

Observations on the nesting behaviour of the spider wasp *Eragenia congrua* (Hymenoptera: Pompilidae), with the first record of the host

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We describe, for the first time, the nesting behaviour of an *Eragenia* spider wasp, *Eragenia congrua*, based on field observations in the Brazilian Amazon. This species was observed nesting in holes at the base of the trunk of a *Jacaranda copaia* tree and provisioning nests with both amputated and non-amputated species of undetermined *Corinna* sp. (Corinnidae) spiders. The spiders are carried forward and grasped at the base of the chelicerae. Nesting is gregarious with females nesting in the same small area on successive days.

Keywords: Pepsinae; Ageniellini; spider; Corinnidae; nest

Introduction

Pompilidae are solitary wasps commonly known as ‘spider wasps’ or ‘spider-hunting robber wasps’ because the female wasps hunt spiders to provision their nests (Day 1988).

Ecological and morphological convergences are known among species of spider wasps, which makes their taxonomy very difficult (Waichert et al. submitted for publication). All pompilids prey on spiders and most species are solitary; however, some species are gregarious and a few are communal (Wasbauer and Kimsey 1985; Weislo et al. 1988; Shimizu et al. 2010). The nesting behaviour of spider wasps is varied; some species dig and construct cells in the soil, whereas others use pre-existing cavities in a variety of substrates, such as holes bored by beetle and in habitation walls (Wasbauer 1995; Fernández 2006). Some spider wasp species are cleptoparasites of other pompilids (O’Neill 2000; Shimizu et al. 2010) and so do not build their own nests, whereas some species construct mud nests in rocks or leaves (Wasbauer 1995; Shimizu et al. 2010).

Nesting biology and behavioural patterns of Nearctic species of Pompilidae have been thoroughly studied (Kurczewski and Kurczewski 1968, 1972; Kurczewski and Spofford 1986; Kurczewski 2010). However, the understanding of nesting and host selection of Neotropical species is scarce and remains unknown for several genera (Wasbauer 1995; Fernández 2006). Consequently, the life histories of many Neotropical genera are unknown and only inferred from their Nearctic relatives

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(Wasbauer 1995; Fernández 2006). Among the Neotropical genera of Pompilidae, the nesting biology of *Eragenia* (Ageniellini) is unknown.

Ageniellini wasps are distributed worldwide, with the highest diversity in the tropics. They exhibit a variety of nesting behaviours. Females of some Ageniellini can be cleptoparasitoids, constructing nests by digging cells in the soil without using water or by softening the soil with water, and building mud and communal nests. The species of this tribe may or may not be specific to a single spider family and provision nests usually with an amputated spider, but variations have been observed (Shimizu et al. 2010). Shimizu et al. (2010) presented an extended list of hosts, ecology and nesting behaviour of species of Ageniellini, but information on the biology of many species of Ageniellini remains unknown or fragmentary.

Eragenia (Ageniellini) contains 16 Neotropical species (Waichert et al. 2014). Nesting behaviour has never been described for *Eragenia*, only host records and host transport behaviour of five species are recognized (Kimsey 1980; Wilson and Pitts 2007; Waichert et al. 2014). Three families of spiders, Ctenidae and Psauridae, and Zoridae, have been described as hosts of *Eragenia*, which may amputate all or some legs of the host (Kimsey 1980; Wilson and Pitts 2007).

We observed for the first time the nesting behaviour of *Eragenia congrua* in the Amazon forest, Brazil. In this paper, we provide and discuss primary information on nesting behaviour of *E. congrua*, including the first host record for this species and the first observation on nesting of the genus.

Material and methods

Study area

The nests were observed in a single tree, located on the border of a walking path found in a secondary Amazon forest at the research campus of Museu Paraense Emílio Goeldi (1°27'05" S, 48°26'40" W), Belém city, State of Pará, Brazil. This forest comprises c.2 ha of protected area and it is surrounded by another reserve, the forest of Universidade Rural da Amazônia. The latter is connected to two other protected areas: Embrapa Amazônia Oriental and Parque Estadual de Belém. The nests were found in an area characterized by rapid-colonization plants, such as *Cecropia* spp., *Tapirira guianensis*, *Euterpe oleracea*, *Lycaonia* sp. and *Hevea brasiliensis*, with a canopy of 10–18 m. The weather is hot and humid, with an annual average temperature of 26°C, the relative air humidity is close to 90%, and the rainfall is between 2300 and 3000 mm/year (Bastos et al. 2002).

Data collection

The observations were carried out once a week during the time period between 0900 and 1700, from August to November 2010. The behaviour of the spider-wasps was video-recorded and photographed with a Sony DSC-H9 camera.

Ten nests were dissected by removing the superficial layer of outer bark adjacent to the nest entrance with a knife. Three features of the dissected nests were recorded: (1) number of cells, (2) cell orientation and (3) tunnel length. The tunnel length was obtained with a small measuring tape.

Scanning electron micrographs were made of female's mandible and metasomal tergum VI to illustrate morphological characters that are behaviourally functional. The structures were previously mounted on stubs, sputter-coated with a gold palladium alloy, and studied with an LEO-1430 at 8 or 10 kV.

Some individuals were collected by hand and identified based on descriptions and comparison to the holotype. The voucher specimens of wasp and spider are housed in the invertebrate collection of the Museu Paraense Emílio Goeldi.

Results

A total of 23 nests were observed, all of them were located in the outer bark at the base of a Jacaranda tree (*Jacaranda copaia*: Bignoniaceae). The base of the tree was covered by mosses and lichens and epiphytes were attached along the trunk and branches (Figure 1A,B). Although the studied site held nearly 15 Jacaranda trees, all females nested in one tree. During the observation period when we observed the wasps, we did not find any nest under construction. The nests consisted of a shallow single cell oriented upward. The tunnel length varied from 9 to 15 mm long.

Up to seven females were observed at the same time in the nesting site (Figure 1C,D). The females and males of *E. congrua* usually walk with the metasoma bent forward and with the wing tip curved downward (Figure 4A). Female wasps did not cooperate in nest provisioning, instead they spent their time hunting and cleaning cells. The peak of activity in the nesting site was between 0800 and 1430, when females would return to the burrow carrying their host. Female–female agonistic behaviour was observed on one occasion. This behaviour took place when one female touched a conspecific female with its antenna. After the contact, the disturbed female flipped its wings toward the other wasp, but no agonistic behaviour was detected when spiders were brought to nests.

Eragenia congrua uses one species of spider as host. All spiders captured by *E. congrua* were identified as an undetermined *Corinna* gr. *ducke* (Corinnidae). Patterns of amputation of the host's legs varied: (1) all legs of the host were amputated and only the pedipalps remained; (2) one leg and pedipalps were intact on the spider; and (3) all legs were left undamaged (Figures 2C,D and 3A–D). The paralysed spiders were grasped by the base of the chelicera tucked beneath the body of the wasp and carried forward to the nest (Figure 2D). The females groomed all the body parts of the spider, including the undamaged areas such as chelicerae, before storing it in the nest (Figure 2C). We did not observe feeding on haemolymph by *E. congrua*.

Upon arrival at the nest, the spider host was dragged backwards into the nest and deposited into a cell. During this time they were held in the wasp's mandibles by the spinnerets (Figure 3A,B). One female placed the host underneath a loose piece of bark while she searched for the nest entrance (Figure 2A).

A single egg was laid diagonally on the side of the abdomen (Figure 3D). After oviposition, females left the nest and closed it up with plant material by scraping off small pieces of wood with the mandibles from the surrounding entrance (Figure 3C,D). The end of the metasoma was used to tightly pack the wood shaving closure (Figure 2B). No individuals were hatched from nests during the months of observation.

We did not observe parasites surrounding or emerging from nests. However, on three occasions females of *E. congrua* chased off *Crematogaster* sp. ants. There was a

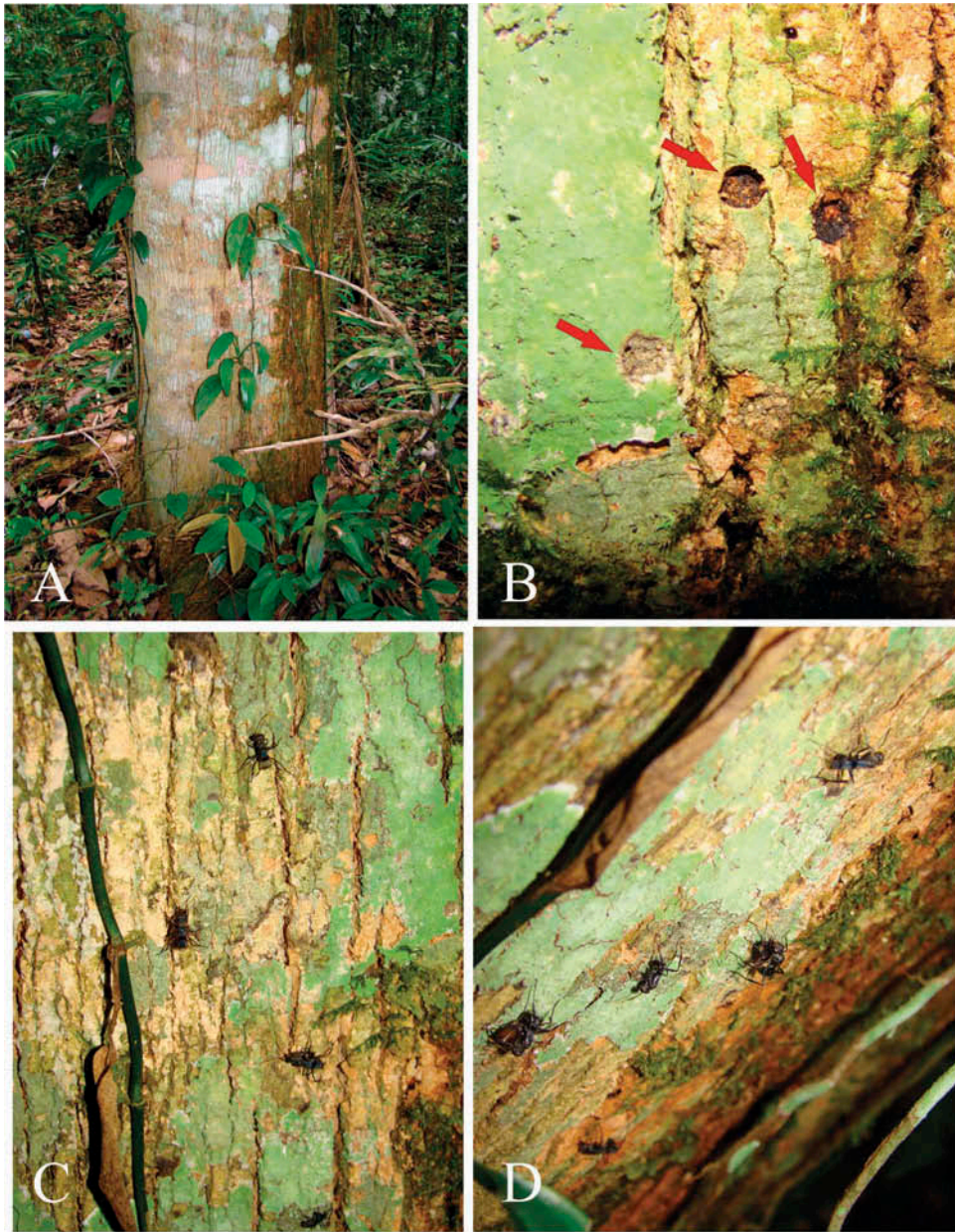


Figure 1. (A) Jacaranda tree (*Jacaranda copaia*) with the nests of *Eragenia congrua*; (B) detail of the bark of Jacaranda tree with three closed old nests of *E. congrua* indicated by arrows. (C, D) Females of *E. congrua* on the bark of a Jacaranda tree.

trail of *Crematogaster* near the nests of *E. congrua*, but these ants were rarely seen in the nesting area.

Males of *E. congrua* were found on leaves of epiphytes at the nesting tree and on low bushes surrounding this tree (about 60–90 cm from the nest entrance). The



Figure 2. (A) Spider host stored underneath a loose piece of bark (indicated by arrow) and *Eragenia congrua* searching for the nest entrance; (B) *Eragenia congrua* filling nest entrance with pieces of wood. (C) *Eragenia congrua* grooming a spider before storing it in the nest; (D) *Eragenia congrua* grasping spider by the base of chelicerae.



Figure 3. (A, B) *Eragenia congrua* inside the nest pulling the spider by the spinnerets; (C) opened nest of *E. congrua* with the host spider in the bottom and entrance closed with pieces of wood; (D) host spider with an egg (indicated by arrow) inside an opened nest of *E. congrua*.

males usually remained motionless, with a short distance between one another. Although the males were in close proximity they did not exhibit aggressive behaviour against each other. Neither attempted nor successful copulation was observed during this study.

Discussion

The nests of *E. congrua* were structurally similar to those described for other species of burrowing wasps (e.g. O'Neill 2000), however, few pompilid species nest in plant tissue (O'Neill 2000). The Japanese species *Anoplius* (*Anoplius*) *eous* constructs the nest cell in rotting wood (Shimizu 1992) and the British species *Dipogon subintermedius* nests in abandoned wood tunnels excavated by beetles (Shaw 1997). The nesting biology of *E. congrua* differs from these species by nesting in the bark of healthy trees. Nesting habits previously recorded for Ageniellini wasps are variable. They have been observed using pre-existing cavities, digging nests in soil, building cells made of mud or masticated vegetal material, or exhibiting cleptoparasitic behaviour (Evans and Shimizu 1996; Shimizu et al. 2010). Despite all of this, this study is the first record of an Ageniellini spider wasp nesting in bark. We did not observe *E. congrua* boring the jacaranda tree bark. It is possible that they are using abandoned nests of wood-boring insects, as do other pompilids (Wasbauer 1995). However, none of the active or abandoned nests, or the nests not yet occupied, were taken by other insects, nor did they contain the remains of exuvia or faecal pellets from previous occupation.

Aculeate wasps that nest in hollow plant stems or in holes in wood usually have morphological modifications associated with this behaviour. It has been suggested that a three-toothed mandible is an adaptation to pith-burrowing (O'Neill 2000). It is true in wasps of the genus *Stigmus* (Sphecidae), for instance (Krombein 1984). In Pompilidae, three-toothed mandible *Dipogon* are confined to woody areas and several species are known to nest in hollow plant stems or in pre-existing cavities in wood (Wasbauer 1995; Evans and Leatherman 2010). Although females of *E. congrua* nest in burrows in the bark, they have a two-toothed mandible (Figure 4B). This may be explained by the fact that the bark of the jacaranda tree is soft. Nevertheless, females of *Eragenia* have distinguished mandibles; they are long, slender, and withdrawn almost completely beneath the clypeus (Waichert et al. 2014). Perhaps it is a morphological change to facilitate excavation.

Another adaptation found in some species of Sphecidae that construct nests in wood is the presence of a narrow and scoop-like pygidial plate (Bohart and Menke 1976; O'Neill 2000). *Eragenia congrua*, as expected of a wood-nesting species, has the pygidial plate narrow and scoop-like, with the tip strongly curved upward (Figure 4C). In addition, the last abdominal segment shows a tuft of strong curved bristles (Figure 4C, D). The scoop-like pygidial plate and the strong bristles are used to scrape and to tamp down small pieces of wood in the nest closure process. Species of *Eragenia* are characterized, and distinguished from other genera of Ageniellini, by having the pygidial plate narrow and covered by thick curved setae (Waichert et al. 2014); hence, it is possible that other species of this genus nest in cavities of trees as well. As this is the first record of nesting behaviour for the genus, further studies are needed to better understand nesting behaviour and morphological adaptations of *Eragenia*.

Communally nesting pompilids demonstrate co-operation in defence, nest building and generational overlap (Evans and Shimizu 1996). *Eragenia congrua* lacks these

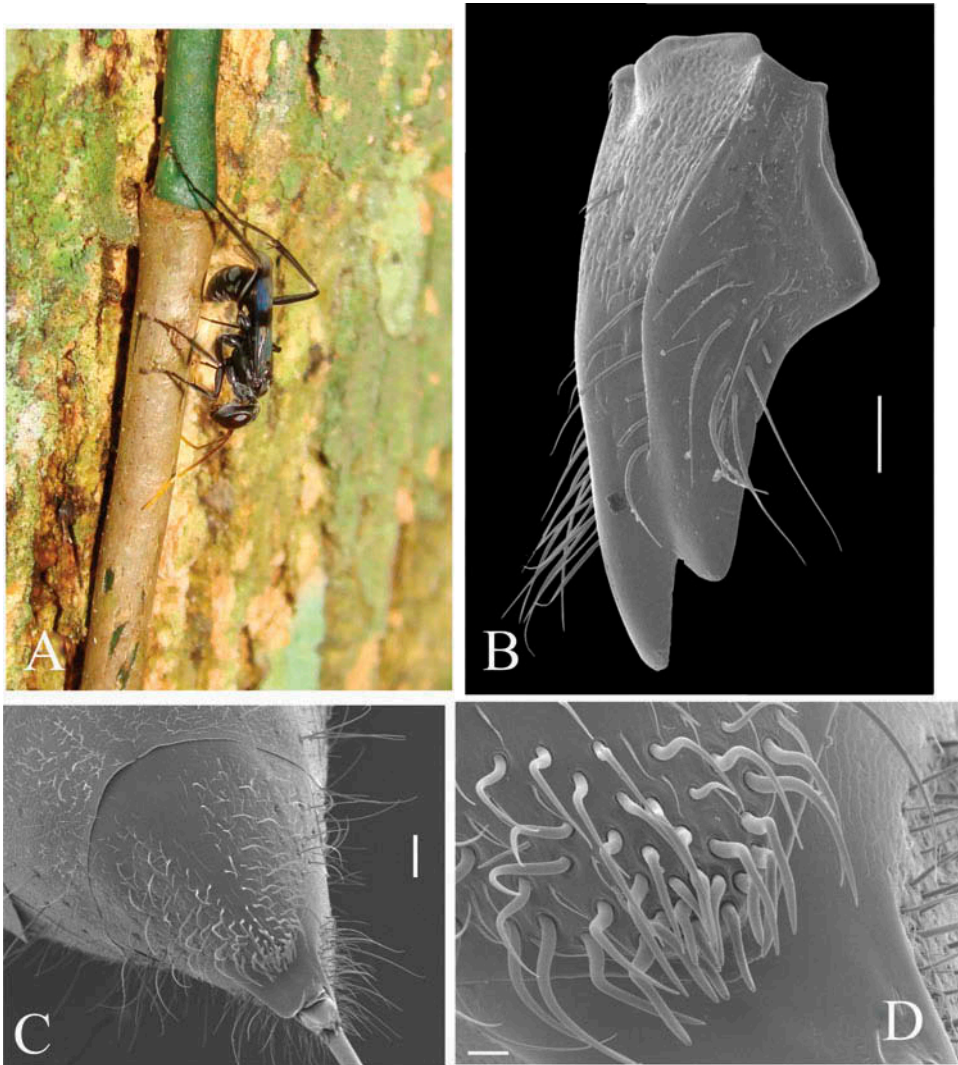


Figure 4. (A) Female of *Eragenia congrua* with bent gaster and curved wing tip; (B) mandible of a female of *E. congrua*; (C) terminal portion of metasoma of a female of *E. congrua*; (D) detail of the bristles in the terminal portion of metasoma of a female of *E. congrua*.

behaviours, and it is therefore assumed to be a gregarious species. However, the utilization of the same nest area by several females of *E. congrua* would be the result of the availability of suitable nesting conditions. Therefore further studies and observations are needed to confirm the gregarious pattern behaviour of this species.

In Ageniellini, there are some communal species (see Evans and Shimizu 1996; Shimizu et al. 2010) but, to our knowledge, only *Ageniella evansi* has been recorded nesting in aggregations deep in a cave (Kurczewski 1995). As this is the first record of the nesting behaviour of *Eragenia*, it remains to be seen if all species of this genus or only *E. congrua* have gregarious nests.

Like most other genera of pompilids, this genus is not specific to a single spider family. The previous host records for the genus *Eragenia* are spiders of the families Acanthoetenidae (now a subfamily of Ctenidae) (Kimsey 1980), Pisauridae (Wilson and Pitts 2007), and Zoridae (Waichert et al. 2014). Currently, about 27 families of spider have been recorded as host to species of Ageniellini (Shimizu et al. 2010), and Corinnidae have been recorded as host only to some species of *Auplopus* (Zanette et al. 2004; Gonzaga and Vasconcellos-Neto 2006). Therefore, this is the first documented record of Corinnidae serving as host of *Eragenia*. In addition, this result suggests that the genus *Eragenia* is oligophagous, since they use unrelated spider families (Corinnidae, Ctenidae, Pisauridae and Zoridae) as hosts. Although *E. congrua* is here reported preying on a single spider species.

Finally, Ageniellini wasps usually amputate all of the legs of the host, but some species leave some or all legs (Evans and Shimizu 1996; Shimizu et al. 2010). Wilson and Pitts (2007) recorded the amputation of some or all the legs of the host of *Priocnemella* sp. probably *Eragenia oliva* or *Eragenia dentata* (Waichert et al. 2014); Waichert et al. (2014) reported a female of *E. oliva* pinned with a spider with all legs. Kimsey (1980) observed *Priocnemella rufothorax*, now *Eragenia micans*, transporting a spider with intact legs and Waichert et al. (2014) reported a pinned specimen of the same species with an amputated spider. *Eragenia congrua* displayed all behaviours described above. Similar intraspecific plasticity has been reported of *Machaerothrix tsushimensis* (Shimizu 2004) and *Auplopus* sp. (Barthélémy and Pitts 2012), both Ageniellini. Therefore, amputation is an inconsistent behaviour in *Eragenia*, which may vary depending on different circumstances. The stimulus that triggers such behaviour remains unknown.

Ageniellini holds a great potential to help understand the states involved in the evolution of parasociality and eusociality in Hymenoptera. Therefore, detailed information on hunting and reproductive ecology of these spider wasps, as presented herein for *Eragenia congrua*, enriches our knowledge on Ageniellini behaviour, a poorly understood group of Pompilidae with the most complex nesting behaviour in the family.

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