

# Reproductive success in a socially polymorphic spider: social individuals experience depressed reproductive success in isolation

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**Abstract.** 1. Correlated individual differences in behaviour across ecological contexts, or behavioural syndromes, can theoretically constrain individuals' ability to optimally adjust their behaviour for specific contexts.

2. Female *Anelosimus studiosus* exhibit a unique behavioural polymorphism: 'social' females are tolerant of conspecifics and aggregate in multi-female colonies, while 'solitary' females aggressively defend their singleton webs from intrusion by adult female conspecifics. Previous work found that social females are also less aggressive toward prey and are more fearful of predators.

3. In this study we quantify potential fitness consequences of these correlated behaviours by examining the potential and realised fecundities of the two phenotypes in naturally occurring colonies, and by quantifying their ability to rear offspring as singleton individuals.

4. There were no differences in the fecundities of laboratory-reared females between the phenotypes, nor were there differences in field-collected brooding females from naturally occurring solitary and social nests.

5. Brooding females from solitary and social colonies that were isolated in new nests for the growing season were both capable of rearing their broods; however, females from solitary nests had significantly greater success.

6. These results suggest a fitness consequence to the reduced-aggression syndrome of social females that may represent a general impediment to the evolution of sociality in spiders.

**Key words.** *Anelosimus studiosus*, behavioural polymorphism, behavioural syndrome, social spider, social structure.

## Introduction

Growing attention is being paid to correlations of behaviours within individuals termed 'behavioural syndromes' (reviewed by Sih *et al.*, 2004). Often focusing on aggression, there is evidence across a wide range of taxa that an individual's behaviour in one context (e.g. prey capture), predicts that individual's behaviour in other contexts (e.g. toward mates, other conspecifics, or predators; Riechert & Hedrick, 1993; Wilson *et al.*, 1993; Maupin & Riechert, 2001; Sih *et al.*,

2003; Bell & Stamps, 2004; Johnson & Sih, 2005, 2007; Nelson *et al.*, 2008; Pruitt & Husak, 2010). Studies in a few key model systems have identified genetic underpinning to these linked behaviour (reviewed by van Oers *et al.*, 2005; Pruitt & Riechert, 2009a), and it is generally presumed these traits are under selection. Some theory suggests behavioural syndromes may constrain evolution, as aggression levels that are adaptive in one context may be maladaptive in another (Arnqvist & Henriksson, 1997; Johnson & Sih, 2005, 2007; Pruitt & Riechert, 2009b). Yet another body of theory suggests that behavioural syndromes are labile over evolutionary time, and are themselves the adaptive result of selection (Bell, 2005; Bell & Sih, 2007; Dingemanse *et al.*, 2007; Herczeg *et al.*, 2009; but see Pruitt *et al.*, 2010).

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In this study we begin to examine the fitness consequences of an aggression-related behavioural syndrome in a socially polymorphic spider, *Anelosimus studiosus*. The majority of individuals in this species are considered subsocial (*sensu* Wilson, 1975), with solitary mothers rearing offspring that disperse at adulthood (Brach, 1977; Jones & Parker, 2002). Solitary females will aggressively defend singleton nests from conspecific adult females. However, at higher latitudes, and in cooler microclimates, colonies containing tens to a few hundred related adult females are regularly observed (Jones *et al.*, 2007; Riechert & Jones, 2008; Pruitt & Riechert, 2009c; Duncan *et al.*, 2010). As in tropical species (Avilés, 1997), social *A. studiosus* cooperate in shared web maintenance, prey capture, and brood care (Furey, 1998). The proposed advantage to social colonies is that, should one female die, other colony members can foster their orphaned brood. A model previously developed by Jones *et al.* (2007) predicts that this advantage is most pronounced in cooler habitats because juvenile development is slowed, and thus, a mother is more likely to die before her brood is independent. Riechert and Jones (2008) developed a simple inter-individual distance test that identified an association between individuals' aggregative tendency and their propensity to form multi-female colonies. Furthermore, evidence suggests that these individual behavioural differences reflect underlying genetic differences rather than mere phenotypic plasticity (Riechert & Jones, 2008; Pruitt & Riechert, 2009a). Taken together, multi-female colonies appear to be an emergent property of the individual behavioural tendencies of colony constituents.

Pruitt *et al.* (2008) recently discovered that the social phenotype of adult *A. studiosus* (as exhibited by spatial attraction/tolerance of conspecific adult females) is part of a behavioural syndrome. Social females were generally less aggressive in attacking prey than were solitary females. Social females were also generally more fearful in simulated predator attacks. It was suggested that the correlation of these behaviours would have fitness consequences and could profoundly affect colony dynamics. Interestingly, a recent large-scale study on *A. studiosus* revealed that populations separated by as much as 37° latitude share similar behavioural syndromes to those observed by Pruitt and collaborators (Pruitt & Riechert, 2009a,b; Pruitt *et al.*, 2010). Thus, at least for *A. studiosus*, the syndrome appears to be an attribute of the species rather than a population-level phenomenon (reviewed in Pruitt *et al.*, 2010). Here, we begin to explore the potential fitness consequences of this behavioural syndrome by examining the fecundity of females from social and solitary colonies, as well as their relative ability to rear broods independently. We ask the following questions: (i) Might the observed reduced-aggression syndrome of *A. studiosus* depress the fitness of singleton social females relative to solitary females? (ii) Is there a difference in the potential and realised fecundities of social and solitary females in naturally occurring colonies? Granted, while these questions fail to address the general adaptive significance of the reduced-aggression syndrome in *A. studiosus*, they will help illuminate how the behavioural tendencies of social females might affect (i) the fitness of colony foundresses and (ii) cases where social

females are not common enough for multi-female colonies to form.

## Materials and methods

### Study species

*Anelosimus studiosus* (Araneae, Theridiidae) is an arboreal comb-footed spider. In the U.S.A. the species ranges from the gulf coast to New England (Brach, 1977; Agnarsson *et al.*, 2007), and is generally most dense along waterways (T. C. Jones, pers. obs.). In solitary colonies, juveniles remain in their natal web with young juveniles being fed by their mother, and older juveniles participating in prey capture and web maintenance (Jones & Parker, 2000, 2002). Adult females are typically intolerant of each other, and they disperse from their natal web upon maturing (Brach, 1977). Spiders in social colonies exhibit similar behaviour, but mothers are indiscriminate about whose juveniles they care for (Furey, 1998). Larger social colonies apparently form by non-dispersal of females (Riechert & Jones, 2008). The majority of colonies throughout the range of *A. studiosus* are solitary, but the proportion of social colonies increasing with latitude from 30°N to 36°N (Jones *et al.*, 2007). In east Tennessee (36°N), solitary colonies are fairly dense along lakes and rivers, but there are isolated 'pockets' where the proportion of social colonies is relatively high. In Tennessee, *A. studiosus* has a seasonal life history. Spiders overwinter in their natal webs as sub-adults and mature by mid-May. Females produce egg cases in June, and offspring hatch 1–3 weeks after parturition. Most brooding females die by September.

### Fecundity measurement: laboratory reared females

To measure the fecundity of different behavioural phenotypes under controlled natal conditions, we collected mature gravid females from a population along a Tennessee Valley Authority managed river system in east Tennessee June 2007 (35°89'N, 84°30'W). The behavioural phenotype of each female was assessed using an inter-individual distance trial (described in Pruitt *et al.*, 2008; Riechert & Jones, 2008), in which individuals that settle near a known social female are labeled as 'social', and those that settle far from the known social female are labeled 'solitary'. Inter-individual distances of female *A. studiosus* exhibit a bimodal distribution (Pruitt & Riechert, 2009c), and the wealth of evidence suggests there is a significant additive genetic component to the behaviour (Riechert & Jones, 2008; Pruitt & Riechert, 2009b). Each female was individually housed and allowed to brood in 500 ml container in the laboratory between 22 and 24 °C with natural lighting conditions. Gravid females were fed four termite workers twice a week until oviposition; when spiderlings emerged this feeding regime was doubled. As the juveniles reached maturity, they were removed from their brood container and isolated in 59 ml containers. The offspring were then maintained on the same feeding regime as gravid females (four termites per week). Upon maturing, female offspring were

run through the inter-individual distance assay, and randomly mated with a laboratory reared, non-sibling male. Matings were performed by placing the male in the web of a mature female and leaving them for 48 h. The males were then removed and the mated females were transferred to 500 ml containers to oviposit. Females and their egg cases were checked twice daily for spiderlings. Spiderlings were allotted 48 h to emerge from the egg case before they were counted. We observed no cannibalism among spiderlings during this time.

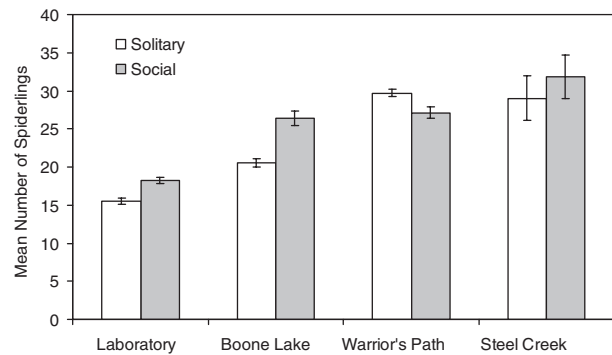
#### Fecundity measurement: field-collected females

To quantify fecundity of field-collected social and solitary females we located three populations in east Tennessee that had both colony types: Boone Lake (36°23'54.85"N, 82°21'53.59"W), Warrior's Path State Park (36°29'42.98"N, 82°28'22.77"W), and Steele Creek Park (36°34'17.16"N, 82°13'58.96"W). At each of these sites, the pockets of social colonies occupied less than 50 m of shoreline and were flanked by solitary colonies. In June 2008 we collected brooding females from solitary and social webs. From Boone Lake and Warrior's Path we collected 25 females of each phenotype (only one female per social colony was taken). Steele Creek is a smaller population and we only collected eight females of each colony type. At this time we also measured the colonies by taking the maximum orthogonal dimensions. This measurement has been shown to correlate strongly with the number of adult females in a colony (Jones & Riechert, 2008).

The spiders were brought back to the laboratory and removed from their webs along with their egg cases. We kept the brooding spiders in 85 × 15 mm Petri dishes under ambient temperature and lighting conditions. The spiders were watered twice a week and fed two *Drosophila melanogaster* per week. The egg cases were checked daily for emergence of spiderlings, which were then counted.

#### Fitness estimates of isolated females

For this experiment we followed a field protocol used to quantify reproductive success in this species (Jones & Parker, 2002; Jones & Riechert, 2008). We collected 25 brooding females from each colony type at Boone Lake and Warrior's Path in June 2008. We placed each spider and her egg case in a foreign solitary web on a Virginia Pine (*Pinus virginiana*) substrate; the former resident spider was removed before the test female was added. These were then placed in 500 ml plastic containers, and kept overnight in the laboratory to allow the new spider to establish residency. The following day, we wired the webs into Virginia Pine at the sites from which they were collected between 1 and 2 m above the water. We made certain that the colonies were at least 50 cm from all other colonies (a distance at which the colonies could not coalesce; Powers & Avilés, 2003; Riechert & Jones, 2008). The colonies were checked 2 days later to confirm that all test females were still present. At the end of the active season in mid-October, colonies were cut from the foliage, transported



**Fig. 1.** Comparison of fecundities of solitary and social phenotypes. Laboratory females were reared entirely under controlled conditions, while the remaining were brooding females collected from different sites. Shown are means with standard errors.

to laboratory, and dissected. We noted both (i) the number of offspring present and (ii) their developmental stage.

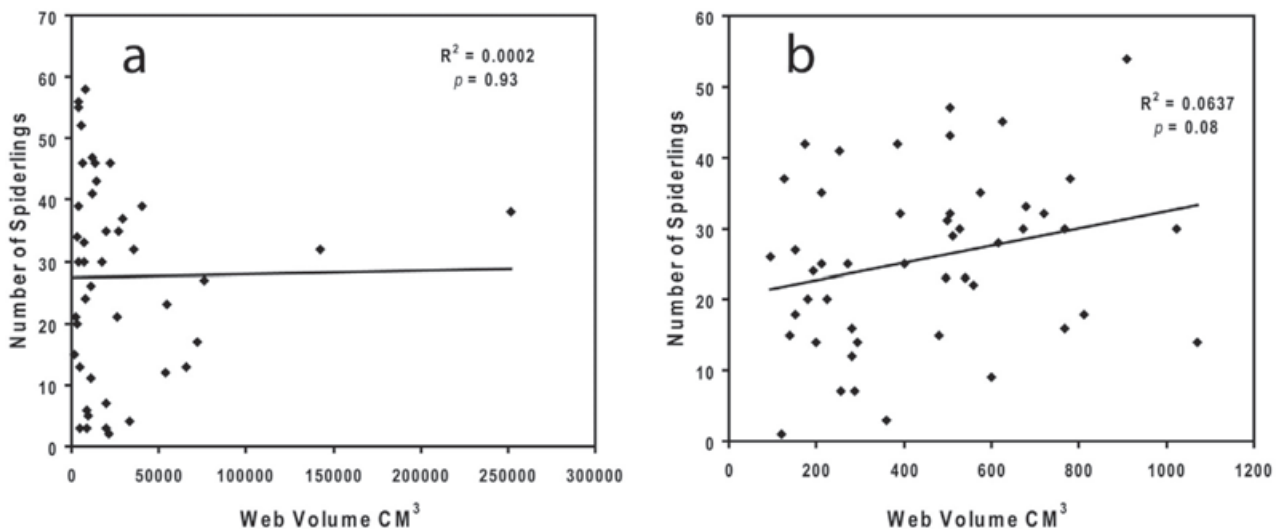
## Results

### Fecundity measurement

Of the 116 brooding females brought into the laboratory, three died before the emergence of spiderlings, and four abandoned their egg cases. These were excluded from analyses because in this species mothers must open their egg cases for juveniles to emerge (Viera *et al.*, 2007). Of the remaining egg cases that were guarded, 14 had no spiderlings emerge. The distribution of egg case failures was not associated with collection site ( $\chi^2_2 = 0.58$ ,  $P = 0.75$ ), or with colony type ( $\chi^2_1 = 0.29$ ,  $P = 0.6$ ). Of those in which juveniles did emerge, fecundity ranged from 1 to 58, and were normally distributed (Ryan–Joiner test  $AD = 0.335$   $P = 0.5$ ) around a mean of 26.6.

We failed to detect a significant difference in the fecundities of the laboratory-reared females of either phenotype (Fig. 1; one-tailed  $T = 1.09$ ,  $P = 0.14$ ). Of the field-collected spiders, the mean fecundities among sites and between social strategies are shown were similar (Fig. 1). There were no differences in fecundity among sites or social strategy detected by GLM (site:  $F_{2,115} = 2.04$ ,  $P = 0.136$ ; social strategy:  $F_{1,115} = 0.00$ ,  $P = 0.986$ ; site × social strategy:  $F_{2,115} = 0.36$ ,  $P = 0.698$ ). However, a *post hoc* test comparing the overall fecundities of Warrior's Path and Boone Lake found that Warrior's Path was higher with marginal significance (BL mean = 19.5, WP mean = 24.8, one-tailed  $T = 1.65$ ,  $P = 0.05$ ). The combined phenotype/colony type fecundities were lower for laboratory-reared spiders (mean = 16.9) than for field-collected females (mean = 26.6; one-tailed  $T = -4.5$ ,  $P < 0.001$ ).

The solitary colonies ranged in estimated volume from 80 to 1071 cm<sup>3</sup> (mean 433.2), and the social colonies ranged from 1248 to 252 000 cm<sup>3</sup> (mean 25292.5). There was no effect of site on web volume detected by one-way ANOVA in either solitary or social colonies (solitary:  $F_{2,57} = 0.09$ ,



**Fig. 2.** Plots of the relationship of web volume to fecundity in field-collected brooding females. (a) Results from social colonies, and (b) results from solitary webs.

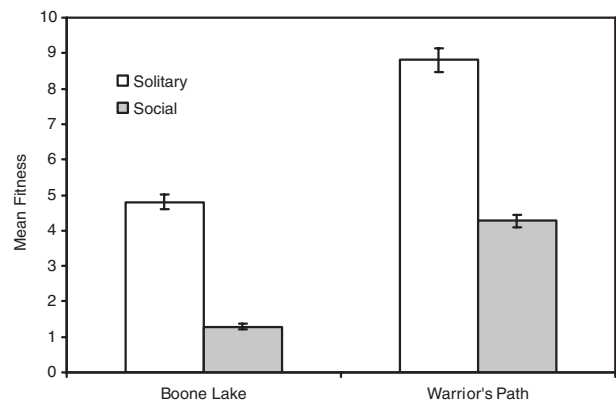
$P = 0.91$ ; social:  $F_{2,57} = 1.84$ ,  $P = 0.170$ ). Again however, a *post hoc* analysis of just Boone Lake and Warrior's Path found significantly higher volumes at Warrior's path in both solitary and social colonies (solitary: one-tailed  $T = 2.8$ ,  $P = 0.004$ ; social: one-tailed  $T = 1.7$ ,  $P = 0.04$ ). There was no effect of estimated web volume on fecundity among the social colonies (Fig. 2a), but there was a non-significant suggestion of a positive relationship between fecundity and web volume among the solitary colonies (Fig. 2b).

#### Fitness estimates of isolated females

In examining the number of juveniles surviving at the end of the growing season, there were clear differences associated with both (i) the colony-type the isolated mothers came from and (ii) between study sites (Fig. 3). A GLM analysis found that females from solitary colonies had significantly higher fitness than those isolated from social colonies ( $F_{1,99} = 10.53$ ,  $P = 0.002$ ), and that females at Warrior's Path had higher fitness than those at Boone Lake ( $F_{1,99} = 14.0$ ,  $P = 0.000$ ). There was no interaction effect between site and colony of origin ( $F_{1,99} = 0.23$ ,  $P = 0.635$ ). An examination of the distributions of complete colony failures (no juveniles at the final census) found that there were no differences associated with colony type of origin ( $\chi^2_1 = 2.19$ ,  $P = 0.14$ ) or with study site ( $\chi^2_1 = 0.68$ ,  $P = 0.41$ ).

#### Discussion

From the fitness estimates of isolated females, it is clear that females from social colonies of *A. studiosus* were less capable of rearing offspring on their own than are females from solitary colonies. This provides evidence to support Pruitt *et al.*'s (2008) assertion that the social females' reduced aggression



**Fig. 3.** Comparison of the numbers of juveniles surviving the first growing season between social and solitary brooding females that were isolated in novel solitary webs. Results from two sites are given with means and standard errors.

towards prey and increased fearfulness could have fitness consequences under some circumstances (e.g. when singleton social females disperse to found new colonies). At this point we have no way to discern which aspect of the syndrome might cause the reduced brood survival of social females (e.g. starvation or predation). Interestingly, there was no difference in the incidence of complete colony failure between females of either phenotype. This finding suggests that both phenotypes are *capable* of rearing offspring on their own; singleton social females are merely less successful. This is consistent with Krafft's (1979) assertion that social spiders display the same behaviours as their solitary congeners, but have simply evolved conspecific tolerance.

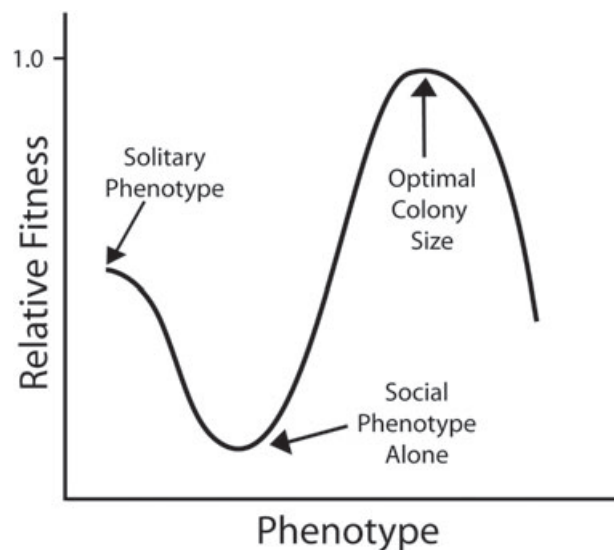
In spiders, clutch size and egg size are related to body condition (Vollrath, 1987; Morse, 1988; Simpson, 1993). The fact that there was no difference in initial fecundity between



females from the two colony types, suggests that females in both colony types are in similar condition at parturition. This, in turn, suggests that the fitness consequences of this reduced-aggression syndrome is mitigated by living in colonies. Conceivably, the reduced individual aggressiveness of social females might also be overcome by cooperative prey capture or colony defence advantages conferred by having nest mates (reviewed by Avilés, 1997; Purcell & Avilés, 2007; Powers & Avilés, 2008; Yip *et al.*, 2008). It was surprising to find that there was no relationship between fecundity and web volume in social colonies. Data from a permanently social congener, *A. eximius*, predicts a reduction of per-capita fecundity with colony size (Avilés & Tufiño, 1998). In contrast, there was a suggestion of a positive correlation between web volume and fecundity in the solitary females. If real, this could suggest that these factors are both related to individuals' condition. Alternatively, habitat itself may affect web volume, which, in turn, affects fecundity. Web volume is known to affect prey capture in this species (Jones & Parker, 2000), and colony success is affected by web substrate (T. C. Jones, unpublished).

The brood fostering model of Jones *et al.* (2007) suggests that in cool climates, where juvenile development is slow, there is an advantage to living in a group where other adults will foster orphaned broods. The model predicts that under these conditions, there will be an increase in individual fitness with colony size reaching some optimum, followed by a decline. In general, this pattern was confirmed empirically (Jones & Riechert, 2008), finding that individual fitness in colonies above 10 spiders was below that of solitary spiders. However, comparisons in that study were made to naturally occurring solitary colonies. Our results here suggest that social females 'should' remain in larger colonies because they are less successful in isolation than their solitary phenotype counterparts. We cannot directly use the data from this study to refine the model parameters as Jones and Riechert (2008) did, because the studies were conducted at different sites. It is clear from this study that all sites are not equal, as the spiders at Warrior's Path were generally more successful than those at Boone Lake. This indicates that a broader scale analysis of the relative fitness of social and solitary colonies across the region is warranted.

In *A. studiosus* and other spiders, the fitness consequences of a reduced-aggression syndrome may significantly constrain the evolution of sociality (Pruitt *et al.*, 2008, 2010). Multi-female colonies are an emergent property of individuals' social phenotype, and thus, social females must be in high enough proportions for colonies to form. If social individuals evolved from solitary subsocial species (as widely believed to be the case; Avilés, 1997), the initial proportion of social individuals in a population could be very low. In such a scenario, the likelihood of social individuals having colony-mates would also be low. Under these conditions, even if multi-female colonies were favoured, there would still be a 'trough' in the adaptive landscape where social individuals (lacking colony-mates) could experience depressed fitness, and such a trough might prove difficult to cross (Wright, 1932; Fig. 4). This hypothesis is consistent with the observation that social spiders are extremely rare (Avilés, 1997; Lubin & Bilde, 2007), and



**Fig. 4.** Illustration of the hypothesised fitness landscape faced by spiders transitioning from subsocial to social strategies. This model assumes that local conditions favour medium-sized colonies and that the solitary phenotype is initially prevalent.

that multi-female colonies are relatively rare in *A. studiosus*, even in areas that seem to favour them (Jones & Riechert, 2008). Future work in the *A. studiosus* system should focus on how such a maladaptive trough could be traversed. For instance, it could be that the shift to social phenotypes occurred across an entire brood, in which case, social individuals would be provided with colony-mates immediately. Alternatively, certain habitat types might favour decreased aggressiveness at some instances in time.

Once multi-female colonies *have* formed, reduced aggressiveness could understandably be advantageous. For example, depressed individual aggressiveness likely diminishes the risk of within-colony conflict over prey, mates and preferred web space (Pruitt *et al.*, 2008; Pruitt & Riechert, 2009a,b,c). Within-colony aggression towards colony-mates might be particularly disadvantageous in *A. studiosus*, because colony members are related on the order of half-sibs (Duncan *et al.*, 2010), and thus, intra-colony aggression could yield indirect fitness costs. Regardless of the summative effects of direct and indirect fitness, selection on aggressiveness must balance the benefits of reduced aggressiveness in a social environment against the depressed fitness of singleton social females identified in the present study.

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## References

- Agnarsson, I., Maddison, W.P. & Avilés, L. (2007) The phylogeny of the social *Anelosimus* spiders (Araneae: Theridiidae) inferred from six molecular loci and morphology. *Molecular Phylogenies and Evolution*, **43**, 833–851.
- Arnqvist, G. & Henriksson, S. (1997) Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology*, **11**, 255–273.
- Avilés, L. (1997) Causes and consequences of cooperation and permanent-sociality in spiders. *Evolution of Social Behaviour in Insects and Arachnids* (ed. by J. Choe and B. Crespi), pp. 476–498. Cambridge University Press, Cambridge, U.K.
- Avilés, L. & Tufiño, P. (1998) Colony size and individual fitness in the social spider *Anelosimus eximius*. *American Naturalist*, **152**, 403–418.
- Bell, A.M. (2005) Differences between individuals and populations of threespined stickleback. *Journal of Evolutionary Biology*, **18**, 464–473.
- Bell, A.M. & Sih, A. (2007) Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, **10**, 828–834.
- Bell, A.M. & Stamps, J.A. (2004) The development of behavioural differences between individuals and populations of stickleback (*Gasterosteus aculeatus*). *Animal Behaviour*, **68**, 339–348.
- Brach, V. (1977) *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. *Evolution*, **31**, 154–161.
- Dingemans, N.J., Wright, J., Kazem, A.J.N., Thomas, D.K., Hickling, R. & Dawray, N. (2007) Behavioural syndromes differ predictably between 12 populations of stickleback. *Journal of Animal Ecology*, **76**, 1128–1138.
- Duncan, S.E., Riechert, S.E., Fitzpatrick, B.M. & Fordyce, J.A. (2010) Relatedness and genetic structure in a socially polymorphic population of the spider *Anelosimus studiosus*. *Molecular Ecology*, **4**, 810–818.
- Furey, R.E. (1998) Two cooperatively social populations of the theridiid spider *Anelosimus studiosus* in a temperate region. *Animal Behaviour*, **55**, 727–735.
- Herczeg, G., Gonda, A. & Merila, J. (2009) Predation mediate population divergence in complex behaviour of nine-spined stickleback (*Pungitius pungitius*). *Journal of Evolutionary Biology*, **22**, 544–552.
- Johnson, J.C. & Sih, A. (2005) Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, **58**, 390–396.
- Johnson, J.C. & Sih, A. (2007) Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Animal Behaviour*, **74**, 1131–1138.
- Jones, T.C. & Parker, P.G. (2000) Costs and benefits of foraging associated with delayed dispersal in the spider *Anelosimus studiosus* (Araneae: Theridiidae). *Journal of Arachnology*, **28**, 61–69.
- Jones, T.C. & Parker, P.G. (2002) Delayed juvenile dispersal benefits both mother and offspring in the cooperative spider *Anelosimus studiosus* (Araneae: Theridiidae). *Behavioral Ecology*, **13**, 142–148.
- Jones, T.C. & Riechert, S.E. (2008) Patterns of reproductive success associated with social structure and microclimate in a spider system. *Animal Behaviour*, **76**, 2011–2019.
- Jones, T.C., Riechert, S.E., Dalrymple, S.E. & Parker, P.G. (2007) Fostering model explains environmental variation in levels of sociality in a spider system. *Animal Behaviour*, **73**, 195–204.
- Krafft, B. (1979) Organisation et évolution des sociétés d'araignées. *Psychology*, **1**, 23–51.
- Lubin, Y. & Bilde, T. (2007) The evolution of sociality in spiders. *Advances in the Study of Behavior*, **37**, 83–145.
- Maupin, J.L. & Riechert, S.E. (2001) Superfluous killing in spiders: a consequence of adaptation to food-limited environments? *Behavioral Ecology*, **12**, 569–576.
- Morse, D. (1988) Relationship between crab spider *Misumena vatia* nesting success and earlier patch-choice decisions. *Ecology*, **69**, 1970–1973.
- Nelson, X.J., Wilson, D.R. & Evans, C.S. (2008) Behavioral syndromes in stable social groups: an artifact of external constraints? *Ethology*, **114**, 1154–1165.
- van Oers, K., de Jong, G., van Noordwijk, A.J., Kempenaers, B. & Drent, P.J. (2005) Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour*, **142**, 1185–1206.
- Powers, K.S. & Avilés, L. (2003) Natal dispersal patterns of a subsocial spider *Anelosimus* c.f. *jucundus* (Theridiidae). *Ethology*, **109**, 725–737.
- Pruitt, J.N. & Husak, J.F. (2010) Context-dependent running speed in funnel-web spiders from divergent populations. *Functional Ecology*, **24**, 165–171.
- Pruitt, J.N. & Riechert, S.E. (2009a) Sex matters: sexually dimorphic fitness consequences of a behavioral syndrome. *Animal Behaviour*, **78**, 175–181.
- Pruitt, J.N. & Riechert, S.E. (2009b) Male mating preference is associated with risk of pre-copulatory cannibalism in a socially polymorphic spider. *Behavioral Ecology and Sociobiology*, **63**, 1573–1580.
- Pruitt, J.N. & Riechert, S.E. (2009c) Frequency dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. *Evolution*, **63**, 2966–2973.
- Pruitt, J.N., Riechert, S.E. & Jones, T.C. (2008) Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour*, **76**, 871–879.
- Pruitt, J.N., Riechert, S.E., Iturralde, G., Vega, M., Fitzpatrick, B.M. & Avilés, L. (2010) Population differences in behaviour are explained by shared within-population trait correlations. *Journal of Evolutionary Biology*, **23**, 748–756.
- Purcell, J. & Avilés, L. (2007) Smaller colonies and more solitary living mark higher elevation populations of a social spider. *Journal of Animal Ecology*, **76**, 590–597.
- Riechert, S.E. & Hedrick, A.V. (1993) A test for correlations among fitness linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Animal Behaviour*, **46**, 669–675.
- Riechert, S.E. & Jones, T.C. (2008) Phenotypic variation in the social behaviour of the spider *Anelosimus studiosus* along a latitudinal gradient. *Animal Behaviour*, **75**, 1893–1902.
- Sih, A., Kats, L.B. & Maurer, E.F. (2003) Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, **65**, 29–44.
- Sih, A., Bell, A.M. & Johnson, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.
- Simpson, M.R. (1993) Reproduction of two species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. *Canadian Journal of Zoology*, **71**, 451–457.

- Viera, C., Ghione, S. & Costa, F.G. (2007) Mechanisms underlying egg-sac opening in the subsocial spider *Anelosimus* cf. *studiosus* (Araneae Theridiidae). *Ethology, Ecology and Evolution*, **19**, 61–67.
- Vollrath, F. (1987) Growth, foraging and reproductive success. *Ecophysiology of Spiders* (ed. by W. Nentwig), pp. 57–370. Springer, Berlin, Germany.
- Wilson, E.O. (1975) *Sociobiology*. Belknap/Harvard University Press, Cambridge, Massachusetts.
- Wilson, D.S., Coleman, K., Clark, A.B. & Biederman, L. (1993) The shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.
- Wright, S. (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the Sixth Congress of Genetics*, **1**, 356–366.
- Yip, E.C., Powers, K.S. & Avilés, L. (2008) Cooperative capture of large prey solves scaling challenge faced by large spider societies. *Proceedings of the National Academy of Sciences of the USA*, **105**, 11818–11822.

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