Stingless bees have specialized guards to defend their colonies, study reveals

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Like ants and termites, several species of stingless bees have specialized guards or soldiers to defend their colonies from attacks by natural enemies.

The differentiation of these guardian bees, which are more robust, larger, and in some cases, colored differently from more common worker bees, evolved in the last 25 million years, and coincided with the appearance of parasitic "robber" bees, which represent a major threat to many stingless bee species.

These discoveries were made by a group of researchers at the University of São Paulo (USP) in Brazil, in collaboration with colleagues from EMBRAPA Eastern Amazon in Belém (Pará State, Brazil) and Johannes Gutenberg University Mainz in Germany. The findings have been published in the journal *Nature Communications*.

"Guards also behave differently from worker bees. They don't leave the nest to search for food like foragers. They fly near the colony entrance and are the first to engage in a fight if parasitic bees invade," said researcher Eduardo Andrade de Almeida .

A previous study, published in 2012, had shown that colonies of Tetragonisca angustula (a Brazilian stingless bee species called jataí in Portuguese) are defended by a population of guards approximately 30 percent larger and differently shaped from their nestmates, and that their larger body size compared with workers is directly linked to their

fighting capabilities.

The researchers followed up on this finding by investigating whether task-related worker differentiation is common to stingless bee species, the largest group of eusocial bees with over 500 described species, of which more than 300 are found in Brazil.

To this end, they compared the size and other morphological characteristics of nest guards and foragers for 28 species of stingless bees from different areas of Brazil. They chose species that are both relatively common and ecologically varied, with a range of habitats, nesting habits and foraging methods, and with colony sizes varying from a few hundred to tens of thousands of workers.

They found that guards were significantly larger than foragers in 10 out of the 28 species analyzed. The species with larger guards displayed 10 to 30 percent more variation in overall worker size. The three species with the largest degree of size differentiation were T. angustula and T. fiebrigi (both jataí), and Frieseomelitta longipes.

In several Frieseomelitta species, guards were not only larger, but also displayed darker coloring than other bees in the same colony.

"We found that the difference between workers and guards is far more common among stingless bee species than was previously thought, and that the evolution of guards with a larger body size apparently relates to the risk of attack by parasitic bees," Almeida said.

"This changes some interpretations regarding the evolution of the social behavior of stingless bees and the relationships among them in the nest, for example."

To find out when worker differentiation began and which factors

triggered the process, the researchers analyzed the phylogeny (evolutionary history) of all 28 species of stingless bee included in the study. The results of the phylogenetic analysis suggested that the common ancestor of the species included in the study had similarly sized guards and foragers, and that increased guard size independently evolved five times during the last 20 to 25 million years.

This period, which is recent compared with the start of stingless bee diversification approximately 80 million years ago, coincides with differentiation of the kleptoparasitic genus Lestrimelitta from non-parasitic ancestors.

"The appearance of species belonging to this genus that display highly specialized behavior in terms of invading colonies of other bees to plunder them may have exerted evolutionary pressure on the species targeted by such attacks, favoring the development of defense mechanisms—in this case, guards and soldiers," Almeida said.

Ten of the 28 studied species are known to be victims of Lestrimelitta "robber bees," whose attacks frequently destroy colonies. The researchers found that the victims of robber bees were four times more likely to have larger guards than non-targeted species.

"As these stingless bee species that are targeted by robber bees suffer fewer attacks or are better able to intercept them, they have a chance to increase the survival of their offspring, which is an evolutionary advantage," Almeida said.

More information: Christoph Grüter et al. Repeated evolution of soldier sub-castes suggests parasitism drives social complexity in stingless bees, *Nature Communications* (2017). DOI: 10.1038/s41467-016-0012-y

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