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Web-sharing Sociality and Cooperative Prey Capture in a Malagasy Spitting Spider (Araneae: Scytodidae)

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Web-sharing sociality and cooperative prey capture are reported for *Scytodes socialis*, sp. nov., a spitting spider discovered in a dry deciduous forest in Eastern Madagascar. Transect-based sampling was used to investigate colony demographics, estimate web volume and stratigraphic position, and assess density of colonies at the study site. The social system in *S. socialis* is compared to that of other non-territorial social spiders where multiple juveniles and adults of both sexes live in colonies while maintaining an unbiased sex ratio. While this form of sociality is previously undocumented in Scytodidae, a variety of social systems is found within the family. With future advances in phylogeny, Scytodidae may become a useful system for studying the evolution of sociality including an independent test the "maternal care pathway" to sociality hypothesis.

Cooperative behavior is known for a minute fraction of spider species. Yet various forms of sociality have evolved repeatedly in spiders (Avilés 1997). Two attributes are commonly used to classify spider sociality: territoriality and permanence (Avilés 1997; D'Andrea 1987). Individuals either defend individual territories from colony mates or move freely throughout a colony of unaggressive conspecifics, and social behavior either persists throughout the life of the spider or alternates with an obligate solitary phase. Permutations of all four conditions are known in spiders (see Avilés 1997 for review). Seasonal colonies of non-territorial individuals typically consist of extended mother-to-offspring maternal care. Such spiders are referred to as subsocial. Territorial sociality, whether periodic or permanent, is typically manifested by clusters of individuals within discrete webs connected to other webs in the colony. There is controversy over whether such spiders should be considered social at all because they are not cooperative (Agnarsson 2002, 2004; Kullmann 1972). Non-territorial permanent social spiders are referred to as quasisocial. These include the best studied social spiders (e.g., Avilés 1994; Avilés and Maddison 1991; Johannesen and Lubin 2001; Lubin 1991, 1995; Riechert 1985; Roeloffs and Riechert 1988; Rowell and Avilés 1995; Seibt and Wickler 1988; Smith and Engel 1994). Most quasisocial spiders are highly inbred and exhibit a strongly female biased sex ratio (e.g., Avilés 1993; Avilés 1997; Avilés and Bukowski 2006; Avilés and Maddison 1991; Bilde et al. 2005; Lubin 1991; Riechert and Roeloffs 1993).

Scytodids are best known for their ability to trap prey at a distance by expelling a mixture of venom and gluey silk from their chelicerae (Foelix 1985, 1996). Most scytodids are cursorial, although some species build webs. A small body of literature on sociality in Scytodidae documents two forms of sociality in the group: subsociality, involving extended maternal care (Eberhard 1986; Li 2002; Li et al. 1999; Li and Kuan 2006) and communal territorial web building (Bowden 1991; Bowden and Jackson 1988).

This paper describes a species of web-building scytodid where webs may contain multiple males, females, and juveniles. Multiple nest mates participate in the capture of large prey items. Participants and non-participant web mates were allowed to feed whether or not they participated in the hunt. No aggression between web mates was observed. The sex ratio among adults is unbiased.

METHODS

Scytodes socialis was studied at Forêt de Kirindy field station, 46 km NE of Morondava (20°04.026'S 44°39.434'E, 50 m elev.), a dry deciduous forest in Toliara province, eastern Madagascar, from 20–30 January, 2006.

Sixteen 25 m transects were censused for *Scytodes* webs. The transects were randomly selected grid lines from two plots used primarily for mammal research. Eight transects were censused from each plot. The plots are approximately 1.6 km apart. All *Scytodes* webs found within 2.5 m to either side of the transect line and up to 2.75 m above the ground were collected into plastic bags. Collections included all colony members plus other arthropods, prey remains, exuvia, etc. Additional webs were collected under an unstructured sampling regime.

The size of each web was measured in three dimensions to estimate volume. Corrections were made to compensate for extreme irregularities. The distance from the ground to the bottom of the web was recorded.

The size of each individual collected during the structured sampling was assessed by measuring patella plus tibia I length and carapace length. Patella plus tibia length has been advocated as more useful for distinguishing instars than carapace length (Toft 1976) and has become the standard in social spider literature (Agnarsson and Kuntner 2005; Avilés and Gelsey 1998; Avilés and Salazar 1999). The relationship between number of individuals in a web and its volume was analyzed using linear regression. A regression was also run for web volume against the number of individuals multiplied by patella-tibia length, as in Agnarsson and Kuntner (2005).

Natural history observations were gathered from webs outside of the sample plots. Webs were selected for their size and accessibility, flagged during the day, and monitored over 5 nights for 3-4 hours beginning at dusk.

TAXONOMY.— All measurements are in millimeters and were taken using a reticle in a Leica MZ12.5 dissecting microscope. Illustrations were rendered in Adobe Photoshop (version 6.0) based on digital photographs taken using a Nikon DXM 1200 digital camera mounted on a Leica MZ16 dissecting microscope. Female genitalia were cleared in methyl salicylate (Holm 1979) and slide mounted (Coddington 1983) for photography using a DXM 1200 digital camera mounted on a Leica DM4000 M; multiple images were combined using Auto-Montage (version 5.01). All specimens examined are deposited in the California Academy of Sciences (CAS).

RESULTS

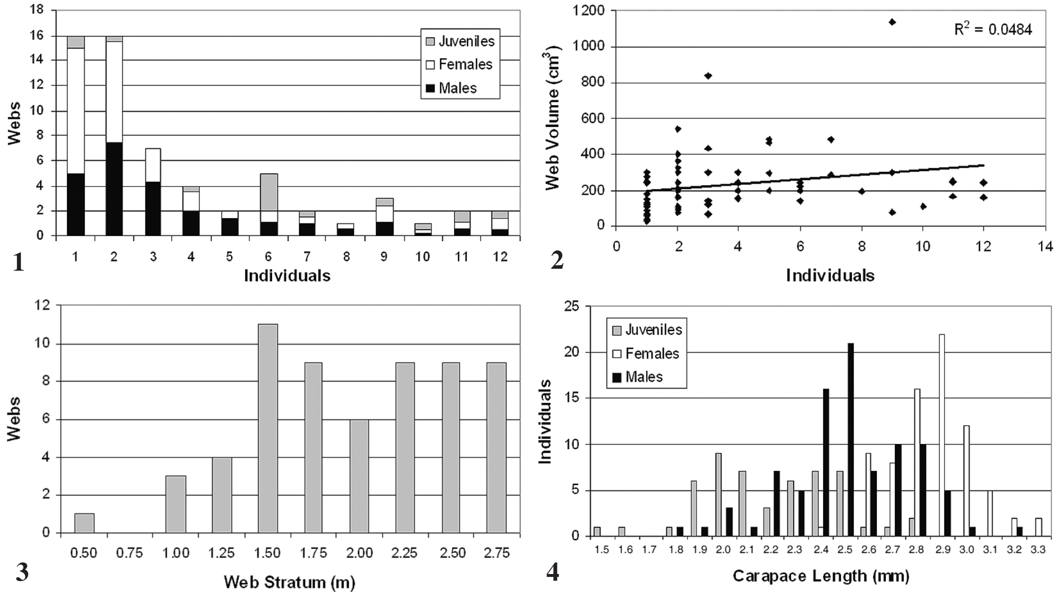
Sixty-one colonies containing 230 *Scytodes socialis* (93♂, 86♀, 51 juveniles) were collected during the structured sampling (Fig. 1). With more adult males collected than females, these data clearly do not indicate a female-biased sex ratio. A χ^2 test confirms that the sex ratio is not significantly different from 0.5 ($p = 0.601$). Transects from the two plots did not differ significantly in terms of number of webs (ANOVA test, $p = 0.25$) or individuals ($p = 0.26$). Webs in transects contained from 1 to 12 individuals; up to 16 individuals, including the unstructured samples. Prey remains found in webs included ants, roaches, and moths.

Webs usually incorporate dead leaves and other debris as well as living leaves and branches

(Figs. 5–6). Mean web volume is estimated at 218.6 cm^3 (8.4×5.8×4.5 cm). Web size is a poor estimator of colony population based either on raw number of individuals (Fig. 2) or number of individuals times a size index (patella-tibia length, not shown; see Agnarsson and Kuntner 2005). Both linear regressions are insignificant.

Webs were concentrated above 1.25 m (Fig. 3). Colonies above the 2.75 m mark were observed but were not collected. Extrapolating from the area sampled during the structured sampling (sixteen 25×5 m transects = 0.2 ha), the forest at Kirindy contains approximately 305 webs and 1150 individual *S. socialis* per hectare not including those above the 2.75 m mark.

Females are larger than males (mean carapace length: female = 2.75 mm, male = 2.43 mm) but males have longer legs (mean patella plus tibia I: female = 4.55 mm, male = 5.35 mm). Using carapace length, juveniles appear to divide into two size classes, apparently representing the penultimate (~2.4 mm) and antepenultimate (~2.0 mm) instars (Fig. 4); a small number of individuals representing younger instars may also be present. The same pattern is not as clear using patella-tibia length (not shown).



FIGURES 1–4. (1) Histogram showing mean proportion of males, females, and juveniles in webs of different population sizes and the number of webs found in each size class during structured sampling. (2) Web volume (cm3) as a function of colony population size for webs collected during structured sampling. (3) Histogram showing the stratigraphic distribution of webs collected during the structured sampling. (4) Carapace length (mm) histogram for all males, females, and juveniles collected during the structured sampling.

NATURAL HISTORY

PREY CAPTURE.— Several instances of cooperative prey capture were observed. On three separate occasions, I observed two individuals participating in the capture of a relatively large prey item (moth or fly; Figs. 7–8). In all three cases, additional colony members eventually joined in the feeding. On another occasion, a moth was caught in a part of the web that was impossible to observe. At least two individuals that had been on the exterior part of the web moved to join in the feeding. No aggressive interactions among colony members were ever observed. Sex/maturity of hunters and feeders could not be determined in the field, but feeders, hunters, and prey remains were collected at the end of an event. From this it is clear that mature males, mature females, and juveniles all participate in prey capture. Individuals were also observed with smaller prey items that they had apparently caught themselves and were not sharing with others (Fig. 9). In one instance, a single female individual attempted to capture a roach about twice her size. The roach became tenuously entangled in silk. The spider appeared to administer a bite to the posterior section of the roach. She then began using her hind tarsi to comb silk over the roach (Fig. 10). The roach eventually escaped. Note that none of her web-mates participated in the prey capture attempt. Roach remains of approximately the size of the escapee suggest that such prey are not beyond capabilities of these spiders, possibly when multiple individuals participate. Access to larger prey may be a driving force in the evolution of sociality (e.g., Nentwig 1985; Powers and Avilés 2003).

The web plays an important role in prey capture. Spiders attack while prey are entangled and delayed by silk. Usually, prey are approached and bitten. Spitting seems to be reserved for more difficult prey when biting fails. A third strategy is to face away from the prey and comb out silk with the fourth tarsi (Fig. 10). The web also seems to assist in prey capture by simultaneously alerting multiple individuals to the presence and location of potential prey.

COURTSHIP AND MATING.— I observed two successful matings and one aborted courtship. Courtship consists of reciprocal leg I taps, mostly from the male as he approaches the female. Mating is venter to venter with both facing the same direction. Copulation takes about one to two minutes. It was not possible to observe individual insertions.

DISCUSSION

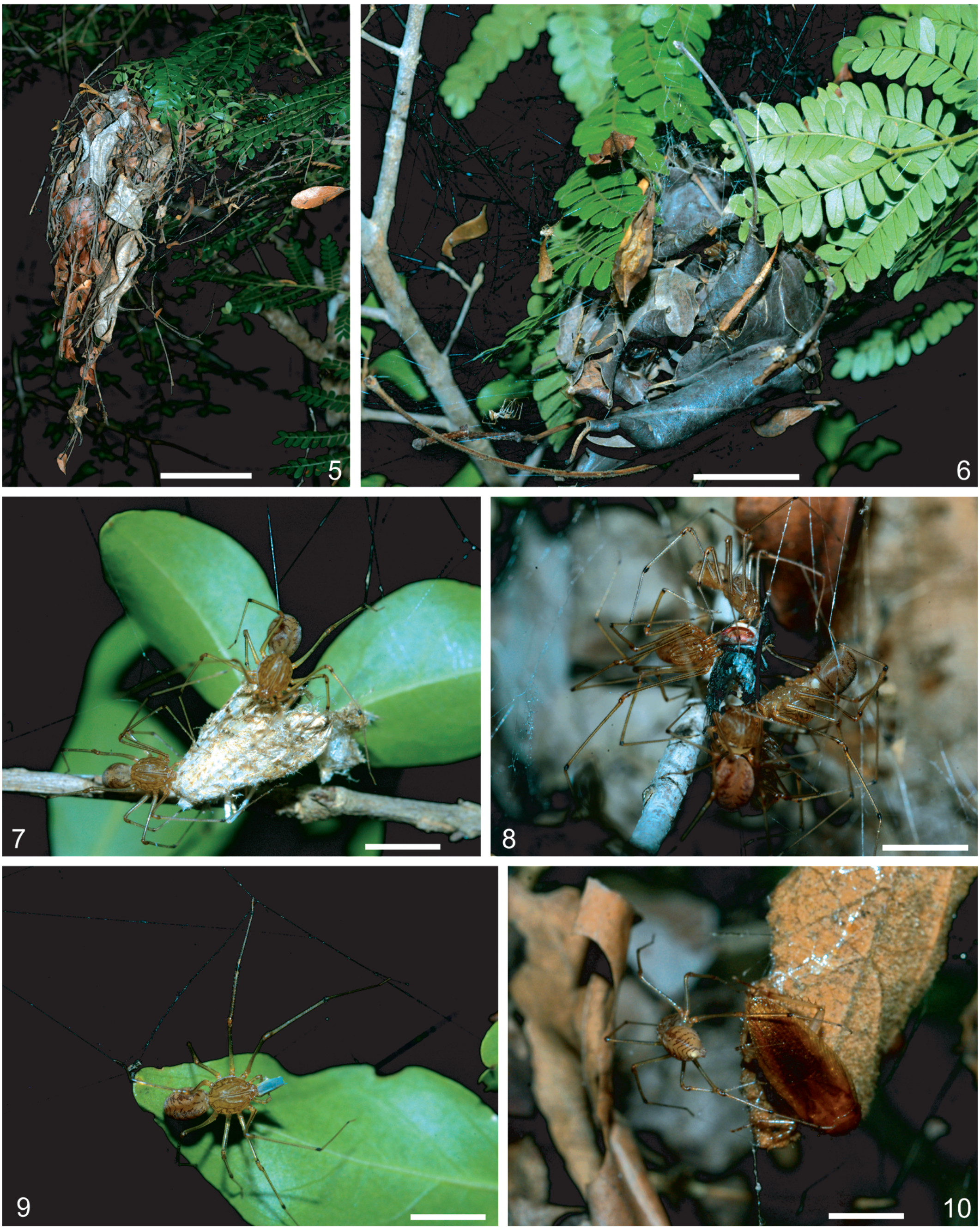
Observations were made over a period of 10 days allowing only a snapshot of the life cycle of *Scytodes socialis*. Most juveniles appeared to be either penultimate or antepenultimate (Fig. 4), suggesting synchronized phenology. Thirty-one of the 61 *S. socialis* webs observed during the structured sampling consisted of *S. socialis* living in non-social situations, either a single individual (5♂, 10♀, 1 juvenile) or a male-female pair (13). Some of these non-social stage collections may represent dispersal or colony founding events. The degree of relatedness among nest mates in *S. socialis* has not yet been established. But given the unbiased sex ratio in this species, it would appear that dispersal is common.

Only five egg cases were collected during this study, and they offer little in the way of hints about the life cycle *S. socialis*. Two egg cases were with solitary females, two were with male-female pairs; one egg case was in a colony with three males, one female, and one juvenile. Four *S. socialis* exuvia were also found in this last web, suggesting that spiders had been there for some time.

SEX RATIO AND COLONY PERMANENCE.— The questions most relevant to compare *S. socialis* to the other social spiders concern colony permanence and whether one or more mothers contribute offspring to the colony.

A female-biased sex ratio is a well-studied phenomenon among highly social spiders that is expected under conditions that favor inbred, strongly subdivided populations where colony growth rate and proliferation are under group selection (e.g., some species of *Achaearanea*, *Agelena*, *Anelosimus*, *Stegodyphus*, etc., see Avilés 1993, 1997; Avilés and Maddison 1991; Lubin 1991; Riechert and Roeloffs 1993).

Scytodes socialis falls into a small class of social spiders where multiple juveniles and adults of both sexes coexist cooperatively while maintaining an unbiased sex ratio. These include the oxyopid *Tapinillus* sp. (Avilés 1994), the sparassid *Delena cancerides* (Rowell and Avilés 1995), and the subsocial thomisid *Diaea ergandros* (Evans 1995).



FIGURES 5–10. Field photographs of *Scytodes socialis*. (5–6) Webs. (7) Two females feeding on a moth. (8) Males, females, and juveniles feeding on a fly. (9) Lone female feeding on a leafhopper. (10) Female using fourth tarsi to pull silk over roach. Scale bars: 5 = 30 mm; 6 = 20 mm; 7–10 = 5 mm.

Among the non-territorial permanent social (quasisocial) spiders, only *Tapinillus* sp. and *Delena cancerides* have an unbiased sex ratio (Avilés 1994, 1997; Rowell and Avilés 1995). Colonies of both species can consist of multiple juveniles and adults of both sexes. Outbreeding in *Tapinillus* is accomplished by dispersing males. So, colonies consist mostly of siblings plus a few immigrant males. Reproduction within colonies is apparently the result of mating between a single male-female pair. In spite of this reproductive monopolization, colonies may contain a few dozen spiders and one atypical web contained hundreds of individuals (Avilés 1994).

Delena cancerides is the only permanent social spider that does not use a prey capture web. Although there is no aggression among colony mates, these spiders are unique among non-territorial social spiders in being extremely aggressive toward conspecifics from other colonies. Given this intercolony aggression, it is unclear how outbreeding is accomplished. Multiple females within the colony contribute offspring (Avilés 1997; Rowell and Avilés 1995).

Unlike *Tapinillus* sp. and *Delena cancerides*, *Diaea ergandros* colonies are non-permanent. Whereas thomisids are not typical web-building spiders, social *Diaea* use silk in nest construction (Evans 1995; Main 1988; see also Jackson et al. 1995). Adult females disperse to establish new colonies after mating. *Diaea ergandros* are unique among subsocial spiders in that offspring continue to cooperate through maturity. Subsocial spiders typically avoid inbreeding by dispersing before they reach sexual maturity (e.g., Avilés 1997; Brach 1977; Nentwig and Christenson 1986). In *D. ergandros*, males mature first, then disperse to other colonies; females mate with siblings or immigrants, then disperse to found new colonies (Avilés 1997; Evans 1995). It is interesting to note that two other social species of *Diaea* exhibit female sex ratio bias. In these species, mating takes place among siblings before dispersal (Avilés 1997; Evans 1995; Main 1988).

How is *S. socialis* similar to or different from these outbred social spiders, especially with respect to colony permanence? For instance, *Diaea ergandros* is an atypical subsocial spider because its colonies persist beyond the maternal care phase into adulthood, yet there is a solitary phase as males disperse for mating and inseminated females disperse to found new colonies. There is no obligate solitary phase in either *Tapinillus* sp. or *D. cancerides*. Reproduction in colonies of *Tapinillus* sp. and *D. ergandros* is the product of a single female. The relatively small population size of *S. socialis* colonies suggests that colony members are the offspring of a single female founder. In fact, colony population size is small in *S. socialis* relative to both *Tapinillus* sp. and *D. ergandros* (Avilés 1994, 1997; Rowell and Avilés 1995). But more observations from across the phenological cycle will be required to determine whether sociality in *S. socialis* conforms better to the *Tapinillus* sp. model (permanent sociality) or the *D. ergandros* model (periodic sociality), or perhaps it differs from both of these in other important ways.

EVOLUTION OF SOCIALITY.— Although sociality is often discussed in terms of discrete classes, it is really a continuum of behaviors involving increasing levels of maternal investment in offspring and conspecific tolerance (Agnarsson 2002, 2004; Avilés 1997; Kullmann 1972; Shear 1970). Subsociality and quasisociality can gradually evolve by extension of maternal care to older and older offspring. This is known as the “maternal care pathway” to sociality, and it predicts that subsociality should precede quasisociality on a phylogenetic tree (Agnarsson 2002, 2004; Avilés 1997). Recent phylogenetic analyses of Theridiidae are consistent with the “maternal care pathway” (Agnarsson 2002, 2004; Arnedo et al. 2004; Miller and Agnarsson 2005).

The evolution of sociality is usually preceded by two adaptations: web building and maternal care (Agnarsson 2002; Avilés 1997; Shear 1970). With rare exceptions (e.g., Sparassidae, Thomisidae), sociality tends to occur within lineages where web building is the norm (e.g., Theridiidae, Eresidae, Agelenidae). Even social members of the typically cursorial family Oxyopidae have non-social congeners that build prey-capture webs (Avilés 1997; Griswold 1983;

Mora 1986). Sociality and web building in scytodids are both rare attributes, yet they seem to be tightly correlated.

Expressions of sociality in Scytodidae are surprisingly diverse, including subsociality with extended maternal care (Eberhard 1986; Li 2002; Li et al. 1999; Li and Kuan 2006), a communal territorial species (Bowden 1991; Bowden and Jackson 1988), and the non-territorial multiple-adult species *S. socialis*. Scytodid colonies with males, females, and juveniles living together in webs have also been observed in South Africa. It is not known if observations of this phenomenon in the Blyde River Canyon region, Mpumalanga and Tonquani Gorge, Magaliesberg Mountains, Northwest Province represent one or two more species (Astri and John Leroy, pers. comm; I. Engelbrecht, pers. comm.). The Blyde River species at least is superficially not very similar to the Kirindy species, raising the possibility of multiple independent origins of non-territorial multiple-adult sociality in scytodids. Sociality is thought to have evolved multiple times within the eresid genus *Stegodyphus* (Kraus and Kraus 1988, 1990) and the theridiid genera *Anelosimus* (Agnarsson 2006) and *Achaearanea* (Agnarsson et al., in press), so such a scenario is hardly unprecedented. Hence, Scytodidae may offer another independent opportunity within spiders to explore the association of sociality with putative social preadaptations such as maternal care and web building, and the consequences of sociality for mating system and sex ratio. The answers to these questions will depend on new advances in the study of scytodid natural history, phylogeny, and systematics.

TAXONOMY

Family Scytodidae Blackwall, 1864
Genus *Scytodes* Latreille, 1804

Scytodes socialis Miller, sp. nov.

Figs. 11–18.

ETYMOLOGY.— Epithet *socialis* from the Latin, meaning companionable.

MATERIAL EXAMINED.— HOLOTYPE: MADAGASCAR: **Toliara:** Forêt de Kirindy field station, 46 km NE Morondava, elev. 50 m, 20°04.026’S, 44°39.434’E, 20–30 January 2006, H. Wood, J. Miller, 1♂ (CAS). OTHER MATERIAL EXAMINED: Same locality as holotype: 178♂ 184♀ 98 juveniles in 109 vials (1 vial per colony; CAS).

DIAGNOSIS.— Distinguished from *Scytodes oswaldi* Lenz 1891, the only scytodid previously known from Madagascar, by its smaller overall size and shorter legs (female *S. oswaldi* total length: 5.5, legs I-IV: 9.5, 7.3, 5.3, 7.6; see Description below for measurements of *S. socialis*; see also Remarks).

DESCRIPTION.— MALE (Holotype from Forêt de Kirindy, Toliara, Madagascar): Carapace brown with dark markings (Fig. 11); abdomen light brown with pattern of dark obliquely transverse markings (Fig. 11). Legs light brown with dark markings; femora I–III with one ventral longitudinal stripe, femur IV with two ventral longitudinal stripes; tibiae and metatarsi with dorsal longitudinal stripe for proximal ~¾ of length, distal tip dark; tarsi without distinct markings.

Palpal bulb 0.78 long, 0.29 wide at the base; basal part nearly spherical with an elongate, gently tapering stalk; distal part narrows abruptly to a glossy black tip; no apophyses present (Figs. 15, 16). Tip of cymbium with tight cluster of three strong prolateral macrosetae.

Total length 5.70. Carapace 2.71 long, 2.04 wide; sternum 1.54 long, 1.03 wide; prosoma 1.94 high; legs (see table top of next page).

FEMALE (from Forêt de Kirindy, Toliara, Madagascar): Markings as in male (Figs. 12–14). Tip of palpal tarsus with tight cluster of four strong prolateral mactosetae subtending the palpal claw.

	Leg I	Leg II	Leg III	Leg IV	Pedipalp
Femur	4.76	3.53	2.46	3.44	0.66
Patella	0.62	0.59	0.63	0.65	0.25
Tibia	5.15	3.53	2.20	3.29	0.41
Metatarsus	7.12	4.56	2.63	3.69	—
Tarsus	1.04	0.82	0.65	0.75	0.76
Total	**18.69**	**13.03**	**8.57**	**11.82**	**2.08**

Vulva covered by oblong lightly sclerotized plate (Figs. 17-18). Duct leaves bursa ectally, curves mesally toward spermatheca (Fig 18). Pair of positioning plates located posterior to epigastric furrow (Fig. 17). Positioning plates striated, wider than long with longest axis obliquely transverse (Figs. 17–18).

Total length 6.77. Carapace 2.95 long, 2.28 wide; sternum 1.58 long, 1.09 wide; prosoma 2.49 high; legs:

	Leg I	Leg II	Leg III	Leg IV	Pedipalp
Femur	3.78	2.99	2.07	2.98	0.61
Patella	0.66	0.64	0.66	0.70	0.25
Tibia	5.05	2.95	1.76	2.81	0.41
Metatarsus	6.58	3.63	2.25	3.16	—
Tarsus	0.89	0.76	0.61	0.73	0.62
Total	**17.96**	**10.97**	**7.35**	**10.38**	**1.89**

CHAETOTAXY: Tibiae I–III with two retrodorsal, one mediodorsal, two prodorsal trichobothria; tibia IV with one additional prodorsal trichobothrium. Retrodorsal and mediodorsal trichobothria distal; one prosorsal trichobothrium distal, others proximal. Distal-most trichobothrium is mediodorsal; distal prodorsal trichobothrium positioned between retrodorsal trichobothria. Metatarsi with one trichobothrium near distal tip. Palpal tibia with three retrodorsal, one mediodorsal, two (rarely three) prodorsal trichobothria.

VARIATION.— FEMALE (*n* = 86): carapace length 2.3–3.2, patella-tibia I length 3.9–5.3; MALE (*n* = 93): carapace length 1.8–3.1, patella-tibia I length (4.1–6.7).

DISTRIBUTION.— Known only from the type locality in western Madagascar.

REMARKS.— One scytodid species was previously recorded from Madagascar: *S. oswaldi* from Nosy Be, known only from the female. I have not been able to obtain type material of *S. oswaldi* (probably destroyed) and it will be challenging to recognize *S. oswaldi* specimens based on the text description and figures alone. However, Lenz (1891) gives a table of measurements that can be used to separate *S. oswaldi* from *S. socialis* (see Diagnosis, above). Despite sustained arthropod collecting efforts spanning over 10 years by California Academy of Sciences personnel and collaborators, no additional specimens of *S. socialis* were found in the collection. However, a number of undescribed species have been collected that resemble *S. socialis*.

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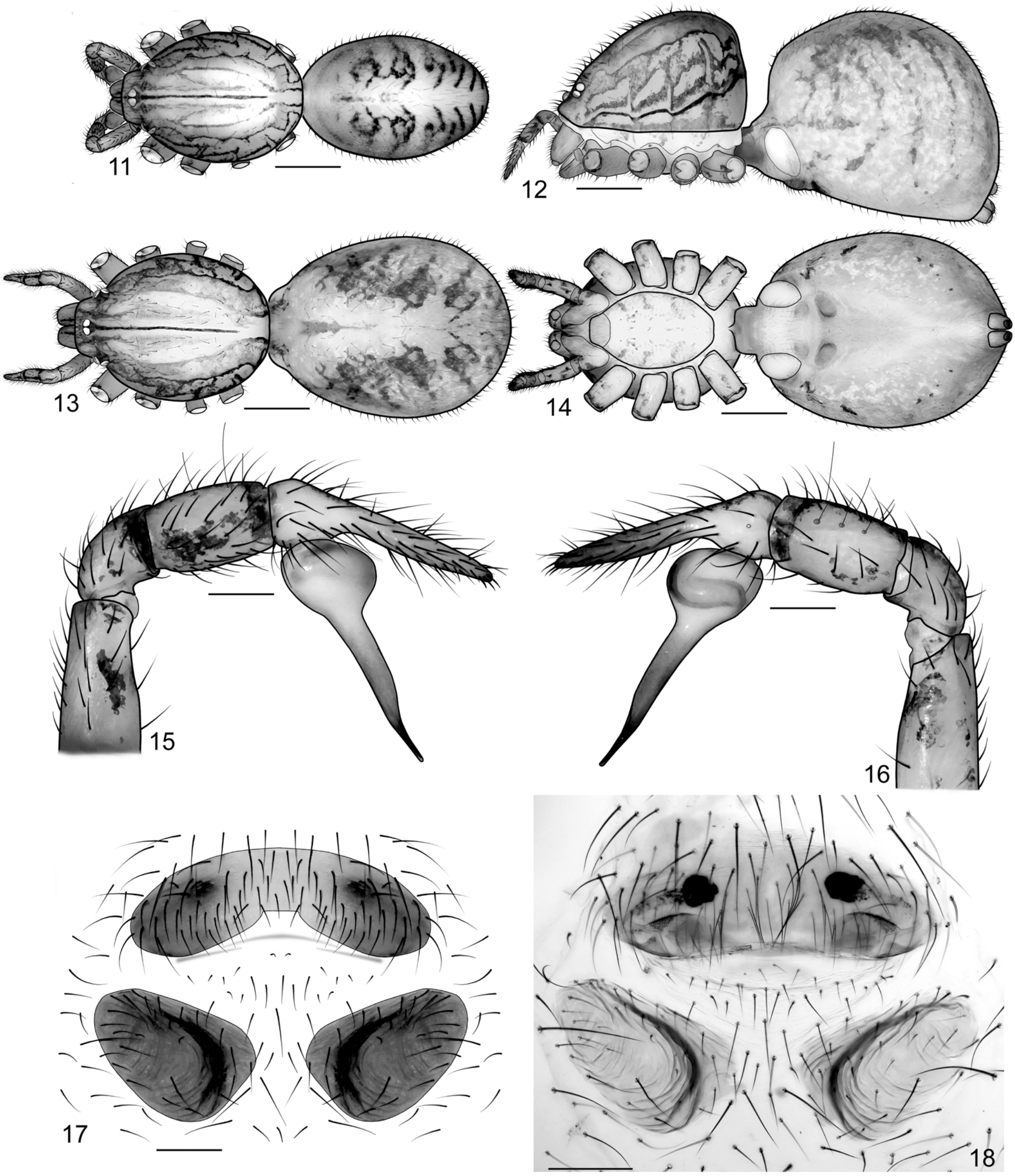

FIGURES 11–18. *Scytodes socialis*. (11, 15–16) Male. (12–14, 17–18) Female. (11, 13) Habitus, dorsal. (12) Habitus, lateral. (13) Habitus, ventral. (15–16) Palp. (15) Prolateral. (16) Retrolateral. (17–18) Vulva. (17) Ventral. (18) Photograph of cleared vulva, dorsal. Scale bars: 11–14 = 1 mm; 15–18 = 0.2 mm.

Lenz's types in the Lübeck collection. Special thanks to Charles Griswold for his generous support. Gratitude for logistical assistance is extended to Brian Fisher, Balsama Rajemison, Rin'ha Harinhala, Evert Schlinger, and Mike Erwin. Thanks to the staff at the Forêt de Kirindy field station.

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