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Unveiling the mutualistic associations between ants (Hymenoptera) and Lepidoptera in the ecosystems

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Ants, 'the little things that run the world' are one of the most successful hymenopteran social insects belonging to the family Formicidae with more than 28,413 species under 514 genera in 23 subfamilies, which invaded most of the geographic regions peaking in the tropics and subtropics (Antweb, 2022). The abundance of this ubiquitous, small creatures with colossal ecological roles are estimated as $20x10^5$ individuals on earth with a biomass of 12 mega tones of dry carbon (Schultheiss *et al.*, 2022). The successful evolution of ants mainly depend on the myriad of interactions exhibited in between species and with other species in the ecosystem. These associations may be mutualistic, competitive or parasitic in nature and a clear understanding of these interactions still remain a challenge to the scientific community.

Ants were evolved during the Cretaceous period, about 140 Mya whereas the first report of ant- arthropod association give proof from 80 Mya. The association between ants and honeydew-producing insects were considered to have major ecological and economic significance and most of these interactions were mutualistic in nature (Helms, 2013). The insect orders *viz.*, Hemiptera and Lepidoptera were documented as the major groups exhibiting mutualistic association with ants. About 17 families of Lepidoptera entered into associations with ants, of which the family Lycaenidae entered into mutualistic associations with more than 53 genera of ants worldwide. About 3841 species of Lycaneidae and 308 species of Riodinidae were associated with ants (Pierce *et al.*, 2002; Pierce and Dankowicz, 2022).

The ant-caterpillar associations may be obligate or facultative. Obligate ant associates are unable to complete their life cycle in the absence of ants whereas facultative ant associates are only sometimes found in association with ants. The lepidopteran caterpillars provide honeydew secretion to ants and in return ants offer protection to the larva from predators. The mutualistic associations between Lepidoptera and ants are mediated mainly through chemical and acoustic signalling.

Chemical signalling

The chemical signalling is performed with the help of specialized organs in the larva of lycaneids *viz.,* dorsal nectary organs, pore cupola organs, and tentacle organs. The most important organs determining the ant-Lepidoptera association is dorsal nectary organ on the seventh abdominal segment of the caterpillar that produces nutritious secretions for ants. This specialized exocrine gland is considered similar to the honeydew gland of hemipterans. These secretions were rich in carbohydrates (13–19%), serine (20-40 mM) and trace amounts of methionine (Pierce *et al.,* 2002; Daniels *et al.*, 2005). The quality and quantity of these secretions determine the persistence of attendant ants in tending the caterpillar.

The pore cupola organs are single celled epidermal glands, distributed over the body of caterpillar that appease the aggressive ants to prevent them from attacking the soft bodied caterpillar by secreting an amino acid based chemical substance (Daniels *et al.*, 2005).

The lycaneid larvae also possess an eversible pair of tentacle organs on the eighth abdominal segment, innervated by a small bipolar sensory cell that secrete a volatile compound functioning as a signal to ants when a caterpillar is being attacked. This gland secretions mimic ant alarm pheromones and communicate the distress situation to the attendant ants (Gnatzy *et al.,* 2017).

Acoustic Signalling

The acoustic signalling in Lepidoptera is mainly concerned with mating traits and defensive behaviour. However, in case of lycaenid caterpillar, sound production play a critical role in interceding the association with ants. The acoustic organ in caterpillars located at the inter-segmental region of segments 4–5, 5–6, or 6–7 working through file-and-scraper mechanism. Besides, a vibratory papillae on the distal edge of the prothorax with concentric grooves is also noticed in some Riodininae larva. The caterpillar oscillates the body parts to create low amplitude calls that travels through the substrate and receiving these substrate borne vibrations may elicit an investigative response in ants.

In addition to these mechanisms, the larva associated facultatively with the ants possesses a thicker cuticle than that of obligate ant associates as an additional defense mechanism (Dupont, 2012).

Examples of ant- Lepidoptera interactions

Several examples of ant-lepidopteran association mediated through chemical and acoustic signalling are observed in the ecosystem. The association with *Aricoris propitia* (Lepidoptera: Riodinidae) and fire ants (*Solenopsis saevissima)* are arbitrated through both type of signalling and all larval stages are tended by ants. The fourth instar stage of this caterpillar exhibited a peculiar behaviour as it devour the host plant during night and rest during the day time inside an underground shelter constructed and guarded by ants (Kaminski and Filho, 2012).

The chemical secretions of lycaenid only act as nutritive rewards but also as manipulative drugs that modify the behaviour of ants. The secretions from dorsal nectary organ of *Arhapala japonica* larva alter the locomotory activities of their tending ants, *Pristomyrmex punctatus* workers. The attending ants fed on these secretions recorded with a lower level of dopamine level in the brain that may result in the manipulation of ant behaviour (Hojo *et al.,* 2015). Likewise, the tentacle organ secretion of the caterpillar *Shirozua jonasi* contains dendrolasin that mimic alarm pheromones of the attendant ants.

In the ecological perspectives, obligate ant associates are more vulnerable to extinction, as they are more prone to invasive ants, habitat destruction and climate changes. As per IUCN statistics, more than 70% of threatened species of Lycaneidae and Riodinidae are ant associates that highlight the importance of ant- Lepidoptera interactions in the ecosystem.

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