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SHORT COMMUNICATION

SUBSOCIALITY IN *HELVIBIS THORELLI* KEYSERLING 1884 (ARANEAE, THERIDIIDAE, THERIDIINAE) FROM FRENCH GUIANA

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ABSTRACT. Preliminary observations on *Helvibis thorelli* (Theridiidae) in French Guiana suggest a typical subsocial behavior in this species, with nests consisting of a mother and her offspring who collaborate in prey capture. Communal feeding occurs over several juvenile instars. Subsociality has previously been described in three theridiid genera (*Achaearanea*, *Anelosimus*, *Theridion*) and predicted to occur in further genera of the subfamily Theridiinae. Our findings support this prediction and have important implications for comparative studies as they add another independent observation of social behavior: current phylogenetic knowledge implies subsociality evolved independently in each of these genera.

Keywords: evolution of sociality, maternal care, communal feeding

Subsociality is rare but phylogenetically scattered in spiders with about 30–40 species distributed in Amaurobiidae, Eresidae, Lycosidae, Pisauridae, Salticidae, Scytodidae, Thomisidae, and Theridiidae (Avilés 1997; Agnarsson et al. 2006). Subsocial spiders form ephemeral colonies consisting of a single mother and offspring; these colonies typically persist until the spiderlings disperse close to adulthood (Schneider 2002; Powers & Avilés 2003), although the exact timing of dispersal may depend on food availability (Schneider 1995; Kim 2000). Subsociality entails not only extended maternal care and mutual tolerance (e.g., Salomon et al. 2005 and references therein) but also cooperation between individuals within a colony, where juveniles actively partake in the colony functions (Agnarsson et al. 2006), for example in prey capture (Kim et al. 2005). Three theridiid genera, *Achaearanea*, *Anelosimus*, and *Theridion*, are known to contain subsocial species and current phylogenetic evidence suggests subsociality evolved independently in each genus (Agnarsson 2002, 2004, 2005, 2006; Avilés et al. 2006; Agnarsson et al. 2006). The phylogenetic distribution of subsociality is important in understanding the evolutionary history of social behavior. Social spiders form permanent colonies that contain anywhere from a few to over 10,000 individuals. In these colonies siblings will mate with each other and dispersal is rare (Avilés 1997). As far as known, social species occur only within subsocial lineages, although detailed phylogenetic evidence supporting this is, thus far, only available in Theridiidae (Agnarsson 2004, 2005, 2006). All available evidence, therefore, suggests that social spiders evolved from subsocial ancestors (e.g., Avilés 1997; Schneider 2002; Agnarsson 2004, 2006; Bilde et al. 2005; Agnarsson & Zhang 2006; Agnarsson et al. 2006). Subsociality, in turn, has only evolved in lineages where maternal care beyond care of the egg sac is common (Avilés 1997; Agnarsson 2002, 2004; Schneider 2002). The link between maternal care and subsociality led to a prediction: because maternal care in theridiids optimized to the ''lost colulus clade'' (*Anelosimus* plus Theridiinae, see Agnarsson 2004 fig. 102), additional discoveries of subsocial species could be predicted within that node (Agnarsson 2004; Agnarsson & Kuntner 2005; Miller & Agnarsson 2005). Here we corroborate this prediction and report the discovery of subsociality in a fourth genus in the lost colulus clade, *Helvibis*.

We made observations on subsocial *Helvibis thorelli* Keyserling 1884 colonies (Figs. 1–6) on three

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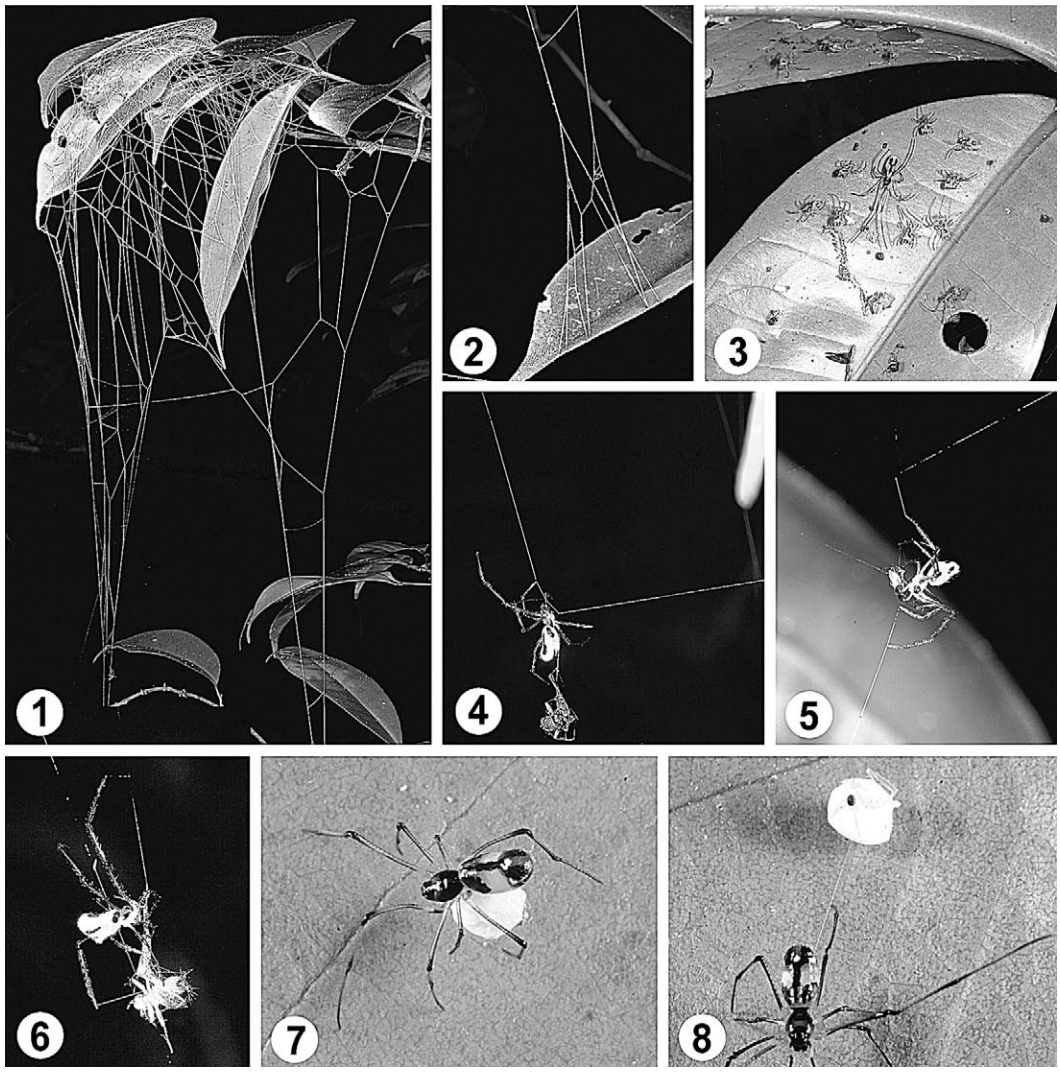

Figures 1–8.—*Helvibis thorelli*. 1. Subsocial web, ~80 cm tall. 2. Attachments of web. 3. Adult female and nine 4th or 5th instar juveniles resting under leaf. 4. Female transporting prey to retreat, attached to the spinnerets and held with one leg IV. 5. Subadult male catching a phlobotomine fly. 6. Female wrap-attacking a cricket. 7. Female with egg sac; photo by M. Kuntner. 8. Female pulling eggsac with a line attached to the spinnerets and held with one leg IV, the same way a prey is carried back to the retreat; photo by M. Kuntner.

consecutive nights (18–20 September 2005) at the Les Nouragues Field Station, on the ''Montagnes Balenfois'' massif, Commune Règina, French Guiana (4°04′08.64″N, 52°40′08.20″W). The field station is placed in an 85 km^2 tract of undisturbed lowland blackwater rainforest at approximately 50 m elevation. Vouchers from this study are deposited in the National Museum of Natural History, Smithsonian Institution.

We saw dozens of *H. thorelli* (Figs. 1–8) webs in this forest. The spiders rested against the underside of live leaves. The webs typically consisted of a network of lines densely-spaced near the resting site with longer and sparser lines further away, which attached the web to other leaves and, in some cases, to the ground (Figs. 1, 2). All the long lines, and some of the short lines, are sticky along almost their entire length, but the ends of the long line segments are non-sticky, unlike typical ''gumfoot'' webs of some theridiids (e.g., Agnarsson & Coddington 2006) but identical to the web of the social *Theridion nigroannulatum* Keyserling 1884 (Avilés

et al. 2006). Nearly all the webs we saw contained a single female, about a third of them guarding an egg sac (Figs. 7, 8; egg sacs contained on average 20 eggs, range 14–24, $n = 5$), while three webs contained the mother and her offspring. Two webs contained a mother and small, probably first or second instar, juveniles and one contained the mother and 13 large juveniles, which, based on the presence of two subadult males, we estimated as 4th or 5th instars (Figs. 1–6). The latter subsocial web was constructed under two adjacent leaves (Fig. 1). The spiders rested in close proximity to each other (Fig. 3). Animals interacted frequently, mostly by touching the first pair of legs without aggression.

We observed prey capture and feeding, under dimmed white light, on naturally caught and introduced prey in two of the subsocial webs. First, in the web containing large juveniles, a phlebotomine fly impacted one of the long sticky lines. After a few minutes, spiders noticeably reacted to the vibrations caused by its struggling. A juvenile responded first by descending on a sticky line adjacent to the line adhering to the prey. Shortly thereafter, the mother descended on the line containing the prey and began a typical sticky silk wrap attack (e.g., Griswold et al. 1998) on the fly before biting. Both spiders walked slowly but apparently without difficulty on the gluey silk line but spun another non-sticky line while walking. The mother wrapped and left the prey at the impact site, and both juvenile and mother ascended rapidly to the leaf retreat on their newly spun non-sticky lines. A few minutes later, the mother descended again in a fast descent down the non-sticky line, cut the prey loose, and carried it on a line attached to the spinnerets and held with one leg IV to the edge of the retreat where she continued to wrap it. Two juveniles approached the mother and prey, but she broke away from them and resumed wrapping. Approach of juveniles and maternal turning away was repeated several times until the mother left the prey and two juveniles began feeding on it together. Later, two additional juveniles began to feed as well. No aggression was seen between the individuals during this behavioral sequence.

We then entangled a small (< 1 cm) cricket on two long sticky lines. Several minutes later the mother reacted to the vibrations by descending and subduing the prey as previously described. A juvenile then arrived at the prey site and appeared to bite and wrap the prey simultaneously with the mother. The animals again left the prey at the attack location, and returned towards the retreat. Before reaching the retreat, the mother returned and started cutting the prey free from the web, thereby destroying several of the long sticky lines. She returned to the retreat with the prey attached as before and eventually juveniles began to feed on the prey. A second phlebotomine fly impacted the web, was detected, attacked, carried to the retreat, and eaten by a subadult male using the same behaviors as the mother (Fig. 5). Finally, a beetle impacted the web and after at least a five minute delay, the mother approached, touched it repeatedly with her first legs but did not wrap it. She returned to the retreat and the beetle eventually broke loose. We also observed prey catching in one of the subsocial webs with small juveniles, where prey handling was identical, except that the small juveniles did not react in any way to prey getting stuck in the web or to the mother attacking but stayed in the retreat.

Even though only a few colonies were seen, *H. thorelli* clearly behaves like a typical subsocial theridiid spider: a nest is founded by a solitary female, a colony consists of a mother and her offspring that disperse near adulthood, colony members exhibit non-aggressive interactions, communal prey attack and feeding is demonstrated, and the mother catches prey that is then left for the juveniles to feed on. This constitutes the known fourth independent origin of subsocial behavior in theridiids, one each in *Anelosimus*, *Achaearanea*, *Theridion*, and *Helvibis*. Both molecular (Arnedo et al. 2004) and morphological (Agnarsson 2004; Agnarsson et al. 2006) data place *Helvibis* in Theridiinae, although morphology places it as sister to *Theridion* and molecules as sister to *Chrysso*. Both placements require the novel origin of subsociality in *Helvibis* as the two genera are primitively solitary.

The discovery of subsociality in *Helvibis* corroborates predictions derived from the phylogenetic distribution of maternal care (Agnarsson 2002, 2004; Agnarsson & Kuntner 2005), and provides another evolutionary replicate for comparative studies of subsocial behavior and the evolution of sociality. Recently, co-workers have discovered additional social and/or subsocial species: e.g., *Anelosimus oritoyacu* Agnarsson 2006, *A. guacamayos* Agnarsson 2006, *A. puravida* Agnarsson 2006, *A. dubiosus* (Keyserling 1891), and *Theridion nigroannulatum* Keyserling 1884 (Marques et al. 1998; Agnarsson 2006; Avilés et al. 2006). Probably many more subsocial and social spider species await discovery. More fieldwork is an urgent priority.

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