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Sex matters: sexually dimorphic fitness consequences of a behavioural syndrome

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There is growing evidence that correlated behavioural traits, or behavioural syndromes, influence behavioural evolution in some taxa. Few studies, however, investigate whether the effects of a syndrome are the same for both sexes. We test whether variation in social tendency, inferred from interindividual distance, is correlated with other aspects of behaviour in male comb-footed spiders, *Anelosimus studiosus*. We compared these results to those from previous studies on female social tendency to determine (1) whether both sexes share the same behavioural syndrome and (2) whether its effects on mating success are the same for both sexes. Trait types in the syndrome analysis include foraging behaviour, antipredator behaviour, exploratory behaviour and activity level. Our results suggest male *A. studiosus*, like females, can be categorized into two social classes: an aggregative (social) class and an intolerant (asocial) class. Social males (i.e. those with lower interindividual distance scores) were generally less aggressive towards prey and predators, and were less active. Furthermore, we provide evidence from a parent/offspring breeding study for an additive genetic component to male social tendency (heritability = 0.32). To determine the influence of the male syndrome on mating success, we performed staged male–male contests between social and asocial males for access to females. We found that male social tendency was the single best predictor of success in these trials, with asocial males outperforming social. This finding is opposite to the trend observed in female *A. studiosus*, where social females experience higher mating success. We propose that the diametrically opposed mating outcomes between the sexes could generate evolutionary conflict.

Correlated behavioural characters (i.e. behavioural syndromes) are a taxonomically diverse phenomenon, having been described in vertebrates (Dingemanse et al. 2003; Sih et al. 2003; Bell 2005) as well as invertebrates (Hedrick 2000; Riechert et al. 2001), and are of evolutionary importance because of their potential to shape adaptation (Dall et al. 2004; Sih et al. 2004). While some evidence suggests behavioural syndromes may limit trait optimization (e.g. Johnson & Sih 2005), other investigators suggest that syndromes may themselves be the result of selection (Cheverud 1996). For example, when choosing an oviposition site, it may be adaptive for maternal host plant preference to covary with offspring chemical tolerances. Selection should then favour mutations that link these functionally dissimilar traits (Futuyma 1983), and the resulting syndrome would be adaptive (Wolf & Brodie 1998).

Some evidence suggests behavioural syndromes can constrain adaptation; because selection must act jointly on the correlated behavioural characters in a syndrome, the outcome is a phenotype that reflects a balance of the effects of each trait on fitness. Behavioural correlations between sexes with differing trait optima are another way in which correlated characters may constrain adaptation (Manning 1963; Partridge 1994). The effect of behavioural correlations between the sexes is particularly interesting because the phenotypes are not merely correlated across contexts and/or situations but are expressed in completely different individuals. For example, in zebra finches, *Taeniopygia guttata*, redder bills in males are favoured by females, but females with lighter coloured bills achieve greater longevity. An evolutionary conflict arises because bill colour is strongly phenotypically correlated between the sexes (Partridge 1994). Evolutionary conflict between the sexes may also occur in systems where males and females share the same behavioural syndrome but experience differing selection pressures. This potential for conflict has received inadequate attention from the behavioural syndromes literature (but see Dingemanse et al. 2004).

Spiders are a common taxa in behavioural syndromes research (Sih et al. 2004), and are well known for showing similar syndromes of aggression across distantly related families (Agelenidae: Riechert & Hedrick 1993; Pisauridae: Arnqvist & Henriksson 1997; Johnson & Sih 2005; Theridiidae: Pruitt et al. 2008). The most thoroughly studied system to date is the desert spider *Agelenopsis aperta* (Araneae, Agelenidae), which shows ecotypic variation in

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aggressiveness: riparian populations tend to be fearful and nonaggressive, while arid populations show little fear and are highly aggressive (reviewed in Riechert et al. 2001). The aggression syndrome described in *A. aperta* includes agonistic behaviour, antipredator behaviour, territory size, latency to attack prey, diet breadth, degree of superfluous killing and prevalence of sexual cannibalism (Maynard Smith & Riechert 1984; Riechert & Maynard Smith 1989; Riechert & Hedrick 1993; Maupin & Riechert 2001) and influences individual fitness in this spider (reviewed in Riechert et al. 2001).

Despite a wealth of research on the fitness consequences of behavioural syndromes in spiders, there has been a strong bias towards emphasizing females in these investigations (Arnqvist & Henriksson 1997; Johnson & Sih 2005; Pruitt et al. 2008), and to our knowledge, no investigation has explicitly compared the effects of a syndrome on male versus female fitness. The researcher bias for female-centred investigations may be because males of most spider species lose much of their behavioural repertoire at maturity (Foelix 1996). Males and females of most species share similar environments and selective pressures as juveniles, but after maturation, their environments and selective pressures diverge (e.g. males leave their webs in search for females and they engage in male–male contests). Thus, a behavioural syndrome shared by the two sexes may come under different or even opposing selection for males and females post maturation. The researcher bias for females might yield an incomplete and misleading concept of the adaptive value of a behavioural syndrome.

Females of the temperate comb-footed spider, *Anelosimus studiosus* (Araneae, Theridiidae) show a polymorphism in social behaviour: they can defend their nests against intrusion by female conspecifics (asocial) or cooperate with them in brood care, foraging and web maintenance (social) (Furey 1998; Riechert & Jones 2008). Pruitt et al. (2008) recently described an aggression syndrome in female *A. studiosus*, where decreased aggressiveness of social females towards conspecifics was correlated with a decrease in aggression in other kinds of behaviour (e.g. antipredator behaviour, foraging behaviour, activity level). Although this syndrome places social females at a selective disadvantage with respect to competition for food, this disadvantage may be offset by differential mating success if (1) males prefer the chemical signal of social females and (2) asocial females show high frequencies of precopulatory cannibalism, which would decrease their probability of mating (Pruitt & Riechert, in press).

In this study we investigated (1) whether males display the same behavioural syndrome as that described in females, (2) whether the social tendencies of males show a significant heritability (i.e. additive genetic variation), thus allowing the trait to respond to selection, and (3) the extent to which existing syndromes influence male–male competition for mates. We consider the contribution that competition between males might have in favouring the spread of one phenotype versus the other.

METHODS

Study Species

Anelosimus studiosus is a common inhabitant of understory vegetation along waterways throughout most of the eastern United States. The species is unique among social spider species in that it shows a social behaviour polymorphism (described above). The frequencies of the asocial and social phenotypes shift with increasing latitude and vary among different temperature sites within the same latitude (Jones et al. 2007; Riechert & Jones 2008). The social phenotype is in the minority in all populations sampled to date, but it increases in frequency with increasing latitude to a maximum of 14% at 36° in eastern Tennessee (Riechert & Jones 2008). At many sites *A. studiosus* are found at high densities, and individuals of both phenotypes are forced to coalesce their webs, and often come to occupy adjacent web space. Thus, there is potential for competition between phenotypes for food, preferred web space and mates to influence the evolutionary outcome of the behavioural polymorphism.

Collection and Laboratory Maintenance

For our breeding study, juvenile females of both social tendencies were collected along a river system managed by the Tennessee Valley Authority in eastern Tennessee during May 2008 (35°89′N, 84°30′W). Upon reaching their final moult, we determined the behavioural phenotype of each individual using a 'distance trial' (see Interindividual Distance Test below). A subset of these females ($N = 30$) were then bred with a male ($N = 30$). Males used in our breeding study were collected as juveniles and originated from a web at least 5 m away from the female's source web. Males used in the breeding study were also run though a distance trial prior to mating. Following mating, females were individually housed with their broods in clear plastic containers (500 ml) in the laboratory at 22–24 °C on a 12:12 h light:dark cycle. They were fed termite workers ad libitum twice weekly. Juveniles were removed from their mothers upon reaching the penultimate instar and isolated in 59 ml containers. Upon reaching maturity, male offspring were run through the interindividual distance trial.

Unless otherwise noted, the behavioural assays for our syndrome analysis were performed on a cohort of 80 wild-caught males, collected as late-instar juveniles (each originating from a web at least 5 m distant). Individuals were run through the following trials: interindividual distance; prey attack; superfluous killing; antipredatory; exploratory/boldness. The protocols followed those reported in Pruitt et al. (2008), except that the 'superfluous killing' and 'attack sequence' trials were run on penultimate rather than mature males, because male spiders typically cease feeding on reaching maturity (Foelix 1996).

Interindividual Distance Test

We used an interindividual distance test to determine whether males would show variation in social tendency similar to that described for females (Riechert & Jones 2008). Two males of unknown social tendency were individually marked with fluorescent powder and placed in the centre of clear plastic container ($13 \times 13.5 \times 2.5$ cm). We allowed males 24 h to settle, then recorded the distance between the males and their location with reference to the four corners of the container: *A. studiosus* prefers to settle in the corners of these containers (Riechert & Jones 2008). We scored males as 'social' if they settled in the same corner, and we scored them as 'asocial' if they settled in opposite or adjacent corners. All asocial males received a second confirmatory test with a known social male, because asocial males, which demand more space (J. N. Pruitt, personal observations), may chase away social males. We used the between-individual distance measure from the second, confirmatory trial when calculating the correlations between social phenotype and other behavioural trait scores; this measure allows for the possibility of intermediate phenotypes. In addition to the males used in our syndrome analysis ($N = 80$), breeding study ($N = 30$) and male–male contests ($N = 40$), this test was run on 150 wild-caught males to determine the frequencies of social versus asocial males in wild populations.