

Carmen Viera · Marcelo O. Gonzaga
Editors

Behaviour and Ecology of Spiders

Contributions from the Neotropical
Region

 Springer

Chapter 13

Parental Care and Sociality

Carmen Viera and Ingi Agnarsson

Abstract Spiders are famously aggressive and cannibalistic, and nearly all are solitary. Only about 20–25 out of over 46,000 known species display highly social behavior. Nevertheless, sociality has arisen in multiple families independently in spiders, probably via the ‘maternal care route’, with an apparent concentration of social species in the Neotropics. We review aspects of reproduction and maternal care and how these may interplay with the evolution and maintenance of social cooperative behavior, focusing on Neotropical spiders. We also discuss the behavioral, ecological, and evolutionary contexts in which these behaviors have evolved in spiders, and highlight the unique opportunities that exist for research due to the multiple independent evolutionary experiments that replicated origins of sociality offer. We ponder why social species appear concentrated in the Neotropics, with the outstanding example found in the genus *Anelosimus*. Curiously, highly social *Anelosimus* are restricted to the Neotropics, while the genus is distributed globally and ubiquitously displays extended maternal care. We discuss traits that are shared among these independently derived social species and thus form a part of a social ‘syndrome’. Such traits include absence of dispersal, inbreeding, biased sex ratios, and even shared patterns of colony composition of individuals differing in personality type. Ecologically, social Neotropical spiders are mostly restricted to tropical lowland and mid-elevation forests where prey size tends to be greater than in areas where sub-social species are found. They are especially common in areas of high rainfall, where their very dense 3-dimensional webs may not only allow capture of large prey, but also serve as a predator defense, for examples where ants are particularly common. Neotropical social spiders receive benefits from collaboration in web construction, care of young, nest defense, and prey capture, where they can handle much larger prey than other similarly sized spiders, and more effectively fend off predators. Colonies seem to benefit from a mix of personality types within colonies with both bold and shy individuals being crucial to colony success, but with

C. Viera (✉)

Entomología, Biología Animal, Facultad de Ciencias, Universidad de la República,
Montevideo, Uruguay

Laboratorio Ecología del Comportamiento, Instituto de Investigaciones Biológicas Clemente
Estable, Montevideo, Uruguay

e-mail: anelosimus@gmail.com

I. Agnarsson

Department of Biology, University of Vermont, Burlington, VT, USA

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C. Viera, M.O. Gonzaga (eds.), *Behaviour and Ecology of Spiders*,
https://doi.org/10.1007/978-3-319-65717-2_13

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larger colonies having more shy individuals and thus characterized by lower overall aggression. While sociality seems to offer short-term benefits in certain environments, a switch to an inbred breeding system that is tightly linked to sociality in spiders seems responsible for a loss of genetic variability that may restrict diversification due to vulnerability to climate change, disease, and parasitism.

Social behavior, characterized by long-term cooperation among individuals, is relatively rare, yet is found in many animal groups; the best known examples occur in eusocial insects such as ants, bees, and termites (Wilson 1971, 1975). In such societies, individuals are often morphologically specialized (castes), and most contribute various tasks to the colony as non-reproductive workers, with a single or a few queens bearing all the young of the colony. Many eusocial lineages are characterized by haplodiploidy (males come from unfertilized eggs and are thus haploid), a trait that may facilitate social evolution through increasing relatedness among sisters (Hamilton 1964a, b) and/or by enabling the queen to control sex ratios and produce more of the sex contributing more to the colony: female workers (Gardner and Ross 2013). Other animals can be strictly asocial, where aggression is more characteristic than cooperation among members of the same species. Such is the case for many spiders that are solitary and aggressive, often cannibalistic, and cooperation is absent (Avilés 1997; Bilde and Lubin 2011; Foelix 1982; Yip and Rayor 2014). Perhaps most animal species show behaviors somewhere in between these extremes, ranging from elementary care of young by the mother (simple maternal care, or ‘transient subsociality’ as defined by Yip and Rayor 2014) to highly cooperative behaviors that involve multiple reproductive individuals, rather than a single queen (cooperative sociality or quasisociality, hereafter ‘sociality’) (Avilés 1997; Avilés and Purcell 2012; Bilde and Lubin 2011; Kullmann 1972; Lubin and Bilde 2007; Yip and Rayor 2014). Spiders are an interesting group in the study of sociality, in part because they show this broad range of behaviors, and in part because they lack the apparent (though poorly understood) common correlate of animal sociality, haplodiploidy (Avilés 1997). It has long been apparent that maternal care, where the mother cares for her newly hatched offspring, is a trait shared by species ranging from mostly solitary to those that are highly cooperative (e.g., Burgess 1978; Vollrath 1982; Yip and Rayor 2014). During this stage, juveniles are typically not aggressive towards one another. This observation underlies the prominent hypothesis on the origin of sociality through the extension of juvenile tolerance and web sharing from early instars to adulthood, dubbed the ‘maternal care hypothesis’ (Agnarsson 2002, 2004; Avilés 1986, 1997; Avilés and Gelsey 1998; Avilés and Tufino 1998; Burgess 1978; Grinsted et al. 2014; Smith 1986, 1987; Uetz 1983; Vollrath 1982). Indeed, “subsociality is maternal care that spans several, rather than few, juvenile instars” (Agnarsson 2004: 471), and sociality is then characterized by the absence of dispersal from the natal nest of these cohabiting, tolerant, and cooperative individuals.

Comparative studies across spider species that display the range of social behaviors could cast light on social evolution (e.g., Settepani et al. 2016), and on the role of

early maternal care and tolerance among juveniles in social origins (Avilés 1997; Kullmann 1972). Indeed, the maternal care hypothesis makes an explicit phylogenetic prediction: that social species should phylogenetically nest within clades characterized by shorter-term maternal care and subsociality.

Fortunately, the phylogeny of many of the social spiders is fairly well understood (Agnarsson 2006, 2012b; Agnarsson et al. 2006a, 2007, 2013a, 2015, 2016; Agnarsson and Rayor 2013; Johannesen et al. 2007, 2009b; Liu et al. 2016; Ruch et al. 2015), facilitating such tests (Fig. 13.1). The results have supported the predictions of the maternal care hypothesis in the groups containing the highest number of social species: Theridiidae (Agnarsson 2006; Agnarsson et al. 2006a, 2007) and *Stegodyphus* (Johannesen et al. 2007; Johannesen et al. 2009a, 2009b). These phylogenies imply multiple independent origins of sociality, even among close relatives, and in all cases, highly social lineages are nested within clades that show ancestral maternal care, typically extended maternal care that is characterized as subsociality (see Agnarsson et al. 2006a). Therefore, there is little doubt that the origin of web-sharing sociality in spiders has its root in early maternal care. The most prominent alternative hypothesis, that sociality may have arisen from foraging groups of non-relatives, see for example Avilés (1997), in contrast, has not been supported by any explicit tests, and does not explain this strong phylogenetic concordance between adult cooperation and maternal care of juveniles.

Another interesting taxonomic and phylogenetic pattern is that there seems to be a particular concentration of both species and social origins in the Neotropics (Figs. 13.1 and 13.5) (Agnarsson 2012a, Agnarsson et al. 2006a, Avilés 1997, Avilés et al. 2001). Furthermore, the environment of social spiders, what abiotic factors may facilitate cooperation, and how social level varies with such factors has been particularly well studied in the Neotropics (Avilés et al. 2007, Guevara and Avilés 2007, 2009; Purcell 2011, Purcell and Avilés 2007, 2008). Thus, a focus on available knowledge with regard to parental care and sociality in Neotropical spiders (see also Avilés et al. 2001) seems useful in elucidating the ecological and evolutionary correlates of social behavior in the context of presumably ‘preadaptive’ maternal care. We do not include in our discussion territorial social spiders (e.g., Fig. 13.2), as these have no evolutionary connection to maternal care of young; for a summary of the biology of some Neotropical territorial social spiders see Avilés (1997) and Avilés et al. (2001).

While cooperative behavior has evolved repeatedly in spiders, it is found in only a tiny fraction, less than 0.05%, of spider species (Agnarsson et al. 2006a; Avilés 1997; Bilde and Lubin 2011; World Spider Catalog 2017). The degree of maternal care and cooperation varies across species, but may include collaborating in web construction, prey capture and feeding, nest defense, and cooperative care of egg-sacs and brood (Fig. 13.4). In social species showing high levels of cooperative brood care, some females may lack any reproductive output. However, the characterization of these species as eusocial (Buskirk 1981, Rypstra 1993, Vollrath 1986) is more misleading than useful. First, there is no caste system—though there may be some division of labor (Holbrook et al. 2014, Settepani et al. 2013)—in social spiders (Avilés 1997, Avilés et al. 2001, Avilés and Tufino 1998), and second there is

Fig. 13.2 *Parawixia bistriata* (Araneidae) from Southeastern Brazil. (a) Group of immature spiders resting during the day. (b, c) Prey capture. (d) Spiders leaving the retreat to build their orb webs at night (Photos: M.O. Gonzaga)

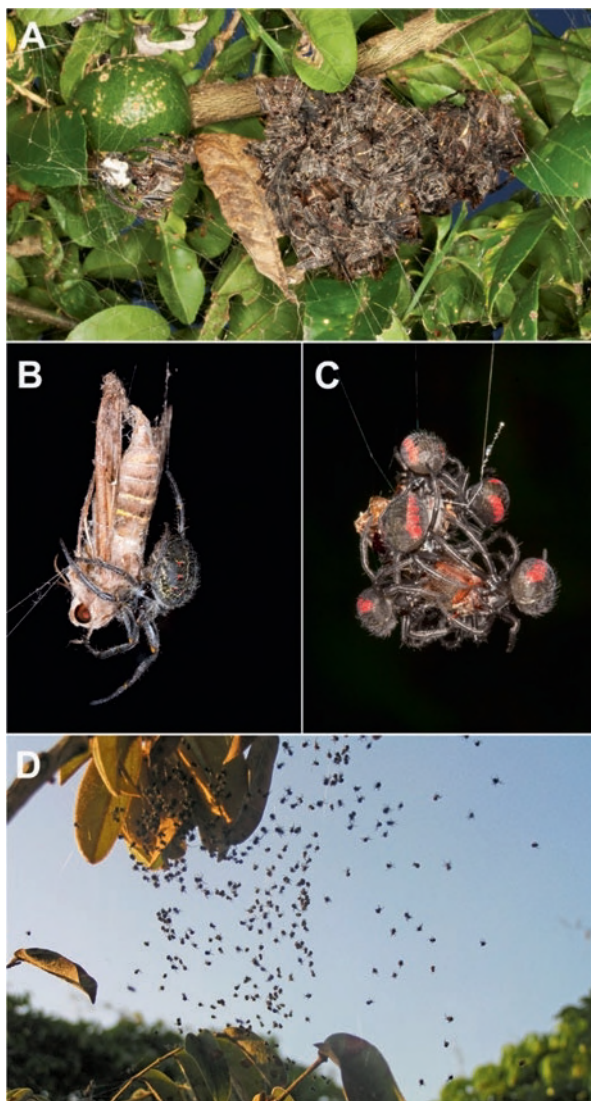


Fig. 13.1 (continued) Nevertheless, social species are scattered, and only a single social pair is recovered (*star*), presumably indicating speciation within a social lineage (*Anelosimus rupununi* and *A. lorenzo*). Sociality in nine species is thus best explained by eight independent social origins. In *Anelosimus*, sociality has only evolved (or been discovered) in the Americas. The social *T. nigroannulatum* is also American, whereas *P. wau* is from Papua New Guinea. Two species that show intermediate social levels are indicated with *green branches* (*A. dubiosus* and *A. jabaquara*). The social *A. eximius*, remains difficult to place, with two alternative topologies (indicated with *circles*) having the highest likelihoods (see also Agnarsson et al. 2007). The resolution of its placement will ultimately affect the number of reconstructed origins of sociality

as yet no evidence available suggesting that the proportion of non-reproductive females in social colonies is higher than the proportion of females of solitary species that fail to reproduce (Agnarsson 2006). More than half of the social spiders belong to the family Theridiidae, and the majority of these to the genus *Anelosimus* (Agnarsson 2005, 2006; Agnarsson et al. 2015, 2016). *Anelosimus* species generally range from social to subsocial (e.g., Avilés 1997; Lubin and Bilde 2007; Yip and Rayor 2014), to species with a very brief period of maternal care of young (e.g., Agnarsson et al. 2006b; Ito and Shinkai 1993). The biology of social spiders in the Neotropics has been the subject of many studies (e.g., Agnarsson 2006; Agnarsson et al. 2006b, 2013a; Albo et al. 2007; Avilés 1986, 1993a, 1994, 1997, 2000; Avilés et al. 2000, 2001, 2006, 2007; Avilés and Maddison 1991; Avilés and Purcell 2011; Brach 1975, 1976, 1977; Buskirk 1981; Cangialosi 1990a, 1990b; Coddington and Agnarsson 2006; Gonzaga and Vasconcellos-Neto 2001, 2002a, b; Grinstead et al. 2014; Guevara and Avilés 2015; Harwood and Avilés 2013; Krafft 1985; Krafft and Pasquet 1991; Kullmann 1972; Levi and Smith 1982; Lichtenstein and Pruitt 2015; Majer et al. 2013; Marques et al. 1998; Nentwig 1985; Nentwig and Christenson 1986; Overal and Silva 1982; Pasquet and Krafft 1989, 1992; Pasquet et al. 1997; Pruitt et al. 2011, 2012; Rypstra and Tirey 1989; Saffre and Deneubourg 2002; Saffre et al. 1999, 2000; Samuk and Avilés 2013; Smith and Hagen 1996; Uetz 1983; Vakanas and Krafft 2001, 2004; Vasconcelos-Netto and Mello 1998; Venticinque and Fowler 1998, 2001; Venticinque et al. 1993; Viera and Albo 2008; Viera et al. 2006, 2007a, b, c; Viera and Garcia 2009; Vollrath and Parker 1992; Vollrath and Rohde-Arndt 1983; Vollrath and Windsor 1986). These studies reveal many shared characteristics of social spiders, despite each social lineage representing an independent evolutionary ‘experiment’. Typically, social spiders have nests with multiple egg-laying females where offspring stay to breed in the natal nest, while subsocial nests consist of a mother and her offspring who disperse at or before adulthood. A dramatic shift in mating system, from outbred to strongly inbred with subdivided population structure, therefore characterizes social spiders (Agnarsson et al. 2013a; Avilés and Bukowski 2006; Avilés and Purcell 2012b; Bilde et al. 2005; Johannesen et al. 2009a; Lubin et al. 2009; Ruch et al. 2009). Differential survival of colony lineages as well as individuals within colonies (multilevel selection), and inbreeding, may have many consequences, including sex ratio bias and loss of genetic variability (Agnarsson et al. 2013a; Avilés 1997; Avilés and Bukowski 2006; Avilés and Purcell 2012b; Bilde et al. 2005; Johannesen et al. 2009a; Lubin et al. 2009; Riechert and Roeloffs 1993; Ruch et al. 2009). Remarkably, nearly all social spiders indeed have highly female-biased sex ratios (Avilés 1986, 1987, 1997; Avilés and Maddison 1991; Avilés et al. 2000; Elgar and Godfray 1987; Lubin 1991; Smith 1986, 1987; Vollrath 1986). There is little to no evidence for dispersal of females between colonies, or for mixing among colony lineages (e.g., Agnarsson et al. 2010b; Avilés 2000; Avilés and Gelsey 1998; Leborgne et al. 1994; Pasquet and Krafft 1989; Vollrath 1982); however, limited male dispersal has been detected (Lubin et al. 2009; Smith et al. 2016). Rather, colony formation is typically by swarm dispersal by multiple individuals, or colony ‘budding’ into two or more daughter colonies (Avilés 1997, 2000; Lubin and Robinson 1982; Saffre and Deneubourg 2002). Individual females may also form new colonies, and individual

males may rarely disperse among colonies. Limited levels of dispersal, for example, have been clearly demonstrated in the African *Stegodyphus* (Berger-Tal et al. 2016; Schneider et al. 2001; Smith et al. 2016). Other traits shared by many social spiders include colony composition of individuals differing in ‘boldness’, and an interplay between boldness, aggression towards prey, and colony size (Pruitt et al. 2011, 2012).

Spiders are diverse on all continents except Antarctica, but this diversity is relatively poorly known outside Europe and North America. Global biodiversity inventories—point estimates based on 1-hectare plots—indicate that species richness is concentrated in the tropics, where the Neotropics are especially diverse (Agnarsson et al. 2013b; Coddington et al. 1991, 1996, 2009; Colwell and Coddington 1994). The number of spider species displaying sociality is also especially high in the Neotropics (Fig. 13.5). Whether that is simply a function of higher diversity in the region, or some other factors, is unclear (see below). One obvious bias is the intensity of study: the Neotropics are by far the best studied tropical region with respect to cooperative spiders, in large part thanks to the efforts of Leticia Avilés and colleagues (e.g., Avilés 1993b, 1994, 1997; Avilés et al. 2001, 2006, 2007; Avilés and Purcell 2011). However, such bias does not easily explain some apparent patterns such as the exclusive occurrence of sociality in Neotropical *Anelosimus*, despite global distribution of the genus (Agnarsson 2012b, Agnarsson et al. 2016) (Figs. 13.1 and 13.5). Hence, the Neotropics for some reason have an inordinate number of spiders that differ from the typical spider in terms of aggression and cooperation. Here we summarize some recent research on parental care and cooperative behavior in Neotropical spiders, to highlight the wealth of recent research in the area and the contribution of this region to understanding of the broader issues of origin of sociality.

Phylogenetics: The Taxonomic Distribution and Origin of Sociality

Analyzing behaviors such as maternal care and sociality using phylogenetic tools is essential to address some basic sociobiology questions. These include whether sociality has evolved multiple times, and if so, in what taxonomic and behavioral contexts. Furthermore, phylogenetics can help answer questions with regard to what the evolutionary causes and consequences of the switch to cooperative behavior are—and in the case of spiders, an associated immediate shift to inbreeding (e.g., Agnarsson et al. 2006a; Avilés 1997; Johannesen et al. 2007). Phylogenetic work to date has yielded two striking patterns regarding the taxonomic distribution of social species, they are simultaneously phylogenetically clustered (non-randomly distributed within a small portion of spider families) and ‘spindly’ (occurring only on isolated phylogenetic branches within these clusters) (Fig. 13.1) (Agnarsson et al. 2006a; Johannesen et al. 2007). Below, we consider the special case of Neotropical social spiders.

Yip and Rayor (2014) offer an excellent review of subsocial spiders and provide a useful framework to discuss the range of behaviors from basic maternal care such as construction of an eggsac, to cooperative behavior where some females forgo reproduction. They refer to as ‘transient subsocial’ those species whose maternal care is limited to care of egg and recently emerged instars, prior to the stage at which they begin to feed (Yip and Rayor 2014). Typically, this is limited to protection of the eggsac and spiderlings as they emerge from it. A large, but unknown, number of spiders offer some protection of the eggsac; this may well be an ancestral behavior for most spiders and will thus not be a focus of this review. Instead, we focus on those species that Yip and Rayor (2014) label ‘subsocial’, showing maternal care beyond the stage at which the juveniles start to feed, up to species showing high levels of sociality like *Anelosimus eximius* (Figs. 13.3 and 13.4) and *Theridion nigroannulatum* (Fig. 13.4).

It is interesting to look at the number and distribution of both subsocial (maternal care) and social spider species worldwide and across the spider tree of life. Yip and Rayor (2014) reviewed the literature and found information on 70 species that they consider subsocial and list in their Table 1. They furthermore estimate an additional 14 subsocial species of Eresidae, bringing the total to 84, plus an unknown number among the genus *Anelosimus*. They included in their list 17/74 *Anelosimus* species (World Spider Catalog 2017); a further eight are social (Agnarsson 2006), but most likely the remainder are all subsocial (under the Yip and Rayor definition). Therefore, there is reasonably good evidence for subsociality in at least 130 spider species. Of course, the actual number is probably vastly greater; we simply lack field observations



Fig. 13.3 *Anelosimus eximius* from Pará, Brazil (Photo: M.O. Gonzaga)



Fig. 13.4 Colonies of *Anelosimus eximius* (above) spanning less than a meter (left) and over 2 m diameter (right) and containing hundreds to over a thousand individuals respectively. Below are females of *Theridion nigroannulatum* collectively defending eggsacs (Photos: Ingi Agnarsson, Matjaž Kuntner)

on most spider species. Nevertheless, if we consider these known species several intriguing patterns emerge. First, these are spread across many spider families and genera, and Yip and Rayer estimated at least 18 independent origins of subsociality in spiders. This is remarkably close to the number of estimated independent origins of quasisociality (Agnarsson et al. 2006a; Avilés 1997), even though not all subsocial lineages have yielded social species. Second, subsocial spiders are found throughout the world; and while they are more common in subtropical or tropical areas, they range to higher latitudes, e.g., in Northern USA and Europe. In contrast, social species are almost entirely constricted to the tropics, apart from populations of the otherwise subsocial *A. studiosus* that is socially polymorphic in certain areas of the USA (Jones

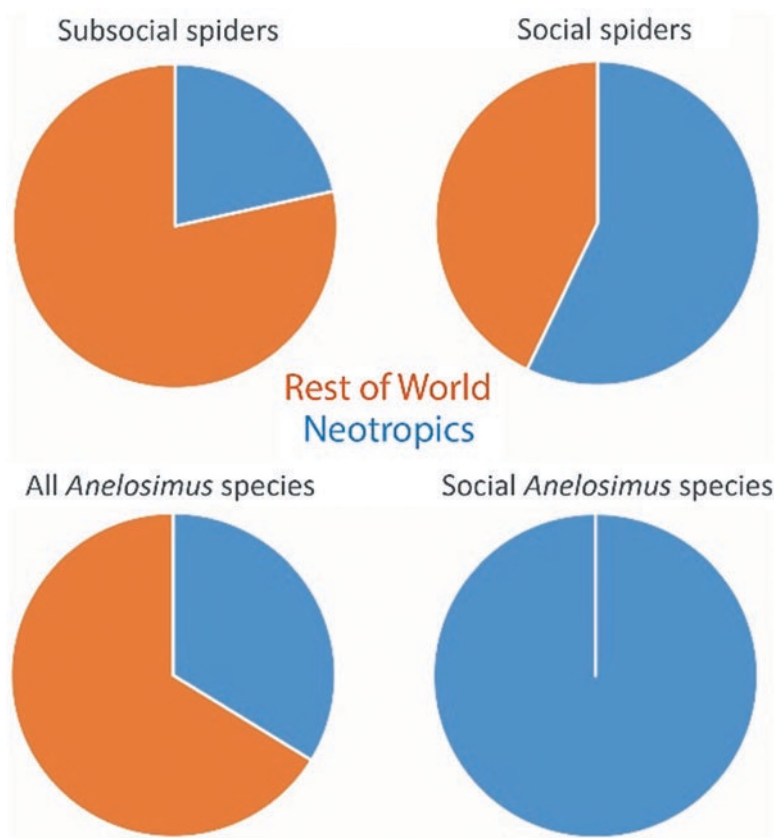


Fig. 13.5 The proportion of social and subsocial spiders in the Neotropics versus the rest of the world. Above, the distribution of subsocial species (*left*), with less than a quarter occurring in the Neotropics, versus social species (*right*) well over half of which are Neotropical. Below, the distribution of all *Anelosimus* species, of which some 30% are found in the Neotropics (*left*), three of all eight social species (*right*)

and Parker 2000, 2002). Subsocial species are not particularly common in the Neotropics, with about 28/130 (21%) of the known species occurring there (Fig. 13.5). Again, in contrast, social species are disproportionately Neotropical where more than half of the social species are found (12/21) (Fig. 13.5).

What could be the reason that the Neotropics have generated more social species, even though the ‘preadaptive’ subsocial trait is not particularly common there? One obvious possibility is knowledge bias. Of the 12 social Neotropical species, five (*Aebutina binotata*, *Tapinillus* sp., *Theridion nigroannulatum*, *Anelosimus guacamayos* and *A. oritoyacu*) were discovered—or for the first time characterized as social—relatively recently by Leticia Avilés (e.g., Avilés 1993b; Avilés et al. 2001, 2006a; Avilés and Purcell 2011). Her efforts researching social spiders in the Neotropics are probably not matched on any other continent, at least not in lowland

rainforest areas where sociality is concentrated (social *Stegodyphus* species are well studied in drier areas of Africa and India (Kraus and Kraus 1988). Without the ‘Leticia factor’, the diversity of Neotropical social spiders would not stand out as clearly. However, there is other evidence that sociality may have evolved more frequently in the Neotropics than expected, based on the distribution of subsocial lineages. The best evidence comes from ecological and phylogenetic research on the genus *Anelosimus*. *Anelosimus* contains 74 species that range in behavior from ‘solitary’ as defined by Agnarsson et al. (2006b) to social (Avilés et al. 2001, 2007), or in other words, in dispersal from natal nest from 2nd to 7th instar to absence of dispersal altogether. Probably none of the species fit into the least social category of Yip and Rayor named ‘transient subsocial’ (dispersal of young prior to commencement of feeding), as in all studied species at least 2nd instar (out of eggsac) spiderlings have been observed in the natal nest. Out of these 74 species, only 25 are found in the Neotropics (~34%), yet all eight social *Anelosimus* are Neotropical (Fig. 13.4), representing no less than 6–7 independent origins of sociality (Fig. 13.1) (Agnarsson 2006; Agnarsson et al. 2007). What could explain the inordinate number of social origins in Neotropical *Anelosimus*? Neotropical *Anelosimus* are certainly better studied than those from other tropical regions; however, some detailed studies on *Anelosimus* elsewhere (Agnarsson 2012b; Agnarsson et al. 2010a, 2015, 2016; Agnarsson and Kuntner 2005) leave no doubt that the vast majority of *Anelosimus* species currently known outside the Neotropics are ‘only’ subsocial. Another possibility could be phylogenetic constraints. For example, if all the social species belonged to a single Neotropical clade, that clade might be characterized by an (as yet unknown) trait that facilitated sociality. However, this is not the case, as social Neotropical *Anelosimus* belong to at least two, distantly related clades (Fig. 13.1) (Agnarsson et al. 2007). The least inclusive clade that contained both of these Neotropical lineages would contain all remaining globally distributed *Anelosimus* lineages (Fig. 13.1). This observation is curious, and merits further scrutiny. However, we can conclude here that, for whatever reason, the Neotropics are rich in social spider species, and are an exciting area where much work has been done and where opportunities exist for a broad range of future studies into the origin and evolution of maternal care and sociality. In the following sections we further explore some of these topics.

Ecology and Sociogeography of Cooperative Spiders

The geographical distribution of species across habitats and landmasses is a central theme of major biological disciplines such as ecology and biogeography (Levin 2009, Losos and Ricklefs 2010). The factors at play are many and diverse, including dispersal ability, geographical history, phylogenetic constraints, and major stochastic events, as well as the ecology and behavior of species. The extent to which behavior of individuals, other than dispersal behavior per se, affects species distribution and diversity has received relatively little attention. For example, their means of dispersal

may afford, or limit, opportunities to cross barriers and colonize distant landmasses. However, other types of behavior such as degree of cooperative behavior and breeding system may also shape species distributions; what might be referred to as ‘socio-geography’. For example, eusociality has allowed insects to dominate many ecosystems, and it has been argued that their extraordinary ecological success in the tropics in fact constrains their diversity (Roubik 1989). The breeding system also relates to biogeographical patterns, e.g., selfing species are more likely to successfully colonize islands. In Neotropical social spiders, Avilés et al. (2007: 783) suggested some sociogeographic patterns. One observation was that “Interestingly, all social spider species appear to occupy a set of habitats more restricted than those available to the phylogenetic lineages in which they occur” (Avilés et al. 2007: 784). As for the particular distribution, they suggested that in the Neotropics “...the absence of subsocial *Anelosimus* species in the lowland rain forest may be due to an increased probability of maternal death in this habitat due to greater predation and/or precipitation, while absence of a sufficient supply of large insects at high elevations or latitudes may restrict social species to low- to mid-elevation tropical moist forests. We refer to these as the ‘maternal survival’ and ‘prey size’ hypotheses, respectively, and suggest that both in combination may explain the geographical distribution of sociality in the genus.” Uetz and Hodge (1990) found that spiders in prey-poor environments were less social than spiders in prey-rich environments. Similarly, populations of *Anelosimus eximius* have both a greater proportion of solitary females and smaller average nest sizes toward the upper end of its elevational range (1000–1300 m) than do populations in the lowlands where prey are larger and more abundant (Purcell and Avilés 2007).

The environmental and biogeographical parallels between altitude and latitude are well known (Stevens 1992; Jimenez-Castillo et al. 2007; Swenson and Enquist 2007). However, altitude and latitude only ‘explain’ the distribution of sociality to the extent that they correlate with environmental and ecological factors that favor or disfavor cooperative behaviors (Avilés et al. 2007). One may suppose that multiple factors play a role, and that these may not always vary in the same manner with altitude and latitude. For example, the widespread species *Anelosimus studiosus* ranges from southern S. America up to northern USA. The species shows clear altitudinal trends across this range. It is restricted to low altitudes at high latitudes, reaches over 3000 m near the equator, and is found at a broad range of altitudes at mid-latitudes (Fig. 13.6). Notably, this species is mostly absent in lowland rainforests where social species are prominent. Even more curiously, in North America, social phenotypes occur in certain populations of this normally subsocial species. Social phenotypes are apparently absent in Florida at 26°N, but appear at about 30°N and increase in occurrence towards 36°N in Tennessee (Riechert and Jones 2008). In either case, it is hypothesized that cooperative behavior is favored in environments where a single female has a high probability of dying before her offspring are able to care for themselves (Jones et al. 2007; Bilde et al. 2007)—the ‘maternal survival’ hypothesis (Avilés et al. 2007). The maternal survival hypothesis may help explain the rarity of subsocial *Anelosimus* species in ‘social habitats’, such as lowland rainforests, where they may experience higher predation risk and frequent web

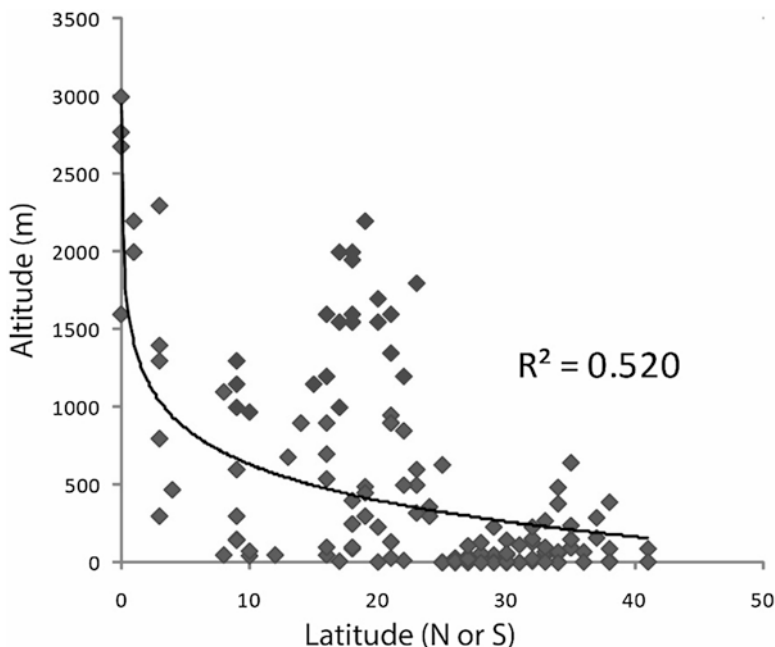


Fig. 13.6 The distribution of the socially polymorphic *A. studiosus* in relation to altitude and latitude. Note the near absence of records from the lowland tropics

damage due to frequent precipitation (see Avilés et al. 2007). In turn, one of the key ecological variables that has been hypothesized to explain the absence of social species from high latitudes and altitudes is prey size (Powers and Avilés 2007, Purcell and Avilés 2008, Yip et al. 2008, Guevara and Avilés 2007, 2009). As colonies grow in both number of spiders and volume of the web, web surface per spider decreases, as does the number of intercepted prey per capita (Yip et al. 2008). Larger colonies therefore increasingly need to capture larger prey items that solitary individuals cannot handle. Accordingly, social species may be absent where sufficiently large prey items are rare. Recently, the hypothesis has received direct support based on an array of empirical data (Powers and Avilés 2007, Purcell and Avilés 2008, Yip et al. 2008, Guevara and Avilés 2007, 2009). Not only do social spider habitats have larger prey than habitats of subsocial species, but also the prey actually caught by social spiders is larger than that which subsocial species catch.

Much work has focused on the ‘typical’ subsocial and social *Anelosimus* species. However, a few species that show unusually short duration of maternal care, and are thus solitary for most of their life cycle, have received less attention. Species such as *A. crassipes* in Japan, (Ito and Shinkai 1993), and *A. pacificus* in Central America (Agnarsson et al. 2006b) have only a brief period of maternal care post emergence of juveniles from eggsac (still fitting Yip and Rayor’s broad definition of subsociality). Similarly, *A. decaryi* and *A. ameliae* from Madagascar and Mayotte (Agnarsson et al. 2010), and *A. potmosbi* and *A. pomio* from Papua New Guinea all share this brief

existence of maternal care. These six, mostly solitary species occupy coastal habitats, often beachfront, where social and typical subsocial *Anelosimus* are nearly entirely absent [*A. kohi* in Malaysia (Agnarsson and Zhang 2006). has been documented in these habitats]. Further, preliminary evidence indicates that a few species occurring in inland habitats at relatively high latitudes have only brief periods of maternal care. These include *A. vittatus* from Europe, and a clade of species from southern S. America (the *ethicus* group as defined by Agnarsson 2005). We note that initial observations on time of dispersal of instars are insufficient to determine level of sociality in observed species. For example, matricide characterizes many of the subsocial–social species, but is (thought to be) absent in most of the less social species. However, a case of matricide was observed in the mostly solitary *A. nigrescens* (Dias et al., *in prep.*). In fact, systematic studies of *Anelosimus* and other spiders that show broad ranges of social behavior within and among species remain an urgent priority. Especially lacking are detailed studies of transient social species and those that show only a brief period of maternal care, as these may offer a unique insight into the early origin of sociality.

It remains unclear to what extent the distribution of solitary *Anelosimus* species follows a latitudinal and/or altitudinal pattern. Latitude clearly plays a role in the example of *A. studiosus*, and *Anelosimus* spiders that differ in social structure clearly differ in global distributions (Fig. 13.7). However, and more broadly, it remains an open question whether the pattern of distribution of solitary, subsocial, and social *Anelosimus* observed in the Americas holds when examining species worldwide. In particular, why no permanently social *Anelosimus* species occurs outside the Americas remains perplexing (Figs. 13.1 and 13.5).

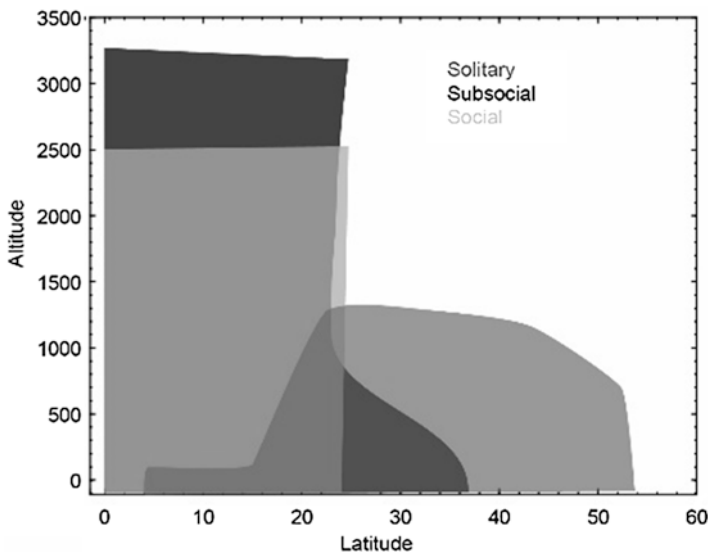


Fig.13.7 A course schematic showing the distribution of solitary, subsocial, and social *Anelosimus* worldwide, in relation to altitude and latitude

Reproductive Aspects of Subsocial Spiders

According to Trivers (1974), parental effort is all the investment that affects the survival success of the offspring. In spiders, parental care is almost synonymous with maternal care, because male contribution to the survival of offspring is very rare, with the exception of *Manogea porracea* (Araneidae), which present amphisexual care (Moura et al. 2017) (Fig. 13.8). In this spider, males protect their brood and keep web integrity in the absence of the mothers. Maternal care is common in many species of spiders, including solitary ones, but the prolongation in time of this behavior is what underlies the formation of more permanent groups.

In a broad sense, nearly all spiders show maternal care, since they build protective sacs for their eggs (Foelix 2011). Another level of investment is added when the spiders take care of the eggsac and the emerged spiderlings during the first instars. These are considered as “solitary” by Wilson (1971) and “transient subsocial behavior” by Yip and Rayor (2014). Agnarsson et al. (2006a) considers the subsocial spiders to be those in which the offspring cooperate in prey capture and web building. We follow here the definition of subsociality of Yip and Rayor (2014)

Fig. 13.8 *Manogea porracea* male close to eggsacs and spiderlings (Photo: M.O. Gonzaga)



in their excellent and exhaustive review about maternal care and subsocial spiders: "... offspring stay together with the parent beyond the age at which they begin to feed, but disperse prior to their own egg-laying and display no alloparental care among adults". Below, we address the importance of extended maternal care in the evolution of sociality from a behavioral context. Furthermore, we consider all reproductive behavior including courtship, mating, and post-mating behaviors which affects parental care and the evolution of sociality.

In social spiders, females cooperate in care of eggsacs and all the spiderlings since their emergence from the eggsac. In many cases (e.g., *Anelosimus eximius*, *A. domingo*, *A. lorenzo*, *Achaearanea wau* and *Stegodyphus dumicola*), a group of females lay the eggsacs more or less synchronously, and then cooperate in taking care of them (Lubin and Robinson 1982, Avilés and Salazar 1999). The high cost of this behavior is shared among all the adult females, not only by the mothers. All females collaborate in colony tasks to assure brood survival and reproductive success. In subsocial spiders, such cooperation among adult females is absent, presumably due to innate intolerance among adult females, as typical of most spiders.

Detailed studies of reproductive behavior can provide us with information about how it relates to parental care and other strategies of survival. Hence, it is necessary to understand the role of all the reproductive cycle in the evolution of sociality. We present a case study focusing on the parental care of the subsocial *Anelosimus viera* from Uruguay. For a better understanding of maternal behavior in this spider—as a model subsocial spider—we describe here all the stages prior to motherhood, beginning with dispersion and male's sexual tactics. We analyze the fights of males for access to females, spermathecal induction, courtship, and mating. Finally, we summarize other maternal behaviors.

Dispersal from the Maternal Nest

Avilés and Gelsey (1998) highlight the lack of the dispersal phase characterizing the transition from subsocial to social spiders. In subsocial spiders, the colony is a family group lasting until the dispersal of the new generation, usually at the subadult stage. Avilés and Gelsey (1998) found that subadults of both sexes dispersed during the mating season. The same process has been studied in other subsocial species, such as *A. studiosus* and *A. viera*. The sex ratio prior to dispersal in *A. jucundus* and *A. studiosus* is 1:1, but in *A. viera* it is approximately 2:1 female-biased (Viera et al. 2007a). Not all individuals necessarily disperse; rather, one or more females can remain in the natal nest. This process opens the possibility of 'new' colonies—natal nests of non-dispersing females—starting the next cycle as a multi-female colony. Thus, polymorphism in colony type and size is observed in the field. Gonzaga and Vasconcellos-Neto (2001) found that in the *A. jabaquara*, a species showing levels of sociality somewhat intermediate between 'typical' subsocial and social species, large adult females are more likely to leave the natal nest, while those females remaining tend to be relatively small. They conclude that the high costs of

dispersal and colony foundation may favor dispersal of large females. Jones and Parker (2000, 2002) analyzed the cost and benefits associated with delayed dispersal in *A. Studiosus*, and found more benefits than costs to both mother and offspring. Most females disperse at the subadult stage, while one or a few females remain in the maternal nest. Males all abandon the natal nest at or near adulthood, a common strategy in most organisms to avoid inbreeding but mostly absent in highly social spider species (Viera et al. 2007a). As seen in many other subsocial species such as *Anelosimus arizona* (Powers and Avilés 2003), Ferreira et al. (*in prep.*) observed in *A. viera* that the amount of available food resources is an important factor determining the timing of dispersal—females dispersed later from well-fed colonies.

Cooperative Behavior Prior to Dispersal

Trophalaxy is a complex and frequent behavior between mothers and offspring in social arthropods. It seems widespread in social spiders but rarer in subsocial species (Avilés and Gelsey 1998). One extraordinary case of regurgitation among subadult *A. viera* has been observed (Viera et al. 2005). Subadult females provided supplementary food to their brothers previous to their dispersal. Males, on average, reach adulthood in six or seven molts, earlier than females, which need seven or eight molts (Viera et al. 2007a). Subadult sisters potentially regurgitate food to their brothers to accelerate the male's maturity. Alternatively, altruistic food sharing among all colony individuals may yield greater overall survival. To test these alternatives, we designed an experiment grouping subadult males and females of different body condition, mixing starved individuals with individuals fed *ad libitum*. The results demonstrated that regurgitation was always from overfed to starved individuals, and strongly biased from females towards males. Males fed by females reached greater size and had a relatively longer first pair of legs than males which did not receive food via regurgitation. The allometric growth of front legs make sense; since the first legs are used in male–male ritualized fights, males with longer first legs have a higher probability of winning contests (Gómez et al. 2015). Thus, food donations from females to their brothers may increase inclusive fitness by assuring better access of brothers to females.

Intolerance among Adult Females

Like other subsocial spiders, individuals of *A. viera* show relatively high inter-individual tolerance, which breaks down at adulthood, when adult females become aggressive among themselves. This aggression limits the degree to which nests are founded by more than one adult female, and thus the level of sociality the species displays. Within subsocial colonies, collaboration and cooperation is extensive among juveniles and with their mother. But unlike social spiders, adult subsocial females do not collaborate in key

tasks such as prey capture and cooperative care of young. Furthermore, the presence of another female inhibits a female from attempting capture of prey. Female intolerance and territoriality were described by Furey (1998) in *A. studiosus*, and have also been observed by Viera et al. (2007a) in *A. viera*. Adult females which remain in the natal nest show intolerance among themselves, and agonistic behavior similar to inter-male contests (Viera et al., in prep.) Experiments in *A. viera* using the methodology proposed by Susan Riechert (*com. pers.*) demonstrated that within multi-female colonies, each female is territorial and avoids any contact with other females, especially when guarding eggsacs (Tambasco et al., *in prep.*). In these experiments, females were forced to encounter other and fight females, and were able to steal eggsacs from other females after winning a contest. This intolerance and aggressive behavior lead to avoidance, and lack of any cooperative behavior related to social benefits such as prey capture and caring for brood. Lack of cooperation among subadult females results in a higher per-capita cost of brood care than in social species.

Preparing for Mating

The sexual behavior of social species is poorly known. We assume that sexual behavior will be relatively simple due to inter-individual tolerance, such as absence of sexual cannibalism and other aggressive interactions toward the males. In many solitary spiders, males avoid female aggression by behaviors such as prolonged and complex courtship, and providing nuptial gifts. However, aggression is not absent between males. They fight for access to females, and may use waiting strategies to get eventual mating, as was also observed by Lubin and Bilde (2007) in the African social spider *Stegodyphus dumicola*. Male fights are ritualized and, at least in experimental conditions, can escalate, to result in serious injuries and death (Albo et al. 2007). Ritualized fights begin with the contenders using the first legs to push into a position facing each other, probably to compare strength. Generally, the larger male wins the contest, but the smaller animal (loser) can flee the arena before a fight escalates. However, frequently the loser male remains completely still near the couple (winning male and female) as a ‘satellite male’, and awaits an opportunity for a later mating once the winning male has left (Fig. 13.9). Females readily accept these satellite males. The potentially dangerous waiting is rewarded by reproductive success, because both first and second males apparently fertilize eggs in equal proportions, with no evidence of sperm priority (Lorieto et al. 2010).

Behavioral patterns involved in male–male conflicts include silk thread tension, vibration, persecution, ritualized fighting, and grappling. The two last behaviors occur in few cases, and when both males have similar body condition. In the ritualized fighting, the males confront venter-to-venter and facing upwards, contacting leg tarsi and vibrating their bodies intensively, but causing no damage. In the grapple, males face each other, crossing legs and biting each other chelicerae to chelicerae, usually finishing with injuries or death to one of the individuals (Albo et al. 2007; Rojas and Viera 2016).

Fig. 13.9 Couple of *Anelosimus viera* and a satellite male (Photo: C. Rojas)



Both the first and second mating male show high percentages of paternity. These results make it difficult to explain the escalated fights for access to female, suggesting that other factors may have greater importance. For example, that there may be cryptic female choice in this species (Lorieto et al. 2010), or that the waiting strategy is costly in other ways, such as in risk of predation.

Sexual Strategies

Males can encounter two kinds of scenarios when they are searching for females; individual nests (uni-female nest) with one subadult or adult female, and communal nests (multi-female nest) containing two or more females of different instar subadults (pre-penultimate, penultimate, and adult female) (Albo et al. 2007). The scenario determines the sexual strategies and preferences of males (Viera and Albo 2008; Rojas and Viera 2015). Viera and Albo (2008) made an experimental design simulating a multi-female nest of *A. viera*, allowing males to choose between females of different age and reproductive status. These multi-female nests consisted of one mature female, one recently molted adult female, and one subadult (penultimate) female. Females of different reproductive status were attractive to males, as they courted at least one female per colony irrespective of reproductive state. When two males were exposed to nests containing only one subadult female, they fought for access to the females described above.

After winning a contest and before mating with the female, the males—like all spider males—must perform sperm induction. Although sperm induction occurs in every sexual encounter, it has not been well described except some cases in big spiders (Mygalomorphae) and in six species of the *Theridion varians* group (Theridiidae) by Knoflach (1998). Rojas and Viera (2016) made a detailed description of the sperm induction behavior in *A. viera*. This behavior can occur prior to or after courtship, before re-mating with the same female, or before mating with

another female. The sperm-induction description was done observing males after first mating. The duration of the entire process of sperm induction (sperm web construction + emergence of sperm drop + filling the palps) takes approximately 5 min. The sperm induction can happen before, in the middle, or at the end of interactions with a female.

Adult females assume a characteristic mating posture upon accepting a male (Fig. 13.10). Non-mature females are receptive and accept courtship and mating attempts, assuming the adult female mating posture, resulting in a peculiar behavior called pseudocopulation common in cobweb spiders (Knoflach 1998, Albo et al. 2007) or non-conception behavior, observed also in *Anelosimus studiosus* (Pruitt et al. 2011). The possible function or advantage of this behavior has been explored for both sexes involved (Rojas and Viera, *in prep.*). This behavior was found to be very common in subadult females, perhaps to retain in the nest males to mate with. Since the sex ratio is biased toward females, the probabilities of encounters decline through the reproductive season. On the other hand, males that remain in the nest with subadult females can copulate with virgin females without fights with other males. We observed in experimental conditions that females can easily accept males to mate with if they were pseudocopulated before, without male individual recognition (Viera and Rojas, *in prep.*). Furthermore, we did not find differences in the time of maturity between pseudocopulated and non-pseudocopulated subadult females, indicating that earlier maturation is not elicited by pseudocopulating behavior. Males also courted more frequently pseudocopulated females than the naïve females. This situation was observed by Pruitt and Riechert (2011) in *A. studiosus*, where prior sexual experience facilitated mating. According to Burghardt (2005), the pseudocopulation is probably sexual proof, and it is expected to reduce the latency to mating. For males that fight to access females, it is advantageous to be accepted more quickly, in order to avoid other males (Foellmer and Fairbairn 2005; Albo et al. 2007; Rojas and Viera 2015). Pruitt and Riechert (2011) found in *A. studiosus* that females invest more energy in the brood from the males with which they pseudocopulated than from those from males with which they did not.

Fig. 13.10 Mating of *Anelosimus viera*, showing the female receptive posture (Photo: C. Rojas)



Maternal Behavior

Although the existence of brood recognition by the mothers is not known, only mature and copulated females care for foreign eggsacs. (Viera et al. 2007c). Mothers can adopt foreign eggsacs, implied by cleaning maneuvers and permanent contact with them. This behavior is energetically expensive, as eggsacs are large and females stop eating during this process (21 days) in *A. viera* (Viera et al. 2007b) The next stages of brood care are very demanding and need a great energy and time investment, also in other subsocial species like *A. studiosus* (Fig. 13.11).

The spiderlings are not able to open the eggsac to hatch. Their natural or ‘adopted’ mothers must make a hole in the eggsac to allow the spiderlings to exit (Fig. 13.12).

Although mothers cannot recognize their own brood, they have an internal clock that is activated externally by movements of spiderlings inside of the eggsacs. This precision mechanism is adjusted at the oviposition event. We have in laboratory condition experiments exchanged eggsacs of different age, and the mothers opened

Fig.13.11 (a) *Anelosimus studiosus* female with eggsac. (b) *A. viera* with eggsac (Photo A: M.O. Gonzaga; B: M. Trillo)

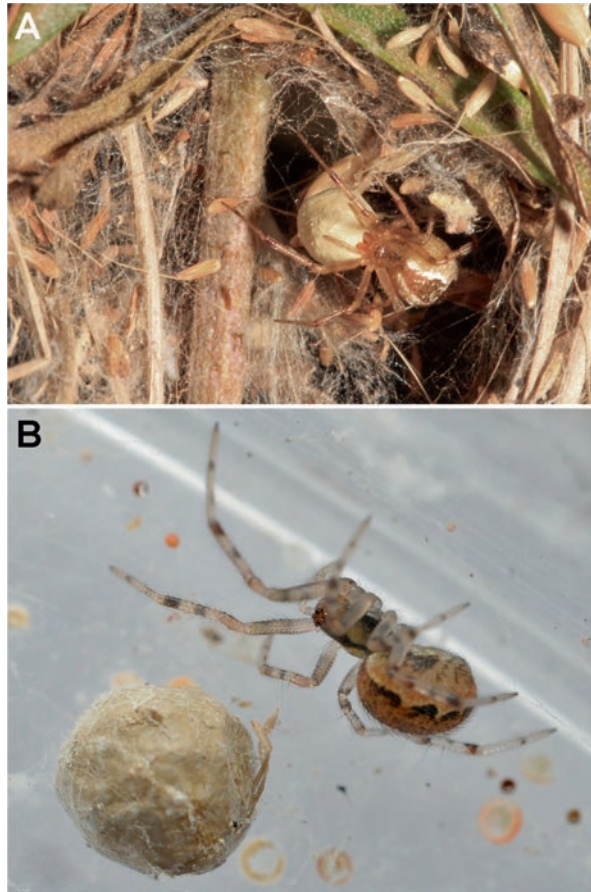
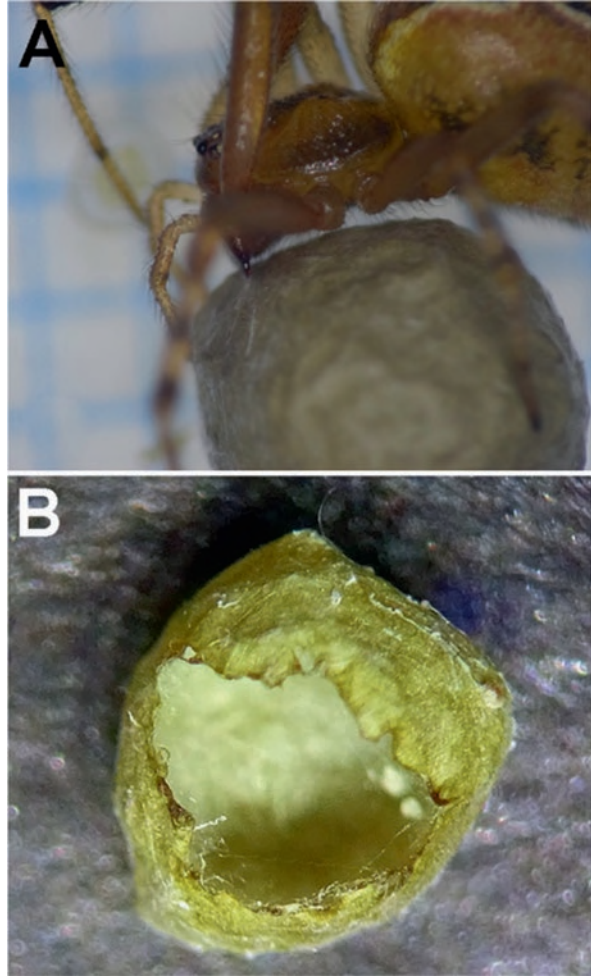


Fig. 13.12 (a) Mother opening the eggsac (*Anelosimus viera*). (b) Eggsac showing a large hole (Photo A: M. Santana; B: C.Rojas)



the eggsacs when the time coincided with the expected time of hatching based on the date of their own eggsac-laying (Viera et al. 2007c). The mother cares for her brood continuously after the exit of spiderlings, and in this period we can point to the differences with the behavior of solitary spiders. Most solitary spiders show maternal behavior in protecting the eggsac, but maternal care ceases when the spiderlings emerge from the eggsacs. In some solitary spiders there is further maternal care; for example, in *Lycosa* the mother carries the spiderlings on her body for a while. But the effort and the complexity of parental investment by the subsocial spiders are remarkable, and individual investment is greater than in the social spiders, which can share the labors with other females of the same nest.

When the brood comes out of the eggsacs, the spiderlings are unable to feed by themselves and need their mother's help. Providing nutrients to the young during maternal care is one of the mechanisms that can affect growth and survival of the

young, and their reproductive success. Salomon et al. (2011) found that maternal nutrition affects offspring performance via maternal care in a subsocial spider. The subsocial spider mother's investment in future reproduction by feeding her young was clearly illustrated by Reinhold (2002) for many taxa, highlighting the important role of extended maternal care.

Initially, the spiderlings are fed by regurgitation from the mother; and later the mother kills prey, tears it apart, or predigests it, and offers it to the spiderlings. During this process, the mother does not feed herself, waiting to eat after satiating her brood. Furthermore, mothers regurgitate to the spiderlings in a 'frozen' posture with open chelicerae, avoiding possible injuries (Fig. 13.13).

This process does not occur in adult virgin or mated females without brood (Viera et al. 2007c). Such females are tolerant and can care for the eggsacs, but do not open them nor feed the spiderlings by regurgitation. This intolerance among adult females in subsocial species, according to the maternal survival hypothesis, may help to explain the rarity of subsocial *Anelosimus* species in 'social habitats', such as lowland rainforests where they may experience higher predation risk and frequent web damage due to frequent precipitation (see Avilés et al. 2007).

The ability of brood to feed without the mothers' help is very important in uni-female nests where there are not other females that can help. Spiderlings have been found to depend on their mother until the 4th instar in the subsocial *A. studiosus* (Brach, 1977). In *A. viera*, Ghione et al. (2004) found that the spiderlings are capable of feeding by themselves already at the first instar, while they improve their prey-capture efficiency in later instars. This early independence from mothers makes these subsocial spiders similar to solitary spiders, as the premature death of the mothers would not rule out the survival of the young. In multi-females nests, subadult females can collaborate in cooperative capture and donate it to the younger ones. However, the presence of the mother in subsocial spiders is absolutely necessary for the care and opening of the eggsac. A final effort of maternal investment is to offer the body as food for its young, a common behavior in social spiders and others showing maternal care beyond the first feeding of spiderlings, such as in *Amaurobius ferox* (Kim et al. 2000)

Fig. 13.13 Mother of *Anelosimus viera* feeding spiderlings



To summarize, subsocial spiders are a good model to examine the traits that underlie the evolution of permanent cooperative sociality. Multipronged approaches focusing on (1) phylogeny, (2) reproductive behavior, especially maternal care, and (3) ecological and abiotic factors relating to sociality are necessary to gain a holistic understanding of the evolution of social life in arthropods. A synthesis combining these approaches may also help to explain why no permanently social *Anelosimus* species occur outside the Americas. However, we do not attempt such a synthesis here, as more behavioral studies on reproductive aspects are needed to develop a species-level database for comparative purposes, as are further studies of biotic and abiotic factors in shaping the origin and distribution of sociality. Thorough comparative studies uniting these approaches with an explicit focus on evolutionary replica—independent origins of sociality—will probably offer the next major insights into social evolution in spiders and other animals.

Acknowledgements We are grateful to two anonymous reviewers who improved the final version of the chapter, and to Marcelo O. Gonzaga, Carolina Rojas, Mariana Trillo, and Martín Santana for photos. Viera also thanks the support of Sistema Nacional de Investigación (ANII), Comisión Sectorial de Investigación Científica (CSIC) and Programa de Desarrollo de las Ciencias Básicas, UdelaR, Uruguay.

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