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Natural History of the Mealybug-Tending Ant, *Acropyga epedana*, with Descriptions of the Male and Queen Castes

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ABSTRACT

The mealybug-tending ant *A. epedana* is an obligate coccidiphile with trophophoretic queens. Trophophoresy is defined as the behavior of a foundress queen transporting a trophobiont on her mating flight for the establishment of a new mealybug "herd" in her new colony. Both the male and queen of *A. epedana* are described here for the first time. Observations on a laboratory colony of *A. epedana* suggest that the ants obtain most, if not all, of their energy requirements from the mealybugs they tend. When offered a variety of food items ranging from dead insects to sugary substances (e.g. honey, sugar water), the ants refused them and even acted aggressively towards the dead prey items. Observations of a laboratory colony also revealed a peculiar body jerking behavior suggestive of a form of vibrational communication, though its exact function remains to be studied.

KEYWORDS: *Acropyga*, Arizona, Formicinae, mealybug, Pseudococcidae, trophobiosis

INTRODUCTION

The ants of the genus *Acropyga* are all hypogaecic (living entirely underground), surviving primarily by tending mealybugs (Hemiptera: Pseudococcidae) on underground roots for their honeydew (Weber 1944; Williams 1998). This mutually beneficial relationship is called trophobiosis (Hölldobler and Wilson 1990) and the partners are known as trophobionts. *Acropyga* species are all thought to be obligate coccidophiles (see Williams 1998; Johnson et al. 2001, for review); the ants are dependent on the mealybugs for survival. All *Acropyga* species investigated to date have been found with mealybugs in their nests (Weber 1944; Williams 1998). Though many ant species are known to harvest honeydew from hemipterans, *Acropyga* have taken the relationship further. Several species have been observed in which queens emerge from their nests for their mating flight each holding a mealybug in the mandibles (Bünzli 1935; Wheeler 1935; Brown 1945; Eberhard 1978; Prins 1982; Buschinger et al. 1987; Williams 1998; Johnson et al., 2001). The mealybug that each queen carries presumably serves as the parent from

which a new generation of mealybugs will be started in the newly founded ant colony (Weber 1944; Williams 1998). The behavior of a foundress queen transporting a trophobiont on her mating flight for establishment of a new mealybug "herd" in her new colony will be termed trophophoresy.

The mealybugs utilized by *Acropyga* all belong to the subfamily Rhizoecinae, and it is likely that the mealybugs are not able to survive independently of the ants for they have never been collected outside of *Acropyga* nests (Williams 1998). The complexity of the relationship between *Acropyga* and the mealybugs is scarcely understood, but it appears to be analogous to what has evolved between attine ants and the fungal species that they "farm." Flanders (1957) found that *A. fuhrmanni* stores its own eggs with those laid by the pseudococcids found in the nest. It has also been observed that *A. fuhrmanni* move mealybugs from underground chambers where roots are found to chambers without roots. Flanders (1957) speculated that the ants switched mealybugs between roots in order to regulate the amount of honeydew produced in a colony and to protect the roots from overuse by the mealybugs.

Fossil evidence suggests that the trophophoretic behavior of *Acropyga* ants is ancient. Johnson et al. (2001) discovered in Dominican amber *Acropyga* queens that were either holding a mealybug or with a mealybug nearby in the amber matrix. The amber dates from the Miocene, so the intimate relationship of *Acropyga* and mealybugs is at least 15-20 million years old (Johnson et al. 2001). Given that most extant formicines display some level of trophobiosis (Hölldobler and Wilson 1990), and that recently discovered formicine ant fossils date back to the mid-Cretaceous about 90 million years ago (Grimaldi and Agosti 2000), trophobiotic activity by ants is likely a very ancient behavior. The number of times trophophoresy originated among the formicines is at present unknown. Trophophoresy among formicines is known to occur only in *Acropyga*, however the monophyly of the genus has recently been called into question (Agosti 1991; Bolton 1995). It is possible that trophophoretic behavior arose at least one other time in the ants, in a species of the genus *Tetraponera* (subfamily Pseudomyrmecinae), a species where queens have been observed to be trophophoretic (Klein et al. 1992).

Unfortunately, little is known about *Acropyga* biology, but understandable because all *Acropyga* species are hypogaeic and small (typically less than 2.5 mm in total length). Workers never forage on the surface, so finding the ants usually requires a concerted effort.

We made observations on *A. epedana*, and have included descriptions of the previously undescribed reproductive castes. Collection of the male caste in *Acropyga* species is especially important because the male genitalia are often the only means by which species can be reliably identified, and because they provide important phylogenetic characters for the genus (LaPolla, unpublished data). *A. epedana*, with the most northern distribution of any New World *Acropyga*, has been collected only in southeastern Arizona (United States). The species was originally described from four worker specimens (Snelling 1973), and to date nothing is known about the species habits. This study suggests that *A. epedana* is an obligate coccidophile and that it is trophophoretic.

MATERIALS AND METHODS

All specimens available for study were examined, including specimens from the collections of the Los Angeles County Museum and Museum of Comparative Zoology, and three nests collected by JSL and UGM in August 2001 just outside the borders of the Southwestern Research Station (GPS location 31° 53.32' N, 109° 12.48' W; 1676 m elevation; approximately 5 miles west of Portal, Arizona). Two nests collected by JSL and UGM were brought back to the laboratory for behavioral

observations. These colonies were placed in plastic nest boxes (7.5 cm x 7.5 cm) with a 1 cm thick layer of moistened plaster on the bottom to ensure a humid nest environment. Some dirt from the collection site allowed the ants to construct tunnels and chambers. Because the ants were extremely photophobic observations were made under subdued light. The ants were videotaped to record behavioral observations. The larger colony was offered an aphid after about five hours in captivity, and then offered a range of food items after two weeks in captivity: a halictid bee, sugar water, and honey. The two insect prey items were frozen and thawed before being placed in the nest box. The sugar water and honey were presented by soaking a piece of paper towel in the sugar or honey solution, allowing the paper to dry, then reconstituting it with a small amount of water.

Morphological terminology follows Bolton (1994). All measurements are given in millimeters. Anatomical abbreviations are as follows: **AL** (alitrunk length): The length of the alitrunk in lateral view from the anterior most point of the pronotum to the posteriormost point of the metapleuron. **CI** (cephalic index): $HW \times 100 / HL$. **EI** (eye index): $EL \times 100 / HW$. **EL** (eye length): The maximum length of the eye. **EW** (eye width): The maximum width of the eye. **HL** (head length): The length of the head proper, excluding the mandibles measured in full-face view from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin. **HW** (head width): The maximum width of the head in full-face view. **SI** (scape index): $SL \times 100 / HW$. **SL** (scape length): The maximum straight line of the antennal scape excluding the condylar bulb. **TL** (total length): The total length of the specimen ($HL + AL + GL$).

RESULTS AND DISCUSSION

Systematic Treatment

Acropyga epedana Snelling, 1973

Snelling, 1973: 7, figure 1 (worker).

Male: (figures: 1a-c)

Measurements ($n=3$).— TL: 2.00- 2.13 HW: .419- .425 HL: .410- .424 SL: .330- .374 EL: .132- .144 EW: .108- .114 THL: .726- .775 GL: 2.00- 2.13 CI: 100.5- 102.4 SI: 78.8- 88.0 EI: 31.0- 34.0

Diagnosis.— Antennae 12 segmented; mandible with two distinct teeth, occasionally a smaller tooth is present at basal angle; genitalia with rectangular shaped parameres, which curve towards each other apically; cuspi and digiti meet apically forming an oval-shaped space between them in ventral view; ventral side of penis valves without teeth; apical tips flattened and laterally expanded.

Description.— Head: brownish-yellow and covered with fine pubescence; apex darker brownish-yellow, with three prominent ocelli; eyes large, in frontal view bulging out from outline of head; antennae 12 segmented; scapes surpass posterior margin, by about the length of the first two funicular segments; clypeus with several long hairs on anterior margin, though clypeus generally less pilose than the rest of the head; mandibles with two distinct teeth, an apical tooth and a basal tooth, a smaller tooth is occasionally present at basal angle; a large gap exists between anterior clypeal margin and inner mandibular margin. Thorax: yellow to brownish-yellow, darker along segmental margins; pronotum short and collar-like; anterior of mesonotum rounded, dorsum flat, covered in short, suberect hairs; scutellum distinct, roughly oval, slightly lighter than mesonotum, with fewer suberect hairs covering dorsum; propodeum with fewer short, suberect hairs than other parts of the thorax; declivity at ca. 45° angle. Gaster: petiole erect and short, triangular in lateral view with a rounded apex; gaster brownish-yellow with more brown dorsally; covered in a fine pubescence, with a few scattered

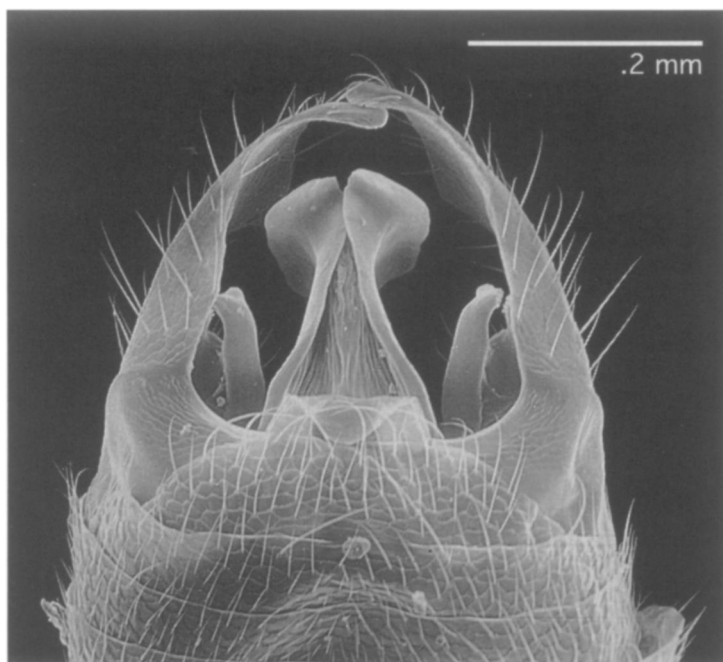


Figure 1a. Dorsal view of *A. epedana* male genitalia.

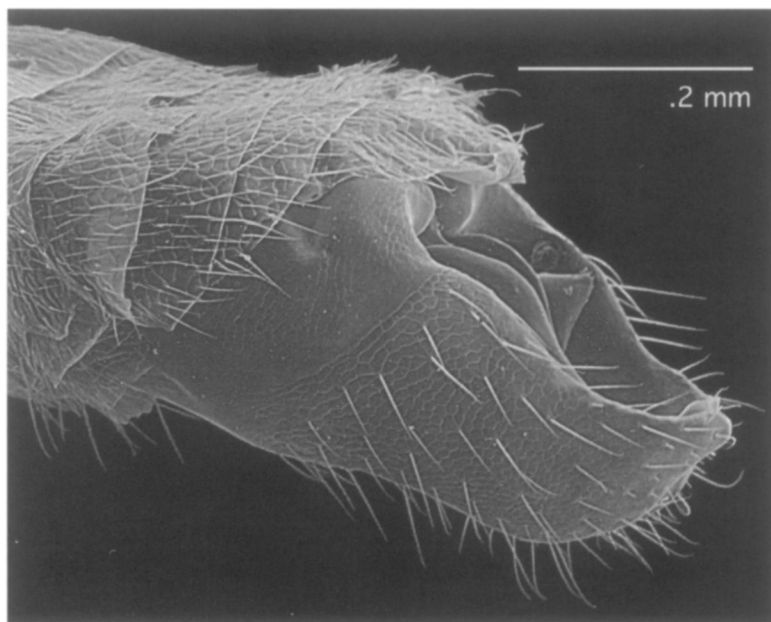


Figure 1b. Lateral view of *A. epedana* male genitalia.

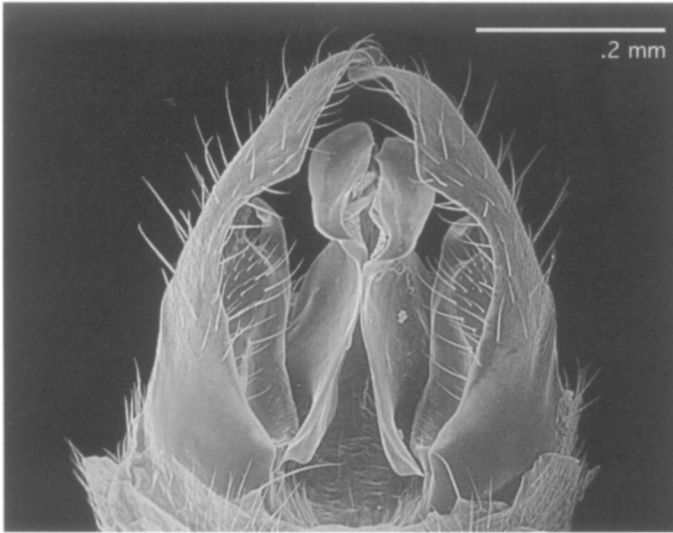


Figure 1c. Ventral view of *A. cpedana* male genitalia.

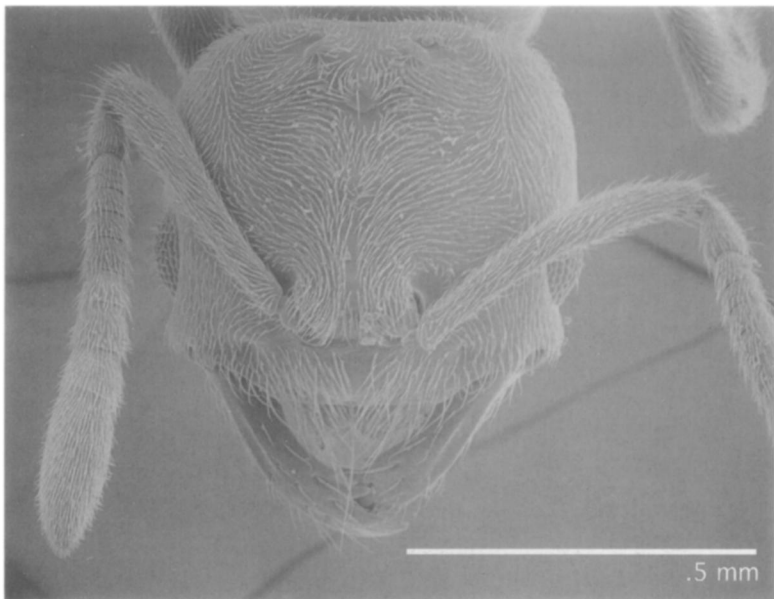


Figure 2: Head of *A. cpedana* female in full frontal view.

suberect hairs present. Genitalia: parameres long, rectangular, curving towards each other apically; anteriorly parameres without hairs, the posterior ends with scattered erect hairs; volsellar lobes distinct, with many erect hairs; cuspi cylindrical, with short, peg-like teeth at the apex; digiti elongate with apical end roughly anvil-shaped; dorsal tip of digiti with short, peg-like teeth where they meet the cuspi, forming an oval-shaped space between them in ventral view; ventral side of penis valves without teeth; apical tips flattened and laterally expanded.

Queen: (Figure 2)

Measurements (n=6).— TL: 3.03- 3.17 HW: .592- .612 HL: .571- .602 SL: .443- .485 EL: .126- .147 EW: .105- .113 THL: .854- .956 GL: 1.51- 1.71 CI: 100.3- 111.0 SI: 74.5- 80.7 EI: 21.3- 24.0

Diagnosis.— Yellow to brownish-yellow; antennae 11 segmented; slender mandible with three distinct teeth, occasionally a smaller tooth is present at basal angle.

Description.— Head: yellow to brownish-yellow, darker along segmental margins; slightly broader than long and covered with a fine pubescence; apex slightly darker with three prominent ocelli; eyes large, positioned towards the anterior margin at lower 1/4 of side; eyes break lateral margins when viewed in full frontal view; antennae 11 segmented and incrassate; scape reaches to slightly passes posterior margin; posterior margin entire, with scattered, short, erect hairs; clypeus wide, medially slightly convex with several (usually around 12 or fewer) long, erect hairs, the longest hair placed medially; mandible infuscated with three distinct teeth, occasionally a smaller tooth is also present at basal angle; a large gap exists between anterior clypeal margin and inner mandibular margin. Thorax: yellow to brownish-yellow, darker along segmental margins; pronotum short and collar-like; anterior of mesonotum rounded, dorsum flat, covered in short, suberect hairs; scutellum distinct, roughly oval, slightly lighter than mesonotum, with fewer suberect hairs covering dorsum; propodeum with fewer short, suberect hairs than other parts of the thorax; declivity at ca. 45° angle. Gaster: petiole erect and short, triangular in lateral view with a rounded apex that is occasionally concave; gaster yellow to brownish-yellow darker along segmental margins; covered in a fine pubescence, with a few scattered suberect hairs present.

Material Examined.— USA: Arizona: Cochise Co.; 3.1 miles west of Montezuma's Pass; elev. ca. 1676 m; 14 August 1969 (coll. RR Snelling); USA: Arizona: Santa Cruz Co.; Pajarito Mtns; 8 miles W. jct. I-19 on Rt. 289 at FSR 221 (Walker Canyon); elev. ca. 1052 m; 10 August 1998 (coll. SP Cover); USA: Arizona: Cochise Co.; 13.8 mi NW jct. Rt. 80 on FSR 74; elev. ca. 1757 m; 18 August 1993 (coll. SP Cover); USA: Arizona: Cochise Co.; ca. 5 miles west of Portal, near Southwestern Research Station (31°53.32' N, 109°12.48' W; 1676 m elevation) 13-14 August 2001 (coll. JS LaPolla and UG Mueller); USA: Arizona: Cochise Co.; 0.4 mi. NW Southwestern Research Station (31°53.20' N, 109°12.24' W; elev. ca. 1737 m); 15 August 2001 (coll. SP Cover).

NATURAL HISTORY AND DISTRIBUTION NOTES

Distribution.— Though *A. epedana* is presently known from 5 sites in southeastern Arizona, it probably ranges south into Mexico through the Sierra Madre Occidental mountain range. *A. epedana* appears to only occur at higher elevations (where annual rainfall is greater) between 1676 m - 1052 m, in open oak/juniper woodland habitat.

Nest Description.— Nests collected in August 2001 were all located in open oak/juniper woodlands, with sparse growth of grasses being the dominant ground cover. Nests were always found entirely underground, with no indication

on the surface of an underlying nest. Nests were often found in areas exposed to direct sunlight throughout the day but always under large stones, though the tunnels and chambers of the nests usually went far beyond the perimeter of the nest covering stone. Nests were typically about 10 cm below the surface and reached a depth of about 30 cm, where a series of diffuse tunnels and loosely differentiated chambers were found. There appeared to be no central nesting area, as queens and brood were found throughout. Tunnels ran laterally through the soil and were often penetrated by roots. Chambers were not distinct, consisting of little more than lateral expansions of tunnels. Workers, queens, brood, and mealybugs were found in both tunnels and chambers. The nest structure of *A. epedana* strongly resembles that described for *A. paramaribensis* (Bünzli 1937). Snelling (1973) reported collecting of specimens from under a large stone in oak/juniper woodland. SC has observed another nest under a rock in open Emory oak woodland.

Mating Flight.—Based on the collection of alates it appears that mating flights probably occur from late July through mid-August. SC observed a dealate female on 18 August 1993 under a rock, in a small chamber; a pile of eggs was near her, indicating she had recently completed her mating flight. JSL and UGM found alate females and males in three separate nests from 13–14 August 2001 near the end of the monsoonal rain season when the ground is moist. Moisture is likely an important factor in timing alate release both because the thin cuticle of *A. epedana* is probably quite susceptible to water loss, and because the ground is easier to tunnel into. Increased moisture may also explain why *A. epedana* specimens have only been collected in August. We suspect that at least part of the colony moves towards the surface as the ground becomes moistened, and the time for releasing alates approaches. During the rest of the year, the ants probably move deep within the soil, making collecting them very difficult. Bünzli (1935) found that drying topsoil was responsible for vertical nest movements of *A. paramaribensis* deeper into the soil.

Polygyny.—All three nests collected in August 2001 had numerous dealate and alate queens. The presence of multiple dealate queens strongly suggests that *A. epedana* is a polygynous species. *A. urichi* was described by Weber (1944) as possessing two dealate queens in a nest, while another species, *Acropyga* morpho-species 1, has also been observed with multiple, dealate queens present in colonies (collection label data). Both these species are probably polygynous. Bünzli (1935) found both the occurrence of pleometrosis (founding of a colony by multiple queens), and the acquisition of young queens by established colonies in *A. paramaribensis*, suggesting multiple possible origins of polygyny in that species. How polygyny originates in *A. epedana* is unknown. The apparently widespread occurrence of polygyny in *Acropyga* species is interesting because it has implications on the trophobiotic relationship with their mealybug species. For instance, is it possible that polygyny brings about genetic diversity in mealybug herds, since otherwise the mealybugs of a colony would only be derived from the parent mealybug brought along during the queen's initial mating flight? At this time it is unclear, but interestingly Malsch et al (2001) found widespread occurrence of polygyny in obligate coccidophilous *Pseudolasius* species, though in those species queens were not trophophoretic and mealybugs may have been acquired through colony fission. Whether or not *Acropyga* species practice colony fission is unknown, but that method of mealybug acquisition remains a possibility that should be investigated, since, like the *Pseudolasius* species investigated by Malsch et al. (2001), it seems that polygynous *Acropyga* species have diffuse, decentralized nests.

Mealybug Association.—Unidentified rhizoecine (Hemiptera: Pseudococcidae: Rhizoecinae) mealybugs were found in nests from two localities (Pajarito Moun-

tains and the Chirachua Mountains [August 2001 site]). SC discovered a colony (Pajarito Mountains site) of *A. epedana* along the edge of a dry creek gully under a rock in light shade. The nest was in open Emory oak woodland, with a ground cover of scattered grasses. When the nest was disturbed (the rock was lifted up and the nest was located) alate queens (but not nearby workers) picked up mealybugs in their mandibles and attempted to escape, suggesting that queens are trophophoretic. Alate queens picking up mealybugs upon nest disturbance has also been observed in the Australasian species, *A. acutiventris*, a known trophophoretic species (Wheeler 1935).

One live nest from the 2001 collection was brought back to the lab for observation. Ants refused all food (sugar, honey, dead insects) offered to them after two weeks of captivity in the laboratory nest box, indicating that *A. epedana* is an obligate coccidophile. Most ant species, even other presumably obligate coccidophiles such as *Acanthomyops* species (Wing 1968; Hölldobler and Wilson 1990) except sugar water and/or honey (T.R. Schultz, pers. comm.), but both these substances were refused by *A. epedana*. Ants responded in an aggressive fashion to an aphid a few hours after the nest was collected, and to a halictid bee about two weeks after the nest was collected. The encounters occurred when a foraging ant came across the specimen. The forager immediately antennated the potential food item, and after a minute it pulled its gaster underneath its body, tapping the insect with a liquid droplet emitted from the acidopore, then ran away from the dead insect. Within 15 minutes more ants would gather and react in a similar fashion, bending their gasters (largely under their bodies, though a few pulled their gasters over their bodies to reach the insect) and leaving a droplet on the insect, then run away. The attacks on the specimens lasted for about 30 minutes. No attempts to grab or dismember the insect was made.

The nest was kept alive for three weeks and by the end of the third week the ants still had not visibly eaten anything. But a fungus had infected the nest box. This covered the nest box, except for the area where ants kept their brood and mealybugs. Apparently the ants kept this area fungus-free.

Worker Behavior.— Worker ants displayed extreme photophobic behavior. Whenever workers were exposed to light, they immediately moved in the direction opposite of the light's origin. In the field workers hid under pieces of dirt or vegetation when exposed to sunlight. When nests were opened, workers immediately picked up nearby brood and mealybugs in their mandibles and tried to escape into tunnels in the ground.

In the laboratory, worker ants constructed a series of tunnels and chambers out of loose dirt in the nest box. Workers moved brood and mealybugs into small chambers (ca. 5 cm to 10 cm long, ca. 2 cm high) constructed from the dirt. Brood and mealybugs were mixed together in loosely constructed piles. Workers meeting in tunnels occasionally engaged in a "body jerking" behavior. Ants jerked their bodies forward horizontally 3-6 times, lightly hitting another ant in front of it (total duration was always less 5 seconds, typically lasting about one second). "Body jerking" elicited a similar display by the recipient ant. the two ants would then separate and pass by each other. The behavior usually occurred with the worker ants being head to head, but several times it was observed that an ant would simply bang into the side (usually hitting the thorax) of another ant in a "body jerking" fashion.

Similar behavior has been observed in ants only in the attines, in a behavior Weber (1957; 1972) termed "jigging." Weber (1957; 1972) described "jigging" as a defensive behavior (elicited when ants were exposed to a sudden stimulus such as a puff of air, or to sudden light) in which the ant would stand with its last two pair of legs in place while the rest of the ant's body and forelegs moved up and down in a vertical plane. The duration of an event was typically less than a minute.

Weber (1957; 1973) **also recorded other ants nearby often reacting in a similar fashion, though not all of them did so.** Kveskin (submitted) further detailed attine "jigging" behavior through high-speed cinematography and determined in a series of experiments that "jigging" is triggered by the presence of collembolan inquilines in gardens of fungus-growing ants, suggesting that "jigging" may be an anti-collembolan defense or a collembola-related alarm signal to other workers.

The "body jerking" behavior observed in *A. epedana* appears to differ from attine "jigging" in several ways: *Acropyga* "body jerking" was performed horizontally, not vertically as seen in attines; in attines there never appeared to be contact between ants; though Weber (1957; 1972) and Kveskin (submitted) report that attines "jig" with their mandibles open and fore- and midlegs lifted off the substrate, the "body jerking" behavior of *A. epedana* did not appear to be a defensive response, because *Acropyga* workers were not seen to open their mandibles and they did appear to react to an intruder. The colony was observed in subdued light and the behavior did not appear to be triggered by the presence of light. Even under fairly dark conditions, *Acropyga* ants **still** displayed the "body jerking" behavior. "Body jerking" behavior in *Acropyga* could be a form of vibrational communication, as has been observed in other insects, though more study is needed.

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