The meat-eating bees

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In the intricate web of the natural world, dietary habits play a crucial role in shaping the behaviour, physiology and ecological interactions of species. Among the myriad of dietary specializations, the phenomenon of meat-eating in bees presents a fascinating deviation from the norm. While most bees are renowned for their role in pollination and their diet of nectar and pollen, a unique subset of stingless bees, commonly referred to as vulture bees, has evolved to consume carrion. The existence of vulture bees, particularly within the genus Trigona, challenges conventional perceptions of bee behavior and ecology. These bees have developed specialized adaptations that enable them to thrive on a diet primarily composed of decaying meat, a stark contrast to the floral resources utilized by their pollen-collecting relatives.

Necrophagy in bees

Necrophagy is feeding on carrion or feeding on liquids exuded from carrion. There are two types of necrophagy in bees viz., facultative and obligate necrophagy. Facultative necrophagous bees primarily feed on nectar and pollen and sporadically on fresh animal carcasses for supplementing their floral diets (Dorian and Bonoan, 2021) which is seen in bumble bees like Bombus terrestris (L.), Bo*mbus ephippiatus* Sayand in many stingless bee genera *Partamona, Scaptotrigona*, and *Oxytrigona*. Whereas, obligate necrophagous bees are never found visiting flowers, instead they feed on fruits and extrafloral nectaries for their carbohydrate requirement and fresh animal carrion for protein and has been found only in three closely related *Trigona* species: *Trigona hypogea* Silvestri, *T. necrophaga* Camargo & Roubik and *T. Crassipes* (Fabricius) (Hymenoptera: Meliponinae).

Distribution and nesting behaviour of obligate necrophagous bees

Trigona hypogea and *T. crassipes* are found in Amazon basin and Guianas, while, *T. necrophaga* is endemic to Panama (Camargo and Roubik, 1990). Trigona hypogea is the smallest among these three and has hypogeous or ground nesting habit whereas, *T. crassipes*,the largest among these, construct nests within cavities of living tress at 2 – 10 m height and T. *necrophaga*, construct nests within cavities of living trees of 46-70 cm diameter, with their entrances 1.2-8.0 m above ground level. Just like pollinivorous stingless bees, necrophagous bees are eusocial, live in perennial colonies, exhibit social organisation and divides the task among themselves. Nest structure is basically same like that of any other meliponine bee. Inside a bee colony, there will be a queen, thousands of workers, and hundreds of males (Camargo and Roubik, 1990).

Adaptations in bees for necrophagy

There are few morphological adaptations that allowed the bees to forage on carcass.

(a) Toothed mandibles: Obligate necrophagous stingless bees have toothed mandibles i.e., they have five teeth in the mandible including three teeth in the apical region. Mandibles of pollinivorous stingless bees lacks apical tooth and have a blunt apical region. The teeth allowed the stingless bees to tear open the skin and to feed within.

(b) Reduced corbicula: Corbicula is a structure on hind tibia of bees that enables bees to collect pollen and in order to collect pollen, corbicula should have a concave surface on its outer side with hairs and bristles. Hind tibia of necrophagous bees is very slightly expanded toward its apex and not concave on its outer surface and the reduced corbicula makes them inefficient to forage on flowers and collect pollen.

(c) Lack of setae in labial palpi of workers: All other species of *Trigona* have giant setae or long,

wavy hairs that are used to gather pollen from tubular anthers, which is greatly reduced in these three necrophagous *Trigona* spp. (Roubik, 1982).

(d) Specialised gut microbiome: Figueroa et al. (2021) found that pollinivorous stingless bee species harboured specialised gut microbiome that helped the bees in necrophagy. Microbes including A*cetobacter, Commensalibacter, Apilactobacillus* and other *Lactobacilli* were abundant in the gut of necrophagous bees and these microbes are believed to have a role ingut acidification as an important adaptation for carrion feeders. Further, lactic acid bacteria are known to prevent spoilage and growth of pathogenic bacteria in preserved meats via acidification, bacteriocins, and H_2O_2.

Food sources and maturation of honey by necrophagous bees

Trigona hypogea has two different food sources: (i) protein source - flesh from carcass and (ii) carbohydrate source - fruits and extrafloral nectaries. Bees remove flesh with the mandibles, cooperatively excavate holes in the bodies, and then move within the body cavity. Each feeding site appears wet and the bees masticate one spot for many minutes, imbibing liquid. Forager bees deposit animal protein into storage pots without involving the receptor bees. They also collect juice from fruits and extrafloral nectaries and deposit them in honey pots. These bees never visit flowers. Protein collected from animal carcasses deposited in special pots is mixed with honey and these pots remain open for about 19 h. They were then filled, capped, and allowed to mature for about two weeks. During this period, the animal-derived materials degraded into simple compounds and was ready for use by the bees. The stored substance was paste-like when placed in the pots and had the same colour as that of source from which it was collected. In the later days, the material became viscous, and after maturation it is honey-like, yellowish and homogeneous. The level of free amino acids increase as the level of soluble protein decreases during maturation. Simultaneously, sugars (total and reducing) increased as the bees added honey to the carrion-based mixture in the pots (Noll et al., 1996).

Predatory behaviour

Predatory nature of *T. hypogea* on living brood of social wasps was documented by Mateus and Noll (2004). They observed that bees removed immatures (larvae and pupae) from their cells by opening capped cells, chewed using their mandibles and, after the larval tissues were completely macerated, they were swallowed and the bees left behind only some brood remains (exoskeleton) that were probably impossible to macerate. This shows that *T. hypogea* is not only necrophagic but also takes advantage of living animal protein opportunistically and the predatory nature might not be an aberrant behaviour, but merely a lesser-known part of the bees' normal repertoire.

Conclusion

Meat eating bees or vulture bees feed on carrion for protein and on extrafloral nectaries and fruits for carbohydrate. It is still controversial if the honey they produce is from the meat they eat or from extrafloral nectaries. Bees are evolved from carnivorous wasps during cretaceous period and pollinivory paved way for their huge diversity. However, vulture bees have switched back to their ancestral lifestyle to tap the advantages of animal protein over pollen and may help them to survive competition by partitioning and repartitioning niche space.

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