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Does the solitary parasitoid *Microplitis pennatulae* use a combinatorial approach to manipulate its host?

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Abstract

Host manipulation is a strategy used by some parasites to enhance their transmission. These parasites use a combination of neuropharmacological, psychoneuroimmunological, genomic/proteomic, or symbiont-mediated mechanisms to manipulate their hosts. Bodyguard manipulation occurs when parasitized hosts guard parasitoid pupae to protect them from their natural enemies. Bodyguard-manipulated hosts exhibit altered behaviours only after the egression of parasitoid prepupae. Behavioural changes in post-parasitoid egressed hosts could have resulted from their altered physiology. Previous studies have shown that gregarious manipulative parasitoids induce multiple physiological changes in their host, but the physiological changes induced by solitary manipulative parasitoids are unknown. *Microplitis pennatulae* Ranjith & Rajesh (Hymenoptera: Braconidae) is a larval parasitoid of *Psalis pennatula* Fabricius (Lepidoptera: Erebidae). After the egression of parasitoid prepupae, *P. pennatula* stops its routine activities and protects the parasitoid pupa from hyperparasitoids by body thrashes. In this study, we looked into the physiological changes induced by the solitary manipulative parasitoid, *M. pennatulae*, in its host, *P. pennatula*, during various stages of parasitization. We considered octopamine concentration and phenoloxidase (PO) activity as biomarkers of physiological change. We also examined whether *M. pennatulae* has a symbiotic virus and whether the wasp transfers it to the host during parasitization. We found that octopamine concentration was low in the pre-parasitoid egressed host, but it was elevated after the parasitoid egressed. Phenoloxidase activity was lower in the pre- and post-parasitoid egressed host than in the unparasitized host. We also detected symbiotic bracovirus (BV) in the wasp ovaries and isolated the BV virulence gene from the parasitised host. Our study suggests that solitary parasitoids also induce multiple physiological changes to influence the host behaviour to their advantage, as is the case with the gregarious parasitoids.

Introduction

Parasites adopt several strategies for their transmission and survival. Of these, host manipulation is an advanced strategy that ensures parasites greater transmission success. Manipulative parasites can alter the behaviour and physiology of their hosts. For example, the protozoan *Toxoplasma gondii*, an apicomplexan parasite, has two hosts belonging to two trophic levels. The primary host of *T. gondii* is a rat, and its definitive host is a cat. Once infected with the parasite, the rat becomes attracted towards the odour of cat urine, despite innate aversion. The altered behaviour increases the predation rate of the rat, and consequently the transmission rate of the parasite (Berdoy et al., 2000). Parasite infection also elevates the concentration of dopamine in the host brain, which plays a critical role in the altered host behaviour (Gaskell et al., 2009).

Some parasitic wasps (hymenopteran parasitoids) also induce behavioural alterations in their hosts through so-called bodyguard manipulation (Brodeur & Vet, 1994). Bodyguard-manipulated hosts protect the parasitoid pupae from their natural enemies (Brodeur & Vet, 1994; Grosman et al., 2008; Harvey et al., 2011; Maure et al., 2011; Mohan & Sinu, 2017). These manipulative parasitoids are koinobionts that feed only on host fat body and haemolymph (Harvey et al., 2008). Their hosts are often alive even after the parasitoid pre-pupal egression (Harvey & Malcicka, 2016). Live hosts protect the parasitoid pupae by thrashing their body or regurgitating fluids from the gut (Harvey et al., 2008). Even the mere physical presence

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