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Original Article

Spider aggressiveness determines the bidirectional consequences of host–inquiline interactions

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Individual behavioral variation (aka behavioral types [BTs]) can alter the nature of species interactions. Here, we explore the performance consequences of behavioral variation in heterospecific dyads of the social spider *Anelosimus studiosus* and two of its most common inquilines (*Larinioides cornutus* and *Theridion murarium*). We determined the BTs of *A. studiosus* (docile vs. aggressive), determined the aggressiveness of their inquilines, and released dyads in the field for 40 days. We assessed the performance of *A. studiosus* and its inquilines using egg case mass and change in body mass, respectively. In the absence of inquilines, we found that aggressive *A. studiosus* outperformed dociles, however docile *A. studiosus* outperformed aggressives in the presence of inquilines. Aggression in *T. murarium* had a large effect on *A. studiosus* fecundity and its own performance, though this trend was not observed in *L. cornutus*. The performance of host and inquiline was simultaneously maximized when dyads were composed of opposing BTs: docile *A. studiosus* with aggressive *T. murarium* and vice versa. Thus, our data demonstrate bidirectional impacts of behavioral variation in a host–inquiline interaction and reveal that the traits that yield the greatest success in one species may depend on the representation of traits in another associated species.

Key words: behavioral type, inquiline, personality, species interaction, temperament.

INTRODUCTION

An emphasis on functional diversity, particularly at the level of individual variation, is experiencing a renaissance in both community and behavioral ecology (Werner and Peacor 2003; McGill et al. 2006; Bolnick et al. 2011). Both intraspecific and interspecific variation in functional traits can drive ecological and evolutionary processes (Réale et al. 2007; Sih and Bell 2008; Sih et al. 2012), in part, because subtle differences in key functional traits (e.g., behavior) can predictably shift the number, intensity, and nature of the species interaction that individuals and/or species will experience (Bolnick et al. 2003, 2011). The consequence of behavioral variation is particularly intriguing, because it is a more “cryptic” form of functional diversity that frequently goes unnoticed in community ecology (Sutherland 1996). However, studies across diverse taxa have identified repeatable intraspecific variation in behavioral traits that are consistent across time and/or ecological contexts (e.g., *Daphnia*, Duffy 2010; spiders, Pruitt et al. 2008; mammals, Réale et al. 2000; etc.). Such repeatable individual differences in

behavior are often called “personality types” or “behavioral types” (BTs), and correlations among such BTs are commonly referred to as “behavioral syndromes” (Sih et al. 2004). BTs are regularly observed along trait axes like shyness–boldness, exploration–avoidance, and docile–aggressive (Réale et al. 2007).

In cases where a single species has an inordinate influence on community dynamics and species interactions (e.g., keystone species, ecosystem engineers, etc.), intraspecific variation in key functional traits could be particularly influential for community dynamics—potentially changing the outcome of species interactions, shaping the presence and magnitude of trophic cascades, and determining the prevalence and diversity of other ancillary species (Jones et al. 1994; Menge et al. 1994; Shanks 2002; Sih and Watters 2005; Pruitt and Ferrari 2011). For example, ecosystem engineers like reef-building corals make drastic modifications to the physical environment via their own living structures (Jones et al. 1997), which, in turn, can modulate biotic processes and ameliorate stressors for heterospecifics (Jones et al. 1997; Hastings et al. 2007). Autogenic ecosystem engineers, like corals, are those that shape their environment by either their own body or via biomaterials that they themselves create. Social spiders (i.e., those that form large multifemale colonies) are yet another example of an

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autogenic ecosystem engineer. Social spiders throughout the world construct elaborate “silken reefs” that can house >100 foreign species of arthropod (Perkins et al. 2007; Pruitt and Riechert 2011b) and numerous vertebrate species (e.g., Hylid frogs, sun birds, tree-roosting bats, field mice, etc.; Pruitt JN, Grinsted L, Riechert SE, personal observation). These silken reefs serve as complex, species-rich biological communities with stunning community dynamics (e.g., trophic cascades, predictable metacommunity dynamics) (Pruitt and Ferrari 2011; Pruitt and Riechert 2011b).

The behaviorally polyphenic social spider *Anelosimus studiosus* (Araneae, Theridiidae) builds multifemale colonies consisting of an assortment of individuals exhibiting discrete aggressive and docile BTs (Furey 1998; Jones et al. 2007; Pruitt et al. 2008). Aggressive females are more active and exhibit considerable aggression toward predators, prey, and colony mates; in contrast, docile individuals are less active and rarely engage in agonistic bouts (Pruitt et al. 2010). *Anelosimus studiosus* lives in relatively small colony sizes containing only two to a few hundred individuals (Riechert and Jones 2008), and conspecific colony members participate in shared alloparental care, collective web maintenance, and cooperative prey capture (Furey 1998; Jones et al. 2007; Riechert and Jones 2008). The preponderance of evidence available to date suggests that spider sociality is driven by foraging benefits, whereby group living allows social spiders to overwhelm large prey that are otherwise inaccessible to singleton spiders (Nentwig 1985; Yip et al. 2008).

Like other social spiders, *A. studiosus* webs serve as habitat for >100 species of arthropod, and the most numerous of which are foreign, heterospecific spiders (Perkins et al. 2007; Pruitt and Riechert 2011b). These web associates commonly benefit by their association with *A. studiosus* via increased foraging success and reduced susceptibility to predation (Pruitt and Ferrari 2011; Pruitt, Cote, et al. 2012). Due to favorable conditions for heterospecifics, social spider colonies often sequester diverse assemblages of heterospecific araneofauna (Avilés et al. 2006; Perkins et al. 2007), insects (Deyrup et al. 2004), and, occasionally, vertebrates. The interactions between *A. studiosus* and its heterospecific web associates can vary dramatically. Henceforth, we will refer to web associates as “inquilines,” which is defined as an animal that resides in a domicile constructed by another species of animal (Hölldobler and Wilson 1990). In *A. studiosus*, the interactions between host colonies and inquilines are often exploitative, where inquilines act as kleptoparasites (Agnarsson 2003) or predators on their host (Perkins et al. 2007). However, host–inquilines interactions can also be commensalisms (e.g., reduced predation risk for inquilines with no cost to hosts), mutualisms (e.g., cooperative foraging), or entirely neutral (e.g., no interspecific interactions) (Perkins et al. 2007; Pruitt and Riechert 2011b; Pruitt, Cote, et al. 2012). The nature of these interactions is determined, in part, by the BTs present within the host colony: groups containing aggressive *A. studiosus* experience depressed body condition and fecundity when living with inquilines, whereas groups composed entirely of docile *A. studiosus* experience increased reproductive output when living with low numbers of inquilines (Pruitt and Ferrari 2011; Pruitt 2012; Pruitt, Cote, et al. 2012). However, why inquilines benefit colonies of all docile females but not those containing aggressive females remains unknown. Moreover, whether intraspecific variation in the BTs of inquilines can also impact the host–inquiline interaction remains entirely unexplored. This second point echoes a weakness shared by nearly the entirety of the behavioral syndromes literature, because the vast majority of investigations are single-species oriented and fail to simultaneously

consider behavioral variation in multiple interacting individuals (argued in Pruitt, Stachowicz, et al. 2012; Sweeney et al. 2013; McGhee et al. forthcoming).

We argue that variation in the interactions between *A. studiosus* and its inquilines might be a consequence of variation in occurrence of interspecific, cooperative prey capture. Specifically, in a previous study, we noted that some colony inquilines will attack prey with their hosts and engage in simultaneous feeding (Pruitt, Cote, et al. 2012). We propose that the nature of host–inquiline interactions will be a function of the BTs of both individuals involved. In particular, we hypothesize that aggressive *A. studiosus* will exhibit increased fecundity when living with docile inquilines, whereas docile *A. studiosus* will exhibit increased mass gain and fecundity with aggressive inquilines. Similarly, we hypothesize that inquilines will gain more mass when living with a host with an opposing BT. Therefore, the performance metrics that we will measure (fecundity and mass gain) should be maximized in pairs of contrasting BTs. These hypotheses are based on the previous observation that *A. studiosus* colonies are more effective at cooperative prey capture and group feeding when they are composed of a mixture of docile and aggressive individuals. Moreover, data from a variety of test systems have revealed bidirectional, positive effects of behavioral variation on the performance of interacting individuals, from social insects to primates (Nonacs and Kapheim 2007). Thus, we predict that similar dynamics could play out in interspecific (i.e., host–inquiline) interactions: both hosts and inquilines will enjoy 1) greater performance and 2) exhibit greater incidence of cooperative prey capture when aggressive hosts are paired with docile inquilines and docile hosts are paired with aggressive inquilines. In the studies herein, we aim to 1) determine if the overall performances of both hosts and/or inquilines are dependent on the BTs of one or both interacting species and 2) assess how the BTs of hosts and inquilines influence incidence of individual versus cooperative prey capture events. These objectives are designed to elucidate whether host–inquiline interactions depend on the behavioral tendencies of one, both, or neither interactor and explore how the role of solitary and cooperative prey capture in determining the nature of host–inquiline interactions.

METHODS

Study system, collection, and laboratory maintenance

Spiders were collected as mid-instar juveniles along a riparian habitat in East Tennessee (Melton Hill) in April 2010. Colonies of *A. studiosus* were collected by placing webs within a cloth pillowcase and trimming the supporting branches using pruning shears. We allotted a minimum of 5-m distance between each colony that we collected. Inquilines were collected haphazardly within adjacent habitats. *Theridion murarium* (Araneae: Theridiidae; $n = 103$) and *L. cornutus* (Araneae: Araneidae; $n = 62$) are two of the most common web associates found in *A. studiosus* colonies; both species occupy 20–60% of wild colonies (Perkins et al. 2007; Pruitt and Riechert 2011b). *Theridion murarium* is comparable in size to *A. studiosus* (≈ 5 mm) and lives its life within the colony: it lays its eggs therein and is commonly mistaken by researchers for *A. studiosus* itself. In contrast, *L. cornutus* has a less intimate association with *A. studiosus*. It resides within the colony during daytime hours but builds its own structurally unique foraging orb-web each evening. Spiders were then transported to laboratory at the University of

Tennessee, Knoxville. On arrival, spiders were sorted by hand, and all spiders were isolated into 590mL deli cups, each containing a small ball of tangled poultry wiring to facilitate web construction. Spiders were reared to maturity within these containers by providing an ad libitum meal twice weekly (crickets for *L. cornutus* and termites for *A. studiosus* and *T. murarium*), so as to control for any influence of life stage or hunger state during the experiment. Containers were misted weekly with a spray bottle containing tap water, in order to provide spiders with a water source.

On reaching maturity, 1 female *A. studiosus* per source colony was haphazardly selected for inclusion in our experiments. Each *A. studiosus* had its BT assessed using the interindividual distance test described below and was mated randomly to a male from a different source colony. As spiders store sperm from previous mating bouts, this allows us to use fecundity as a metric of individual fitness after experimentation (Foelix 1996). Three days later, the web of each female was then treated with one of 3 experimental treatments (described below). To minimize any paternal effects in offspring quality, we completely randomized the identity of the sire and its source colony with dam identity and experimental treatment.

On reaching maturity, *T. murarium* and *L. cornutus* were run through 3 “latency of attack” assays (described below), in order to determine their aggressiveness. A randomly selected individual of either species was then placed within a host colony and transplanted into the field.

Determination of female *A. studiosus* behavioral tendencies

We used an interindividual distance measure to rapidly assess females’ behavioral tendencies. We know from previous studies that interindividual distance measures are highly repeatable ($r = 0.5–0.72$), heritable ($h^2 = 0.32$), and tightly correlated with numerous aspects of females’ aggressive behavior (e.g., latency to attack prey, response toward predators; Pruitt et al. 2008, 2010; Pruitt and Riechert 2009b). Females with larger interindividual distance scores are more aggressive in virtually all respects.

Two females of unknown behavioral tendencies were individually marked using a fast-drying paint marker atop their cephalothorax prior to being assayed. We then placed 2 females within a clear, rectangular container (12 cm × 12.5 cm × 2.5 cm) and allowed them 24 h to settle and construct webs. Females that settled close to each other (<7 cm) were scored as *docile*. In contrast, females that settled far apart (>7 cm) were scored preliminarily as *aggressive* (Figure 1). A bimodal distribution in the frequency of aggressive versus docile BTs suggests these determinations represent 2 distinct BTs (Pruitt and Riechert 2009a). A length of 7 cm corresponds to natural lull or break in the distribution of interindividual distance measures in all social *Anelosimus* (Pruitt and Riechert 2009a; Pruitt et al. 2011). All females that were scored as “aggressive” in their first trial were then repaired with a known docile individual in a second confirmatory test. A confirmatory test was required because large interindividual distance scores can result from trials in which 1 female is aggressive and 1 is docile,

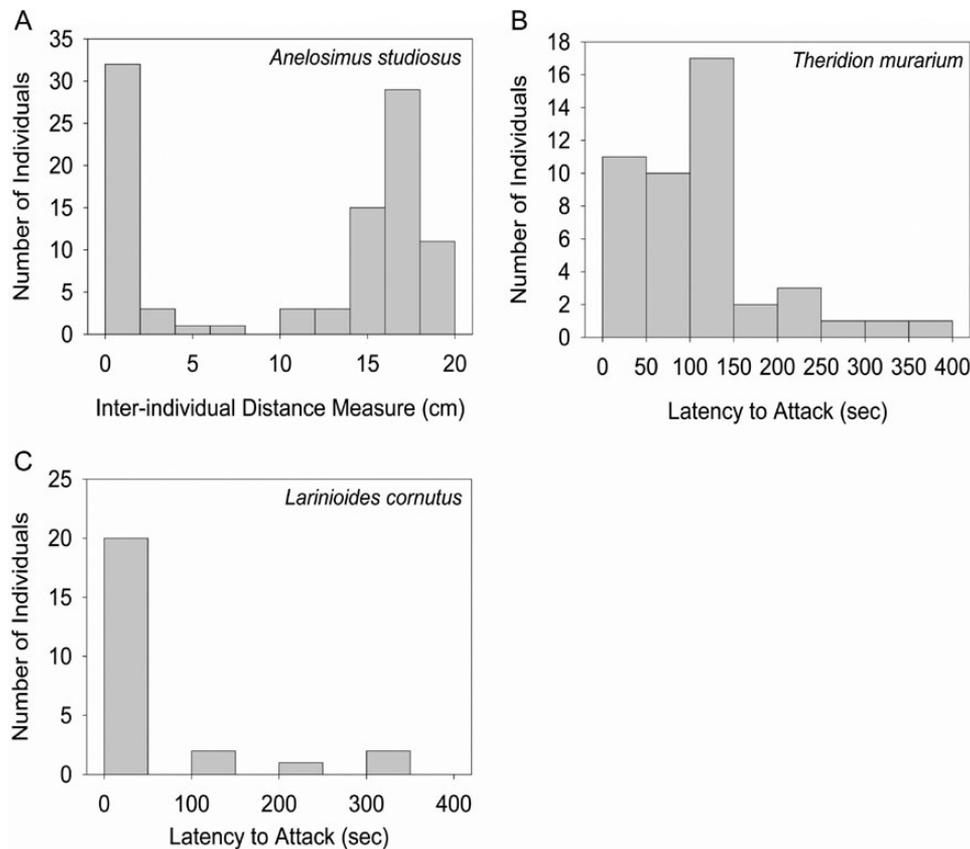


Figure 1 Frequency histogram of (a) female *Anelosimus studiosus* BTs ($n = 98$) as determined from interindividual distance measures and distribution of (b) *Theridion murarium* ($n = 46$) and (c) *Larinioides cornutus* ($n = 25$) BTs as determined from staged prey events.

because aggressive females demand space. We used the distance measures from females' second confirmatory test when assigning females to a given behavioral tendency (docile or aggressive).

Determination of inquiline behavioral tendencies

We assessed the aggressiveness of *T. murarium* and *L. cornutus* using staged predator–prey interactions and measuring individuals' latency to attack prey. “Latency of attack” trials were performed 24 h after a maintenance meal, in order to control for individuals' hunger state. A partially immobilized prey item was placed centrally into the capture surface of the spiders' webs, and we subsequently measured the time elapsed between the prey item's initial struggling movements and the moment when the spider made contact with the prey item. *Larinioides cornutus* were presented with 2-week-old crickets, and *T. murarium* were presented with termite workers. In contrast to the binary nature of *A. studiosus* BTs (i.e., discrete aggressive vs. docile groups), the aggression level of these spider inquilines exists along a gradient, which we score as a continuous variable. Therefore, there is no distinct gap between “aggressive” and “nonaggressive” inquilines, only a value that corresponds to their relative aggression level. We assayed each individual 3 times, in order to test whether individuals' latency to attack was repeatable. Repeatability is an important factor in the predictive power of behavioral traits and is instrumental to the BT literature (Bell et al. 2009). “Latency of attack” assays were separated by 3 days each.

Species associations and colony placement

Prior to staging associations between *A. studiosus* and its web associates, we weighed and individually marked all spiders, using a laboratory balance (Mettler-Toledo, LLC; Columbus, OH) and the marking protocol described above. We placed one of 3 different entities into the webs of each *A. studiosus*: a black glass bead (to control for a foreign object in the colony; $n = 50$), a *T. murarium* ($n = 50$), or a *L. cornutus* ($n = 50$). Associations between *A. studiosus* and its web associates were paired randomly using a random number generator and were given 3 days in laboratory to acclimate and build webbing before colonies were placed out in the field.

Colony placement localities were selected based on the presence of preexisting colonies of comparable size as indicators of habitat quality. At each locality, the resident colony was removed using pruning shears and replaced with a randomly selected experimental colony. Experimental colonies were adhered to the foliage using topiary guide wires. Colonies were then checked daily for the next 4 days to confirm that neither *A. studiosus* nor its web associates dispersed. In instances where spiders dispersed ($n = 3$), we were able to track the dispersal route of spiders using the dragline silk that extended from their source colony to their postdispersal locality. Postdispersal spiders were replaced within their source colonies, after which time, we did not observe any further dispersal behavior.

We checked colonies every other day for the next 40 days to observe whether female *A. studiosus* had produced an egg case. After producing an egg case, female *A. studiosus* guard their egg cases by clasping them within their chelicerae. We encouraged females to abandon their egg case by gently prodding their prosoma with a pencil eraser. We then massed females' egg cases using a portable balance (within 0.0001 g) and returned it to the female within 1 h. Egg case mass was our proxy for female fecundity because it is highly correlated with the number of eggs therein ($r = 0.62$) (Pruitt and Ferrari 2011). To estimate the performance of *L. cornutus* and

T. murarium, we recollected colonies at the end of 40 days and massed the heterospecifics. We used the change in mass of both web associates as our estimate of their performance. Mass gain and individual mass are highly correlated with fecundity in many species of spider (Foelix 1996). Mortality in the field reduced our sample sizes for each treatment (isolated *A. studiosus*, $n = 27$; *A. studiosus* with *T. murarium*, $n = 45$; *A. studiosus* with *L. cornutus*, $n = 25$).

Participation in prey capture

To assess how the BTs of *A. studiosus* and its web associates influence participation in prey capture, we staged prey capture events in the field. We used a standardized vibratory stimulus to elicit prey capture behavior for all of our host–inquiline associations (described above). We simulated a prey capture stimulus by placing a 2 cm fragment of dried oak leaf within the capture thread of the colony and then vibrated the leaf using a handheld vibratory device to produce a consistent, repeatable stimulus (GoVibe-Purple). We allotted 30 s of acclimation time between leaf placement and the initiation of the vibratory stimulus. A 6-cm aluminum thread extended from the tip of the vibratory device and was used to make contact with the leaf. We vibrated the leaf for 8 min or until both spiders attacked. For each instance, we noted whether *A. studiosus*, its web associated, or both species attacked. All instances where both species attacked were cooperative in nature (i.e., both spiders seized the leaf with their chelicerae at the same time). We repeated this test every 4 days, for 40 days (10 trials/colony).

Statistical methods

In order to verify the repeatability of inquiline behavioral tendencies, we used a nested ANOVA to partition measured variance into within-individual versus among-individual variability. A significant model suggests that there is more behavioral variability between individuals than within an individual. The resulting intraclass correlation coefficient scores were used as estimates of repeatability (Boake 1989; Falconer and Mackay 1996).

To analyze *A. studiosus* fecundity, we first used a 2-way ANCOVA with the independent variables: *A. studiosus* BT, treatment (i.e., whether the spider was isolated or living with a *T. murarium* or *L. cornutus*), and BT \times treatment. *Anelosimus studiosus* mass was included as a covariate. The mass of the host spider must be accounted for as it may be related to body condition and size and could influence their interspecific interactions (Foelix 1996). Subsequently, we used an ANCOVA with the same terms as before, but included inquiline BT as an independent variable. Using these 2 analyses allows us to ascertain the explanatory value of including the BT of both the host and inquiline spider in determining the nature of their interaction.

To analyze inquiline mass gain in *T. murarium* and *L. cornutus*, we used a 2-way ANCOVA with *A. studiosus* BT, inquiline BT, and *A. studiosus* BT \times inquiline BT as independent variables. *Anelosimus studiosus* mass, *A. studiosus* prosoma width, and inquiline prosoma width were included as covariates. Because *A. studiosus* “isolated” replicates were devoid of inquilines, separate models were run for each inquiline species.

To analyze the data documenting the frequency of solitary versus cooperative prey capture in response to an artificial prey stimulus, we used a nominal logistic regression with the independent variables *A. studiosus* BT, inquiline BT, and *A. studiosus* BT \times inquiline BT. Treatments were treated as a “by” effect and were analyzed

separately. Post hoc tests comparing the incidence of cooperative prey capture between BTs of *A. studiosus* and its inquilines were performed with 2-tailed Fisher’s Exact tests.

RESULTS

BT assays

The repeatability of our latency to attack measures was quite high for both inquilines: *L. cornutus* ($F_{24,50} = 7.21$, $P < 0.0001$, repeatability = 0.77) and *T. murarium* ($F_{45,92} = 2.77$, $P < 0.0001$, repeatability = 0.58). Thus, both species exhibit stable intraspecific variation in the rapidity with which they attack prey (Figure 1).

Anelosimus studiosus fecundity

When we excluded inquiline BT, our combined model predicting *A. studiosus*’ egg case mass was highly significant ($F_{6,90} = 10.21$, $P < 0.0001$, $R^2 = 0.41$). For this model, we detected a highly significant interaction effect of *A. studiosus* BT \times treatment ($F_{2,90} = 27.57$, $P < 0.0001$; Table 1 and Figure 2): aggressive females produced 68% heavier egg cases than docile females in the absence of inquilines, whereas docile females produced 44–59% heavier egg cases than aggressive females in the presence of inquilines. No other independent variables were significant in our model (Table 1).

Similarly, when we simultaneously consider the BTs of both *A. studiosus* and its inquilines, we found that only *A. studiosus*’ BT influenced its fecundity when living with *L. cornutus* ($F_{1,18} = 5.48$, $P = 0.03$, $R^2 = 0.30$; Figure 3 and Table 2). In these circumstances, docile *A. studiosus* produced 40% heavier egg cases than their aggressive counterparts, regardless of the BTs of *L. cornutus*. In contrast, when living with *T. murarium*, with whom *A. studiosus* shares a more intimate association, *A. studiosus* fecundity was determined by the interaction of BTs of both *A. studiosus* and *T. murarium* ($F_{1,39} = 19.77$, $P < 0.0001$, $R^2 = 0.61$; Figure 3 and Table 2). Specifically, aggressive *A. studiosus* produced heavier egg cases when they were paired with nonaggressive *T. murarium*, whereas docile *A. studiosus* produced heavier egg cases when they were paired with aggressive *T. murarium*. Thus, complementary and opposing aggressive/docile BT combinations yielded heavier egg cases for *A. studiosus*. For reference, in dyads composed of high-performing BT combinations (i.e., those containing opposing BTs), *A. studiosus* produced 166–230% heavier egg cases than individuals within dyads composed of low-performing BT combinations (Figure 3). An a posteriori power analyses showed that, for the *A. studiosus*–*T. murarium* pairs, given our standard error of the residual error ($\sigma = 0.000464$) and the raw effect size ($\delta = 0.000334$), the power to detect a significant effect at our sample size ($n = 45$) is 0.997. For the *A. studiosus*–*L. cornutus*

pairs ($\sigma = 0.000858$; $\delta = 5.985e^{-6}$), the power to detect a significant effect at our sample size ($n = 25$) is 0.05. However, a further calculation of the number of observations necessary to detect a significant effect (i.e., the “least significant number”) at a power of 0.80 is $n = 78\ 940$. The unachievably high value of this number of necessary observations lends evidence to the notion that the lack of a significant interaction in this model term is biologically meaningful and not an artifact of the sample size.

Inquiline mass gain

Our combined model predicting change in mass of *L. cornutus* was nonsignificant ($F_{6,24} = 0.64$, $P = 0.69$, $R^2 = 0.18$; Table 2 and Figure 3). In contrast, our combined model predicting the change in mass of *T. murarium* was highly significant ($F_{6,45} = 3.17$, $P = 0.012$, $R^2 = 0.22$; Table 2 and Figure 3). We detected a significant BT \times BT interaction on mass gained by *T. murarium* ($F_{1,39} = 5.36$, $P = 0.03$), where aggressive *T. murarium* gained more mass when they were associated with docile *A. studiosus*, but less aggressive *T. murarium* gained more mass when they were associated with aggressive *A. studiosus*. Thus, opposing aggressive/docile BT combinations yielded greater mass gain for *T. murarium*. For reference, *T. murarium* in dyads with opposing BT combinations gained 166–300% more mass than those within dyads composed of low-performing BT combinations (Figure 3).

Division of prey capture

The results of our nominal logistic regression predicting the incidence of singleton versus cooperative prey capture in heterospecific dyads showed that aggressive *A. studiosus* attack prey on their own 40% of the time on average, whereas docile *A. studiosus* attacked prey solitarily only 14% of the time on average ($\chi^2_{4,20} = 26.27$, $P < 0.0001$; Figure 4). Additionally, *L. cornutus* engaged in solitary prey capture 28% of the time, whereas *T. murarium* engaged in solitary prey capture only 18% of the time ($\chi^2_{8,20} = 138.54$, $P < 0.0001$; Figure 4). All other predictor variables were nonsignificant (Table 3). Cooperative prey capture was relatively rare, which prohibited our ability to predict its occurrence in our combined model: aggressive *A. studiosus* engaged in cooperative prey capture with *L. cornutus* in 2 out of 120 events and with *T. murarium* in 5 out of 170 events; docile *A. studiosus* engaged in cooperative prey capture with *L. cornutus* in 0 out of 130 events and with *T. murarium* in 11 out of 90 events. However, post hoc tests comparing the incidence of cooperative prey capture between docile and aggressive *A. studiosus* revealed no difference in the incidence of cooperative prey capture with *L. cornutus* (2-tailed Fisher’s Exact test, $P = 0.23$). In contrast, docile *A. studiosus* engaged in cooperative prey capture with *T. murarium* in 12% of trials, whereas aggressive *A. studiosus* performed cooperative prey capture in 2% of trials (2-tailed Fisher’s Exact test, $P = 0.005$).

DISCUSSION

Understanding how individuals’ behavioral traits shape their niche remains a core goal of the animal personalities literature (Sih et al. 2012). In the study presented here, we explored how intraspecific behavioral variation influenced the outcome of species interactions in a host–inquiline system. First, we explored how variation in host BTs influenced their fecundity when living with heterospecifics. Second, we explored whether/how simultaneous consideration of both host and inquiline BTs changed the results and interpretations

Table 1

Summary of the effect tests of parameters predicting the egg case mass of *Anelosimus studiosus* when living isolated or with one of 2 inquilines: *Larinoidea cornutus* and *Theridion murarium*

Independent variable	df	F-ratio	P-value	Model R^2
Treatment and <i>Anelosimus</i> fecundity				0.41
<i>Anelosimus</i> BT	1,90	2.55	0.11	
Treatment	2,90	2.54	0.08	
Treatment \times BT	2,90	27.57	<0.0001	
<i>Anelosimus</i> mass	1,90	0.06	0.80	

Bold values are statistically significant.

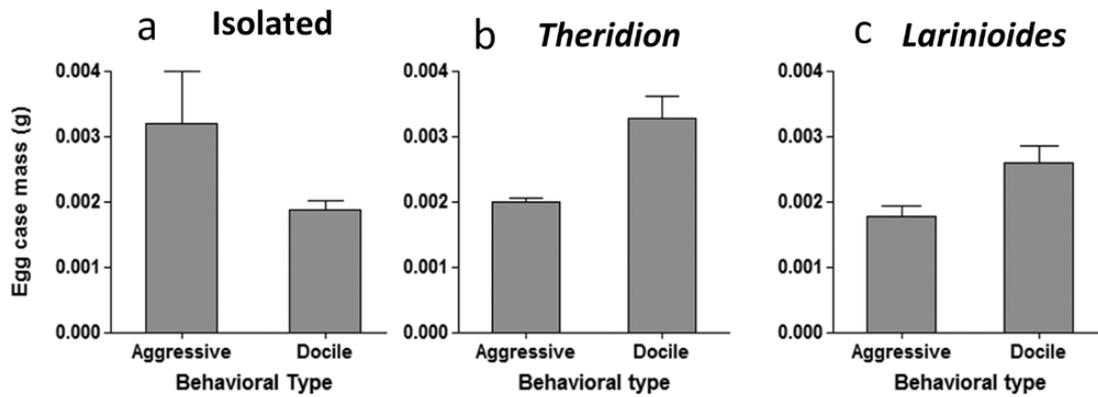


Figure 2

(a) Aggressive *Anelosimus studiosus* females had greater fecundity than docile females in the absence of inquilines, (b) and (c) though docile females had greater fecundity in the presence of inquilines ($F_{2,90} = 27.57$, $P < 0.0001$).

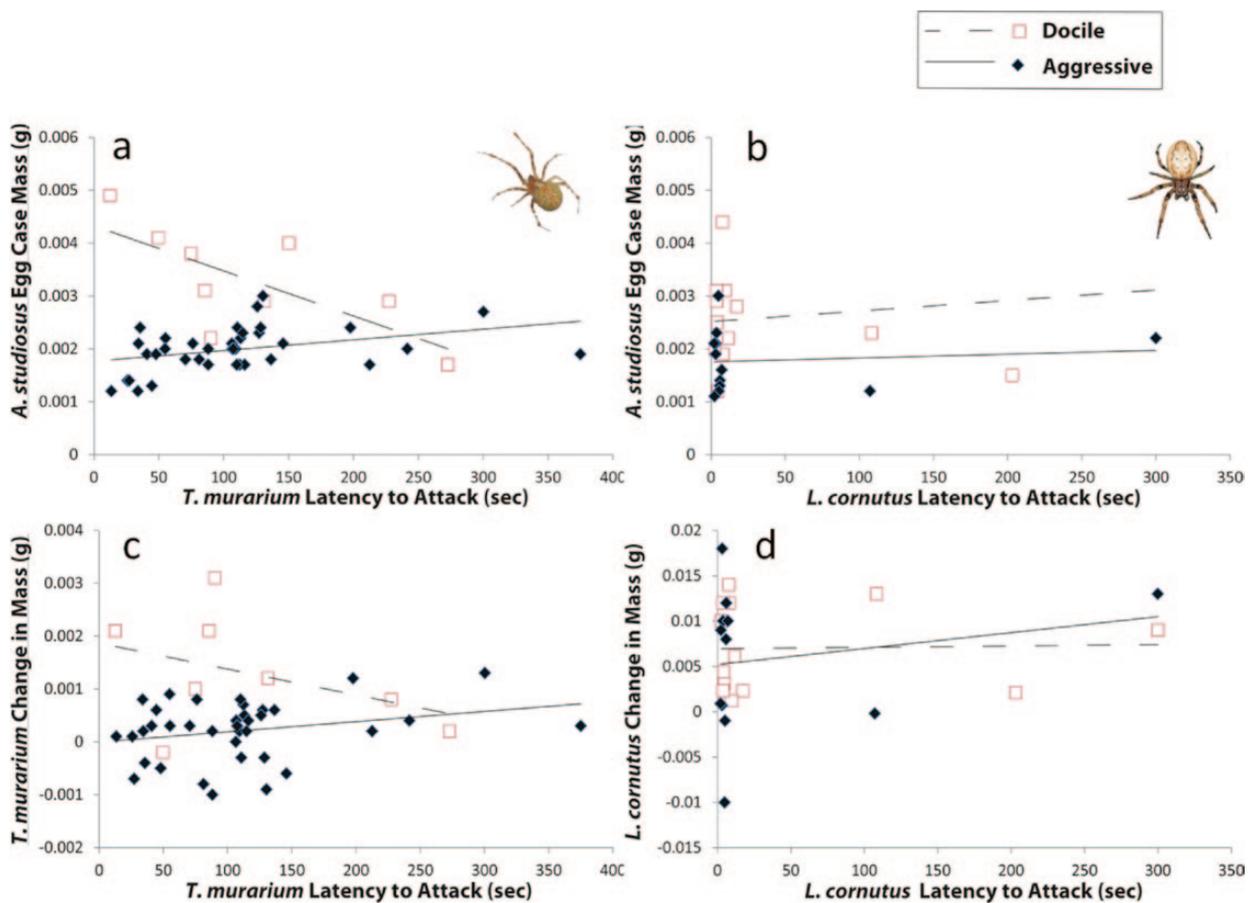


Figure 3

(a) When living with *Theridion murarium*, *Anelosimus studiosus* fecundity was determined by the interaction of both *A. studiosus* and *T. murarium* BTs ($F_{1,39} = 19.77$, $P < 0.0001$, $R^2 = 0.61$). (b) In contrast, the BT of *A. studiosus* was the sole predictor of its fecundity when living with *L. cornutus* ($F_{1,18} = 5.48$, $P = 0.03$, $R^2 = 0.30$). (c) The change in mass of *T. murarium* was highly dependent on both its own aggression and the BT of *A. studiosus*: aggressive *T. murarium* performed better were associated with docile hosts and docile *T. murarium* gained more mass when they were associated with aggressive *A. studiosus* ($F_{1,39} = 5.36$, $P = 0.03$, $R^2 = 0.66$). (d) Alternatively, the change in mass of *L. cornutus* living with *A. studiosus* was not dependent on its own aggression nor the BT of its host ($F_{6,24} = 0.64$, $P = 0.69$, $R^2 = 0.18$).

of our data. And third, we investigated how BTs of both host and inquilines unite to shape the incidence of individual versus cooperative prey capture, which is a known determinant of success in social spiders (Ward and Enders 1985; Yip et al. 2008; Pruitt, Oufiero, et al. 2012). Our results generally confirm previous findings that

solitary aggressive *A. studiosus* exhibit greater fecundity than solitary docile individuals (Jones et al. 2010) and that the presence of inquilines reverses this trend: docile individuals outperform aggressive individuals in the presence of inquilines. The effects of inquiline BT on host fecundity and inquiline mass gain differed between the 2

Table 2
Effects test from two 2-way ANCOVAs predicting *Anelosimus studiosus* fecundity and body mass gain in 2 inquiline species

Independent variable	df	F-ratio	P-value	Model R ²
Inquiline BT and <i>Anelosimus</i> fecundity				
<i>Larinooides cornutus</i>				
<i>Anelosimus</i> BT	1,18	5.48	0.03	0.30
Inquiline BT	1,18	0.63	0.44	
<i>Anelosimus</i> BT × inquiline	1,18	0.001	0.97	
BT				
<i>Anelosimus</i> prosoma width	1,18	0.39	0.54	0.66
Inquiline prosoma width	1,18	0.19	0.67	
<i>Anelosimus</i> mass	1,18	0.50	0.49	
<i>Theridion murarium</i>				
<i>Anelosimus</i> BT	1,39	57.83	<0.0001	0.66
Inquiline BT	1,39	8.30	0.006	
<i>Anelosimus</i> BT × inquiline	1,39	19.77	<0.0001	
BT				
<i>Anelosimus</i> prosoma width	1,39	1.61	0.21	0.18
Inquiline prosoma width	1, 39	0.05	0.82	
<i>Anelosimus</i> mass	1,39	0.09	0.77	
Inquiline BT and inquiline mass gain				
<i>Larinooides cornutus</i>				
<i>Anelosimus</i> BT	1,18	0.51	0.48	0.18
Inquiline BT	1,18	1.70	0.21	
<i>Anelosimus</i> BT × inquiline	1,18	0.33	0.57	
BT				
<i>Anelosimus</i> prosoma width	1,18	0.05	0.83	0.22
Inquiline prosoma width	1,18	0.0003	0.99	
<i>Anelosimus</i> mass	1,18	2.32	0.15	
<i>T. murarium</i>				
<i>Anelosimus</i> BT	1,39	0.0016	0.97	0.22
Inquiline BT	1,39	0.81	0.37	
<i>Anelosimus</i> BT × inquiline	1,39	5.36	0.03	
BT				
<i>Anelosimus</i> prosoma width	1,39	10.95	0.002	0.22
Inquiline prosoma width	1,39	1.59	0.21	
<i>Anelosimus</i> mass	1,39	3.48	0.06	

Separate models were run for each inquiline species. Bold values are statistically significant.

species of inquiline considered. We found that the BT of *L. cornutus* had no effect on the outcome of the host–inquiline interaction, whereas the BT of *T. murarium* had large impacts both on its own mass gain and the fecundity of *A. studiosus*. Specifically, we found that the performances of both *T. murarium* and *A. studiosus* were maximized when dyads were composed of opposing BTs: docile *A. studiosus* with aggressive *T. murarium* and aggressive *A. studiosus* with docile *T. murarium*. Therefore, the BTs of hosts and inquilines jointly shaped the outcome of their interaction, but only for *T. murarium*, which exhibits a more intimate association with its host.

The vast majority of studies on animal personality are correlative, single-species oriented, laboratory studies. Although these approaches have notable advantages, much of the interest in these studies is predicated on their ability to predict/inform how BTs shape individuals' ecology in the field. One of the strengths of the *A. studiosus* system is the ability to experimentally construct species associations with individuals of known behavioral tendencies and then track the performance of multiple interactors in situ. Our data demonstrate that the predictability of *A. studiosus* fecundity was improved when we considered BT variation in 2 species for associations between *A. studiosus* and *T. murarium* ($R^2 = 0.61$ vs. 0.32), but not for associations between *A. studiosus* and *L. cornutus* ($R^2 = 0.30$ vs. 0.32). Similarly, we detected strong effects of inquilines BTs on mass gain for *T. murarium* but not for *L. cornutus*. We propose that the reason that we detected effects of inquiline BT for *T. murarium* but not for *L. cornutus* is because of differences in the way either

species interacts with its host: *T. murarium* spends the majority of its life cycle within the host colony, whereas *L. cornutus* merely retreats within the host colony during the day or for feeding. Thus, we argue that *T. murarium* BTs have a detectable impact on the performance of hosts and inquilines because it exhibits a consistent, highly intimate association with its host. Although, admittedly, the negative result observed in *A. studiosus* and *L. cornutus* pairs may also stem from a lack of statistical power.

Interestingly, for *T. murarium*, the effects of inquiline BT on 1) its own mass gain and 2) its host's fecundity were contingent on the BTs of its host: *A. studiosus* enjoyed higher fecundity and *T. murarium* enjoyed greater mass gain when individuals of either species were paired with opposing BTs (Figure 2). This intriguing pattern closely resembles the BT × BT interactions that are observed among female *A. studiosus* in the absence of inquilines: both aggressive and docile females enjoy higher fecundity when they are associated with females of unlike phenotypes (Pruitt and Ferrari 2011; Pruitt and Riechert 2011a). Although the precise mechanisms for these BT × BT interactions remain unknown, we conjecture that the similar patterns observed both 1) among *A. studiosus* and 2) between *A. studiosus* and *T. murarium* could be driven by the same mechanism: division of labor. Consistent with this hypothesis, a number of recent studies on social spiders from different families (*Stegodyphus*—Eresidae, *Anelosimus*—Theridiidae) have documented division of labor within colonies and that variation in individuals' task performance is associated with their behavioral and/or morphology traits

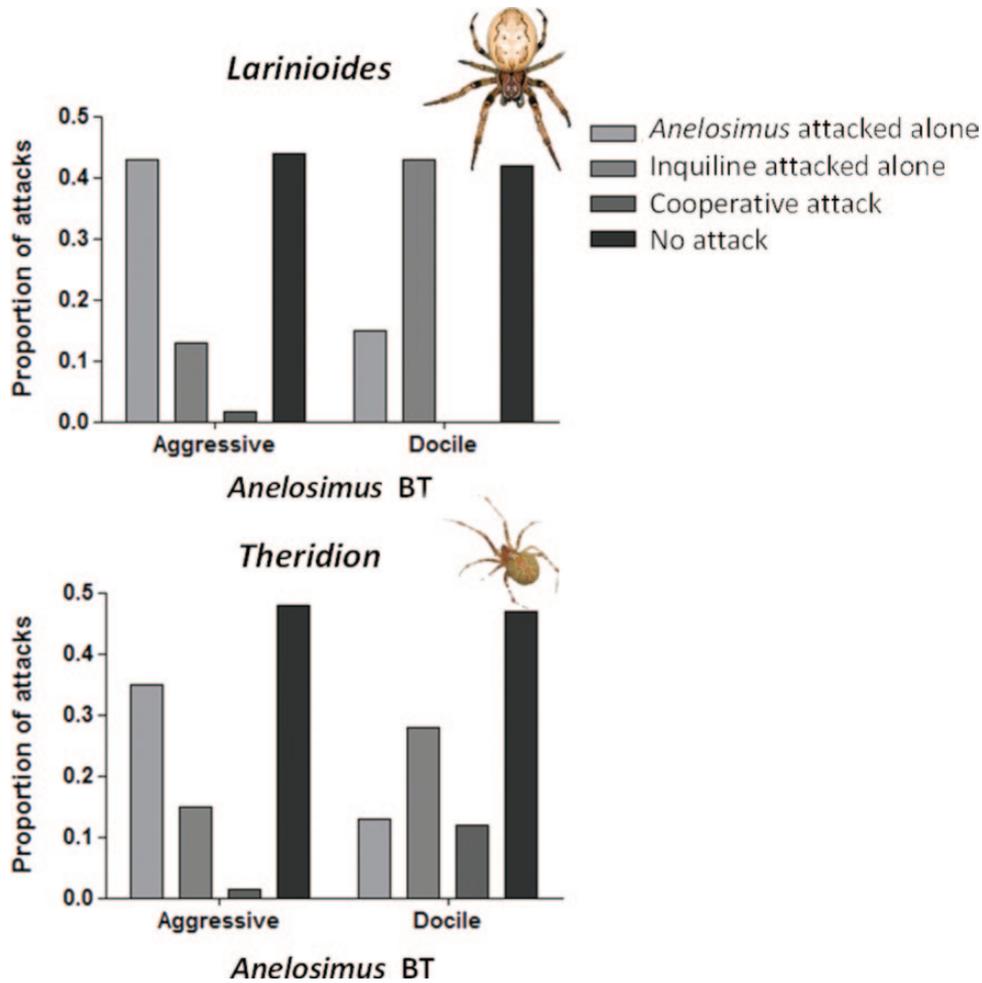


Figure 4

Aggressive *Anelosimus studiosus* are more likely to attack prey solitarily than are docile individuals ($\chi^2_{4,20} = 26.27$, $P < 0.0001$). Additionally, *Larinioides cornutus* is 31% more likely than *Theridion murarium* to attack prey solitarily ($\chi^2_{6,20} = 138.54$, $P < 0.0001$). Cooperative prey capture was rare, though our data suggest that docile hosts are more likely to engage in cooperative prey capture with 1 inquiline, *T. murarium*, than are aggressive hosts (2-tailed Fisher’s Exact test, $P = 0.005$).

Table 3

Effects test from a nominal logistic regression on the division of attacks by either *Anelosimus studiosus* or its inquiline

Independent variable	df	χ^2	<i>P</i> -value	Model <i>R</i> ²
Division of attacks				
<i>Larinioides cornutus</i>				
<i>Anelosimus</i> BT	3,9	41.20	<0.0001	0.11
Inquiline BT	3,9	3.84	0.28	
<i>Anelosimus</i> BT × inquiline BT	3,9	0.46	0.93	
<i>Theridion murarium</i>				
<i>Anelosimus</i> BT	4,12	35.87	<0.0001	0.05
Inquiline BT	4,12	2.04	0.73	
<i>Anelosimus</i> BT × inquiline	4,12	4.87	0.30	
BT				

Inquiline species was included as a “by” effect. Bold values are statistically significant.

(Pruitt and Riechert 2011b; Settepani et al. 2012). Whether similar mechanisms are at play in multispecies interactions is unknown. However, our data from staged prey capture events (discussed below) may help shed light on this subject.

In heterospecific dyads, the BTs of the host, *A. studiosus*, but not the inquilines shaped participation in prey capture. As suggested by their long latencies to attack prey during laboratory trials (Pruitt et al. 2008), docile *A. studiosus* did not readily attack during our staged prey capture events. Instead, inquilines were more likely to engage in prey capture than their docile hosts: both *L. cornutus* and *T. murarium* were more likely to attack prey individually than docile *A. studiosus* (Figure 3). Thus, the reduced foraging tendencies of docile *A. studiosus* may be compensated, in part, by their inquilines’ propensity to engage in prey capture. In contrast, aggressive *A. studiosus* readily attacked during our staged prey capture events, whereas their inquilines were less likely to attack either individually or cooperatively with their aggressive hosts (Figure 3). Taken together, whether the host, inquiline, or both interactors engaged in prey capture depended on the BT of the host spider, but not their inquilines. We argue that these data could hold explanatory power for why docile *A. studiosus* benefit by their association with inquilines, whereas aggressive *A. studiosus* are negatively impacted by their association (Pruitt and Ferrari 2011; Pruitt, Cote, et al. 2012). Specifically, our results suggest that docile *A. studiosus* could benefit from their inquilines by their involvement/assistance with prey capture. However, aggressive *A. studiosus* are potent foragers

on their own and their inquilines are less likely to engage in prey capture. Thus, under these circumstances, it is plausible that inquilines might parasitize their aggressive hosts by adopting scrounging strategies or might impinge on each other's ability to capture prey via aggressive interference (argued in Pruitt, Oufiero, et al. 2012).

We argue that the silken reefs of *A. studiosus* are a promising and possibly general model for exploring the effects of behavioral variation on community dynamics. By building large communal webs that provide benefits to heterospecific occupants, social spiders sequester a vast diversity of inquilines, thereby producing an “infracommunity” similar to the level of organization in within-host parasite communities (Holmes and Price 1986). An infracommunity is defined as a subset of the component ecological community whose structure is determined by host traits, parasite species (i.e., inquilines, in this case), and emergent interactions within and among constituents (Bush et al. 1997). Within silken reefs, social spiders and inquilines engage in nuanced interactions including kleptoparasitism, commensalisms, ammensalisms, and mutualisms that differ based on the BTs of the host (Pruitt and Ferrari 2011; Pruitt, Stachowicz, et al. 2012) and its inquilines (data herein). Thus, for at least some community members, individuals of similar behavioral tendencies (aggressive *A. studiosus* and aggressive *T. murarium*) may share more in common, functionally speaking, than individuals of the same species that exhibit opposing BTs (aggressive *A. studiosus* vs. docile *A. studiosus*). Therefore, for this community of predators, binning individuals into functional groups in terms of their behavioral tendencies, rather than their species identity, could be a more powerful predictor of their functional roles. Multispecies associations, like those between *A. studiosus* and its inquilines, have been noted in many other taxa such as mixed-species bird flocks or fish schools, where individuals can retain the advantages of sociality (e.g., augmented foraging, reduced predation risk, etc.) while reducing the associated costs of monospecific group living (e.g., competition for resources) (Morse 1970). Additionally, as seen between *A. studiosus* and inquilines, mixed-species groups of vertebrates regularly engage in division of labor and/or task sharing (e.g., vigilance, Ragusa-Netto 2002; alarm calling, Morse 1970). The extent to which BT × BT interactions innervate other mixed-species groups remains an intriguing frontier for both behavioral ecology and community ecology. However, our findings here suggest that consideration of BT variation in these systems will hold tremendous explanatory power for the way these systems behave ecologically.

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