

## Extraordinary Predation by the Neotropical Army Ant *Cheliomyrmex andicola*: Implications for the Evolution of the Army Ant Syndrome<sup>1</sup>

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### ABSTRACT

Workers of the genus *Cheliomyrmex* are unique among the New world army ants (subfamily Ecitoninae) in that their mandibles are armed with elongate, spine-like teeth. We present the first prey records for this genus. *Cheliomyrmex andicola* prey on large-bodied ground dwelling invertebrates and, possibly, on vertebrates. Unlike other army ants, *C. andicola* workers use their sting during prey capture. The workers' unusual mandibles and potent stings may be adapted for piercing and gripping the integument of nonarthropod prey animals, and for rapidly subduing large-bodied prey, respectively. The genus *Cheliomyrmex* may be the sister taxon to other Neotropical army ants (Ecitoninae), and *Cheliomyrmex* shares features of mandibular morphology and prey selection with Old World driver ants in the genus *Dorylus*. Mass cooperative foraging, an important element of army ant behavior, may have arisen in part as an adaptation for exploiting large-bodied prey.

### RESUMEN

Las obreras del género *Cheliomyrmex* son únicas entre las hormigas cazadoras del Nuevo Mundo (subfamilia Ecitoninae) por tener las mandíbulas dotadas de dientes alargados y aciculares. Presentamos la primera documentación registros de presa para este género. *Cheliomyrmex andicola* depreda invertebrados terrestres de tamaño grande, y posiblemente vertebrados. En contraste con otras hormigas cazadoras, las obreras del *C. andicola* utilizan su aguijón durante la captura de su presa. Las mandíbulas inusuales y las picaduras potentes de las obreras pueden ser adaptaciones para perforar y sujetar la piel de presa no-artrópoda, y para someter presa grande rápidamente. El género *Cheliomyrmex* podría ser el taxón hermano de las demás hormigas cazadoras Neotropicales (Ecitoninae), y comparte características de morfología mandibular y selección de presa con las hormigas cazadoras del Viejo Mundo del género *Dorylus*. El forrajeo cooperativo en masa, un elemento importante del comportamiento de estas hormigas cazadoras, pudo haberse presentado en parte como una adaptación para aprovechar presa grande.

*Key words:* Ecitoninae; Ecuador; mandibular modification; sting.

AMONG EUSOCIAL INSECTS, ARMY ANTS EXHIBIT an unusual type of foraging behavior that involves the obligate coordination of large groups of workers. Raid parties that comprise thousands to hundreds of thousands of workers, depending on the species of army ant, cooperate to locate, subdue, and harvest prey (Topoff *et al.* 1980, Gotwald 1995). In the Neotropics, dramatic foraging raids conducted above the soil and leaf litter surface by the swarm-raiding species *Eciton burchellii* and *Labidus praedator* have long attracted the interest of tropical biologists (Darwin 1839, Wheeler 1921, Schneirla 1971), and led to studies suggesting their role as keystone predators in tropical forests (Boswell *et al.* 1998, 2000; Roberts *et al.* 2000).

Relative to the few surface-raiding species, most army ant species are obscure because they seek prey primarily beneath the leaf litter or in the soil (hypogaecic foraging). Little is known about the behavior, diet, and impacts on litter/soil communities of the

less conspicuous hypogaecic army ants (Berghoff *et al.* 2002, 2003). However, surveys of several Neotropical localities suggest that lowland wet forests can support army ant guilds that comprise approximately 20 species, most of which are partially or fully hypogaecic in behavior (Rettenmeyer *et al.* 1983, Quiroz-Robledo *et al.* 2002). Here, we report observations of foraging and predation by rarely observed hypogaecic army ants in the genus *Cheliomyrmex*. As the sister taxon to the other genera in the New World army ant radiation (subfamily Ecitoninae; Brady 2003), *Cheliomyrmex* may provide information about the early stages in the evolution of the army ant life style.

We conducted surveys of army ant density and diversity at four Neotropical wet forest sites (La Selva Biological Station, Costa Rica, 10°26'N, 83°59'W, 50 m elevation, 10 June–10 August 2003; Barro Colorado Island, Panama, 9°10'N, 79°50'W, 50 m elevation, 19 July–24 August 2003; Santa Maria, Venezuela, 10°22'N, 67°49'W, 650 m elevation, 1 August–7 September 2003; Tiputini Biodiversity Station, Ecuador, 0°38'S, 76°09'W, 200 m elevation, 24 September–16 October 2003). We searched for army

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ant raid columns using standardized trail-walk surveys. At each site, we walked loop trails that were approximately 3 km long at a rate of 1.5 km/h. When army ant raids were encountered, we recorded time, ground surface temperature, weather conditions, forest type (terra firme or varzea; primary, second growth, or treefall gap), topography (level, slope, or ridge top), soil moisture, and the substrate that the ants were using. We recorded similar data when we opportunistically encountered army ant raids at other times.

*Cheliomyrmex* colonies were encountered only at the Ecuador site. We collected workers from two *Cheliomyrmex andicola* foraging raids. During raid 1 on 26 September 2003 at 1030 h, we encountered a large *C. andicola* raid column in primary terra firme forest, exiting from soil-covered foraging trails that the ants had constructed on a slope. The sky was clear, and ground surface temperature was 25.9°C. Beneath the raised tunnel of soil particles that the ants had constructed, we found the partially consumed carcass of a snake (1 cm in diameter and 10 cm long). Most of the snake's scales and skin had been removed. *Cheliomyrmex andicola* workers were observed chewing on the snake and carrying away bits of flesh in their mandibles. As we dug near the carcass, the ant workers responded by biting and stinging our hands. The workers clung to our skin, and we noted that their stings were more painful than those of other army ants from the site (e.g., *Eciton burchellii* and *Eciton hamatum*). We collected ant workers and samples of snake flesh into 70 percent ethanol. During raid 2 on 1 October 2003 at 1205 h, during a brief rain shower, our attention was drawn by rustling sounds in the leaf litter on a slope in a partially cleared area of terra firme forest adjacent to the station buildings. A subterranean column of *C. andicola* workers erupted from the soil in pursuit of a fleeing giant earthworm (possibly a species in the genus *Martiodrillus*; Zicsi 1990). Several hundred ant workers emerged from the soil and ran over the leaf litter in the direction taken by the worm. Five *C. andicola* workers mounted the worm and were biting and apparently stinging its body. After the worm crawled for a distance of 3 m down slope from where it exited the soil, its body contracted from over 40 cm in length to approximately 20 cm in length. The worm abruptly stopped moving and became rigid on the soil surface within 10 sec of exiting the soil, and was then unresponsive to human touch. We assumed that the worm was either paralyzed or dead. We lifted the worm to examine it, and we collected ant workers from its body and from the raid column as it arrived where the worm came to rest. Workers collected from both raids had no prey (other than snake flesh at raid 1) in their mandibles.

Our observations demonstrate that *Cheliomyrmex* workers can subdue large-bodied, fast moving prey, and that the workers actively pursue fleeing prey. Although we could not determine whether *Cheliomyrmex* workers had killed the snake, we note that they are apparently unique among Neotropical army ants in that they remove and consume vertebrate flesh. Neotropical swarm-raiding army ants occasionally sting and kill small vertebrates (lizards, snakes, and nestling birds), but these are not consumed as prey (Schneirla 1971). The consumption of flesh from large-bodied animals by *C. andi-*

*cola* is shared with Paleotropical driver ants in the genus *Dorylus* (Gotwald 1995).

We propose that *Cheliomyrmex* colonies regularly forage for large prey in the soil or under the leaf litter. The rapidity with which the giant earthworm became immobile after being stung suggests that *Cheliomyrmex* venom is toxic and/or paralytic. We, and other researchers who have collected *Cheliomyrmex* workers, noted that their stings are more painful than those of other army ants (Gotwald 1971, Villareal *et al.* 1995). Other investigators have also noted that when *Cheliomyrmex* workers bite, they adhere to human skin (Gotwald 1971, Villareal *et al.* 1995). Larger-bodied *Cheliomyrmex* workers possess sickle-shaped mandibles that are armed with elongate, spine-like teeth (Fig. 1; Gotwald 1971). Worker ants' mandibles are typically triangular in shape (Fig. 1), and modified mandibular morphology (e.g., elongated teeth or hairs) is often associated with the evolution of a specialized diet (Wilson 1989, Brandão *et al.* 1991). Mandibular morphology of *Cheliomyrmex* workers is unusual among ants, and unique among the New World army ants (Ecitoninae). The strongly toothed mandibles of the larger size classes of *Cheliomyrmex* workers resemble those seen in some Old World army ants (Dorylinae; Gotwald 1995), but are not shared by other ecitonines. We hypothesize that the mandibular morphology in *Cheliomyrmex* is an adaptation for the successful capture of large-bodied prey. *Cheliomyrmex* workers that locate large prey items bite them, and the workers may be difficult to dislodge because of their toothed mandibles.

We have found no previous records of prey taken by *Cheliomyrmex* species. Most Neotropical army ants are largely or exclusively carnivorous, and many species prey most heavily on colonies of other social insects (Rettenmeyer *et al.* 1983, Gotwald 1995). However, the subterranean foraging activity of most species hinders observations of predation. *Cheliomyrmex* colonies typically raid and nest underground (hypogaeically). Gotwald (1971) suggested that *Cheliomyrmex morosus* conducts raids in the upper 15 cm of soil. Both of our encounters of *C. andicola* foraging raids were on slopes, as were Gotwald's (1971) observations of *C. morosus* in Mexico. Hypogaecic raids may be especially likely to come to the surface along slopes, or in other areas of uneven surface terrain. There are records of ecitonines preying on annelids (Rettenmeyer *et al.* 1983), although to our knowledge, army ant predation on animals as large as giant earthworms, and feeding on vertebrate flesh, have not been noted in the Neotropics.

Brady's (2003) phylogenetic analysis of army ants suggests that *Cheliomyrmex* may be the sister group to the rest of the New World army ants (Ecitoninae), which in turn are the sister taxon to the old world army ants (Dorylinae). The genus *Cheliomyrmex* shares features of mandibular morphology and prey selection with Old World driver ants in the genus *Dorylus*. We propose that mass cooperative foraging, an important and defining element of army ant behavior (Brady 2003), may have arisen in part as an adaptation for exploiting large-bodied prey. If so, then exploitation of smaller prey items would have arisen convergently in the remaining New World army ants, and in some Old World army ants as well (Brady & Ward *in press*).



FIGURE 1. Frontal views of the head capsules of five ecitonine workers collected from the Tiputini Biodiversity Station in Ecuador. Top, from left to right, *Cheliomyrmex andicola*, *Niewamyrmex cristatus*, *Eciton burchellii*. Bottom, from left to right, *Labidus praedator*, *Nomamyrmex esenbeckii*. Scale bar = 1 mm.

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