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Social spiders: mildly successful social animals with much untapped research potential

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In some ways, social spiders are a biological novelty item. They are not extraordinarily successful either evolutionarily or ecologically, and their societies suffer a variety of disadvantages that render them more brittle than other social systems. Yet, from an empiricist's perspective, these attributes make them uniquely poised for addressing a variety of research questions. Here we provide a brief overview of the biology of social spiders for the general reader. We then highlight a variety of ecological and evolutionary challenges suffered by these animals that renders them at risk of extinction in the short and long term. We finally discuss how these hardships have given rise to a variety of individual and group level adaptations that are rare or entirely absent in other spiders, as well as in most other social animals. Throughout this article, we highlight gaps in our current understanding of these creatures and draw attention to some of the more promising frontiers for future research. To this end, we have two goals. First, we would like to draw the attention of general behavioural ecologists interested in social evolution to the biology of social spiders, and emphasize a variety of reasons why one might consider these animals for their next research question. Second, for those already inculcated in the social spider literature, we hope that this article will raise the reader's consciousness to various underexplored but promising avenues for future research. With the right research question, social spiders promise to be a high-profile and high-throughput model system.

The evolution of sociality is often viewed as a key evolutionary transition (Maynard Smith & Szathmary, 1995). This is, in part, because group living can radically alter the selective landscape where other traits evolve (Moore, Brodie, & Wolf, 1997; Wolf, Brodie, Cheverud, Moore, & Wade, 1998). In its most extreme cases, sociality can give rise to adaptations that cannot be sustained in nonsocial environments. Highly altruistic traits, such as sterile castes in social insects, are possibly the most broadly appreciated example of such traits (Abbot et al., 2011). However, group living can also give rise to a variety of other novel trait types, at both the individual and group level (Gardner & Grafen, 2009). In this review and perspectives paper, we consider the degree to which group living has caused novel adaptations in a taxon better known for aggression towards conspecifics: spiders.

Of the nearly 47 000 described species of spider, fewer than 30 exhibit permanent cooperative sociality (Avilés & Guevara, 2017). Social spiders differ from other kinds of group-living spiders, namely colonial spiders and subsocial spiders, in a few respects. Colonial spiders aggregate together in conglomerate webs but maintain individual subterritories within these aggregations; thus, individuals within these aggregations generally do not cooperate directly. Subsocial spiders live in cooperative family groups composed of a single mother and her offspring, but those offspring develop aggressiveness towards their siblings sometime in their development, and will disperse prior to their penultimate moult. Social spiders, which are hypothesized to have evolved from subsocial ancestors, never develop aggressiveness towards their siblings and instead remain within their natal web generation after generation and cooperate in a variety of tasks (Avilés, 1997).

Social spiders are characterized by cooperative prey capture, group web construction, shared colony defence, alloparental care and high degrees of tolerance towards conspecifics (Avilés, 1997; Lubin & Bilde, 2007; Fig. 1). With few exceptions, spider sociality is restricted to the tropics (Furey, 1998; Guevara & Avilés, 2015). Although social spiders are not speciose, several genera (e.g. *Stegodyphus* and *Anelosimus*) exhibit a wealth of both intraspecific and interspecific variation in their degree of sociality, and this variation

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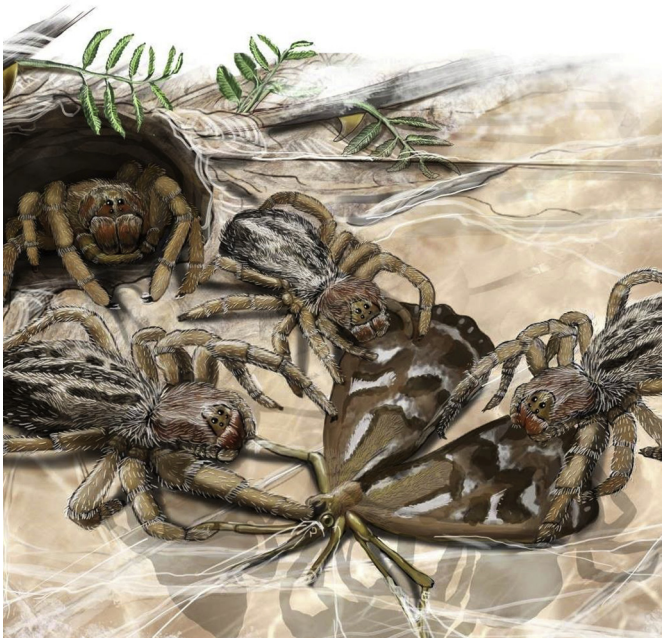

Figure 1. Social *Stegodyphus* engaged in cooperative prey capture. Artist: Mesa Schumacher.

helps illuminate the ecological drivers and evolutionary consequences of sociality in these animals (Powers & Avilés, 2007; Purcell & Avilés, 2007).

This paper consists of three parts. First, we briefly review the most prominent hypotheses for why sociality has evolved rarely but repeatedly in spiders. We detail how social spiders differ from their subsocial ancestors, and how specific selective advantages may have given rise to the transition from subsociality to sociality. Second, we outline the ecological challenges brought about by group living, and the adverse effects that these challenges have on individual fitness and group performance. Finally, we discuss some adaptations that have emerged in response to the ecological challenges of group living in spiders. We contrast these traits against situations where the pre-existing traits of subsocial spiders may have helped ease the transition to permanent social living. Throughout this paper we highlight promising avenues for future study. We do not intend this paper to be an exhaustive review of social spider biology. A comprehensive review of social and colonial spiders has recently been published (Avilés & Guevara, 2017) and several earlier reviews on these animals are also available (Avilés & Guevara, 2017; Avilés, 1997; Buskirk, 1981; Lubin & Bilde, 2007). We instead consider this paper a roadmap for empiricists interested in harnessing the experimental potential of these animals and an opportunity to showcase some of their extraordinary biology.

SOCIAL SPIDER BIOLOGY

Why Are They Social?

Social spider research for the last 40 years has largely been devoted to answering the question: why are social spiders social? Noting that nearly all social spider species belong to genera that build dense three-dimensional webs, Avilés and Guevara (2017) argued that the most immediate benefit of group living in spiders is retaining the protection afforded by the natal nest and sharing the costs of its maintenance, followed by a need for surrogate caregivers for the offspring in adverse environments. According to these authors, accessing large prey is vital for these animals, but is actually a secondary benefit of group living for them. Yet, ample evidence suggests that assistance with at least three types of task, web maintenance and defence, prey capture and alloparental care, has a hand in guiding social evolution in these animals.

Before delving into the biology of different social spider systems, we first note that the evolutionary antecedent to prolonged sociality in spiders is subsociality (Yip & Rayor, 2014). Subsocial spiders are characterized by prolonged obligate parental care and tolerance of conspecifics as juveniles (Bilde & Lubin, 2001; Jones & Parker, 2002; Miller & Agnarsson, 2005). They assist each other in web maintenance and cooperative prey capture. However, the early tolerance towards conspecifics exhibited by subsocial spiders is eventually replaced by aggression at some point prior to maturity, but the precise switching point varies between species (Avilés & Harwood, 2012) and with food availability (Kim, 2000). This latent aggressive behaviour results in premating dispersal in subsocial spiders, and the exchange of genetic material between colony lineages via the dispersal of males between webs (Avilés & Gelsey, 1998; Powers & Avilés, 2003; Ward & Lubin, 1993). Social spiders, in contrast, never develop this latent aggression towards conspecifics and instead remain for their lifetimes in communally cooperative societies. The finding that many subsocial species occasionally form multifemale colonies in some habitats but not others suggests that the evolutionary tipping point from subsociality to sociality in spiders is reasonably common and experimentally accessible (Jones, Riechert, Dalrymple, & Parker, 2007; Riechert & Jones, 2008). The immediate and most pressing question is therefore: what are the environmental factors (e.g. climatic conditions, enemy abundances) that contribute to the transition from subsociality to prolonged sociality?

Neotropical rainforests have favoured the repeated evolution of sociality in the genus *Anelosimus* (Agnarsson, Avilés, Coddington, & Maddison, 2006). These habitats are characterized by intense rain that damages spiders' webs (Purcell & Avilés, 2008), frequent attacks by predatory ants (Hoffman & Avilés, 2017) and the presence of large insect prey (Powers & Avilés, 2007). In such environments group-living spiders enjoy the benefits of reduced per capita energy investment in web repair following rain (Riechert, 1985; Riechert, Roeloffs, & Echternacht, 1986). Colonies are also more likely to survive sieges by ants than individual spiders in a solitary web (Purcell & Avilés, 2008). Group living helps to ensure that at least some colony members survive such attacks in order to reproduce or to provide obligate parental care to orphaned spiderlings (Jones et al., 2007). The formation of large colonies, however, is only possible in the lowland tropical rainforest where large prey are available for large colonies to capture and subdue cooperatively (Guevara, Gonzaga, Vasconcellos-Neto, & Avilés, 2011; Rypstra, 1993; Yip, Powers, & Avilés, 2008). As insect size decreases with increasing elevation, so the relative social complexity of the spiders decreases (Avilés et al., 2007). Subsocial spiders, in contrast, are excluded from lowland rainforest environments as single mothers are unable to repair the damage caused by intense rain and survive attacks by ants and other predators (Hoffman & Avilés, 2017; Purcell & Avilés, 2008).

A second genus of spider that has iteratively evolved permanent sociality is the Old World genus *Stegodyphus*. Like *Anelosimus*, social *Stegodyphus* appear to have evolved multiple times from subsocial ancestors (Johannesen, Lubin, Smith, Bilde, & Schneider, 2007), and the distribution of social species is largely restricted to habitats with greater precipitation and productivity (Majer, Svenning, & Bilde, 2013). These include savannah habitats in southern Africa, Madagascar and India. Social *Stegodyphus* experience many of the same selection pressures as social *Anelosimus*, implying that a similar recipe of selection pressures has given rise to sociality

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