The ecological consequences of temperament in spiders

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Abstract Ecological and evolutionary studies on spiders have been featured prominently throughout the contemporary behavioral syndromes movement. Here we review the behavioral syndromes literature devoted to spiders, and identify some ways in which behavioral syndromes can impact the function of spiders in ecological communities. We further highlight three general themes within the behavioral syndromes literature for which spiders have served as front running model systems: (1) how trait correlations beget performance trade-offs, (2) the influence that behavioral trait variants have on interspecific interactions and (3) mechanisms that aid in maintaining behavioral variation within- and among-populations. Research on behavioral syndromes continues to grow at an impressive rate, and we feel the success of behavioral syndromes studies in spiders bodes well for their continued prominence [Current Zoology 58 (4): 589–596, 2012].

Keywords Animal personality, Behavioral type, Behavioral syndrome, Social insects, Social spider

1 Introduction

Within animal behavior, much attention has recently focused on examining individual differences in behavior, which are variously referred to as individual temperaments, personalities, behavioral tendencies, behavioral types, or behavioral syndromes (Sih et al., 2004a; Sih et al., 2004b; Reale et al., 2007). This area has been the focus of much research over the last several years because of the potential for trait correlations to constrain optimization of behavior across contexts, but also because behavioral variation begets individual-level niche variation (Bolnick et al., 2003; Dingemanse and Reale, 2005; Reale et al., 2007; Reale et al., 2010). Although there is a bias in behavioral syndrome’s literature towards vertebrate systems, invertebrates offer unparalleled opportunities to address long-standing and unresolved questions in this field. Here we offer a general review of behavioral syndrome’s studies using spiders as model test systems, and highlight some of the ecological implications of behavioral syndromes for which spiders have served as general models.

2 Aggressiveness and Shy-Bold Syndromes

To a very large extent, we owe the prototypical “aggressiveness” and “shy-bold” syndrome axes to early work on spider test systems. These classic axes of behavioral variation refer to individuals’ degree of aggressiveness towards predator, prey, and/or mates (aggressiveness) and their response towards aversive and/or novel stimuli (shy-bold), respectively. Spiders are quintessentially aggressive, gluttonous predators (Pruitt and Krauel, 2010; Trubl et al., 2011): they exhibit polyphagous foraging tendencies (Foelix, 1996); many species exhibit high incidence of cannibalism, both sexual and otherwise (Elgar 1991; Arnegast and Henriksson, 1997; Schneider and Elgar, 2001; Johnson and Sih, 2005); spiders frequently subdue prey and consume meals much larger than themselves (Foelix, 1996; Pruitt and Krauel, 2010); and, any degree of sociality or tolerant behavior is exceedingly rare (< 0.1% of approximately 37,500 described species)(Aviles, 1997; Agnarsson, et al., 2006; Bilde et al., 2007; Lubin and Bilde, 2007). Given the markedly aggressive behavioral tendencies of spiders, much arachnological research has focused on determining the costs and benefits of aggressive versus passive/docile behavior in spiders. Consequently, aggressiveness syndromes have been documented in a disproportionately large number of spider species and across a broad diversity of ecological contexts, including foraging behavior, anti-predator responses, activity-levels, sexual behavior in both males and females, and social behavior (Table 1).
Table 1  A summary of the research testing repeatability of individual behavioral tendencies in spiders and whether the study detected a cross-contextual behavioral syndrome

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
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<th>Behavioral Syndrome</th>
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<td></td>
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<td>Kralj-Fišer et al., 2012</td>
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<td>Johnson and Sih, 2007</td>
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<tr>
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<td></td>
<td></td>
<td>Habitat selection: choosiness</td>
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3 Trade-offs

A focal construct of behavioral syndromes is that there is the potential for correlation among traits to generate maladaptive “spillovers”. Or, in other words, because traits are linked, selection acting on one context
may inadvertently cause ancillary trait shifts in other contexts. The inference drawn is that selection must average the costs and benefits of a particular temperament across various ecological contexts, thereby preventing behavior from being optimized. While there has been recent research that challenges the constraining potential of syndromes (Bell, 2005; Dingemanse et al., 2007), context-general trade-offs are still widely accepted and some of the best examples have come from spider models (Arnqvist and Henriksson, 1997; Johnson and Sih, 2005).

Aggressiveness syndromes in spiders may lead to a number of trade-offs. One that has received much attention is referred to as the ‘aggressive spillover hypothesis’, and is used to explain incidences of sexual cannibalism. Females of many spider species will cannibalize males either before, during, or after mating (Elgar, 1991; Arnqvist and Henriksson, 1997; Schneider and Elgar, 2001; Huber, 2005). Although sexual cannibalism during or after mating has intuitive benefits (i.e., females have obtained sperm and may gain energetic benefits), pre-copulatory sexual cannibalism is a risky behavioral pattern for females, particularly if they are virgin, because virgin females may risk killing off all of their potential suitors prior to mating and thus remain unmated (Arnqvist and Henriksson, 1997; Johnson and Sih, 2005). Thus females could be effectively sterilized by their unrestrained aggressiveness. The spillover hypothesis posits that pre-copulatory cannibalism may develop as an epiphenomenon of selection on aggressiveness in other contexts; aggressiveness is often favored during foraging or territorial encounters, and as a result of trait-linkage or pleiotropy, aggressive females are also predicted to exhibit higher incidences of sexual cannibalism. Data from a number of test systems have supported this hypothesis by detecting associations between females’ aggressiveness and their probability of attacking or consuming mates: fishing spiders (Johnson and Sih, 2005; Johnson and Sih, 2007), funnel-web spiders (Riechert and Hedrick, 1993; Riechert et al., 2001), and cob web weavers (Pruitt et al., 2008; Pruitt and Riechert, 2009b; Pruitt et al., 2011b). In some systems, this leads to females which attack every male they encounter (Riechert et al., 2001; Pruitt et al., 2011b). Alternatively, in the case of non-aggressive behavioral types, females sometimes even flee from every male which attempts courtship (Riechert et al., 2001). Thus, extremes on both sides of the aggression continuum can effectively sterilize female spiders.

Recent studies indicate that the males of some spider species, at least, can distinguish among females of different behavioral tendencies based on chemical cues released by females (Pruitt and Riechert, 2009b), and this may further disfavor aggressive females. As would be expected, given the high probability of being cannibalized by a female of the aggressive phenotype, males have been found to preferentially choose low-risk, non-aggressive females (i.e., females that are unlikely to cannibalize their mates)(Pruitt and Riechert, 2009b, Johnson, et al., 2011). Thus, in these circumstances, the danger of aggressiveness sterilizing aggressive females is even greater than indicated by rates of female cannibalism on males, because aggressive females’ encounter rates with males are predicted to be lower than those of non-aggressive females.

Aggressiveness syndromes can also produce trade-offs as a result of conflicting pressures during foraging and anti-predator encounters, because the shy-bold and aggressiveness axes of behavior are commonly correlated. The funnel-web building spider Agelenopsis aperta (Araneae, Agelenidae) has long been the focus of behavior trait correlation studies. Consistent individual differences in aggressiveness and boldness produces trade-offs in this species both across ecological contexts and in specific situations within them. For instance, because aggressive individuals generally exhibit broader diets (Riechert, 1991), they grow at a faster rate but suffer greater risk of injury owing to their tendency to attack dangerous prey. Moreover, in A. aperta, aggressive individuals are more likely to attack potential predators (Riechert and Johns, 2003) or resume foraging rapidly following simulated predator threats (Riechert and Hedrick, 1990; Riechert and Hedrick, 1993). Both of these high risk behavioral patterns can result in decreases in individual fitness: experimental results indicate as many as 40% of the local population of this spider species succumbs to avian predators each week during the spring nesting season of avian predators (Riechert, 1993a; Riechert and Hedrick, 1993). Variation in behavioral types is maintained within some populations of A. aperta owing to gene flow among locally-adapted populations (Riechert, 1993b; Riechert et al., 2001).

The general aggressiveness syndrome documented in spiders may also hold explanatory power for why sociality is exceedingly rare in these taxa. Even among social spiders, individuals exhibit repeatable variation in their behavioral tendencies. Highly social individuals are not only tolerant towards each other, but also exhibit reduced aggressiveness towards predators, prey, and
mates (Riechert 1985; Pruitt et al., 2010; Pruitt et al., 2011). These correlations are maintained within populations (Pruitt et al., 2008; Pruitt et al., 2010), across populations (Pruitt et al., 2010), and across species (Pruitt et al., 2011), suggesting that the behavioral aggressiveness syndrome of spiders has the potential to genuinely constrain trait evolution and limit the ecological conditions under which sociality may evolve. Although these highly-conserved correlations need not imply absolute constraints on behavioral evolution, populations and species primarily diverge along multivariate ‘lines of least resistance’ generated by interdependence (e.g., through shared proximate underpinnings) of traits constituting the behavioral syndrome.

Why are aggressive traits interdependent in spiders? Models of the spider *Agelenopsis aperta* suggest temperament is controlled by levels of antagonistic hormones (Smith and Riechert, 1984) which together increase or decrease individuals’ tendency to escalate or flee during contests. This conclusion was further supported by breeding experiments completed on population crosses (Riechert and Smith, 1989). Thomas Jones recently provided direct evidence in support of Maynard Smith and Riechert’s predictions (Jones et al., 2011). In this new study, octopamine and serotonin were found to have opposite effects on antipredatory behavior (i.e., length of death feigning or thanatosis) exhibited by the orb-weaving spider *Larinioides cornutus* (Aranea; Araneidae). If temperament is controlled by antagonistic hormones, it is not surprising that there would be an interdependence in behavior across contexts: hormone levels typically have broad ranging, pleiotropic effects in animals.

If interdependence of behavior across contexts is forced by an underlying hormonal mechanism, this could significantly affect the evolutionary pathway to sociality in the spiders. Thus, if selection were to favor increased social tendencies in some populations/species, selection must be ‘relaxed’ enough in associated traits to permit that change. Thus, sociality might not readily evolve in populations experiencing selection for aggressiveness towards prey and/or predators. The relationship between social tendencies and prey availability has been investigated in related species of the comb-footed spider genus *Anelosimus* (Araneae, Theridiidae: *A. eximius, A. guacamayos*), and as expected, sociality is more common and pronounced in environments with greater prey densities, and particularly, larger prey sizes (Rypstra, 1986; Kim 2000; Aviles et al., 2007; Guevara and Aviles, 2007; Powers and Aviles, 2007; Yip et al., 2008). One interpretation of these data is that sociality is only permitted to evolve in environments where selection for aggressiveness towards prey is reduced, such as the lowland tropics where prey abundance is predictably high (Riechert, 1985; Pruitt et al., 2010). As it happens, ≈98% of social spider species are restricted to the tropics.

### 4 Species Interactions

Individuals’ behavioral tendencies can shift the number, strength, and nature of interspecific interactions, and nowhere is this more thoroughly characterized than in spiders. In general, more aggressive, bold, and active individuals are thought to experience a greater number of species interactions (Sih et al., 2012). Understanding how trait differences impact species interactions is important because it has implications both for the environments in which various temperaments are favored, and conversely, for how individuals will impact their broader community. For example, aggressive individuals commonly exhibit broader diet breadths than do non-aggressive individuals (Riechert, 1991), and active individuals are thought to experience a greater encounter rate with heterospecifics of virtually every sort (e.g., prey, competitors, predators) (Sih et al., 2012). Thus, in terms of connectivity within a community, bold, aggressive, and active individuals are predicted to experience greater connectivity.

An individual’s temperament can also influence the magnitude of its interactions with heterospecifics and this can impact the success of temperaments in different environments. For instance, bold, aggressive, and active individuals commonly enjoy greater rates of encounter with prey, but suffer greater susceptibility to predation (Biro et al., 2004; Biro et al., 2006). Thus, relative to non-aggressive individuals, aggressive spiders are expected to have more intense interactions with both predators and prey (Riechert, 1993a). This, in turn, impacts how aggressive individuals perform in different environments. In general, aggressive behavioral types tend to outperform non-aggressive individuals in low resource, low predation environments whereas non-aggressive individuals tend to thrive in resource rich, high predation environments (Riechert and Hedrick, 1990; Riechert, 1993a; Riechert et al., 2001).

Although ecologists are already familiar with the idea that trait differences can impact the number and magnitude of species interactions, the mechanisms by which trait differences impact the nature of species interactions (e.g., competition, predation, mutualism) is poorly un-
understood. As above, trait-dependent species interactions can impact the differential success of various types of temperament in different environments. These interactions, however, add an additional layer of complexity because of their potential to create non-intuitive feedbacks between population and community ecology. For instance, in the social spider, Anelosimus studiosus (Araneae, Theridiidae), females exhibit a marked polymorphism in temperament and can be categorized into “docile” or “aggressive” behavioral phenotypes (Riechert and Jones, 2008). Multi-female colonies show significant levels of variation in their behavioral phenotypic composition (Pruitt and Riechert, 2009a, Pruitt et al., 2011). Numerous studies have shown that the composition of behavioral types within a colony can impact all aspects of their ecology (Jones et al., 2007; Pruitt and Riechert, 2011b; Pruitt and Riechert, 2011a). Anelosimus studiosus colonies are ecologically important because they serve as habitat for a many other spider species which, by and large, have a negative impact on the survival and reproductive output of A. studiosus colonies (Perkins et al., 2007; Pruitt and Riechert, 2011b). However, upon finer examination, whether particular heterospecific spider species hurt or harm host colonies they invade actually depends on the mixture of host behavioral types present. If aggressive behavioral types are present in an A. studiosus colony, heterospecifics are found to have a negative impact on colony performance (incidentally the heterospecific spiders also grow at a slower rate in these colonies.) In contrast, in colonies of all docile behavioral types, heterospecifics can actually benefit their host colony by assuming the aggressive role typically adopted by ‘aggressive’ A. studiosus: they subdue prey and lay disproportionately large amounts of silk (Pruitt and Ferrari, 2011; Pruitt et al., 2012). Thus, the mixture of behavioral types (trait variants) within A. studiosus colonies changes the nature of their interactions with heterospecifics (ammensalism to mutualism), and under some circumstances, heterospecifics can play important functional roles within their hosts’ society.

Data also suggest trait-dependent interactions could facilitate the spread of docile A. studiosus colonies across landscapes via the following sequence: (1) some habitats contain enough foreign spiders that they invade colonies of A. studiosus; (2) foreign spiders disfavor colonies containing aggressive females, driving them to extinction, but benefit colonies of all docile females; (3) docile colonies persist in the environment and begin to occupy the resources previously consumed by other colonies; (4) because docile colonies increase in representation, this is expected to further increase the number and diversity of heterospecific spiders in this habitat, via their mutualistic interaction; (5) this cycle continues until other external factors limit the density of heterospecifics present, or alternatively, the system becomes internally unstable.

5 Factors Maintaining Behavioral Variation

In general, evolution is characterized as an optimizing agent that tends to eliminate all but the most “fit” of trait variants. However, even a cursory glance of any behavioral trait can reveal an exquisite diversity in the kinds of strategies employed by organisms, even within a single population. Identifying the factors that help maintain this variation is a perennial goal in behavioral ecology and behavioral syndromes research exemplifies this goal. In this review, we focused on the factors known to maintain genetic variation in behavioral tendencies within spider populations.

Perhaps the most obvious mechanisms maintaining behavioral variation in all systems (spiders or otherwise) are context-specific performance trade-offs. Trade-offs are important in maintaining behavioral variation because if one strategy could be successful under all conditions, it would be everywhere. In a world without trade-offs, indeed, one strategy could come to occupy all niche space. However, countless studies in the behavioral syndromes literature have documented severe trade-offs associated with temperament: growth versus survivorship (Biro et al., 2006; Stamps, 2007), current versus future reproductive success (Pruitt and Krauel, 2010), foraging versus mating success (Johnson and Sih, 2005; Pruitt and Riechert, 2009b), performance in high versus low predation environments (Hedrick and Riechert, 1989; Riechert and Smith, 1989; Riechert, 1993a). These mechanisms can help maintain genetic variation in behavioral types both across landscapes, and within populations that experience finer spatial and temporal variation in their environment. Thus, at its most basic level, it is a heterogeneous environment paired with context-dependent performance trade-offs that is arguably the key mechanism maintaining behavioral variation.

A second mechanism that is commonly used to explain behavioral variation within populations is negative frequency dependent selection, or a rare type advantage. Under these circumstances, strategies are predicted to
do well at low representations within populations, but suffer reduced performance as they approach numerical dominance. A convenient example comes from work on social spiders, where colonies are composed of a mixture of aggressive versus docile behavioral types (Pruitt and Riechert, 2009a; Pruitt et al., 2011). At low representation within colonies, the aggressive phenotype dominates interactions with colony mates and consumes a disproportionately large amount of food (Pruitt et al., 2008; Pruitt and Riechert, 2009a). However, as the representation of the aggressive phenotype increases, violent interactions among aggressive individuals can lead to injury or even death for one or more interacting individuals (Pruitt and Riechert, 2009a). Under such circumstance, docile individuals outperform their aggressive counterparts by employing a kind of sneaker strategy, where they scavenge uneaten prey while avoiding direct conflict. The outcome is such that colonies of mixed behavioral type outperform monotypic groups (Pruitt and Riechert, 2011a). As a consequence of such negative frequency dependent foraging effects, colonies may be drawn towards a mixture of both phenotypes (Pruitt and Riechert, 2009a).

A third, more novel mechanism that can help maintain behavioral variation within spider populations is that of “social heterosis” or “behavioral type complementarity” (Nonacs and Kapheim, 2007; Nonacs and Kapheim, 2008). Both terms describe a situation where the nature of individuals’ interactions depends on their temperament types, and individuals of various phenotypes enjoy greater success when they associate with unlike individuals. Thus, demes of individuals composed of unlike phenotypes enjoy greater survival success and reproductive output than monotypic demes, and this favors the development and persistence of within-deme behavioral variation (Pruitt et al., 2008; Pruitt and Riechert, 2011a; Pruitt et al., 2011). Again, some of the best data on spider test systems is derived from work on social spiders. The *Anelosimus* genus is outstanding among spiders because sociality has evolved multiple times independently across the genus (Agnarsson et al., 2006; Agnarsson et al., 2007; Agnarsson et al., 2010). The evolution of sociality in this genus is associated with depressed aggressiveness, increased fearfulness, and reduced activity-levels relative to subsocial species (Pruitt, Riechert, & Aviles unpublished data). However, more interestingly, social species also exhibit greater variation in their behavioral tendencies, and data reveal that groups composed of a mixture of high and low-aggressiveness individuals gain more mass and enjoy higher survivorship than do monotypic groups. The resulting inference is that positive interactions among behavioral types could be a major factor maintaining behavioral variation within social groups, and indeed, within social species of spider. How the colony-level personalities types emerge from the behavioral types of their constituents has not been thoroughly considered in spiders, and we feel this is a promising avenue for future research (reviewed by Pinter-Wollman, 2012).

6 Conclusions

Behavioral syndromes have important implications in terms of how individuals interact with their biotic and abiotic environments, as well as how social systems can evolve. In spiders, three general themes have emerged for how syndromes impact the ways in which individuals interact with their biotic and abiotic environments. (1) Behavioral syndromes generate context-specific performance trade-offs as a result of a general aggressiveness syndrome in spiders. (2) Temperament shapes the way individual spiders interact within their community. This suggests that the behavioral syndrome could shape community dynamics and conversely, that community structure could influence the maintenance of behavioral syndromes. (3) A multitude of variance-sustaining mechanisms aid in maintaining behavioral variation within- and across species of spider. Among social spiders, positive interactions among trait variants seem particularly influential in this regard. Although the fitness consequences and proximate mechanisms generating behavioral syndromes have received a tremendous amount of attention, only now is the behavioral syndromes literature turning its attention to the ecological impacts of behavioral syndromes. Given our rich preexisting understanding of how behavioral syndromes impact spiders; interactions with the abiotic and biotic communities they exist in, we feel this bodes well for the continued prominence of spider research in this thriving field.

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