

- Scorza (10), who found an increase in percent iRBC but also a decrease in hematocrit and RBC counts in the lizard *Tropidurus torquatus* when infected with *P. tropiduri*. The infections studied by Scorza were experimentally induced by inoculation with whole blood from malarious donors and reached very high parasitemia (up to 7800 per 10,000 RBC). Such massive infections are rarely observed in *Sceloporus* with natural infections (observed range: 25 to 4000 per 10,000 RBC) but are frequently observed in experimental infections in this species.
13. Oxygen consumption was measured according to the methods of A. F. Bennett and T. T. Gleeson, *Physiol. Zool.* 49, 65 (1976). Animals were held in captivity for approximately 1 month before measurement; infected and noninfected lizards were size-matched.
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 16. Burst speed and distance running ability were measured as described in A. F. Bennett, *Anim. Behav.* 28, 752 (1980).
 17. Broken tail frequencies: males = 49 percent for infected, 42 percent for noninfected (N , 731; $\chi^2 = 3.44$, $P > .05$); females = 36 percent for infected and 33 percent for noninfected (N , 628; $\chi^2 = .36$, $P > .05$). As larger *S. occidentalis* are more likely to be infected as well as to have broken tails, only animals in a restricted size range (61 to 70 mm body length) were used in this analysis.
 18. We thank R. W. Schall for assistance in fieldwork and figure preparation; J. E. Simmons for advice and facilities at the University of California, Berkeley; the staff of the Hopland Field Station; and T. J. Bradley, J. M. Herbers, B. Heinrich, and R. Huey for comments on the manuscript. Work was supported by an NIH postdoctoral fellowship to J.J.S. and NSF grant PCM77-24208 and NIH grant K-04 AM00351 to A.F.B.

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Obligate Necrophagy in a Social Bee

Abstract. *The social bee Trigona hypogaea uses carrion instead of pollen as a protein source. Nests lack stored pollen, pollen is absent in larval provisions, and corbiculae for pollen transport on worker hind legs are reduced. Glandular secretions of 20 percent protein content appear to replace stored pollen. Toothed mandibles, pheromonal recruitment to resources, and aggressive foraging behavior facilitated evolution of necrophagy in this tropical forest bee lineage.*

Highly social bees are anomalous among bees and Hymenoptera. All are native to tropical forest, and all but four species (Apinae) lack a functional sting. The remainder are the Meliponinae, a pantropical group of at least 400 species (1-7). Stingless bees display immense diversity in resource use. In addition to nectar, pollen, spores, homopteran exudates, sap and resin, also used by apines, they collect mud, feces and carrion (1-9). Necrophagy by stingless bees had not been studied carefully, and this behavior was thought to involve collection of nest construction material or liquid exudates from carcasses (1, 6, 10). Study of *Trigona* (*Trigona*) *hypogaea* Silvestri in the wet lowland forest of eastern Panama shows that this species partly digests animal flesh, then transports it to the nest, where it is regurgitated to other bees. No other protein sources are used by *T. hypogaea*, and pollen transporting structures have been lost, making this species an obligate necrophage.

Nests of *T. hypogaea* lack stored pollen. In four dissected nests, I found abundant stored honey but no indication of pollen (11). Microscopic analysis of brood provisions from cells containing eggs revealed the absence of pollen grains, the primary brood food of normal bees. Other highly social bees provide a mixture of hypopharyngeal gland secretions, honey, and pollen for the brood (1). Brood provisions of *T. hypogaea* appear to be largely glandular. Some storage pots in nests contained a substance that was approximately 20 percent pro-

tein, comparable in color and quality to larval cell provisions (12). Furthermore, colorimetric protein assay of these substances gave identical results to that of worker hypopharyngeal secretions of *Apis mellifera* (12). Pollen carried by foragers to nests of stingless bees is first placed in storage pots, from which it is taken by workers to provision brood cells prior to deposition of an egg. Newly emerged adult bees consume stored pollen, necessary for glandular development (1). Stored glandular secretions have probably taken the place of pollen as food for brood and young adult bees.

Trigona hypogaea is not unique among

Trigona in rending and visiting animal flesh, and several other species, primarily of the subgenus *Trigona*, are known to do so (1, 6, 10). However, these species maintain colony stores of pollen, used as the primary protein source (1, 13). *Trigona hypogaea* and its subgenus differ significantly from all other *Trigona* in possessing five large, pointed teeth on each mandible (Fig. 1A). This structural adaptation has led to many unique behavioral and ecological attributes, often associated with the propensity of these species to rob flowers and attack competitors for food and nest sites (2, 14, 15). Toothed mandibles and associated aggressive foraging behavior probably preadapted this lineage to the harvest and defense of large, compact nonfloral protein sources.

Trigona sensu stricto combines the advantages of toothed mandibles with massive recruitment and communication behavior, features that are analogous with social mammalian carnivores that dominate resources by aggression and sheer number (16). The subgenus *Trigona* deposits a pheromone trail between resources and the nest; bees arrive at resources rapidly and in large numbers, sufficient to displace competitors (1, 15). I watched *T. hypogaea* deposit trail pheromones on plants between the nest and animal resources; it recruited rapidly and aggressively deterred dipteran competitors while foraging at animal carcasses.

In Panama, observation colonies recruited several hundred foragers in 2 hours to freshly killed large lizards (*Amyva* species) and toads (*Bufo marinus*). A large dead lizard placed 15 meters from one nest was located by bees within 8 hours. Groups of 60 to 80 bees

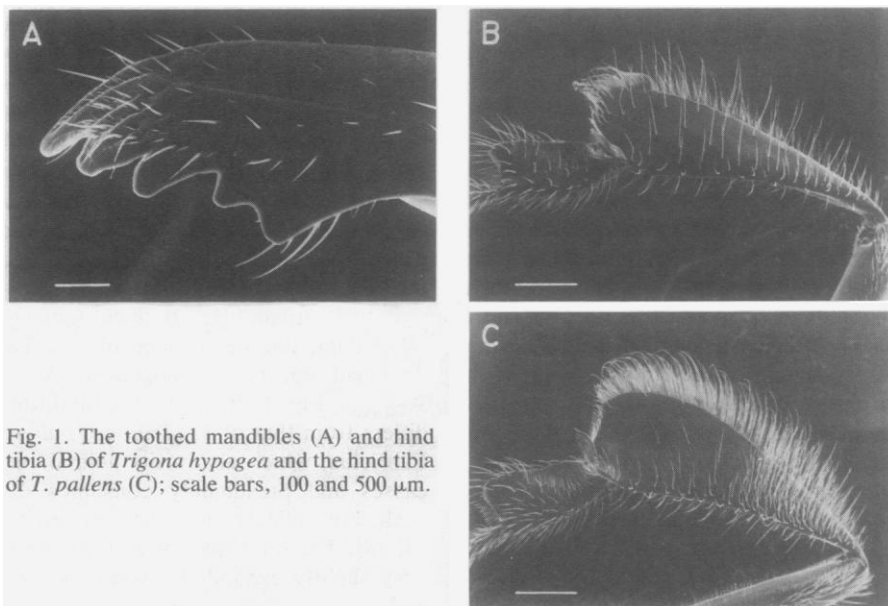


Fig. 1. The toothed mandibles (A) and hind tibia (B) of *Trigona hypogaea* and the hind tibia of *T. pallens* (C); scale bars, 100 and 500 μ m.

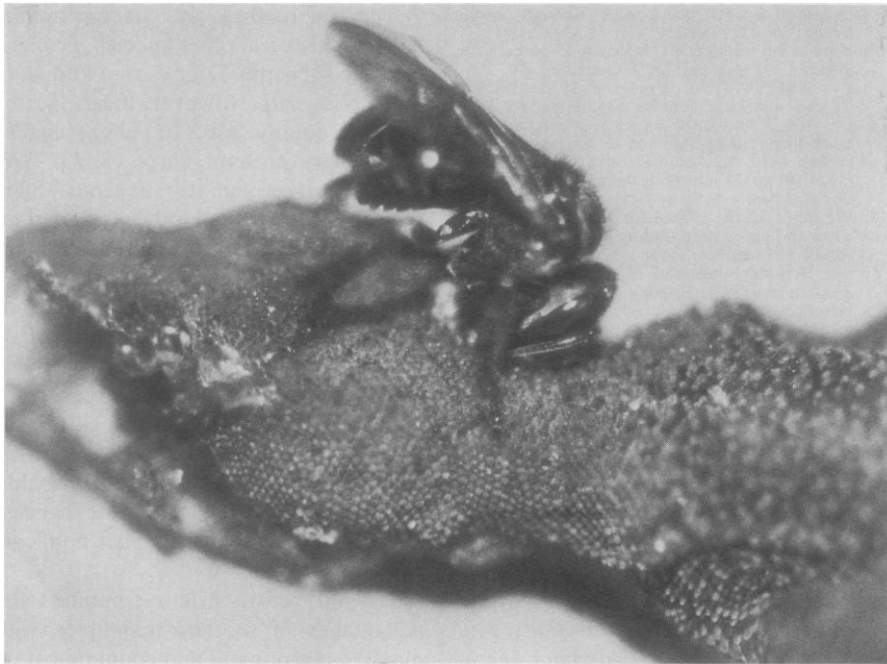


Fig. 2. A worker of *Trigona hypogea* harvesting the flesh of a small lizard, *Gonatodes albigularis*.

removed the skin, entered the body, and reduced much of the carcass to a skeleton during the next 2 days. In 8 hours bees removed feathers and flesh from the cranium of a freshly killed passerine. Small resources, such as a freshly killed lizard *Gonatodes albigularis*, were visited by two or three bees at one time (Fig. 2). Two *Physalemus pustulosus*, a frog 4 cm long, were located and reduced to skeletons by the bees within 6 hours. This bee also visits carcasses of monkeys, snakes, fishes, and large insects (6), and it readily harvested commercial pork and poultry. In foraging experiments performed in Panama, the animal flesh had not noticeably putrefied before being discovered by the bees, and flies seeking oviposition sites were chased from the carcasses and their vicinity by foraging *T. hypogea*. Ants of the genus *Crematogaster* also foraged at animal flesh in one experiment but rarely attempted to bite or harass the bees. In contrast, a polybiine wasp attracted to the bait was killed and partly consumed by the ants. Ants had discovered the resource before the bees, but for 2 days after bees arrived, the ants confined most foraging to nocturnal hours. Ants are a significant necrophagous group in tropical forests (10), yet they appear to avoid *T. hypogea*. Chemical and other interactions between the bees and ants may lead to diurnal-nocturnal resource partitioning of animal carcasses.

The bees masticate and consume flesh at the feeding site. They do not carry pieces of flesh to the nest, but appear to

hydrolyze it with a secretion produced by either mandibular or salivary glands, which gives the feeding site a wet appearance. Individual bees captured while feeding, then forced to expel the contents of their crop were carrying a slurry of flesh, measuring between 37 and 65 percent dissolved solids by volume (17). Bees tagged while foraging in the morning continued to depart and arrive at a carcass throughout the day, suggesting that animal food is passed by trophallaxis to other workers in the nest. Nest mates may then convert flesh into glandular substances. Considering animal flesh rots and would be unsuitable as stored food, its metabolic conversion is essential to allow storage (12). No indication of carrion was detected in honey stores or elsewhere in nests of *T. hypogea*.

The efficiency with which *T. hypogea* locates and harvests animals has apparently led to the most distinctive structural feature of the species: a hind leg with a drastically reduced corbicula, or pollen basket (Fig. 1B). Schwarz (6) described the contour of the hind tibia as "suggestive of a baseball bat." In the absence of other data, the significance of this feature had not been recognized. As is shown in Fig. 1, B and C, the hind tibia differs from that of *T. (Trigona) pallens* Fabricius, which also visits animal carcasses and presumably consumes the flesh, but collects and stores pollen (6, 13, 18). The hind tibia of *T. hypogea* is very slightly expanded toward its apex and not concave on its outer surface,

where pollen is carried by normal bees. Hairs and bristles are present on the inner surface of the middle and hind basitarsi, as are combs on the apex of the hind tibia, which allow transfer to the corbiculae of substances gathered by stingless bees (18). I frequently observed resin collection by colonies maintained for observation up to 5 months, but pollen collection never was seen. Thus, complete loss of grooming structures associated with a corbicular load would not be expected.

Now that the adaptive syndrome of flesh feeding has been recognized for stingless bees, further studies may focus on complementary adaptations of feeding biochemistry (12) and the adaptive significance of facultative or obligate necrophagy in perennial colonies of tropical forest bees.

DAVID W. ROUBIK

Smithsonian Tropical Research

Institute, APO Miami, Florida 34002

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11. Silvestri collected type specimens of *T. hypogea* in Brazil and mentioned storage pots "for honey and for pollen" in the nest; J. M. F. Camargo (personal communication) has seen one nest in Amazonia, and it had no pollen pots. Silvestri did not microscopically examine pots that did not contain honey. I have found six nests in Panama, each in the wet forest (greater than 3500 mm rainfall annually) between the Caribbean and Pacific coasts 85 km east of Panama City. This bee was not previously known from Panama and is not found in more westerly localities (13).
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17. Bees (24) were taken while foraging or when arriving at the nest, and the contents of crops were collected in 50- μ l capillary tubes, then measured for dissolved solids with a Bellingham and Stanley refractometer. Crop contents were light brown, unlike floral nectar, and foragers arriving at carcasses had empty crops.
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19. This paper is dedicated to the memory of Robert Silberglied, whose honest intelligence and enthusiasm will be missed by many. I thank S. L. Buchmann for preparing protein analyses and SEM photographs, and Smithsonian Institution for Scholarly Studies grants 1234S102 and 1234S201.

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