

Behavioural trait variants in a habitat-forming species dictate the nature of its interactions with and among heterospecifics

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Summary

1. Although ecologists commonly categorize species in terms of their functional roles, function diversity occurring at the level of the individual is often dismissed.
2. Multi-female colonies of the spider *Anelosimus studiosus* serve as habitat for a myriad of arthropods, and colony members display notably polymorphic behavioural tendencies: females exhibit either an ‘aggressive’ or ‘docile’ behavioural phenotype.
3. We manipulated the phenotypic composition of colonies (100% aggressive, 50% aggressive and 50% docile, 100% docile) and tested its effects on species interactions between *A. studiosus* and its web associates, and among the web associates themselves.
4. We found that the phenotypic composition of *A. studiosus* colonies significantly impacted interactions within their web. In colonies of all aggressive females, the relationship between *A. studiosus* (–) and its web associates (+) was exploitative and web associates negative impacted each other’s performance. In colonies of all docile females, the relationship between *A. studiosus* (+) and its web associates (+) was facilitative and web associates positively influenced each other’s performance. Colonies of mixed phenotype had intermediate interactions.
5. Our data suggest that (i) the mixture of behavioural trait variants within groups can mediate the nature of both direct and indirect species interactions, and (ii) community structure can affect which social group compositions enjoy highest fitness.

Key-words: behavioural syndrome, caste frequency distribution, intraspecific variation, personality, temperament

Introduction

Species in a community necessarily interact with each other, and an organism’s interactions are fundamental to its fitness and function within an ecosystem. Interactions are typically categorized by their net fitness effects on pairs of species (e.g. competition, exploitation, mutualism), and to a lesser extent, on the mechanisms generating these effects (Holt 1977; Schoener 1983; Spiller & Schoener 2001). By and large, the central tendency in ecological theory is to implicitly assume the outcomes of species interactions are invariant. However, it has also been suggested that the outcome of species interactions might depend on the attributes of the specific individuals/genotypes involved

(Johnson & Agrawal 2005; Vellend & Geber 2005; Crutsinger *et al.* 2006; Hughes *et al.* 2008; Genung *et al.* 2010), and arguably, understanding the factors mediating species interactions is critical to elucidating how communities look and function (Schoener & Spiller 1996; Schoener, Spiller & Losos 2001; Stachowicz 2001; Bracken, Gonzalez-Dorantes & Stachowicz 2007).

Altered species interactions across biotic and abiotic gradients have been documented in a few studies (Stachowicz & Hay 1999; Rudgers & Strauss 2004; Holland & DeAngelis 2009; Lee, Kim & Choe 2009); in contrast, examples of intraspecific trait variants mediating species interactions are rarer (Yu & Pierce 1998; Lankau & Strauss 2007; Piovita-Scott 2011), perhaps owing to the fact many community studies overlook intraspecific trait variation (but see Lankau & Strauss 2007; Bolnick *et al.* 2011), either ignoring it entirely (reviewed in Bolnick *et al.* 2003; Sih *et al.* 2004; Reale *et al.*

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2007) or merely manipulating genetic diversity at neutral loci and disregarding functional differences among individuals (Hughes & Stachowicz 2004; Johnson & Agrawal 2005; Vellend & Geber 2005; Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006; Hughes *et al.* 2008; Genung *et al.* 2010; Bailey 2011). We argue, however, that in instances where single species have large effects on their community (e.g. habitat-forming species, ecosystem engineers, keystone predators), intraspecific trait variants have the potential to shape the interactions of whole suites of species, including those not directly involving the keystone species itself (Bolnick *et al.* 2003, 2011). In some cases, it might merely be the trait diversity of key community players that mediates species interactions and promotes species richness. For instance, in the habitat-forming species *Solidago altissima*, subtle trait differences among genotypes are associated with predictable changes in the associated arthropod community structure, and genotypic richness within plots is positively associated with arthropod diversity (Crutsinger *et al.* 2006). However, in other systems, specific trait variants can experience altered species interactions and thereby alter community structure (e.g. Stimson 1970; Shanks 2002; Pruitt & Ferrari in press). For example, in the owl limpet (*Lottia gigantea*), aggressive, territorial individuals maintain large territories free of other herbivores, and thereby create refugia for palatable microalgae and newly recruited macrophytes; in contrast, non-territorial roving *L. gigantea* graze down palatable algal species, which results in reduced species richness on multiple spatial scales (Stimson 1970; Shanks 2002).

To investigate how the attributes of key community players affect species interactions, we use the spider *Anelosimus studiosus*, for two reasons. Firstly, *A. studiosus* builds multi-female colonies that serve as habitat for a variety of arthropod species (> 100 species) (Perkins, Riechert & Jones 2007; Pruitt & Riechert 2011b) and thus has the potential to mediate the nature of interspecific interactions occurring within its webs. Secondly, *A. studiosus* exhibits a marked within-species behavioural polymorphism, whereby females exhibit either an aggressive active or docile inactive behavioural type (BT, hereafter 'aggressive' and 'docile'). Aggressive females are more active, aggressive towards prey, bold towards predators and exhibit greater incidence of sexual cannibalism than docile females (Pruitt & Riechert 2009b; Pruitt *et al.* 2010). Although aggressive females consume a disproportionately large amount of food (Pruitt & Riechert 2009a), their presence in multi-female colonies is beneficial because they facilitate the capture of high-quality prey (Pruitt & Riechert 2011a), and they attack and deflect a suite of exploitative araneofauna that commonly invade colonies (Pruitt & Riechert 2011b). Furthermore, because aggressive females demand space and chase away docile females, individuals' BTs can be easily identified by assaying their inter-individual distance (Pruitt *et al.* 2010). Taken together, *A. studiosus* is particularly well suited to test whether and how intraspecific behavioural variants shape species interactions across a community.

The goal of our study was to test the effect of BTs on the performance of *A. studiosus* and two common web associates,

Argyrodes elevatus and *Theridion differens* (Araneae, Theridiidae). We first measured the performance of all three species in isolation and then compared those to their performances when co-occurring. We also assessed whether interactants' performances differed among *A. studiosus* colonies of various BT compositions: 100% aggressive, 50% aggressive and 50% docile, 100% docile. Specifically, we asked: (i) does including 'colony BT composition' significantly improve the predictability of interspecific interactions in this community, as compared to more traditional approaches where intraspecific variation is ignored? (ii) If yes, does colony BT composition affect the *nature* and/or *magnitude* of interspecific interactions within the web of *A. studiosus*, both between *A. studiosus* and its web associates, and among the web associates themselves? If, in fact, the nature of interspecific interactions changes as a function of colonies' BT composition, this could have important implications for the trait mixes that result in the highest fitness at different sites, and conversely, divergent colony compositions at different sites could change the representation of other species within the broader araneofauna community.

Materials and methods

STUDY SPECIES

The web associates *A. elevatus* and *T. differens* are two of the smallest (4–7 mm) web associates commonly found in *A. studiosus* colonies (Perkins, Riechert & Jones 2007) and are similar in size to *A. studiosus* (4–5 mm). Given their size, it is unlikely that either species preys on mature *A. studiosus* directly, but at least one species (*A. elevatus*) is a known kleptoparasite of other spiders (Whitehouse *et al.* 2002; Agnarsson 2003). All three species are common tangle-web spiders in the Eastern United States; *A. elevatus* and *T. differens* occur in > 25% of *A. studiosus* colonies at warm sites (Perkins, Riechert & Jones 2007). It should be noted that *A. elevatus* and *T. differens* are not commonly observed in association outside of *A. studiosus* colonies, and thus, *A. studiosus* appears to be the nuclear species of their association.

BEHAVIOURAL TYPE BIOASSAY

It is the BTs of females that structure spider societies (Aviles 1997; Lubin & Bilde 2007), and thus, in the present study, we limit our focus to females. We used a well-established assay to determine female BT (Riechert & Jones 2008). Two females of unknown behavioural tendency were individually marked with fluorescent powder and placed in the centre of a clear plastic container (13.5 × 13.5 × 2.5 cm). After 24 h of settling time, we measured the distance between them. All females that exhibited an inter-individual distance greater than zero (i.e. they were not in direct contact) were run through a second confirmatory test with a known docile female (i.e. one that previously exhibited an inter-individual distance score of zero). This second test is necessary to differentiate the two types of females, because aggressive females demand space and chase away docile females. Females that exhibited an inter-individual distance < 7 cm in the second confirmatory test were categorized as 'docile', and females that exhibited an inter-individual distance > 7 cm were categorized as 'aggressive'. Seven centimetres corresponds with a natural break in the

distribution of inter-individual distance measures between the two phenotypes (Pruitt & Riechert 2009a; Pruitt, Riechert & Harris 2011). Inter-individual distance scores are both repeatable and heritable and are highly correlated with other aspects of individual aggressiveness (Pruitt, Riechert & Jones 2008; Pruitt & Riechert 2009c).

ARTIFICIALLY RECONSTITUTED COLONIES

Our experimentally reconstituted colonies were composed of six size-matched ($\pm 3\%$ body mass), randomly mated, and individually marked females of known BT. The average colony size at our field site is 5.22 females (SD = 1.45) (Pruitt & Riechert 2009a). Experimental colonies were constructed with three BT compositions: 100% aggressive, 50% aggressive and 50% docile, and 100% docile. For comparison, naturally occurring colonies exhibit tremendous variation in their phenotypic composition, with the average colony containing 41.67% aggressive females, but range from 0% to 86% aggressive females (Pruitt & Riechert 2009a). Females were assigned to experimental colonies within 1 week of their maturation and painted with a unique pair of coloured dots atop their cephalothorax using fast-drying modelling paint. Colonies were first housed in 473 mL, clear plastic cups, each containing a tangled ball of poultry wiring to facilitate web construction. After 4 days of web construction, spiders were provided a meal of two immobilized 2-week old crickets. Forty-eight hours after this meal, heterospecifics were added to the colonies in one of the six treatments: one *A. elevatus*, two *A. elevatus*, one *T. differens*, two *T. differens*, one *A. elevatus* and one *T. differens*, or a control glass bead (hereafter termed 'isolated' colonies). Prior to entry, each heterospecific was weighed and marked with a unique sequence of coloured dots. Heterospecific was size-matched for our study ($\pm 15\%$ each others' body mass). Heterospecifics were given 2 days of acclimation before colonies were transplanted out to our field site.

Our experimental colonies were placed along a disturbed riparian habitat in east Tennessee (36.30904°N, 84.21106°W). Colony localities were opportunistically selected using the presence of pre-existing *A. studiosus* colonies as an indicator of habitat quality. At each location, we removed a pre-existing colony of similar size (i.e. volume) and replaced it with an experimental colony. Experimental colonies were wired to the foliage using topiary wires. Colonies were positioned by braiding the wires through the poultry wiring and then around adjacent supporting branches. Experimental colonies were checked every 24 h for the next 30 days. A minimum of nine colonies of each BT composition and treatment (i.e. isolated, *A. elevatus*, *T. differens*, etc) were established at our field site, for a total of 228 experimental colonies. Roughly 14% of colonies experienced emigration during the course of our study, and in these circumstances, colony members left in a mass-dispersal event within 1 week of being transplanted. We removed these colonies from our analyses and they are not included in the total count of colonies established (i.e. we attempted to transplant 265 colonies). We detected no significant relationship between mass-dispersal events and BT composition ($\chi^2_2 = 2.65$, $P = 0.27$).

Colonies were checked every other day for egg case production. In *A. studiosus*, females slowly increase in body mass postmaturity and dramatically shrink in size after parturition. Parturition events are easily recognizable in *A. studiosus* by females' abruptly decreasing in size, and subsequently, they can be observed guarding their egg cases. Postparturition females were encouraged to abandon their egg cases by prodding them gently. Egg cases were weighed with a portable balance (NA60-4; Napco Precision Instruments, Shenzhen, Guangdong, China) and returned to their mothers. We used egg case mass as our estimate of colony members' fitness because egg case mass is corre-

lated with number of offspring produced by spiders (Foelix 1996) and fledged in *A. studiosus* (Jones, Pruitt & Riechert 2010). Mortality in this study was exceedingly low (10 individuals) during our experiment.

After 30 days, colonies were recollected, and heterospecifics were weighed. We used change in body mass over the 30-day period as our estimate of heterospecifics' performance. We measured the performance of one randomly selected focal individual, per heterospecific species, per colony in our study. As with *A. studiosus*, heterospecific mortality was exceedingly rare (two *T. differens*, one *A. elevatus*).

HETEROSPECIFIC PERFORMANCE IN ISOLATION

Heterospecific performance trials were run concurrently with our assessments of colony performance. To assess the performance of heterospecifics in isolation, we released individual *A. elevatus* and *T. differens* at locations adjacent to our experimental colonies. Before release, individuals were weighed, individually marked and placed in a 473 mL clear plastic container. Each enclosure contained a ball of poultry wiring to facilitate web construction. Spiders were then given 48 h to acclimate before being transplanted into the field. Release localities were selected using the presence of pre-existing *A. studiosus* colonies as indicators of habitat quality. We first removed the pre-existing colony and then replaced it with a singleton *A. elevatus* ($N = 9$) or *T. differens* ($N = 8$) using the wiring protocol described previously. Notably, we could not make experimental associations between *A. elevatus* and *T. differens* outside of *A. studiosus* colonies because one of the species always dispersed; however, in nature, these species are never observed in association outside of *A. studiosus* colonies. Spiders were checked daily for the next 30 days by visually scanning foliage for evidence of webs. Spiders were recollected after 30 days and transported to laboratory at the University of Tennessee where they were reweighed. The placement of experimental *A. studiosus* colonies vs. isolated heterospecifics was randomized among localities.

STATISTICAL METHODS

Performance of Anelosimus studiosus colonies

We used a 3×6 design to test the effects of BT composition (100% aggressive, 50% docile and 50% aggressive, 100% docile) and treatment (isolated, one *A. elevatus*, one *T. differens*, two *A. elevatus*, two *T. differens*, one *A. elevatus*, one *T. differens*) on colony members' egg case masses. For *A. studiosus*, we averaged the egg case masses of all females within a colony and use a single averaged value per test colony. We included colony member starting mass as a covariate in our analysis. Following the significant interaction term BT composition \times treatment, we compared egg case masses in each treatment and BT composition combination using ANOVA with *post hoc* Tukey tests. Test statistics for all Tukey pairwise comparisons can be found in our electronic supplementary materials (Appendix S1).

Performance of web associates

We used a 3×3 design to test the effects of colony BT composition (i.e. 100% aggressive, 50% docile and 50% aggressive, 100% docile, isolated) and competitive environment (singleton individual within a colony, conspecific competitor, heterospecific competitor) on change in mass for both heterospecifics. Following the significant interaction term BT composition \times competitive environment, we used ANOVA with *post hoc* Tukey tests to assess differences in change in mass among treatments and colony compositions vs. isolated individuals

(i.e. those not within *A. studiosus* colonies). Test statistics for all Tukey pairwise comparisons can be found in our electronic supplementary materials (Appendix S1).

Models with vs. without behavioural types

We looked at the AICc scores and adjusted R^2 of previously mentioned models with (as earlier) and without including colonies' BT compositions. These comparisons permitted us to quantitatively assess the benefits of considering intraspecific behavioural variants in our models: for heterospecifics, we tested their performance under various competitive environments, irrespective of colonies' BT composition; for *A. studiosus*, we tested the effects of associating with varying densities and compositions of heterospecifics, but again, irrespective of BT composition.

Results

ANELOSIMUS STUDIOSIUS EGG CASE MASS

Our combined model predicting colony member egg case mass was highly significant ($F_{35,192} = 8.11$, $\text{adj } R^2 = 0.52$,

$P < 0.0001$). We detected significant effects of treatment ($F_{5,228} = 4.17$, $P = 0.001$) and BT composition ($F_{2,228} = 6.19$, $P = 0.001$); however, as evidenced by the significant interaction term treatment \times BT composition ($F_{10,228} = 22.02$, $P < 0.0001$), the effects of treatments differed among colonies with different BT compositions. Colonies containing aggressive females experienced their highest fitness in the absence of heterospecifics (Fig. 1) and generally suffered depressed fitness as the number of web associates increased. In contrast, colonies of all docile females experienced their lowest fitness when devoid of heterospecific web associates and enjoyed increased fitness with a greater number or diversity of web associates.

HETEROSPECIFIC MASS GAIN

Our models predicting mass gain by *A. elevatus* ($F_{17,91} = 4.11$, $\text{adj } R^2 = 0.34$, $P < 0.0001$) and *T. differens* ($F_{17,90} = 4.67$, $\text{adj } R^2 = 0.37$, $P < 0.0001$) were highly significant. Although we detected several significant main effects for both species (Table 1), both models contained a

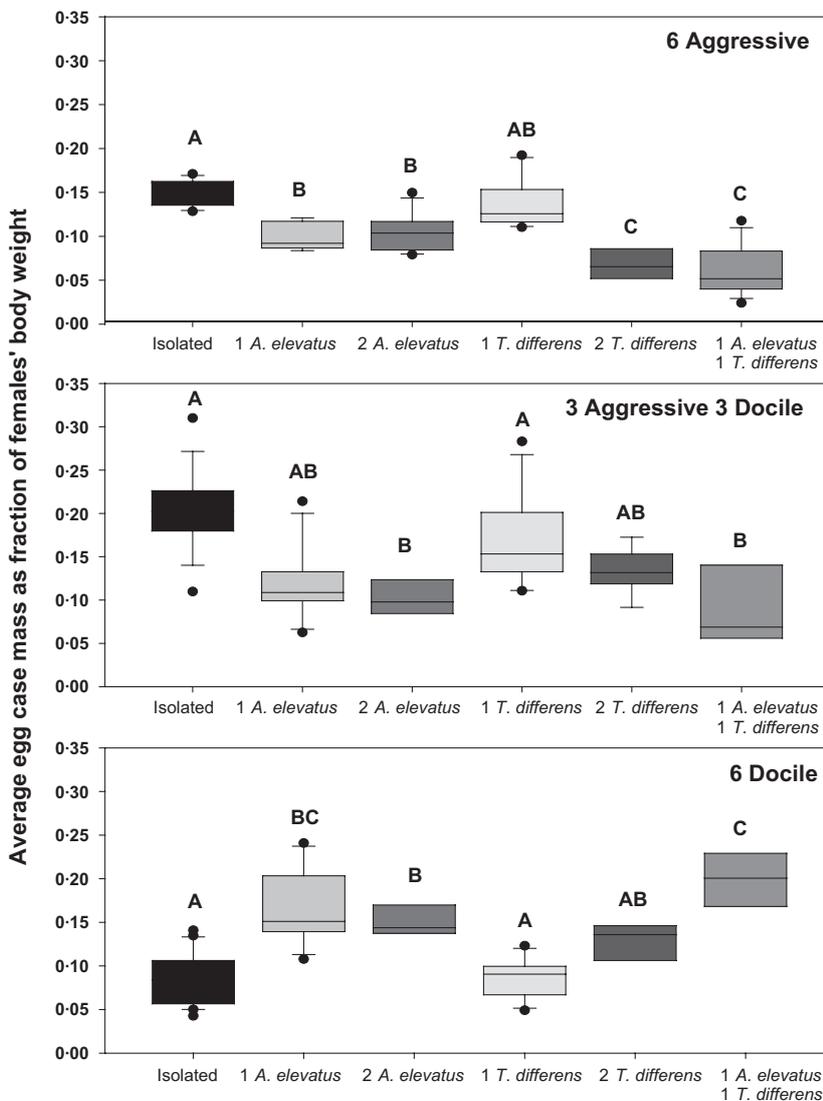


Fig. 1. Box plots of the egg case masses as a fraction of females' body weight (egg case mass/females' pre-mating body mass) of *Anelosimus studiosus* in colonies of various behavioural type (BT) compositions and treatments (one *Anelosimus elevatus*, one *Theridion differens*, etc). 'Isolated' refers to colonies without heterospecific web associates. Vertical shaded bars represent interquartiles range, and vertical lines represent the 90th and 10th percentiles. Within BT compositions, bars not sharing letter flagging are significantly different at $\alpha = 0.05$ using *post hoc* Tukey tests.

significant interaction term between BT composition and competitive environment. Thus, the performance consequences of the competitive environment differed among colonies with different BT compositions (Table 1). In colonies containing aggressive females, adding more web associates (whether conspecifics or heterospecifics) depressed the mass gain of both *A. elevatus* and *T. differens* (Fig. 2); that is, web associates' interactions tended to be competitive in nature. However, in colonies of all docile females, adding more web associates increased mass gain for both *A. elevatus* and *T. differens* (Fig. 2). In other words, colonies of all docile females appear to beget facilitative relationships among their web associates.

SUMMARY STATISTICS WITH VS. WITHOUT BEHAVIOURAL TYPES

For comparison, including data on intraspecific trait variation (i.e. BTs) always resulted in a more informative model using AICc model selection criterion, which penalizes for superfluous terms (Akaike 1987; Burnham & Anderson 2002), and models including BTs always boasted adjusted R^2 s far exceeding those of comparable models (Table 2).

Table 1. Effect tests for combined models predicting egg case mass of *Anelosimus studiosus* and mass gain of heterospecifics. Bolded terms are deemed significant at a Bonferroni corrected $\alpha = 0.007$

Source	d.f.	F-ratio	P
<i>A. studiosus</i> egg case mass			
Treatment	5,228	4.17	0.001
BT composition	2,228	6.91	0.001
Starting mass	1,228	1.61	0.21
Treatment*BT composition	10,228	22.07	< 0.0001
Treatment*starting mass	5,228	1.21	0.31
BT composition*starting mass	2,228	1.48	0.23
Treatment*BT composition*starting mass	10,228	0.98	0.46
<i>Argyrodes elevatus</i> mass gain			
Competitive environment	2,108	1.77	0.19
BT composition	2,108	8.81	0.0003
Starting mass	1,108	0.22	0.64
Competitive environment*BT composition	4,108	4.20	0.004
Competitive environment*starting mass	2,108	0.73	0.39
BT composition*starting mass	2,108	2.71	0.03
Competitive environment*BT composition*starting mass	4,108	0.97	0.43
<i>Theridion differens</i> mass gain			
Competitive environment	2,109	0.27	0.77
BT composition	2,109	3.85	0.02
Starting mass	1,109	12.25	0.0007
Competitive environment*BT composition	4,109	7.32	< 0.0001
Competitive environment*starting mass	2,109	8.42	0.0004
BT composition*starting mass	2,109	8.16	0.0005
Competitive environment*BT composition*starting mass	4,109	4.66	0.002

BT, behavioural type.

Discussion

Understanding how species interact with their biotic and abiotic environment is the fundamental goal of ecology. The way ecological theory has classically characterized species interactions implicitly assumes interactions are relatively fixed. In contrast, a more recent body of literature has demonstrated that species interactions can be remarkably fluid: varying across environmental gradients, and occasionally, depending on the traits of the interactants. Here, we experimentally demonstrate that the influence of trait variants extend beyond mere dyadic interactions and can have both direct and indirect effects on a whole suite of species interactions. Specifically, we demonstrate that the BT compositions of *A. studiosus* colonies not only change how colonies interact with their web associates, but how web associates interact with each other (Fig. 3). Our data indicate the functional traits of key community players can have far-reaching implications for how communities function.

Intraspecific variation in key community players can shape the way communities look and function. In recent years, data have emerged from several systems documenting the effects of intraspecific variation on various community attributes. By and large, these data come from studies in plant ecology, where manipulating genetic variation in key habitat-forming species (e.g. *Zostera marina*, *S. altissima*, *Oenothera biennis*) alters various community attributes: succession, primary production, population growth rates, biodiversity (Hughes & Stachowicz 2004, 2009; Johnson & Agrawal 2005; Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006; Genung *et al.* 2010). However, there is a paucity of similar data from animal systems, and among the plant literature, remarkably few studies implicate which functional traits are responsible for the documented trends (Hughes, Stachowicz & Williams 2009). In contrast, our study approaches the topic by manipulating the frequencies of known, genetically influenced behavioural variants (Pruitt & Riechert 2009c), and measuring their effects on a suite of species interactions, both direct and indirect. Our data reveal that the effects of intraspecific trait variation are far reaching: influencing the way peripheral species interact with key community players, and the way peripheral species interact with each other. Specifically, relative to colonies containing aggressive females, we found that colonies of all docile females beget an environment of facilitation: heterospecifics negatively impacted colonies with aggressive females, resulting in the production of small egg cases; in contrast, heterospecifics had positive effects on colonies of all docile females (Fig. 1). Additionally, heterospecifics reduced each other's mass gain in colonies containing aggressive females, but increased each other's mass gain in colonies of all docile females (Fig. 2) (see Fig. 3 for summary).

Although we presently lack data on the mechanisms generating differences in species interactions among colonies, we feel the topic is worth further speculation. In the absence of heterospecifics, colonies containing a mixture of docile and aggressive females experience highest fitness (Laboratory: Pruitt & Riechert 2011a; Field: Pruitt & Ferrari 2011).

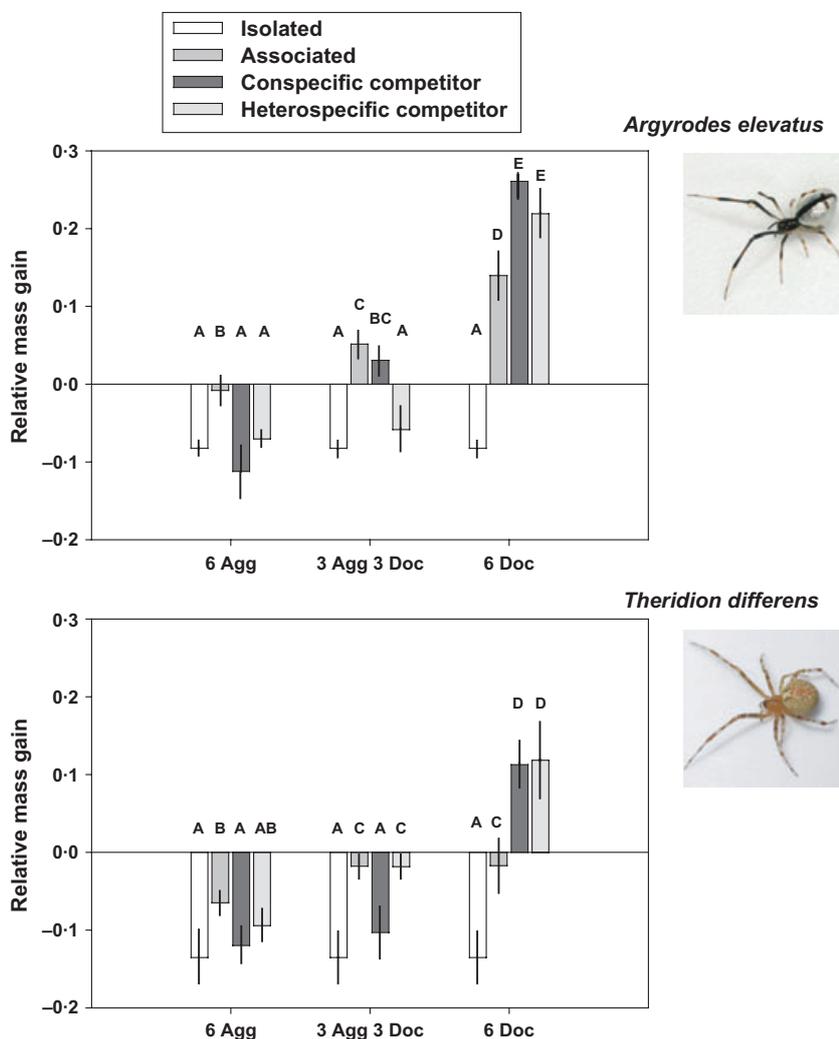


Fig. 2. Mean \pm SE bars of relative mass gained (change in mass/starting mass) by heterospecific web associates in colonies of various behavioural type compositions and treatment vs. isolated individuals. Bars not sharing letter flagging are significantly different at $\alpha = 0.05$ using *post hoc* Tukey tests. *Isolated*: not associated with an *Anelosimus studiosus* colony; *Associated*: singleton associated with a colony; *Conspecific Competitor*: two conspecifics associated with a colony; *Heterospecific Competitor*: two heterospecifics associated with a colony.

Table 2. Details of the combined analyses comparing model fit with and without regard to the BT composition of *Anelosimus studiosus* colonies. For comparison, including BTs always resulted in a more informative model using AICc model selection criteria, the Akaike weights (W_i) of BT-included models resemble one, and the R^2 s are more than twice those of models without regard to BTs. Δ AICc refers to the difference in AICc scores between our BT-included and BT-excluded models

Response variable	With BTs						Without BTs						Δ AICc
	F	d.f.	P	R^2	AICc	W_i	F	d.f.	P	R^2	AICc	W_i	
<i>A. studiosus</i> egg case mass	8.11	35,192	<0.0001	0.52	-2970.14	>0.9999	1.57	11,216	0.11	0.03	-2841.92	1.12×10^{-24}	128.22
<i>Argyrodes elevatus</i> mass gain	4.11	17,91	<0.0001	0.34	-1095.99	>0.9999	0.86	5,103	0.51	0.03	-1073.1	2.47×10^{-12}	22.89
<i>Theridion differens</i> mass gain	4.67	17,90	<0.0001	0.37	-1172.44	>0.9999	1.48	5,102	0.20	0.02	-1142.94	3.73×10^{-18}	29.5

BT, behavioural type.

This trend stems from the fact that aggressive females, by virtue of their short latencies to attack prey, facilitate the capture of large high-quality prey, whereas docile females contribute disproportionately to web maintenance (J. N. Pruitt & S. E. Riechert 2011a; unpublished data). However, at high representations within social groups, aggressive females spend extended periods of time engaging in conflicts over prey, and this behaviour results in time and energy wasted (Pruitt & Riechert 2009a). Unfortunately, without

aggressive females around to capture prey, colonies of all docile females experience woefully reduced prey capture success and fecundity. We propose that, in the absence of aggressive *A. studiosus*, heterospecifics effectively assume their role within colonies: possessing the ancestral (aggressive) character state, heterospecifics attack prey rapidly, capture more prey than they can consume and perhaps leave uneaten prey to be scavenged by docile *A. studiosus*. In other words, for groups of all docile females, heterospecifics may

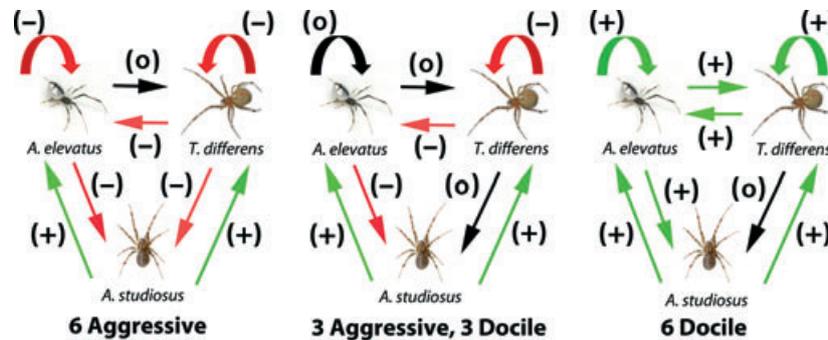


Fig. 3. Diagram summarizing the net species interactions between *Anelosimus studiosus* and heterospecific web associates and among the web associates themselves. Arrows pointing towards *A. studiosus* indicate the effect heterospecifics had on the egg case masses of colony members, and arrows faced towards *Argyrodes elevatus* or *Theridion differens* indicate the effects other species had on mass gained by the focal species.

be contributing to colony function in important ways. However, when aggressive females are present, the representation of aggressive individuals (conspecifics plus heterospecifics) is too high, and this results in a greater number of competitive/agonistic interactions and globally reduced foraging performance. Taken together, our current hypothesis is that colonies containing a mixture of docile and aggressive females experience greatest fitness, and this benefit is irrespective of whether the aggressive individuals are *A. studiosus* or heterospecific web associates. This hypothesis could also help explain why colonies of mixed BT (50 : 50) experience interactions more similar to colonies of all aggressive females than docile females (Fig. 3), because the greatest changes in colony dynamics occur at compositions ranging between 10% and 40% aggressive females (Pruitt & Riechert 2009a). Or, in other words, colonies containing >40% aggressive females experience little change in (i) the frequency of within-colony agonistic interactions, (ii) prey capture success and (iii) food wastage (Pruitt & Riechert 2009a, 2011a).

Finally, our findings also have implications for the interplay of eco-evolutionary dynamics between population biology and community structure (Lankau & Strauss 2007). In the absence of foreign web associates, colonies of mixed BT enjoy superior fitness. However, in many populations of *A. studiosus*, a disproportionately large number of colonies are composed of all docile females (Furey 1998; Riechert & Jones 2008). We propose that variation in the abundance of heterospecific araneofauna might bias the success of colonies in favour of all docile females via the following sequence: (i) groups of docile females are less likely to repel foreign spiders (Pruitt & Riechert 2011b); (ii) colonies of docile females enjoy higher fitness by associating with heterospecific araneofauna and increase the fitness/abundance of their associates (Figs 1 and 2); (iii) this facilitative relationship begets an environment, rich in heterospecific araneofauna, that negatively impacts neighbouring colonies containing aggressive females, causing colony collapse (Pruitt & Riechert 2011b); (iv) docile females then come to occupy habitats previously occupied by colonies of other BT compositions. Interestingly, this verbal model resembles the dynamics of those in the literature on disease transmission, where carriers (doc-

ile colonies) facilitate the spread of selective agents (heterospecific spiders) that spread and negatively impact competitor fitness (aggressive colonies), thereby facilitating the spread of carrier phenotypes. As it happens, colonies of docile females commonly occur in dense 'pockets' of high abundance, and their distribution is not obviously associated with any aspect of the abiotic environment (Furey 1998; Riechert & Jones 2008). Although this scenario requires further investigation, the plausibility of such sequences makes *A. studiosus* a highly tractable model with which to test contemporary theories on eco-evolutionary dynamics.

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Supporting Information

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Appendix S1. All pairwise Tukey tests.

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