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# BEHAVIOR OF NESTING *EPISYRON CONTERMINUS POSTERUS* (FOX) AND ITS CLEPTOPARASITE *EPHUTA S. SLOSSONAE* (FOX) (HYMENOPTERA: POMPILIDAE, MUTILLIDAE)

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*Abstract.*—Behavior of the nesting spider wasp, *Episyron conterminus posterus* (Fox) and its cleptoparasite, *Ephuta s. slossonae* (Fox) were studied near Lake Annie in the sand pine scrub of Archbold Biological Station, Lake Placid, Florida. Nest burrows of *E. c. posterus,* 5.0–8.5 cm in length, were usually dug at a 45° angle into sandy, unvegetated soil. Excavation of several empty burrows prior to provisioning a nest was commonly observed. Each nest was provisioned with a single araneid spider, *Eustala anastera* (Walckenaer). Prey capture occurred prior to nest digging, and the paralyzed spider was cached on low vegetation near the nesting site. Spiders were dragged by their legs into the nest. Closure and concealment of the burrow quickly followed nest provisioning. Behavior of receptive female *Ephuta* and their attracted males is described. Details of female searching behavior, inspection of empty *Episyron* burrows, and entry into a closed, provisioned nest are provided. We report here for the first time, a mutillid probably feeding upon the host egg on the spider prey, and ovipositing within the body of its host's prey. A review of the known or suspected hosts of *Ephuta* suggests that the latter are obligate cleptoparasites of Pompilidae (spider wasps).

*Key Words:* *Episyron, Ephuta,* spider wasp, mutillid, cleptoparasite, empty burrows, Pompilidae, Mutillidae

Early in April, 1993 and 1995, we observed the behavior of *Episyron conterminus posterus* (Fox), and its cleptoparasite, *Ephuta s. slossonae* (Fox) at the Archbold Biological Station (ABS), Lake Placid, Florida. Observations of the wasps were made near Lake Annie along a narrow section ca 325 m long of a sand road paralleling Florida State Road 70 (Fig. 1).

## *Episyron conterminus posterus* (Fox) (Fig. 2)

Nesting and prey records for *E. c. posterus* have been reported by a number of observers (Krombein, 1979; Kurczewski, 1981; Kurczewski and Spofford, 1986). It was the most abundant pompiline at ABS where it nested principally in unvegetated white sand. Mark Deyrup (personal communication) collected over 655 individuals in three Malaise traps during his 1986 ABS insect survey.

Prey hunting and transport.—The wasps hunted for prey in the sand pine scrub adjacent to the nesting sites. We did not witness prey capture, but three spiders taken from wasps or their nests were females of the araneid, *Eustala anastera* (Walckenaer), ca 7 mm long. Levi (1977) noted that at ABS this spider made its web each evening after dark, and that most webs had been removed by morning. The species makes no


Fig. 1. Excavation site for nest of *Episyron conterminus posterus* in the sand road adjacent to Lake Annie, Archbold Biological Station, Florida.

retreat, but rests on dead branches when not in the center of the web. Such habits make it vulnerable to predation by *Episyron.* Prey capture occurs prior to nest construction. The wasp transports the paralyzed spider to the nesting area by flying with it if the prey is small, or by carrying a larger prey up a low plant, and making a short flight, followed by one or more similar sequences. Near the site where nest digging will be initiated, the wasp drags the spider up a small plant and caches it in the angle between a leaf and the main stem. We watched one female try several times unsuccessfully to drag her spider up a grass blade and get it to stay near the tip.

Nest excavation.—Females ready to initiate nest digging walked rapidly over the sand quite erratically, and occasionally flew low over the ground. Digging of empty burrows was frequently observed prior to digging the burrow that would contain the spider prey. The empty burrows extended downward to the level of damp sand similar to nest burrows. One female was observed digging seven empty burrows before provisioning and closing one of them (Fig. 2). Occasionally, she revisited an empty burrow to remove some sand grains, and then returned to work on the true nest. Most burrows entered the ground at a 45° angle. The raised mounds of sand adjacent to tire ruts appeared to be more attractive nesting sites than the surrounding level ground. Burrows (n = 25) measured 5.0–8.5 cm in length. Burrow openings were circular and ranged from 0.8 to 1.0 cm in diameter. A spoil heap of sand excavated from the burrows fanned out in a triangular pattern on the downslope below the nest openings. The terminal cell was spheroidal, often slightly wider than the burrow diameter, and was always in damp sand.

Nest provisioning.—Once burrow excavation was completed, females brought their paralyzed prey to the nest. These spiders were dragged by the legs, and deposited in front of nest openings. One female was observed pulling and pushing her prey over the sand for a distance of more than 150 cm from where it had been placed. Females then entered their burrows once or twice more, each time bringing sand grains

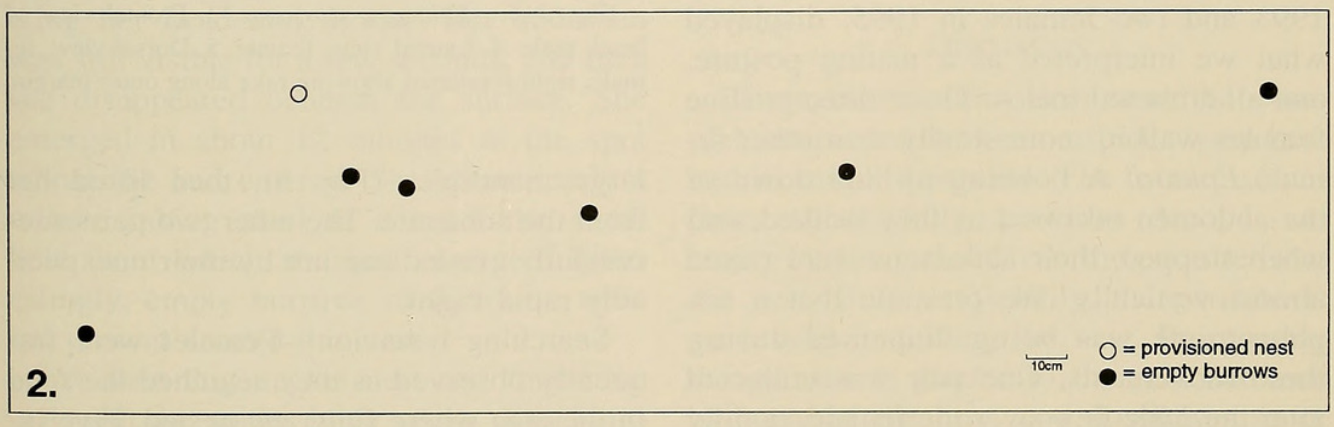



Fig. 2. *Episyron conterminus posterus.* Diagram of nest entrance and position of empty burrows.

to the opening, and kicking them out. Presumably, a cell was being created of the proper dimensions to accomodate the prey. Females inspected their prey, entered their nests, then came to the opening head first, and pulled their spiders inside.

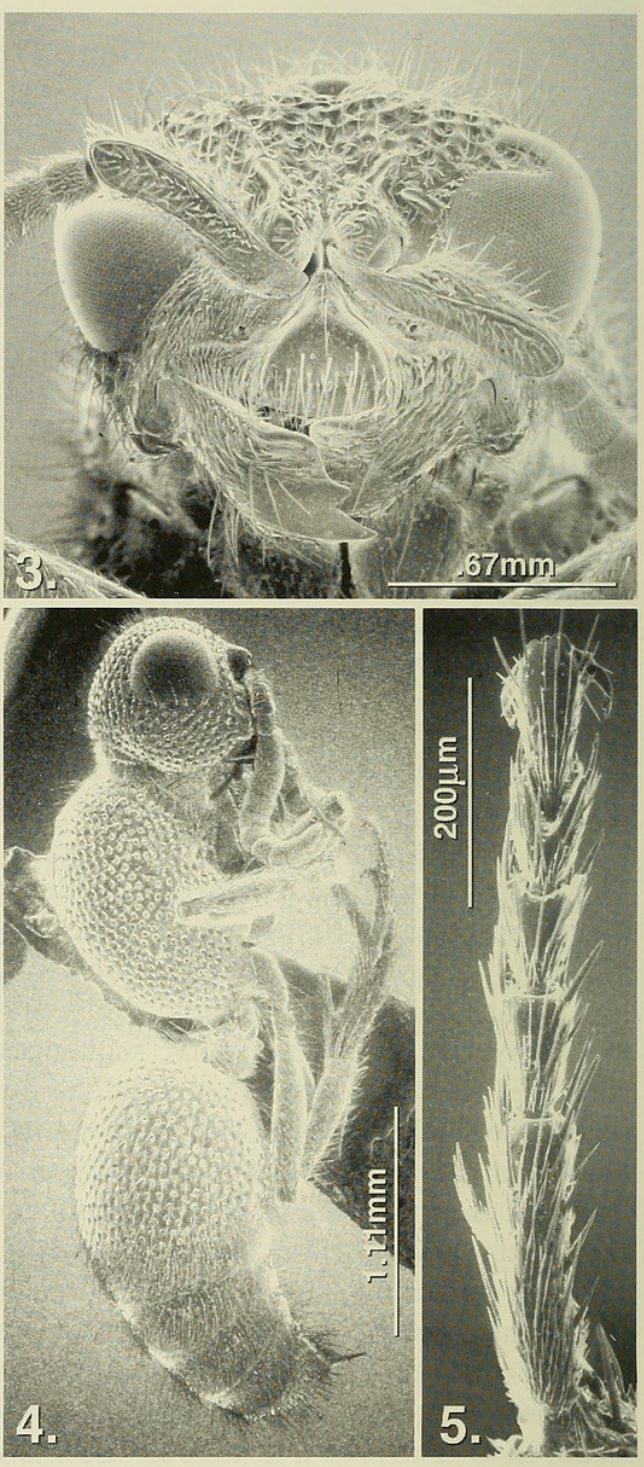
Nest closure.—Within several minutes of placing prey in their nests, females began nest closure and concealment. Appearing at the nest opening, females raked sand from the spoil heap into the burrow to fill it. *Episyron* raked sand down into their burrows and after plugging them nearly to the surface, most of the remaining spoil heap was raked away. Females then raked off the edges of the area where the opening had been, thus obliterating the remaining small depression. Finally, several minutes were spent scattering sand grains over the nesting area. One female, timed from initiation to completion of nest closure, spent 24 minutes plugging and concealing her nest.

*Ephuta slossonae slossonae* (Fox)
(Figs. 3–6)

This small species with females 3.2–4.8 mm long (Fig. 4), was the most common *Ephuta* in the study area. We saw only one female of the somewhat larger *E. puteola* (Blake) in this area.

Mating behavior.—Most of the female *E. s. slossonae* we observed walked over the sand with their abdomens held horizontally. These females appeared to be engaged in searching behaviors and were never observed to attract males.

However, one female observed during 1993 and two females in 1995, displayed what we interpreted as a mating posture, and all attracted males. These three pristine females walked more slowly than other female *Ephuta*. A bobbing up and down of the abdomen occurred as they walked, and when stopped, their abdomens were raised almost vertically. We presume that a sex pheromone was being dispersed during these movements. One pair was collected after the male flew over the female, rapidly pounced, apparently seizing her with his large mandibles (Fig. 3), then lifted her from the substrate. The other two pairs successfully evaded capture by their unexpectedly rapid flight.




Figs. 3–5. *Ephuta s. slossonae*. 3, Frontal view of head, male. 4, Lateral view, female. 5, Dorsal view, female, right foretarsus showing rake along outer margin.

Searching behavior.—Females were frequently observed as they searched the sand in the area where *Episyron* nested. Five individuals were followed continuously for as

long as 35 minutes each. They walked steadily throughout the observation period, but in a highly erratic pattern, turning this way and that. The pattern seemed similar to the erratic path of a spider wasp searching for a suitable nesting site. No *Ephuta* that we followed were ever observed to locate a host nest successfully.

*Ephuta* females did, however, often locate and crawl inside the empty burrows excavated by female *Episyron.* One female *Ephuta* was observed as she searched a nesting area containing five empty burrows. An *Episyron* had just recently provisioned and closed her nest which was roughly surrounded by the empty burrows. The mutillid entered each of these open burrows remaining inside for 30-60 seconds. The sand grains surrounding the burrows also appeared to attract her as she often circled around the spoil heaps upon exiting. Four holes excavated by nesting ants were also present at this site. These too were inspected by the *Ephuta* which entered them but exited immediately.

At an adjacent nesting area, we disturbed an *Episyron* female just as she was in the final stages of closing her nest. In this area traversed by the spider wasp as she concealed her nest opening, we noted a female *E. s. slossonae* searching and showing interest in a small area of several $cm^2$. After a few minutes she began digging into the sand which she excavated with her forelegs, presumably using the weak tarsal rake (Fig. 5) to scratch the sand backward. As she dug, the loose sand above slid down covering her head and thorax. Her abdomen was still visible for a few seconds, and then she disappeared beneath the surface. She emerged in about 12 minutes at the spot where she had entered. She spent nearly a minute raking sand to conceal the small hole from which she had emerged. Interestingly, empty burrows of *Episyron* were not present around this nest.

We then dug up the nest and found the cell with the spider lying on its dorsal surface in damp sand at a depth of ca 7 cm. A wasp egg was not visible on the spider, so the paralyzed prey was placed in a vial of Kahle's solution for further study. Microscopic examination later revealed an oblique cluster of sand grains adhering to the spider's abdominal venter anterolaterally. When the grains were teased away, we found the collapsed and drained *Episyron* egg chorion. It seems probable that the egg had been punctured and fed upon by the *Ephuta.*

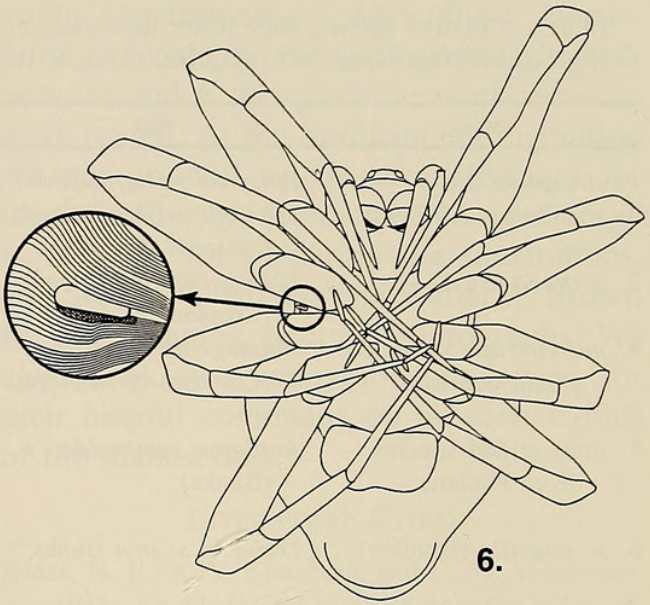



Fig. 6. *Eustala anastera.* Ventral view showing oviposition site on right side of cephalothorax, and, in circle, the egg of *Ephuta s. slossonae* between layers of muscle tissue.

No *Ephuta* egg was visible on the external surface of the spider. Careful dissection of the entire spider revealed a small, slightly curved *Ephuta* egg (ca 0.75 mm long) inserted between layers of muscle on the right side of the cephalothorax just above the second and third coxae (Fig. 6).

## Discussion

These observations document the complex interaction between a spider wasp host and its mutillid parasite. The former, sometimes successfully, provides decoys, i.e. empty burrows, that divert the parasite from the nest. But occasionally, the parasite is successful in finding the nest. Presumably the parasite is guided to the nest entrance by scent of the host, and possibly also of the spider prey, remaining on particles of

Table 1. Taxa of *Ephuta,* their hosts, nest sites, and pertinent references. The taxa are grouped by nest types: 1–2, ground-nesting hosts; 3–5, mud cell hosts; 6, twig-nesting host.

| *Ephuta* | Host | Nest Site | Reference |
|---|---|---|---|
| 1. *slossonae* (Fox) | *Episyron posterus* (Fox) | sand | ibid. |
| 2. *s. sabaliana* Schuster | ? *Anoplius* (*Pompilinus*) *fraternus* (Banks) | salt flats | Krombein, 1979 |
| 3. *scrupea* (Say) | *Phanagenia bombycina* (Cresson) | cocoon of host (presumably in mud cell) | Schuster, 1951 |
| 4. *margueritae xanthocephala* Schuster | *Phanagenia bombycina* (Cresson) or *Auplopus* sp. | Hymenoptera—cocoons under stones (presumably in mud cells) | Schuster, 1951; Krombein, 1979 |
| 5. unidentified species from Panama | *Auplopus esmeralda* (Banks) | mud cell at base of inner surface of fallen palm frond | Kimsey, 1980 |
| 6. *p. pauxilla* (Bradley) | *Dipogon s. sayi* Banks | trap-nest | Evans and Yoshimoto, 1962 |

the substrate that are scattered about the area during nest closure.

*Episyron.*—Evans (1966) defined the term accessory burrows as "... any burrows started from the soil surface in close proximity to the true burrow and made by the same individual." Some species of *Episyron* make empty burrows more or less regularly, usually before construction of the nest, but sometimes afterward. What we recognize as empty burrows were reported in North America for *E. biguttatus* (Fabricius) (Peckham and Peckham 1898; Krombein 1953), *E. posterus* (Fox) (Kurczewski 1963, 1981; Kurczewski and Spofford 1986), and *E. quinquenotatus* (Say) (Peckham and Peckham 1898; Evans and Yoshimoto 1962). These observers reported that the empty burrows were dug before the nest burrow was excavated. None of them noted parasites at the nest sites.

We found that construction of empty burrows was common in the *E. posterus* population at the Lake Annie site. We also noted that empty burrows were usually made before completing the nest and were never used as a source of fill for nest closure. These empty burrows were not trial or test burrows such as those described by Kurczewski (1981) in his opening paragraph on *E. posterus.* Rather they appeared to be deliberate constructions in association with a nest burrow. Mutillids frequently walked into these empty burrows that usually were oriented in a direction differing from that of the nest burrow. We assume that empty burrows play some role in distracting and delaying parasites both during and following *Episyron* nesting.

*Ephuta.*—This is the first record of a mutillid probably feeding on the host egg, and then ovipositing within the body of the host's prey. This type of oviposition is reminiscent of the behavior of the cleptoparasitic pompilid, *Ceropales maculata* (Fabricius). Richards and Hamm (1939) reported the species as ovipositing within the stigmata leading to the lung-book of the spider. Other species of *Ceropales* are known to oviposit similarly.

Considering the oviposition behavior of *E. s. slossonae* in the context of similar behavior in the known species of *Ceropales* raises a question as to whether other species of *Ephuta* also oviposit within the spider prey of the host wasp. The few known or suspected hosts of *Ephuta* are limited to pompilid wasps[1]. Those few suspected

[1] In his listing of species of *Ephuta,* Fattig (1943: 13) mentioned that a male of *E. pauxilla* Bradley "... was taken with *Tiphia transversa* Say" [misspelled *transversata*]. The two specimens on a single pin are in the USNM collection. Both are males, so this odd coupling does not signify a possible host relationship as suggested by Schuster (1951: 14).

hosts of *Ephuta* are limited to pompilid wasps. Those few hosts have diverse nesting habits as noted in Table 1. Two species nest in the ground; three make mud nests in sheltered situations; and one nests in cavities in wood above ground.

*Ephuta s. sabaliana* Schuster is the other probable cleptoparasite of a ground-nesting spider wasp. The host is almost certainly *Anoplius (Pompilinus) fraternus* (Banks). Both species were observed in substantial numbers on the salt flats at Cape Sable, Florida (Evans, Krombein and Yoshimoto 1955; Krombein and Evans 1955). These observers found no other wasp or bee of appropriate size nesting in numbers in the ground. They noted no interaction between *Ephuta* and *Anoplius.* However, the *Anoplius* customarily left its spider prey on the ground while it searched for a nesting site, thus affording an opportunity for *Ephuta* to insert an egg into the spider.

Concerning the other four species of *Ephuta* listed in Table 1, apparently none of the cells was saved from which the mutillids emerged. This is unfortunate; the discovery of a mutillid cocoon *only* in the cells would have established that these species of *Ephuta* have oviposition behavior like that of *E. s. slossonae.*

Closer investigation of pompilids, their spider prey, and associated mutillids is clearly warranted. The available host information, though scanty, suggests that species of *Ephuta* are obligate cleptoparasites of Pompilidae (spider wasps).

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