

SHORT COMMUNICATION

New observations on a neotropical termite-hunting theridiid spider: opportunistic nest raiding, prey storage, and ceratopogonid kleptoparasites

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Abstract. A neotropical spider in the genus *Janula* Strand 1932 is reported as an opportunistic raider in damaged carton nests of the arboreal termite *Nasutitermes ephratae*. These spiders were shown to be attracted to ruptured nests and galleries from which they gather soldier termite prey that they bundle into silk-wrapped balls before suspending them away from the nests. Three species of *Forcipomyia* and one species of *Atrichopogon* (Ceratopogonidae, biting midges), rare associates of spiders, are reported as kleptoparasites on the dangling and immobilized termites.

Keywords: Theridiidae, *Janula*, Ceratopogonidae, *Nasutitermes*, spider foraging, kleptoparasitism, *Forcipomyia*, *Atrichopogon*

During a 2009 undergraduate field course in eastern Ecuador, we deliberately punctured arboreal carton nests of the termite *Nasutitermes ephratae* Holmgren in order to demonstrate how some specialized Reduviidae routinely prey on termites when nests are damaged. As expected (McMahan 1982), termite-hunting assassin bugs (*Salyavata variegata* Amyot & Serville) appeared at the damaged nests, but so did some remarkably specialized theridiid spiders of the genus *Janula* Strand 1932 (identified as *Janula* sp. near *J. erythrophthalma* (Simon 1894), previously in *Episimus* Walckenaer in Latreille 1809, see World Spider Catalog (2015)). *Janula* is close to *Episimus*, where it was formerly placed, and *Janula* plus *Episimus* may be the sister lineage of *Chrosiothes* Simon 1894 (Duran-Barron et al. 2013). The biology of the genus *Janula* was previously poorly known.

Spider specialization on termites is very rare (Pekár & Toft 2014) but, interestingly, the only previously described specialization of a web-building spider on termite prey was of a related genus, *Chrosiothes*, in which *C. tonala* (Levi 1954) builds horizontal lines above the ground from which to grab and envenomize termites (Eberhard 1991). The delicate *Janula* spiders, with a body size of ~2 mm (slightly smaller than that of their termite prey, Fig. 1A, B), promptly attacked termite soldiers defending the periphery of the breach, usually wrapping multiple prey termites together and webbing them to the outside of the nest before suspending the immobilized termites away from the nest or gallery (Fig. 1B). Spiders with prey invariably attracted kleptoparasitic female adult Ceratopogonidae, some of which fed on the immobilized termites. We describe here the details of these novel associations.

We made diurnal observations of termites, spiders and flies at four nests of *Nasutitermes ephratae* between May 4–9, 2009, in a small area of wet forest adjacent to the main buildings of the Estación Científica Yasuní of the Pontificia Universidad Católica del Ecuador (250m, 0°40'41''S 76°23'48''W). No spiders were seen at several nearby nests of arboreal termites of other species. The subject *Nasutitermes ephratae* nests (Fig. 1C) were located more or less at eye level, and when the thin, paper-like shells were ruptured (poked with a stick), numerous soldier termites immediately appeared at the point of damage; spiders appeared shortly thereafter. We noticed no silk lines attached to the nest prior to manipulation. Behavior was documented with both still photography and video, and voucher specimens were

collected. Newly killed termites were set out near two of the four nests to see if the spiders and/or ceratopogonids were attracted to immobilized termites outside the spider's caches. We aspirated Ceratopogonidae from around spiders and their termite prey, stored them in 70% alcohol, and later slide mounted the specimens using the method described by Borkent & Spinelli (2007).

Although we saw no *Janula* spiders on or near intact nests, 1–5 spiders appeared within five minutes of damaging each nest. Prey soldier termites were picked off the periphery of the breach by spiders clinging to the outer nest surface adjacent to the breach. The spiders moved to nearby termites on the nest surface, grabbed them with their legs, and webbed them to the nest surface. Multiple termites were bitten while on or near the nest or gallery prior to being webbed together. Spiders bundled one or more (Fig. 1D) termites into a ball. They then secured silken strands to a nearby leaf or branch, attached a strand to the now immobile bundle of termites, and swung out from the nest with their prey. They proceeded to feed slowly on the termite soldiers where they hung in space away from the termite nest. Some spiders returned to the termite nest to capture further prey, swinging out with prey and adding them to the initial bundle.

Ceratopogonid flies were observed on or around the spider's termite bundles at each of the four observed nests. Each bundle eventually attracted 1–4 flies that hovered nearby (Fig. 1E, F), darted in and out, and briefly (from a few seconds to a few minutes) fed on the wrapped termites. Still photographs clearly show the fly mouthparts inserted into the prey (Fig. 1D). Attending spiders were clearly agitated by the flies, waving their legs at the flies in apparent defense (Fig. 1F). Although no successful attack on a fly was observed, some of the termite bundles included dead ceratopogonids (Fig. 1D), suggesting that kleptoparasitism of *Janula* carries some risk. Flies appeared soon after the termite bundles were hung and persisted throughout the period of observation (up to 24 hours on one bundle). The flies sometimes landed nearby for short periods, but showed no interest in the dead termites laid out nearby. No ceratopogonids were seen on or around the Reduviidae feeding on the termites at the same nests. The ten flies collected on or near the wrapped termites were of four species of blood-feeding Ceratopogonidae in two genera (see below for details of the fly taxa).

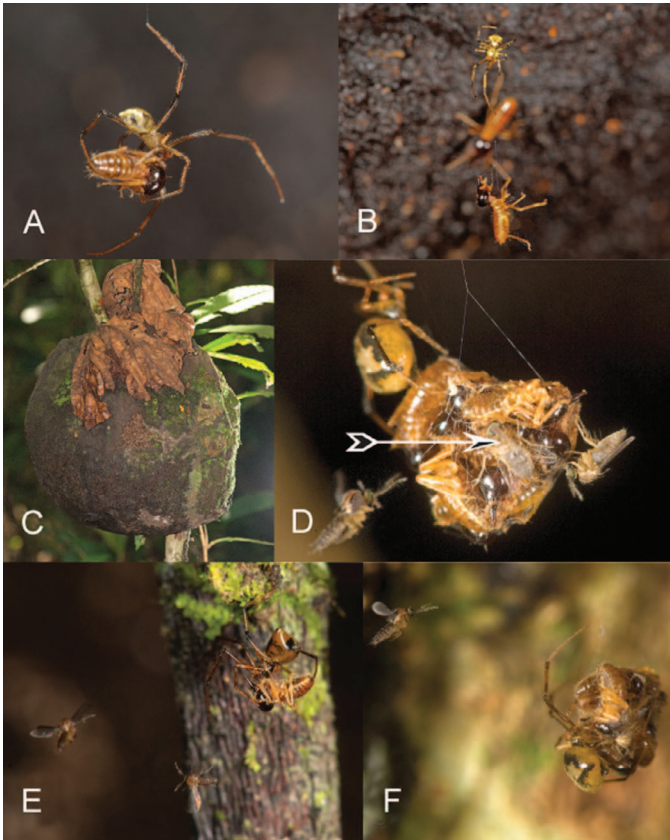


Figure 1.—A) *Janula* sp. with a single soldier of *Nasutitermes ephratae*; B) *Janula* sp. swinging out from a *Nasutitermes ephratae* nest with a single termite (lower termite in the photo) in tow; C) *Nasutitermes ephratae* nest with a breach in the outer wall; D) Female *Forcipomyia* sp. feeding on immobilized termites; the bundle of termites includes at least one dead *Forcipomyia* (arrow); E) *Janula* sp., with a single prey *Nasutitermes ephratae* soldier, fending off two kleptoparasitic female *Forcipomyia* sp.; F) *Janula* sp. with hanging ball of immobilized termites; a female *Forcipomyia* hovers nearby.

Repeated observations of consistent modes of attack, transport and storage of prey by *Janula* spiders on four *Nasutitermes ephratae* nests suggest that termites are an important food source for this spider species. Given these observations and the relative rarity of termitophagy in spiders (Pekár and Toft 2014), we hypothesize that the spider is a specialized termite raider. Spiders were found on all four *N. ephratae* nests observed but were not found on either intact or ruptured nests of other, more abundant termites in the same area, further suggesting that it is a specialized raider of *Nasutitermes ephratae* nests. Additional experimental studies are needed to test these intriguing hypotheses.

Several families of flies are known to be kleptoparasites on spider prey (Sivinski et al. 1999) and are often attracted in groups of numerous individuals that may consist of multiple species (Sivinski et al. 1999; Kuntner & Agnarsson 2010). The frequent appearance of the ceratopogonid flies at each colony, but only on bundled termites, suggested a specialized kleptoparasitic relationship. This relationship is remarkable in that four species of fly were involved and that biting midge and spider associations are rare (Sivinski et al. 1999).

No other *Janula* species is known to attack termites, but one other theridiid species (*Chrosiothes tonala*) has been described as preying on foraging workers and associated soldiers of a subterranean termite, *Tenuirostritermes briciae* (Snyder), in Mexico (Eberhard 1991). This species also immobilizes multiple individuals, transporting them

before hanging them under leaves or stems, often in large masses of 20 or more individuals. *Chrosiothes tonala*, however, has an otherwise very different attack strategy, dropping down on foraging termites on the surface of the ground from above rather than attacking soldiers at a nest breach as in the species considered here. Most theridiid spiders rely on webs to stop and entangle prey, facilitating their capture (Agnarsson 2004). However, both *Janula* and *Chrosiothes* belong to the subfamily Spintharinae (Agnarsson & Veve 2015). Most spintharines appear to be specialists on pedestrian prey, and some physically subdue prey rather than relying on webs. Prey capture strategies are known for only very few spintharines and the observations discussed here suggest that further studies may uncover diverse and unusual prey capture strategies within this subfamily.

Females of many species of the biting midge subfamily Forcipomyiinae feed on insects much larger than themselves, including such hosts as caterpillars, phasmids, wings of Odonata and Lepidoptera, blister beetles and more (Borkent & Spinelli 2007). There are very few observations of Ceratopogonidae female adults feeding on spider prey other than the records of *Atrichopogon* in Downes & Smith (1969). Three unidentified *Forcipomyia* were observed by W. Eberhard (pers. comm.) on a spider web on Isla del Coco, Costa Rica but it was uncertain if they were feeding. One species of *Forcipomyia*, *F. araneivora* Clastrier & Legrand from Guinea, has been observed feeding directly on a spider (Clastrier & Legrand 1991), the only ceratopogonid known to do so.

The subfamily includes two genera, *Forcipomyia* Meigen and *Atrichopogon* Kieffer. The 10 specimens found here all have biting mouthparts and were collected pursuing the spiders and their captured termites. Of these, a single female of *Atrichopogon* (*Lophomyidium*) sp. resembles some undescribed Costa Rican species that can only be distinguished on the basis of male specimens (Borkent & Picado 2004). The genus *Atrichopogon* is large, with 521 described species worldwide (Borkent 2014). However, there are records of feeding for only nine other described species on either true or false blister beetles (Meloidae, Oedemeridae) or the wing of a Lepidoptera. Downes & Smith (1969) observed unidentified *Atrichopogon* feeding on dead insects in a spider web, the only other observation of this genus besides ours of an association with spiders. Three species of *Forcipomyia* were also sampled. Two of these are in the subgenus *F. (Warmkea)* Saunders and are the first records of biting in that group. Six specimens were of *F. galindoi* Wirth and Soria, a species more broadly distributed in the Neotropical Region (Borkent & Spinelli 2007). Two specimens were *F. terrestris* Saunders, a species previously known only from Trinidad (Borkent & Spinelli 2007). One specimen of *Forcipomyia* (*Euprojoannisia* Brèthes) could not be identified to species. All ceratopogonids photographed feeding on the bundled termites were *Forcipomyia* Meigen.

The observations reported here document a previously unknown prey capture strategy of a theridiid spider and confirm persistent kleptoparasitism by ceratopogonid flies attracted to the immobilized termite prey. Given the rarity of ceratopogonids feeding on spider prey, it was unexpected to discover four ceratopogonid species associated with this specialized Ecuadorian *Janula* species. In the light of this finding it would be worthwhile to determine whether the flies feeding from the spider-bundled termites are the same as those seen flying around the spider and prey. This biological system warrants further study to more fully document the natural history of this remarkable termite-hunting spider and its relationship with multiple species of biting midges.

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