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# Iterative Evolution of Increased Behavioral Variation Characterizes the Transition to Sociality in Spiders and Proves Advantageous

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**ABSTRACT:** The evolution of group living is regarded as a major evolutionary transition and is commonly met with correlated shifts in ancillary characters. We tested for associations between social tendency and a myriad of abiotic variables (e.g., temperature and precipitation) and behavioral traits (e.g., boldness, activity level, and aggression) in a clade of spiders that exhibit highly variable social structures (genus *Anelosimus*). We found that, relative to their sub-social relatives, social species tended to exhibit reduced aggressiveness toward prey, increased fearfulness toward predators, and reduced activity levels, and they tended to occur in warm, wet habitats with low average wind velocities. Within-species variation in aggressiveness and boldness was also positively associated with sociality. We then assessed the functional consequences of within-species trait variation on reconstituted colonies of four test species (*Anelosimus eximius*, *Anelosimus rupununi*, *Anelosimus guacamayos*, and *Anelosimus oritoyacu*). We used colonies consisting of known ratios of docile versus aggressive individuals and group foraging success as a measure of colony performance. In all four test species, we found that groups composed of a mixture of docile and aggressive individuals outperformed monotypic groups. Mixed groups were more effective at subduing medium and large prey, and mixed groups collectively gained more mass during shared feeding events. Our results suggest that the iterative evolution of depressed aggressiveness and increased within-species behavioral variation in social spiders is advantageous and could be an adaptation to group living that is analogous to the formation of morphological castes within the social insects.

**Keywords:** adaptive caste demography, behavioral syndrome, temperament, Theridiidae.

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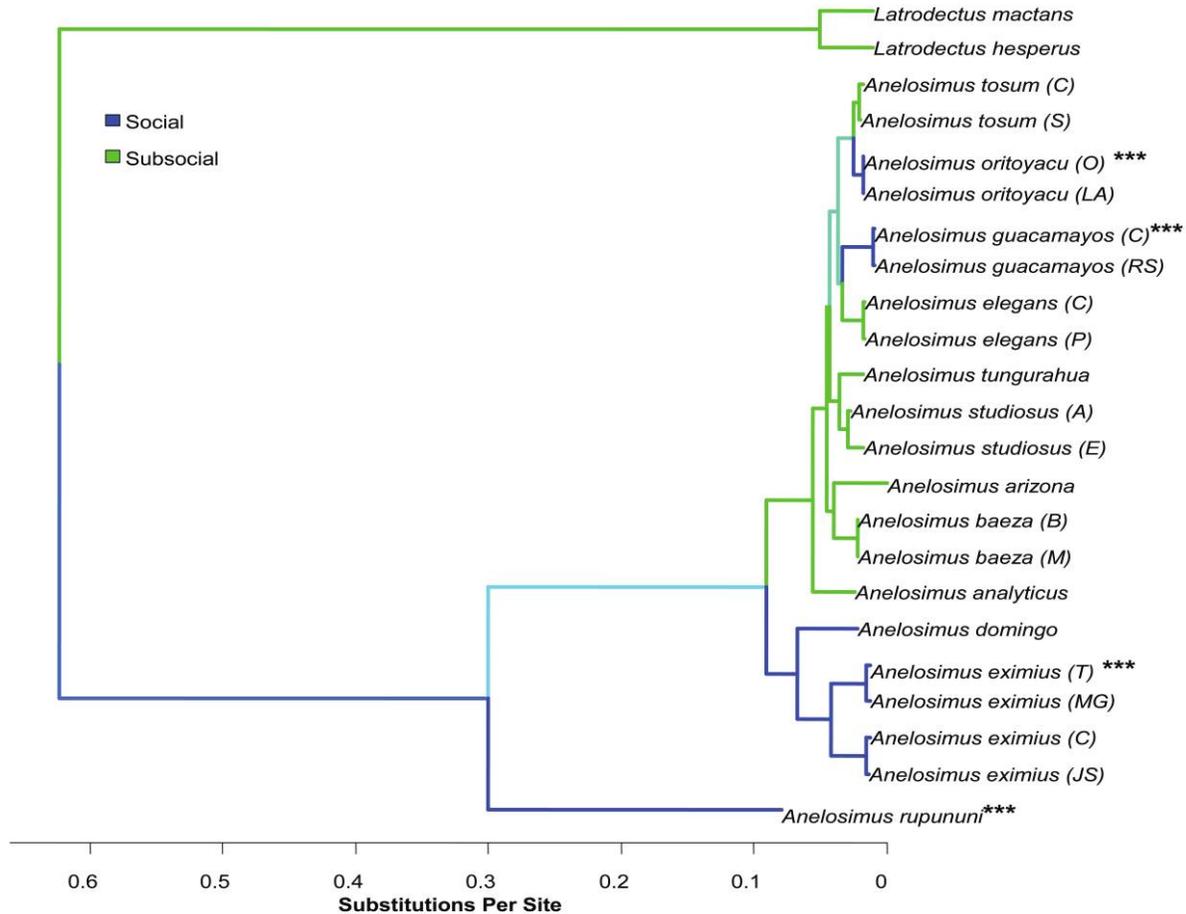
## Introduction

The evolution of sociality is often regarded as a major evolutionary transition, in part because the formation of societies is thought to alter the adaptive landscape in which other traits evolve (Maynard Smith and Szathmari 1995). For instance, the presence of cooperative conspecifics might soften selection for vigilance against predators (Elgar 1989) or, alternatively, group living might generate a selective advantage for greater social and/or Machiavellian intelligence, in which increased intelligence allows individuals to better use and exploit social information (Dunbar 1993). In virtually every cooperative taxon, the transition to group living is accompanied by shifts in traits that are not obviously associated with sociality, and whether or how these ancillary trait shifts are adaptive is typically untested but commonly assumed.

Although basic phylogenetic methods have never been intended to test adaptive hypotheses (Felsenstein 1985), phylogenetically controlled tests for species-level trait associations are frequently taken as evidence for adaptation (Blumstein and Armitage 1997; Ruckstuhl and Neuhaus 2002; Iwaniuk and Arnold 2004; Samuk et al. 2012). A more direct approach to assessing the adaptive value of trait shifts is to stage an evolutionary transition by forcibly creating mixed groups of individuals possessing basal versus derived character states and assessing the effect of trait composition on group dynamics (e.g., division of labor and establishment of hierarchies) and/or performance (e.g., task efficiency, survival, and fecundity). These experiments are typically conducted using closely related, solitary species (Jeanson et al. 2005, 2008; Jeanson and Fewell 2008; Holbrook et al. 2009). We apply this experimental approach to understanding behavioral trait shifts that underlie spider sociality in the study reported here.

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**Figure 1:** Phylogeny depicting the relationship among the *Anelosimus* species assayed in our study and two *Latrodectus* species (outgroup). Colored branches reflect ancestral character state reconstruction using the “pic” method in the ape package for R. Shades of green indicate a subsocial character state, and shades of blue indicate a social ancestor. Asterisks indicate that individuals of this species and site were used in our assessments of individual and group prey capture performance.

Sociality is exceedingly rare in spiders; of the nearly 40,000 species of spiders, only approximately 30 are designated as social (Avilés 1997; Agnarsson et al. 2006; Lubin and Bilde 2007). Although social spiders lack morphological castes, growing evidence suggests that individual variation in age (Rypstra 1993; Ebert 1998) and behavioral tendencies (Pruitt and Riechert 2011a, 2011b) influences the tasks that individuals perform within their groups (e.g., prey capture and colony defense). The genus *Anelosimus* (Araneae, Theridiidae) is outstanding among spiders because sociality appears to have evolved multiple times independently across the genus (Agnarsson 2006; Agnarsson et al. 2006, 2010). Here, we explore the behavioral correlates of sociality in *Anelosimus* and experimentally evaluate the adaptive significance of the trait correlates of grouping behavior and/or sociality using naturally occur-

ring intraspecific trait variants. We can approach this problem experimentally, because although social spiders are, on average, more passive and docile than subsocial spiders, at least some small fraction of individuals in most colonies possess trait variants that resemble those of their more aggressive, subsocial sister taxa (i.e., the evolutionary transition to more passive behavior in social species is incomplete; Pruitt et al. 2011). These nearly complete transitions afford us the unique opportunity to experimentally assess whether and how species-level trait shifts affect individual and group task performance while holding species identity constant. We use this approach with four social species spanning the *Anelosimus* genus (fig. 1).

By characterizing the behavioral correlates of sociality and testing their functional consequences, we hope to begin to elucidate the general selective pressures favoring

sociality in these typically solitary, territorial predators. Toward this end, we examined the following questions: (1) After taking shared evolutionary history into account, is sociality correlated with aggressiveness during foraging, antipredator behavior, or activity level? (2) Is sociality associated with greater intraspecific trait variation, as predicted by classic literature on social insects (Oster and Wilson 1978; Schmid-Hempel 1992) and the recent literature on animal personalities (Bergmüller and Taborsky 2010)? (3) What are the abiotic environmental correlates (e.g., temperature and precipitation) of sociality in this spider system? (4) Are the behavioral traits associated with sociality also associated with improved prey capture success in individual versus group prey capture events?

## Methods

### *Test Species, Collection, and Laboratory Maintenance*

To determine the behavioral correlates of sociality, we collected and assayed a total of 1,113 spiders representing five social *Anelosimus* species (*A. domingo*, *A. eximius*, *A. guacamayos*, *A. oritoyacu*, and *A. rupununi*), seven subsocial *Anelosimus* species (*A. analyticus*, *A. arizona*, *A. baeza*, *A. elegans*, *A. studiosus*, *A. tosum*, and *A. tungurahua*), and two outgroups of genus *Latrodectus* (*L. mactans* and *L. hesperus*; fig. 1). In spiders, social structure is determined by the behavioral tendencies of adult females (Avilés 1997). We thus limited this study to mature females. Also, because several of our test species are rare, we had to be opportunistic in obtaining test subjects. Individuals were returned to their respective colonies after their use in the experiments described below. Our collection localities were as follows: *A. analyticus*, La Julla, California; *A. arizona*, Garden Canyon, AZ; *A. baeza*, Banos and Mindo, Ecuador; *A. domingo*, Cuyabeno and Jantun Sacha, Ecuador; *A. elegans*, Cocodrilo and Pichincha, Ecuador; *A. eximius*, Cuyabeno, Jantun Sacha, Manuel Galendo, and Tena, Ecuador; *A. guacamayos*, Cocodrilo and Rio Solado, Ecuador; *A. oritoyacu*, Lago Agrio and Oritoyacu, Ecuador; *A. rupununi*, Tena, Ecuador; *A. studiosus*, Auburndale, FL, and Quito, Ecuador; *A. tosum*, Suscal and Chunchi, Ecuador; *A. tungurahua*, Banos, Ecuador; *L. hesperus*, Davis, CA; and *L. mactans*, House Mountain, TN.

We collected mature females from their webs and transported them to nearby hostels where they underwent a series of behavioral assays. Care was taken not to collect females with egg cases. Spiders were housed individually (*Anelosimus* in 59-mL cups and *Latrodectus* in 490-mL cups) and given 3 days to construct webs before being provided an ad lib. meal; *Anelosimus* species received termite workers, and *Latrodectus* received 2-week-old crickets. Individuals underwent trials in the order presented

here and were allotted 24 h of recovery time between assays. Individuals were run only once for each trial. We used separate pools of individuals for our behavioral assays and staged prey capture experiments. Individuals used in our prey capture experiments were run through the “interindividual distance” assay and assigned to an experiment on the basis of behavioral scores and body masses. Before their group assignment, females were maintained on a diet of two termite workers twice weekly.

### *Social Tendencies: Interindividual Distance Assay*

Two females of unknown tendency were individually marked with fluorescent powder and placed in the center of a clear plastic container (13 × 13.5 × 2.5 cm). After 24 h of settling time, we measured the distance between them. All females that exhibited an interindividual distance greater than 0 (i.e., that were not in direct contact) were run through a second confirmatory test with a known docile female (i.e., one that previously exhibited an interindividual distance score of 0). This test is necessary to tease apart the two types of females, because aggressive females demand space and chase away docile females. Females that exhibited an interindividual distance of ≤7 cm in the second confirmatory test were assigned to the “docile” behavioral type, and females that exhibited an interindividual distance of >7 cm were assigned to the “aggressive” behavioral type. Seven centimeters corresponds with a natural break in the distribution of interindividual distance measures between the two behavioral types in social *Anelosimus* (Pruitt and Riechert 2009a; Pruitt et al. 2011). For all *Anelosimus* species studied to date, interindividual distance scores are repeatable ( $r = 0.32\text{--}0.66$ ; Pruitt et al. 2008, 2011) and/or heritable (Pruitt and Riechert 2009b). In this study, we used the docile/aggressive behavioral type distinction for assigning females to prey capture trials and used the raw interindividual distance scores (cm) for our comparative analyses.

### *Foraging Behavior*

We offered each female a termite placed at a distance of 2.0 cm and recorded the time from females’ first intention movement until it made contact with the prey (“latency to attack”). Females that exhibited shorter latencies of attack were identified as being more aggressive on a continuum from nonaggressive to highly aggressive.

### *Antipredator Behavior*

To test for individuals’ degree of boldness toward potential predators, each female was placed in a new clear plastic container (13.5 × 13.5 × 2.5 cm) lined with white com-

puter paper, and the lid was closed. We have found that *Anelosimus* species almost universally exhibit a huddle response (i.e., pull in the legs in what is referred to as a “death feign”) in response to the lid closing. We subsequently recorded the behavior of the test female for 10 min. Boldness is estimated as the time elapsed between the placement of the lid on the container and the female’s first motion as she extends her legs or initiates web construction. Females that exhibit shorter latencies to initiate movement are labeled as more “bold” than females exhibiting longer latencies on a boldness continuum.

#### Activity Level

Our assessment of activity levels took place in the container that housed each female. We observed each female for 15 min and counted the number of times that she moved (typically grooming behavior or repositioning); movements were deemed independent if they were separated by 5 s or more of quiescence. Activity trials were conducted between 0800 and 1200 hours each day.

#### Comparative Methods

To determine whether social tendency, as inferred from interindividual distance, is correlated with aggressiveness during foraging, antipredator behavior, or activity level while incorporating phylogenetic information, we used the MECorrPhysig.m Matlab module developed by Ives et al. (2007). Our phylogenetic hypothesis (fig. 1) was modified from the phylogeny presented by Agnarsson et al. (2010) on the *Anelosimus* genus. The phylogeny was modified in two ways. (1) Because we had some taxa that were not included in the original phylogeny (e.g., several populations of some species), the new taxon (B) was added to its closest relative (A) by creating a new internal node halfway up the existing branch for A, creating sister taxa A and B with equal branch lengths, which were half of the original branch lengths of A (Oufiero et al., forthcoming). (2) We included two species of *Latrodectus* as an outgroup to *Anelosimus* with an internal node separating the two species equal to the split between *A. analyticus* and the clade with most of the species in the dataset. The branch lengths for the two *Latrodectus* species were set to equal the height of the longest branch of *Anelosimus*.

We first examined the amount of phylogenetic signal for behavioral traits (both mean trait values and standard deviations) through estimation of the  $K$  statistic using the Physig\_ll.m module for Matlab (Blomberg et al. 2003) to determine whether related species are similar in mean trait values and their amount of variation ( $K = 1$ ). We examined several pairwise correlations using a maximum likelihood estimation in MECorrPhysig.m (Ives et al.

2007). We first examined the correlation between social tendency, as inferred from interindividual distance measures, with species mean aggressiveness during foraging, antipredator behavior, and activity level, while incorporating standard errors into account. Then, to test whether social species exhibit greater behavioral variation than subsocial species, we tested for correlations between species’ mean interindividual distance scores and variation (estimated as standard deviation) exhibited in other behavioral traits (activity level, latency of attack, and boldness). We also examined correlations of species mean behavior with environmental data, again incorporating intraspecific variation in behavioral traits. Climate data were obtained from the International Water Management Institute’s World Water and Climate Atlas (<http://www.iwmi.cgiar.org/WAtlas/Default.aspx>). This climate atlas compiles data from approximately 30,000 weather stations around the world for the period 1961–1990. Finally, we examined the correlation of sociality with species variances for other behaviors. All correlations were examined with and without taking phylogenetic information into account. The results of both approaches were compared through examination of the natural log likelihoods (a higher natural log likelihood suggests a better fit for the phylogenetic model). Our phylogenetic hypothesis is displayed in figure 1.

#### Individual Prey Capture Efficiency

We used individual prey capture trials to assess whether social phenotype (aggressive or docile) was associated with the isolated spiders’ ability to capture prey. We assessed individual prey capture performance in four test species from across the *Anelosimus* genus (fig. 1): *A. eximius*, *A. guacamayos*, *A. oritoyacu*, and *A. rupununi*. We completed this trial of female’s in their home containers 1 day after a routine feeding. Before the trial was initiated, the top of the female’s container was removed, and the bottom surface was cut off. Thus, prey items had the potential to jump or walk out of the top of the web or crawl directly through it. We allowed 60 s of acclimation before presenting the prey item. Three size classes of crickets were used, and crickets were size-matched relative to the test female’s body mass (i.e., small spiders received proportionately smaller crickets). The size classes were small ( $30\% \pm 9\%$ ), medium ( $100\% \pm 9\%$ ), and large ( $200\% \pm 9\%$ ). Females were used in only a single trial and were returned to their source colonies. Prey items were dropped from 1–2 cm over the web in a central position, and incidence of capture success was observed.

**Table 1:** Phylogenetic signal results

Trait	Ln likelihood			
	Phylogeny	Star	<i>K</i>	<i>P</i>
Interindividual distance	−64.04	−69.30	.1086	<.001
Interindividual distance SD	−22.93	2.20	.0124	.483
Boldness	−123.76	−114.63	.0267	.005
Boldness SD	−76.15	−57.18	.0159	.155
Latency to attack	−124.17	−113.64	.0288	.012
Latency to attack SD	−82.10	−65.13	.0217	.091
Activity level	−40.69	−22.55	.0132	.158
Activity level SD	−1.09	19.25	.0111	.321
Body length	−33.28	−72.02	3.8372	<.001

Note: Results were obtained using the *Physig\_ll.m* module for Matlab; *K* is the amount of phylogenetic signal (Blomberg et al. 2003), and *P* value is for the significance of phylogenetic signal. Behavioral traits exhibit low phylogenetic signal; thus although there is significant phylogenetic signal (closely related taxa have similar behaviors for most traits), the *K* statistic is low. On the other hand, body length has very high phylogenetic signal. There is no phylogenetic signal for the standard deviations of our trait measures, which suggests that similar species do not exhibit a similar amount of intraspecific trait variation. Statistically significant *P* values are presented in boldface type.

#### Group Prey Capture Efficiency

We used group prey capture trials to assess the effect of group phenotypic composition on prey capture success and prey extraction efficiency. We assessed group prey capture performance in four test species from across the *Anelesimus* genus (fig. 1): *A. eximius*, *A. guacamayos*, *A. oritoyacu*, and *A. rupununi*. Our experimental colonies were composed of six size-matched ( $\pm 5\%$  body mass), individually marked females of known social phenotype. For identification, females were painted with a unique pair of colored dots using fast-drying modeling paint. Experimental colonies were constructed with four behavioral type compositions: 6 docile individuals, 1 aggressive and 5 docile individuals, 3 docile and 3 aggressive individuals, and 6 aggressive individuals. Colonies were housed in 490-mL clear plastic deli cups (each with a 3-cm diameter hole in the bottom) and were provided with a diet of 3 termite workers twice weekly. Trials occurred 2 days after a routine feeding. Colonies ( $n = 567$ ) were used in only a single prey capture event and were then disbanded and returned to their source colonies. As above, we used three prey size classes in these trials (small,  $30\% \pm 10\%$ ; medium,  $100\% \pm 10\%$ ; large,  $200\% \pm 10\%$ ). Prey items were then dropped from 1–2 cm above the web at a haphazardly selected point above the colony. We then recorded whether the prey item was successfully subdued. To assess the prey extraction efficiency of each experimental group, each female in the group was weighed 6 h before and 24 h after being presented with each prey size class. Females were removed and replaced using an aspirator. We calculated prey extraction efficiency as the sum of the change in mass

of all colony constituents divided by the total mass of the prey item (total  $\Delta$  mass of group constituents/prey mass). This test result could be confounded if the behavioral types differed in resting metabolic rates. To test whether this might be the case, we ran a “no feed” control ( $n = 6$ ) for each species and phenotypic composition (total,  $n = 96$ ). No phenotype effects on mass loss were detected for any group composition or species (paired *t*-tests  $>.10$ ).

#### Statistical Methods

We used multiple logistic regression to test the effects of species identity, body mass, behavioral type (docile or aggressive), prey size (small, medium, or large), and the interaction term species  $\times$  behavioral type on individual prey capture success. We also used multiple logistic regression to test the effects of species identity, body mass, prey size, and colony behavioral type composition (hereafter “BT composition”) on group prey capture success. We used a general linear model to test the effects of species identity, body mass, prey size, and colony BT composition on group prey extraction efficiency.

#### Results

All of our behavioral measures exhibited low, often non-significant phylogenetic signal ( $K < 0.15$ ; table 1). In other words, closely related species often exhibited divergent behavioral tendencies, both in terms of their trait means and standard deviations (i.e., behavioral traits were not highly conserved). Our phylogenetic-corrected correlations reveal

that, among species, variation in social tendency (as inferred from interindividual distance measures) is correlated with a number of behavioral and environmental variables (table 2). First, interindividual distance was negatively associated with latency to resume movement following simulated predator threats (hereafter “boldness”) and latency to attack prey and was positively associated with activity level (table 2; fig. 2). Thus, social taxa tended to exhibit reduced boldness toward predators, reduced aggressiveness toward prey, and reduced activity levels relative to less social taxa. Second, sociality was associated with shifts in trait variation; interindividual distance was negatively associated with standard deviation in boldness and latency of attack. Thus, social taxa tended to exhibit greater variance in associated behavioral traits than did less social taxa. Finally, sociality was associated with a number of abiotic environmental variables; interindividual distance was negatively correlated with annual rainfall and average humidity and was positively associated with greater average wind velocities (table 2; fig. 2). That is, social taxa tended to occur in habitats with greater precipitation, higher humidity, and reduced average wind velocities (e.g., lowland and tropical rainforests).

Our combined model predicting individual prey capture success was highly significant ( $\chi^2_{20} = 49.06$ ,  $R^2 = 0.14$ ,  $P < .0001$ ; table 3). We detected main effects of body mass ( $\chi^2_1 = 4.03$ ,  $P = .04$ ), behavioral type ( $\chi^2_1 = 6.54$ ,  $P = .01$ ), and prey size ( $\chi^2_1 = 33.00$ ,  $P < .0001$ ) on prey capture success. Although all test subjects were better able to capture prey at the small end of the range offered, heavier-bodied females and those exhibiting the aggressive behavioral type enjoyed greater prey capture success in isolation (fig. 3).

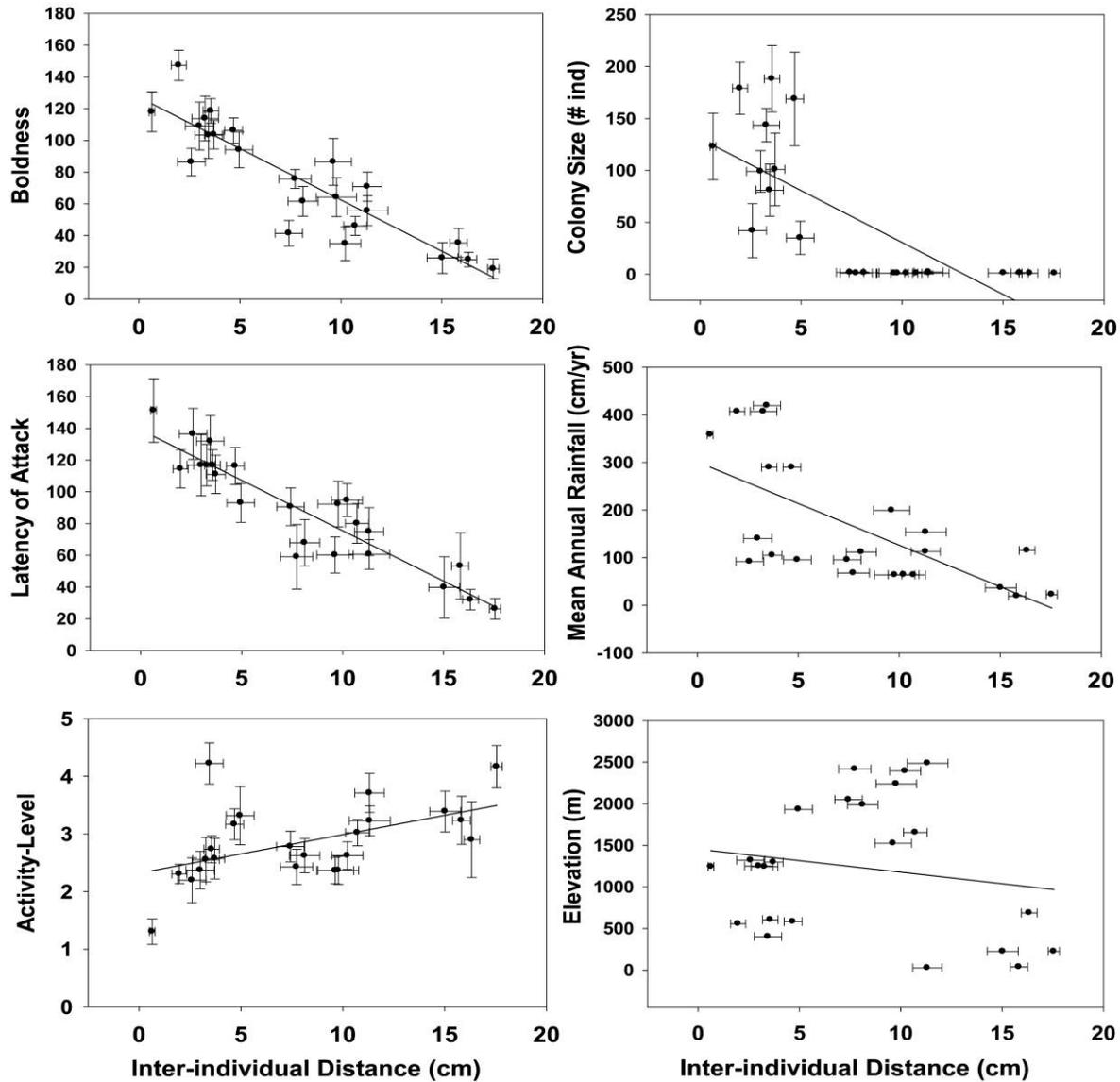
Our model predicting group prey capture success was also highly significant ( $\chi^2_{48} = 227.19$ ,  $R^2 = 0.29$ ,  $P < .0001$ ; table 2). We detected significant main effects of BT composition ( $\chi^2_3 = 50.79$ ,  $P < .0001$ ) and prey size ( $\chi^2_2 = 110.82$ ,  $P < .0001$ ) on group capture success. However, as evidenced by the three-way interaction term “species  $\times$  prey size  $\times$  BT composition” ( $\chi^2_{17} = 40.12$ ,  $P = .002$ ), the effects of all three factors depended on the status of others (fig. 4). For all test species and prey sizes, groups of mixed behavioral types were at least as successful at capturing prey as were monotypic groups, and under many circumstances, groups of mixed behavioral types enjoyed the greatest prey capture success. Thus, in *A. eximius*, 1A5D and 3A3D groups were most effective at capturing medium and large prey; in *A. guacamayos*, 3A3D groups were most effective at capturing medium prey, and 1A5D groups were most effective at capturing large prey; in *A. rupununi*, 1A5D groups were most effective at capturing medium prey, and 3A3D groups were most effective at capturing large prey; and, in *A. oritoyacu*, 1A5D groups

**Table 2:** Correlations between sociality, as inferred from individual distance scores, and behavioral traits and environmental variables

Variable	Star (ML)	Phylogeny (ML)
Behavioral trait:		
Boldness:		
<i>R</i>	-.8788	-.88028
<i>P</i>	<.0001	<.0001
Ln likelihood <sup>a</sup>	-116.85	-113.3403
Latency of attack:		
<i>R</i>	-.85252	-.97354
<i>P</i>	<.0001	<.0001
Ln likelihood <sup>a</sup>	-118.3698	-106.9733
Activity level:		
<i>R</i>	.28785	.57654
<i>P</i>	.1829	.004
Ln likelihood <sup>a</sup>	-38.5568	-33.9979
Boldness SD:		
<i>R</i>	-.7638	-.7891
<i>P</i>	<.0001	<.0001
Ln likelihood <sup>a</sup>	-278.57	-274.44
Latency of attack SD:		
<i>R</i>	-.8148	-.4611
<i>P</i>	<.0001	.02
Ln likelihood <sup>a</sup>	-287.20	-307.20
Activity level SD:		
<i>R</i>	-.4590	-.1848
<i>P</i>	.02	.38
Ln likelihood <sup>a</sup>	-132.48	-137.45
Environmental variable:		
Latitude:		
<i>R</i>	.43	.08
<i>P</i>	.03	.71
Ln likelihood <sup>a</sup>	-107.13	-96.16
Log precipitation per annum:		
<i>R</i>	-0.67	-0.16
<i>P</i>	.0002	.44
Ln likelihood <sup>a</sup>	-39.16	-54.52
Days with rain:		
<i>R</i>	-0.71	-0.39
<i>P</i>	<.0001	.05
Ln likelihood <sup>a</sup>	-135.55	-130.97
Temperature:		
<i>R</i>	-.38	-.05
<i>P</i>	.06	.81
Ln likelihood <sup>a</sup>	-84.19	-107.69
Humidity:		
<i>R</i>	-.47	-.24
<i>P</i>	.017	.34
Ln likelihood <sup>a</sup>	-103.81	-89.10
Average wind velocity:		
<i>R</i>	.73	.46
<i>P</i>	<.0001	.02
Ln likelihood <sup>a</sup>	-16.41	-21.29

Note: ML, maximum likelihood.

<sup>a</sup> A greater natural log (ln) likelihood suggests a better-fit model for a given correlation.



**Figure 2:** Associations between interindividual distance and various behavioral correlates and climatic variables. Error bars represent standard error of the mean.

were most effective at capturing medium prey. The prey capture success of groups composed of a single behavioral phenotype was statistically indistinguishable from each other for the majority of prey sizes and species. However, in *A. oritoyacu* and *A. rupununi*, groups composed entirely of aggressive females were more effective than groups composed entirely of docile females at capturing small prey.

Our model predicting prey extraction efficiency was also highly significant ( $F_{20,233} = 49.06$ ,  $R^2 = 0.14$ ,  $P < .0001$ ;

table 3). We detected significant main effects of prey size ( $F_{2,503} = 7.32$ ,  $P = .007$ ) and BT composition ( $F_{2,503} = 24.01$ ,  $P < .0001$ ) on prey extraction efficiency. However, as evidenced by the three-way interaction term species  $\times$  prey size  $\times$  BT composition, the effects of all three factors depended on the status of others ( $F_{17,503} = 4.01$ ,  $P < .0001$ ; fig. 5). In most test species and prey size classes, groups composed entirely of aggressive females experienced the lowest prey extraction efficiency. Thus, in *A.*

**Table 3:** Table summarizing the effects tests for the terms in multiple logistic and multiple regression models predicting individual prey capture success, group prey capture success, and group prey extraction efficiency

Variable	df	$\chi^2$	F ratio	P
Individual prey capture:				
Species	3	7.52	...	.06
Body mass	1	4.03	...	<b>.04</b>
Prey size	2	33.01	...	<b>&lt;.0001</b>
BT	1	6.54	...	<b>.01</b>
Species $\times$ BT	3	.88	...	.83
Group prey capture:				
Species	3	.27	...	.57
Body mass	1	.26	...	.61
Prey size	2	110.81	...	<b>&lt;.0001</b>
BT composition	3	50.79	...	<b>&lt;.0001</b>
Species $\times$ prey size	5	5.81	...	.44
Species $\times$ BT composition	9	8.67	...	.47
BT composition $\times$ prey size	6	10.64	...	.09
Species $\times$ prey size $\times$ BT composition	18	40.19	...	<b>.002</b>
Prey extraction efficiency:				
Species	3, 304	...	1.71	.18
Body mass	1, 304	...	.45	.37
Prey size	2, 304	...	24.01	<b>&lt;.0001</b>
BT composition	3, 304	...	4.03	<b>.007</b>
Species $\times$ prey size	6, 304	...	4.35	<b>.0008</b>
Species $\times$ BT composition	9, 304	...	7.08	<b>&lt;.0001</b>
BT composition $\times$ prey size	6, 304	...	2.07	.07
Species $\times$ prey size $\times$ BT composition	18, 304	...	4.01	<b>&lt;.0001</b>

Note: Statistically significant *P* values are presented in boldface type. BT, behavioral type.

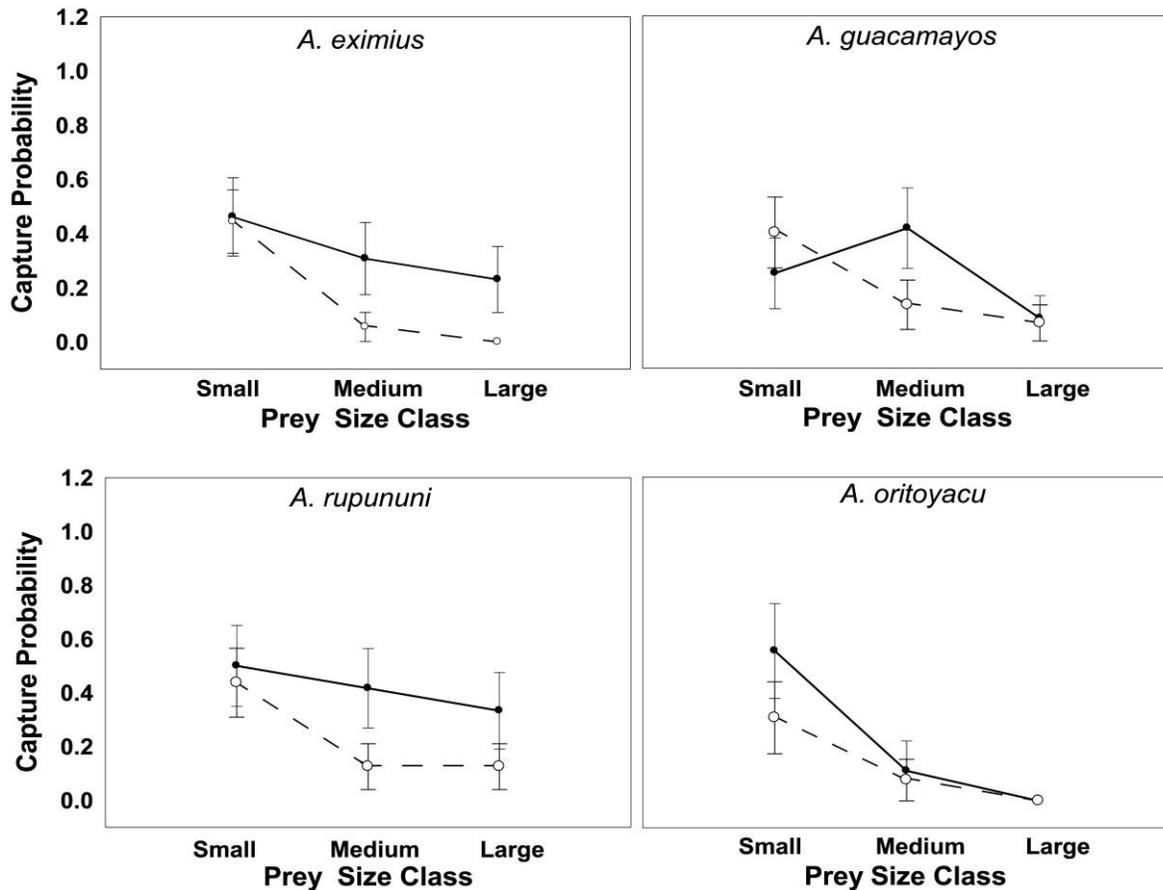
*eximius*, 1A5D groups experienced the greatest prey extraction efficiency; in *A. guacamayos*, 3A3D and 1A5D groups enjoyed higher prey extraction efficiency than monotypic groups, and their efficiencies resembled one another's; in *A. rupununi*, 1A5D groups enjoyed the greatest prey extraction efficiency; and, in *A. oritoyacu*, groups of docile females and mixed behavioral types exhibited greater prey extraction efficiency than did groups composed entirely of aggressive females, but their efficiencies were generally indistinguishable from each other's (fig. 5). After 24 h, prey subdued by groups that consisted entirely of aggressive females were typically moist, decomposed, and pungent smelling, whereas prey subdued by groups of docile females or mixed BT compositions were typically drier, compacted, and faint smelling.

## Discussion

### *Behavioral Correlates of Sociality*

Intuitively, the evolutionary transition from solitary life to living in groups of hundreds or even thousands of conspecifics might require a shift in behavioral tendencies. However, comparative studies that explicitly test for

species-level behavioral syndromes are needed to test this hypothesis. Our data collected on *Anelosimus* species reveal that the evolution of sociality is associated with a shift in a suite of behavioral traits; social *Anelosimus* tend to exhibit longer latencies to resume activity after predator cues, longer latencies of attack, and reduced activity levels relative to their subsocial relatives. Thus, in *Anelosimus*, social species are less aggressive toward prey and more fearful toward predators than are subsocial species (Pruitt et al. 2008, 2010, 2011). These results are consistent with the recent findings of Samuk et al. (2012), which noted that social species exhibit depressed aggressiveness when defending their egg cases. Samuk and collaborators argue that group living has altered (i.e., depressed) the selective advantage of aggressive defensive behavior either (1) because females will aid one another in defending their egg cases or (2) because the larger and more elaborate architecture of multifemale colonies likely reduces the need to actively defend egg cases. Interestingly, in our study, social species also differed in their trait variances; sociality was associated with greater intraspecific variation in latency to resume movement after predator cues and latency to attack prey. Thus, although they are generally less aggressive and more fearful than their subsocial relatives, social species



**Figure 3:** Interaction plots depicting the effects of behavioral type and prey size class on isolated individual prey capture success for aggressive (solid black line, filled circles) and docile (dashed line, open circles) females of *Anelosimus* species. Error bars represent standard error of the mean.

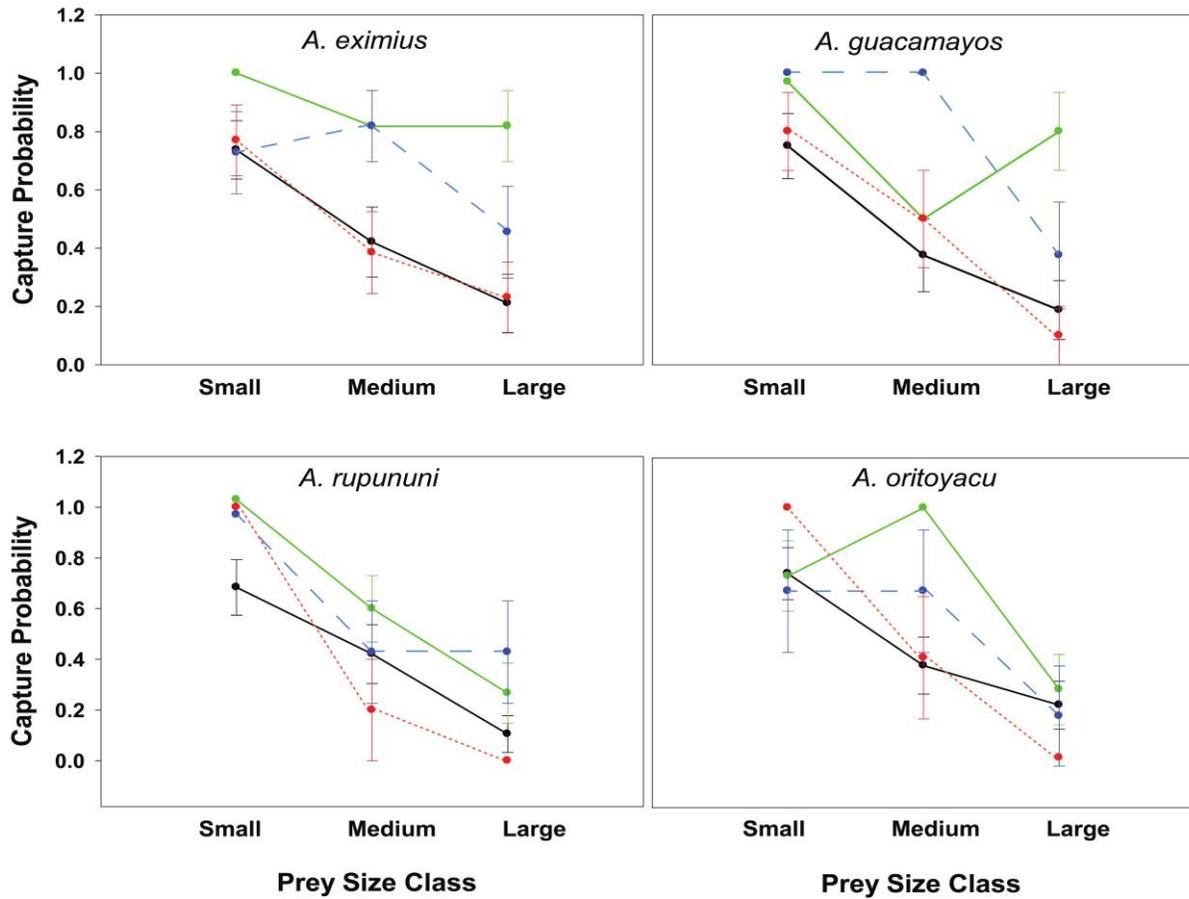
exhibit greater trait variance in several aspects of their behavior.

Increased trait variance within social groups is a hallmark of many animal societies, particularly the social insects (Schmid-Hempel 1992; Burns and Dyer 2008; Pruitt and Riechert 2011*b*). The classic hypothesis from the social insect literature is that within-group trait variation is associated with greater task specialization, amplified division of labor, diminished niche overlap, and increased whole-group fitness (Oster and Wilson 1978; Wilson 1987; Hölldobler 1990). It has even been proposed that a positive relationship among trait variants could be a general mechanism for maintaining diversity (genetic or phenotypic) within social species (Nonacs and Kapheim 2007, 2008; Caesar et al. 2010). Concordant with these hypotheses, we found that social spider species of the genus *Anelosimus*

exhibited greater trait variation than related subsocial species, and this finding raises the question as to whether or how increased behavioral variation influences task performance. That is, if reduced aggressiveness and increased within-group behavioral variation are adaptive for social spiders, we predict docile groups or groups of mixed phenotypes will outperform groups consisting entirely of aggressive females. By parallel logic, because solitary species tend to be more aggressive, we anticipate aggressiveness will be linked with improved performance in isolation and that docility will be disfavored.

#### *Environmental Correlates of Sociality*

Identifying the environmental correlates of sociality within and across species can help elucidate the environments



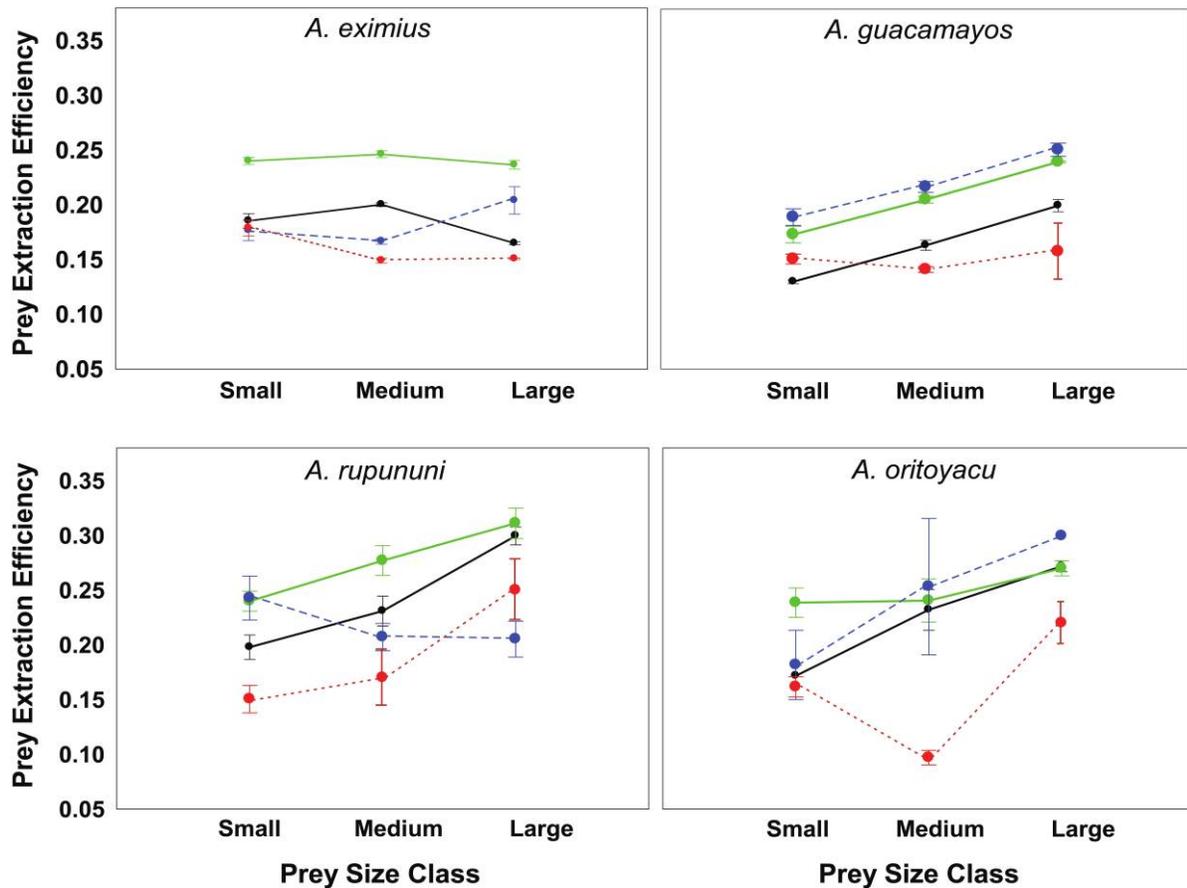
**Figure 4:** Interaction plots depicting the effects of behavioral type and prey size class on group prey capture success for *Anelosimus* species groups of various phenotypic compositions, including 6 docile (black solid), 5 docile and 1 aggressive (green solid), 3 docile and 3 aggressive (blue dashed), and 6 aggressive individuals (red dotted). Error bars represent standard error of the mean.

that favor social living and perhaps provide some evidence for why social species exhibit such divergent behavioral tendencies. Within spiders, a multitude of investigations have tested for associations between habitat parameters and social living using either intraspecific trait variation (Campon 2007, 2008, 2010; Jones et al. 2007; Purcell and Avilés 2007, 2008; Riechert and Jones 2008) or small-scale comparative studies (involving 2–5 species; Guevara and Avilés 2011; Guevara et al. 2011; Samuk et al. 2012). However, to date, no study has simultaneously considered enough species to use comparative analyses to test for an association between sociality and various environmental parameters. Our data demonstrate that, relative to sub-social species, social spiders tend to occur in warm, wet habitats with greater precipitation and lower average wind velocities. This is concordant with a sizable number of

case studies that argue that social spiders tend to occur in the lowland tropics, where colonies encounter larger prey, more ant predators, and greater web damage from rain (Avilés et al. 2007; Guevara and Avilés 2007; Powers and Avilés 2007; Purcell and Avilés 2007, 2008; Yip et al. 2008; Guevara et al. 2011).

#### *Causes and Consequences of Increased Behavioral Variation within Social Species*

The spectacular diversity of behavioral tendencies exhibited across the *Anelosimus* genus raises several questions worth discussing, including (1) what mechanisms generate the increased behavioral variation observed within social species and (2) whether differences among species in personality are the cause or consequence of sociality. With



**Figure 5:** Interaction plots depicting the effects of behavioral type and prey size class on prey extraction efficiency for *Anelosimus* species groups of various phenotypic compositions, including 6 docile (black solid), 5 docile and 1 aggressive (green solid), 3 docile and 3 aggressive (blue dashed), and 6 aggressive (red dotted). Error bars represent standard error of the mean.

respect to the first question, it is important to note that social spider colonies are very highly inbred ( $r \approx 0.80\text{--}0.90$ ; reviewed in Avilés 1997; Lubin and Bilde 2007), and consequently, the increased variation in behavioral tendencies observed within social species is most likely the result of plasticity, not sequence differences. Whether behavioral variation develops in response to variation in the abiotic, biotic, and/or social environments is less clear and awaits further study. However, at least some theory suggests that variation in personality could develop as individuals adopt different social niches within their groups (Bergmüller and Taborsky 2010). With respect to the second question, we argue that reduced aggressiveness has more likely evolved as a consequence of sociality, rather than having acted as a cause of sociality. We favor this hypothesis because docile individuals tend to perform

poorly outside of a social groups (Jones et al. 2010; Samuk et al. 2012), and thus, docile variants are unlikely to persist within exclusively subsocial populations. Other studies have demonstrated that, once grouping has evolved, docile and/or mixed compositions tend to outperform groups composed entirely of aggressive individuals (e.g., honeybees: Hillesheim et al. 1989; social spiders: Pruitt and Riechert 2009a). This is because aggressive compositions engage in excessive amounts of interference competition and infighting.

#### *Individual Prey Capture Efficiency*

One hypothesis for why social and subsocial spiders differ in their behavioral tendencies is that the behavioral traits favored in individual versus group foraging scenarios

might differ. Most spiders are quintessentially aggressive predators; they exhibit polyphagic foraging tendencies, a suite of adaptations for feast-or-famine existence, and intense aggressiveness toward food, rivals, and mates (Foelix 1996). Given this ecology, it is intuitive that aggressive females should enjoy greater performance in isolation. Consistent with this prediction, in all four of our test species, aggressive females were more successful than docile females at capturing prey in isolation, and this advantage was most pronounced when catching medium or large prey (fig. 3; table 3). Thus, as predicted, solitary foraging appears to favor the high levels of aggressiveness that characterize the majority of spider species.

#### *Group Prey Capture Efficiency*

Given that sociality was correlated with reduced aggressiveness and increased within-species trait variation (table 2), we predicted that groups composed entirely of docile females and groups of mixed phenotypic composition would outperform groups composed entirely of aggressive females during staged prey capture events. Consistent with our prediction, we found that groups of mixed phenotypic composition outperformed monotypic groups during staged prey capture events (fig. 4). However, note that our finding that groups of docile females failed to outperform groups composed entirely of aggressive females during prey capture events is contrary to this prediction. Thus, in all four test species, groups of mixed composition enjoyed the greatest prey capture success, and this advantage was most pronounced in encounters with medium or large prey. These data add to the limited number of studies documenting the positive effects of within-group behavioral variation in the laboratory (honeybees: Burns and Dyer 2008; ants: Modlmeier et al. 2012; social spiders: Pruitt and Riechert 2011a) and field (ants: Modlmeier and Foitzik 2011; social spiders: Pruitt and Ferrari 2011). However, our study goes two steps further. First, whereas most studies have tested for functional consequences of within-group behavioral variation in a single test species, our study documents a significant macroevolutionary trend in which social species exhibit greater trait variation. Second, we then tested the functional consequences of within-group variation using multiple test species spanning the *Anelosimus* phylogeny. Thus, the functional consequences of within-group behavioral variation are unlikely to be the result of mere species-specific idiosyncrasies. Consequently, this represents one of the most thorough examples of adaptive within-group behavioral variation to date, which confirms a sizable body of existing theory (Oster and Wilson 1978; Myerscough and Oldroyd 2004; Graham et al. 2006; Burns and Dyer 2008).

Capturing large prey is vital for multifemale colonies,

because as spider societies grow, they experience a reduced surface-area-to-volume ratio. This scaling constraint translates into reduced prey capture potential per colony constituent. The way spider societies overcome this constraint is by capturing larger and larger prey as colony size increases (Yip et al. 2008). Thus, in many ways, spider societies depend on the prevalence of large prey to persist. Our data reveal that within-group behavioral variation confers increased task efficiency during prey capture events, and this advantage is most prominent when attempting to capture high-quality, colony-sustaining prey. We propose these results may explain why we find some, albeit small, proportion of aggressive females present in all social *Anelosimus* species tested and in virtually all *Anelosimus* colonies assayed (Pruitt and Riechert 2009a, 2011b; Pruitt et al. 2011). This is because a mixture of aggressive and docile females best facilitates the capture of large, colony-sustaining prey.

For foraging societies to thrive, they must do more than merely subdue prey. The efficiency with which prey is consumed (collective group mass gain per unit of time) is frequently a key determinant in the success of a foraging group. For instance, in cooperatively hunting mammals, subdued prey must be consumed quickly because rivals (e.g., larger predatory mammals and carrion) can recruit to recent kills and steal prey. Similarly, within spider societies, ants (Furey and Riechert 1989; Purcell and Avilés 2008), parasitic hemipterans (Agnarsson 2006), and even fellow spiders (Agnarsson 2006; Avilés et al. 2006; Perkins et al. 2007; Pruitt and Riechert 2011b) threaten to supplant colony members and steal uneaten or partially consumed prey items. Consuming prey rapidly both diminishes the probability that intruders will recruit to prey and reduces the quantity and quality of food being stolen. Our data reveal that group composition significantly impacts prey extraction efficiency in all four of our test species. Generally speaking, irrespective of prey size, groups of mixed phenotypic composition exhibited greater prey extraction efficiency than monotypic groups, and groups composed entirely of docile females exhibited greater prey extraction efficiency than groups composed entirely of aggressive females. From work on a related species (*Anelosimus studiosus*), we know that, when at high representation, aggressive females will engage in excessive interference competition for contested prey, and these disputes lead to food wastage and increased risk of injury (Pruitt et al. 2008; Pruitt and Riechert 2009a). Similarly, our data suggest here that reduced aggressiveness plays an important role in successfully coordinating prey capture and consumption. Taken together, our data suggest that, as with prey capture efficiency, within-group behavioral variation confers improved prey extraction performance. Here

again, the iterative evolution of increased trait variation in social spiders appears to be advantageous.

### Conclusions and Synthesis

A perennial notion within sociobiology is that the evolution of sociality alters the adaptive landscape in which traits evolve, and one cornerstone prediction from this literature is that the evolution of societies favors increased within-group trait variation (e.g., body size, castes, behavioral tendencies, and signals; Oster and Wilson 1978; Schmid-Hempel 1992; Beshers and Fewell 2001). Here, we demonstrate that social spiders are generally less aggressive toward prey, more fearful toward predators, and less active than their subsocial relatives. However, more interestingly, social species also exhibit greater trait variation than their subsocial relatives, and this finding is consistent with a sizable body of theory from the social insect literature (Oster and Wilson 1978). Given this association, we predicted that aggressiveness would confer greater prey capture success in isolation (since solitary species are more aggressive) and that depressed aggressiveness and greater within-group behavioral variation would confer superior prey capture success during group prey capture events. Consistent with our predictions, we found that aggressive females were more successful at capturing prey in isolation, and during group prey capture events, groups of mixed phenotypes outperformed monotypic groups both at capturing prey and at feeding efficiently. Thus, our data are thoroughly consistent with the long-standing “adaptive within-group trait variance” hypothesis from the sociobiology literature and suggest that the species-level behavioral syndrome described herein is, in fact, functionally adaptive.

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*Anelosimos eximius* traversing a web. Photograph by Jonathan N. Pruitt.