, we performed independent model selection procedures for each of three response variables: latency of emergence, latency of attack, and number of individuals out at night during our web-building assays. For each model, we average colonies' response across all of their observations. To find the best model, we used Akaike information criterion (AICc) and Akaike weights to compare models (Akaike 1987; Burnham and Anderson 2002). We included the following predictor variables in our models: the average body size of colony constituents, the average aggressiveness of colony constituents, the average boldness of colony constituents, and the within-colony variation of all three traits (i.e., variance in body size, aggressiveness, and boldness within each colony). We present here the best three models from each of our model selection procedures. All analyses were completed using JMP 9.0 (JMP 9.0; SAS Institute, Cary, NC, USA).

Results

Individual personality assays

Spiders exhibited consistent individual differences in their boldness ($F_{180,541}=2.03$, $p<0.0001$, repeatability=0.63; Tables 1 and 2; distribution: Fig. 1) and aggressiveness ($F_{178,531}=1.42$, $p=0.002$, repeatability=0.55; Tables 1 and 2; distribution: Fig. 1). We also detected a negative association between individuals' average aggressiveness and their

Table 1 Tests for repeatability in individual and colony-level behavioral assays. ANOVA were used to assess repeatability

	Repeatability	<i>F</i>	<i>df</i>	<i>p</i> value
Individual spiders				
Boldness	0.63	2.03	180, 721	<0.0001
Aggression	0.57	1.42	178, 709	0.002
Colony collective behaviors				
Latency of emergence	0.74	4.21	14, 63	<0.0001
Latency to attack	0.74	4.20	14, 63	<0.0001
Number of web repairers	0.69	3.24	14, 63	0.001

average boldness score (Spearman's $\rho = -0.17$, $p = 0.03$). That is, bolder individuals were generally less aggressive. We also found that individuals with larger prosoma widths were less bold ($F_{1,180} = 5.77$, $p = 0.02$, $R^2 = 0.03$) and more aggressive ($\chi^2 = 5.29$, $df = 1$, $p = 0.02$, Nagelkerke $R^2 = 0.01$). Body condition was not significantly associated with boldness ($F_{1,180} = 3.11$, $p = 0.08$, $R^2 = 0.02$), but individuals which were in better body condition were more aggressive ($\chi^2 = 5.16$, $df = 1$, $p = 0.01$, Nagelkerke $R^2 = 0.01$).

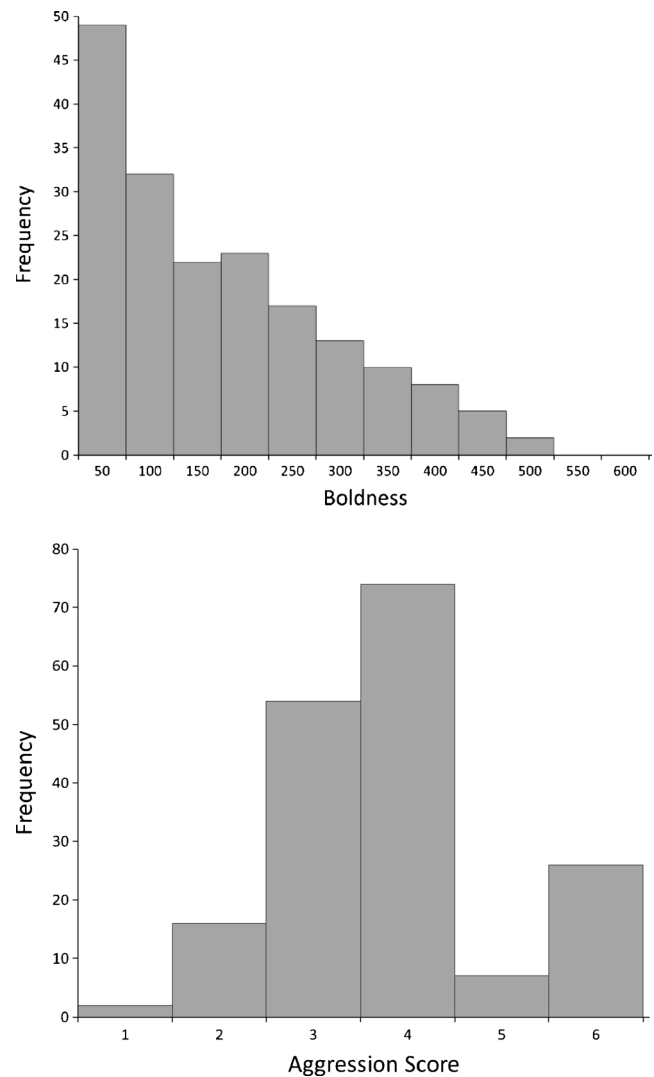
Task performance

Our combined model predicting individuals' participation in prey capture tasks was highly significant ($F_{4,174} = 3.97$, $R^2 = 0.09$, $p = 0.004$, Table 3). Individuals with high body condition indices were less likely to participate in prey capture (PC1; $F_{1,174} = 12.8$, $R^2 = 0.08$, $p = 0.0005$; Fig. 2). However, individuals' tendency to engage in prey capture behavior was not associated with their personality traits (boldness: $F_{1,174} = 0.03$, $p = 0.86$; aggression: $F_{1,174} = 0.72$, $p = 0.40$) or prosoma widths ($F_{1,174} = 1.04$, $p = 0.31$).

Our combined model predicting individuals' participation in standard web building behavior was significant ($F_{4,174} = 2.83$, $R^2 = 0.06$, $p = 0.03$, Table 3). Here, larger individuals were less likely to engage in web construction than smaller individuals (PC3; $F_{1,174} = 8.59$, $p = 0.005$; Fig. 3). No other predictor variables were significant in our model (all $p > 0.5$).

Table 2 Associations between individual-level personality and individuals' body size or condition. Generalized linear models were used to test for associations between individual-level personality and body size/condition

	R^2	F, χ^2	<i>df</i>	<i>p</i> value
Individual spiders				
Boldness vs body condition	0.02	3.11	1, 180	0.08
Boldness vs Prosoma width	0.03	5.77	1, 180	0.02
Aggression vs body condition	0.01	5.16	1	0.01
Aggression vs prosoma width	0.01	5.29	1	0.02

**Fig. 1** Frequency histograms depicting the average personality traits exhibited by individual female *S. dumicola* ($n = 180$). Spiders exhibited consistent differences between individuals in their boldness ($F_{180,721} = 2.03$, $p < 0.0001$, repeatability = 0.63; Fig. 1) and aggression ($F_{178,709} = 1.42$, $p = 0.002$, repeatability = 0.55)

No individual characteristics influenced participation in web repair behavior (PC2; $F_{4,174} = 1.04$, $R^2 = 0.02$, $p = 0.39$, Table 3).

We failed to detect an association between any of our three PC axes (all $p > 0.87$). That is, an individual's propensity to participate in one task had no relationship with its propensity to participate in other tasks. Therefore, the evidence suggests that tasks are not partitioned among individuals, nor are the individuals engaged in one set of tasks significantly more like to engage in others.

Colony-level personality assays

Across 10 days of observation, colonies exhibited consistent differences in their collective behavior (latency of emergence: $F_{14,63} = 4.21$, $p < 0.0001$, repeatability = 0.74; latency to attack:

Table 3 Results of three ANOVAs predicting the relationship between individuals' traits (behavioral tendencies, body size, body condition) and their participation in various colony tasks. The first principle component (PC1) explained 55.7 % of the variation in the number of times first to emerge, number of times first attacker, and number of times joined in attack; PC2 explained 21.7 % of the variation in number of times producing silk 0.87 and number of times repairing the web 0.51; and PC3 explained 15 % of the variation in number of times producing silk and number of times repairing the web

Independent variable	PC1		PC2		PC3	
	<i>F</i> _{4,174}	<i>p</i> value	<i>F</i> _{4,174}	<i>p</i> value	<i>F</i> _{4,174}	<i>p</i> value
Whole model	3.97	<i>0.004</i>	1.03	0.39	2.83	<i>0.03</i>
Boldness	0.03	0.86	1.42	0.24	0.02	0.88
Aggression	0.72	0.40	0.05	0.82	0.39	0.53
Prosoma width	1.04	0.31	2.03	0.16	8.60	<i>0.005</i>
Body condition	12.8	<i>0.0005</i>	0.04	0.85	0.27	0.6

Significant *p*-values are presented in italics

$F_{14,63}=4.20$, $p<0.0001$, repeatability=0.74; number of spiders nocturnally active: $F_{14,63}=3.24$, $p=0.001$, repeatability=0.69). In our best models predicting colony-level personality, colonies' latency of emergence, latency to attack, and the number of spiders engaged in standard web construction were not influenced by the average body size or body condition of the spiders therein (Table 4). The model which best explained the latency of emergence included within-colony variance in individuals' prosoma width and no other predictor variables ($F_{1,14}=5.72$, $R^2=0.31$, $p<0.05$; Table 4, Fig. 4). The model which best explained colonies' latency of attack included only within-colony variance in aggression and no other predictor variables ($F_{1,14}=5.68$, $R^2=0.30$, $p<0.05$; Table 4, Fig. 5). There were no models in which any element of colony composition effectively predicted the number of individuals

engaged in standard web construction (i.e., all $p>0.05$, Table 4), but the single best nonsignificant model included within-colony variance in boldness and no other variables ($R^2=0.05$, $p=0.41$, Table 4).

Discussion

Understanding how the traits and actions of individuals unite to determine social organization and collective behavior is vital to our understanding how such behaviors arise. In particular, the interplay between individual variation, task differentiation, and colony-level behavior/success has been a driving force in the social insect literature for more than four decades. Here we provide evidence that variation in individuals' body size and condition influence their propensity to perform a variety of colony maintenance tasks. This result is intriguing because this trait variation and its resulting task differentiation arises in a cooperative breeding society composed of highly related, inbred individuals of nearly identical age which develop together in synchrony. The once-conventional reasoning in the social spider literature was that these conditions will beget minimal inter-individual trait variation and insignificant levels of task differentiation (Darchen and Delage-Darchen 1986; Whitehouse and Lubin 2005). Our data, in addition to others (e.g., Salomon et al. 2008) undermine this view. Moreover, the best predictors of colonies' collective behavior (i.e., colony-level personality) were always their degree of within-colony trait variation (Table 4): colonies with greater within-colony variation in body size emerged more slowly in response to prey; colonies with greater within-colony variation in aggressiveness took longer to attack prey; and within-colony variation in boldness was

Fig. 2 Individuals with larger than average mass for their body size, an indication of body condition, were less likely to participate in foraging-related tasks (PC1) ($F_{90,174}=12.8$, $R^2=0.08$, $p=0.0005$)

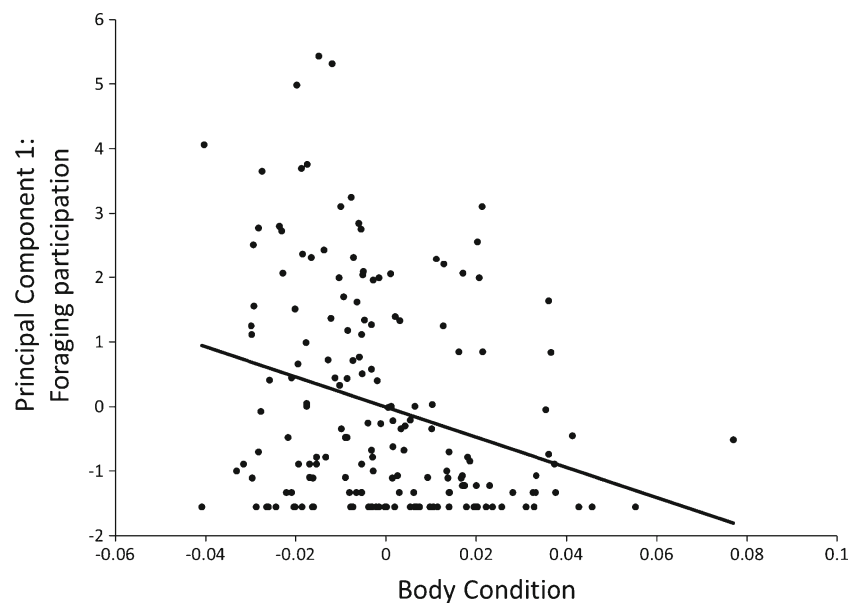
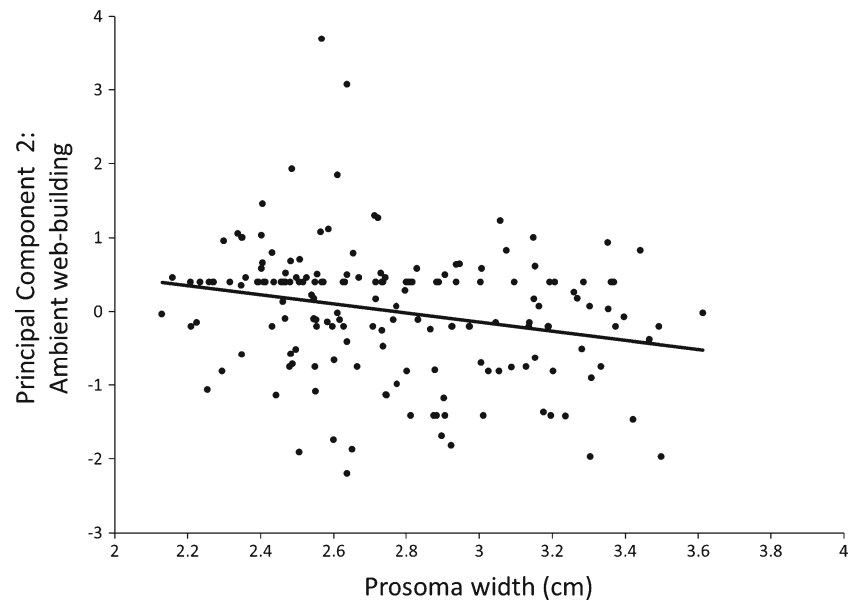


Fig. 3 Larger individuals were less likely to participate in ambient web construction after during colony expansion into a larger environment (PC3) ($F_{53,174}=8.59$, $p=0.005$)



(non-significantly) associated with more individuals engaged in standard web-building behavior. Taken together, our data suggest that inter-individual variation can still play an important role in social organization and collective behavior in societies where basic intuition might predict its absence.

Task differentiation

Task differentiation is argued to be a vital innovation behind the success of the social insects and, by extension, one might predict an absence of such organizational mechanisms in other societies. However, here we show that task differentiation of a strikingly similar nature exists in an “egalitarian” social spider. That is, individuals differed in their propensity to perform various tasks and this was associated with individuals’ traits.

However, we found no evidence for division of labor or the presence of “elite” workers, which characterize the work forces of social insect societies (Robson and Traniello 1999; Pinter-Wollman et al. 2012). In other words, the propensity of an individual to participate in one task (e.g., web building) was neither negatively nor positively associated with its likelihood to participate in other tasks (e.g., prey capture).

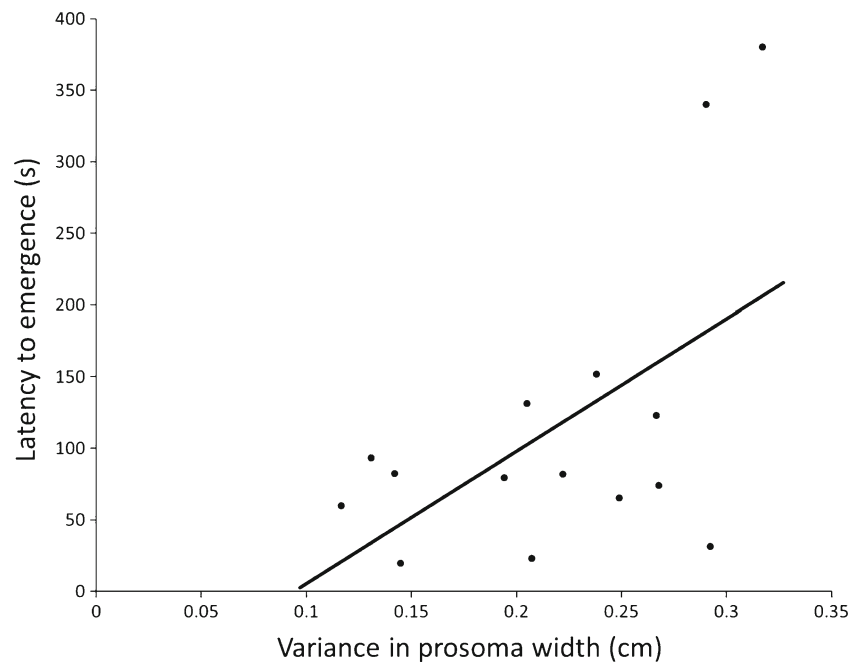
We found that individuals’ tendency to perform different tasks were associated either with their body size (i.e., prosoma width) or with their body condition, but not their personality types. This is surprising because other studies on *Stegodyphus* have found that individuals’ participation in foraging tasks is associated with both their boldness and their body size (Grinsted et al. 2013; Pruitt et al. 2013; Settepani et al. 2013). In contrast, in this study, body condition was the best

Table 4 Model comparison of those obtained via independent model selection procedures predicting latency of emergence, latency of attack, and number of individuals participating in ambient web-building in

experimental colonies. Akaike information criterion (AICc) and Akaike weights are used to compare models

Model variables	R^2	p value	RMSE	AICc	Akaike weight
Latency of emergence					
Variance in prosoma width	0.31	<0.05	91.9592	184.2438	0.42
Variance in prosoma width, Variance in aggression	0.46	<0.05	84.7293	184.4049	0.38
Average colony aggression, variance in prosoma width, variance in aggressiveness	0.56	<0.05	79.3683	185.8055	0.19
Latency to attack					
Variance in aggression	0.30	<0.05	123.3575	193.0561	0.55
Variance in prosoma width, Variance in aggression	0.40	<0.05	119.2152	194.6489	0.25
Average colony boldness, variance in prosoma width, variance in aggression	0.55	<0.05	108.2333	195.1112	0.20
Number of individual nocturnally active					
Variance in boldness	0.05	0.41	0.1113	-17.2546	0.77
Average body condition, Variance in boldness	0.10	0.51	0.1128	-14.2508	0.17
Average body condition, average colony aggression, variance in aggression	0.23	0.38	0.1089	-11.943	0.05

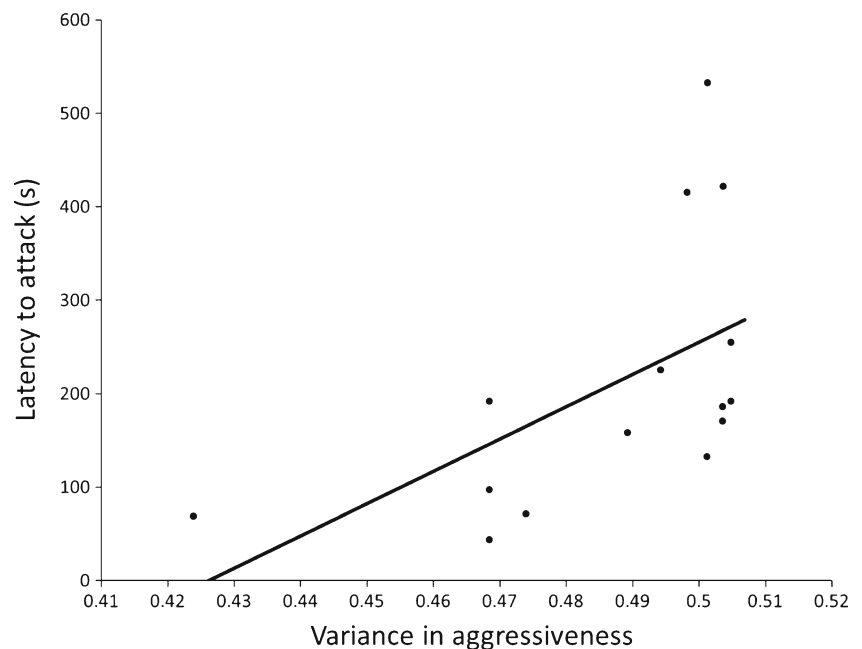
Fig. 4 The latency of emergence from the nest after prey stimulus increased along with within-colony variance in individuals' prosoma width ($F_{1,14}=5.72$, $R^2=0.31$, $p<0.05$). That is, groups with greater among-individual variation in body size took longer to respond to prey stimulus



predictor of individuals' tendency to participate in prey capture, where lower body condition was associated with more foraging activity (Fig. 2). We reason that this may be the result of individuals' recent foraging success, and that satiation diminishes individuals' willingness to engage in further risk-associated behaviors. Additionally, spiders with smaller prosoma widths were more likely to engage in ambient web-building behavior (Fig. 3). Why small individuals become active at night is unknown, but this nocturnal activity pattern may be associated with risk aversion, since the majority of predation on *Stegodyphus* occurs during the day (Henschel

1998) and smaller individuals may be more susceptible to predation. A similar size-based task differentiation has been observed in *Atta* leaf-cutting ants, where small individuals are thought to increase their nocturnal activity as to avoid predation by parasitoid flies (Orr 1992). Lastly, some of the variation in task participation may also be due to differences in the behavior of adjacent life stages. Although *S. dumicola* colonies are age-structured, the colonies collected in the field likely contained both adults and late-stage subadults (i.e., penultimate juveniles) which may differ in their propensity to perform foraging-related tasks.

Fig. 5 Colonies' latency to attack a prey item increased along with within-colony variance in aggression ($F_{1,14}=5.68$, $R^2=0.30$, $p<0.05$; Table 4, Fig. 5). That is, groups with greater among-individual variation in aggression took longer to respond to prey stimulus



Colony-level personality

We detected consistent colony-level variation in collective foraging and web-building behavior. And the best predictor of colony-level behavior was always colonies' degree of within-colony trait variation. First, we implicated within-colony variation in body size as the single best predictor of colonies' latency of emergence. This variable alone explained 31 % of the variation and a modest Akaike weight of 0.42. The second (weight=0.38) and third (weight=0.20) best models predicting colonies' latency to emerge again included within-group variation in body size as well as variation in aggressiveness (Table 4). Likewise, within-colony variation in aggressiveness alone explained 30 % of the variation observed in the colonies' latency to attack a prey item (Table 4) and this univariate model boasted an Akaike weight (0.55) twice that of either rival model. Taken together, we argue that within-colony trait variation is a more informative indicator and important driver of collective behavior than mere average trait values in this species, and thus, differences in within-colony trait variation could have important implications for colony success.

The success of insect societies is often attributed to within-colony trait variation and the resulting division of labor (Oster and Wilson 1979; Wilson 1987). Consistent with this prediction, recent studies on animal personality have shown that within-group variation in behavior and body size is positively associated with productivity: ants (Modlmeier and Foitzik 2011; Modlmeier et al. 2012), social spiders (Pruitt and Riechert 2011a), invasive populations of mosquito fish (Fogarty et al. 2011). Our data here suggest that the positive relationship often described between within-group variation and group success in diverse social taxa (e.g., Swanson et al. 2003; Pruitt and Riechert 2011a; Modlmeier et al. 2012) may be mediated by the consequences of within-group variation on collective behavior. Collective behavior is, fundamentally, a product of the variation in the behavior and/or morphology of individual group members. And, for many systems, variation in collective behavior is a major driver of group success (e.g., Dussutour et al. 2008; Pruitt 2013; but see Jandt and Dornhaus 2013). However, the precise reasons why within-group variation is correlated with differences in colony-level behavior in this system remain a mystery.

Synthesis of social spider literature

A growing body of literature demonstrates the utility of social spiders for studies on the relationship between group composition, collective behavior, and colony success. This is because, although social spiders are not enormously successful in terms of their evolutionary or ecological success (Agnarsson et al. 2006, 2013), they do lend themselves superbly to manipulative experiments on group composition in

the laboratory and in the field. To date, studies on group composition, task differentiation, and colony success have been conducted on nine different species across three genera and two families (Table 5), which together represent an estimated eight independent derivations of sociality (Agnarsson et al. 2006). This diversity of test systems is powerful because it provides us with the opportunity to explore whether generalizable patterns in social organization and colony success emerge iteratively with the evolution of sociality in these organisms. In this final section, we briefly summarize the data available from various social spiders and remark on similar patterns where they occur.

Similar relationships between task differentiation, group composition, and collective behavior/success have been observed in two of the world's most speciose genera of social spiders: New-world *Anelosimus* and Old-world *Stegodyphus*. Significant levels of task differentiation have been noted in eight or nine out of the nine species studied to date, with *S. mimosarum* having conflicting results among studies. Individual personality is the trait most commonly associated with an individual's propensity to perform different tasks (66 % of species), followed by body size (33 % of species). Personality is also the most phylogenetically widespread predictor of task differentiation, encompassing both *Stegodyphus* and *Anelosimus* species, whereas body size is only a significant predictor among social *Stegodyphus*. The fact that similar relationships between individuals' traits and task participation emerge iteratively with the evolution of sociality in spiders either implies that similar trait–task associations evolve de novo with the evolution of sociality or that such patterns emerge as a mere epiphenomenon of group living in spiders. Studies that stage associations among normally subsocial species will help untangle these alternatives.

Group composition has a significant impact on collective behavior in seven of the nine species studied, including both *Anelosimus* and *Stegodyphus*. Here, within-group variation in personality has been associated with collective foraging tasks in all seven species, and variation in body size has been associated with collective foraging behavior in *S. dumicola* only. We argue that these results imply similar mechanistic underpinnings to the collective behavior in diverse spider societies and that personality, in particular, is a major driver. Finally, group composition has notable impacts on colony success in six out of nine of the species studied, including representatives from both *Anelosimus* and *Stegodyphus*. Here again, variation in colonies' personality composition is a consistent driver of colony success in all six species: boasting effects ranging from increased/decreased group feeding success to mediating the productivity and extinction risk of entire societies. Taken together, we argue that personality appears to play a similar orchestrating role in the social organization and success of spider lineages to that of morphological castes in the social insects. If this is indeed the case, then these results

Table 5 Comparisons in the relationship between individual traits and colony social organization and success across nine species of social spider, representing eight independent derivations of sociality (Agnarsson et al. 2006)

Taxon	Range/habitat	Predictors of task participation	Relationship between colony composition and collective behavior?	Relationship between colony composition and colony success?	References
Genus: <i>Stegodyphus</i>					
<i>S. dumicola</i>	Southwest Africa; arid scrub and bushveld	Body size, body condition	Yes—within-colony trait variation and colony members with extreme phenotypes influence collective behavior Unknown	Yes—Colonies containing one very bold individual exhibit greater mass gain and survivorship in laboratory Unknown	This paper; Pruitt and Keiser (in review)
<i>S. mimosarum</i>	East Africa; arid scrub and bushveld	None or body size	Unknown	Unknown	Ward and Enders (1985); Wickler and Seibt (1993); Ainsworth et al. (2002); Grinsted and Settepani (unpublished data)
<i>S. sarasinorum</i>	Southeastern Asia, arid scrub and bushveld	Body size, personality	Yes—the boldness of colonies' boldest constituents is associated with collective behavior	Unknown	Settepani et al. (2013); Pruitt et al. (2013)
Genus: <i>Anelosimus</i>					
<i>A. studiosus</i>	North and South America; temperate deciduous forests	Personality	Yes—colonies with more aggressive individual deploy a greater number of foundresses each year and exhibit greater defensive behavior	Yes—frequency of aggressive females begets ninefold differences in extinction risk and fourfold differences in productivity	Pruitt et al. (2012, 2013)
<i>A. eximius</i>	Central and South America; lowland rainforest	Weight, nutrition, personality	Yes—colonies with aggressive individuals are more effective at capturing prey	Yes—colonies of mixed docile/aggressive composition are more effective at group feeding	Ebert (1998); Pruitt et al. (2012)
<i>A. guacamayos</i>	Central and South America; mid-elevation cloudforest	Personality	Yes—colonies with aggressive individuals are more effective at capturing prey	Yes—colonies of mixed docile/aggressive composition are more effective at group feeding	Pruitt et al. (2012)
<i>A. oritoyacu</i>	Central and South America; mid-elevation cloudforest	Personality	Yes—colonies with aggressive individuals are more effective at capturing prey	Yes—colonies of mixed docile/aggressive composition are more effective at group feeding	Pruitt et al. (2012)
<i>A. rapununi</i>	Central and South America; lowland rainforest	Personality	Yes—colonies with aggressive individuals are more effective at capturing prey	Yes—colonies of mixed docile/aggressive composition are more effective at group feeding	Pruitt et al. (2012)
Genus: <i>Achaearanea</i>					
<i>A. wau</i>	Montane rainforests, Papua New Guinea	Age	Unknown	Unknown	Lubin (1995)

could bode well for the continued growth and cross-fertilization of theory and data derived from both literatures, which have until recently remained largely disjointed.

Conclusions

In the work presented herein, we have (I) identified task differentiation between members of *S. dumicola* colonies, (II) confirmed that colonies vary consistently in their collective behavior, and (III) demonstrated that the relationship between within-colony variation and collective behavior is robust. As noted above, similar relationships between task differentiation, group composition, and colony-level impacts have now been noted in numerous species of social spider, including *S. dumicola*. In our view, the combined weight of data effectively refutes the long-held notion that social spider societies are homogeneous and egalitarian (Whitehouse and Lubin 2005). Instead, the repeated pattern of social organization observed in these systems bears more striking resemblance to classical views of the social Hymenoptera. Thus, these seemingly divergent societies (insects and spiders) may share more behavioral and organizational homoplasies than would have been predicted as recently as 2 years ago.

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