Behavioral and Physiological Changes in *Macrotermes gilvus* (Hagen) (Blattodea: Termitidae) Induced by the Endoparasitoid *Misotermes mindeni* (Diptera: Phoridae)

by

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Abstract

Association of the subterranean termite *Macrotermes gilvus* (Blattodea: Termitidae) with the endoparasitoid *Misotermes mindeni* (Diptera: Phoridae) results in numerous behavioral and physiological changes of the former. These changes can be a defensive response of the host or a colony response to infection or an adaptive modification of the host by the endoparasitoid for the benefit of the latter. However, when the modifications do not benefit either party, these changes may simply be the pathological consequences of infection. This paper summarizes the behavioral and physiological changes in the host *M. gilvus* induced by the endoparasitoid *M. mindeni*.

Key words: termite, host, parasitoid, interaction

Introduction

The process of successful parasitism consists of a sequence of steps, i.e., host habitat finding, host location, host suitability, host acceptance, and host regulation (Vinson 1976, Vinson and Iwantsch 1980, Brodeur and Boivin 2004). These hierarchical steps are indispensable because successful parasitism is an intricate attainment (Brodeur and Boivin 2004). Many interactions between host and parasitoid are regarded as an adaptive response of the host to compensate for the effects of parasitism or an adaptive modification of the host by the parasitoid to create a host environment suited to meet the demands of the latter to ensure successful parasitism (Godfray 1994, Poulin 1995, 1998). Successful parasitism includes host lactation and discrimination , overcoming the host's immune response, and regulating or adapting to the dynamic host environment (Brodeur and Boivin 2004). These intricate host-parasitoid interactions affect numerous key features of ecological organization including community structure, population size and dynamics of the host, long-term population persistence, and geographical distribution (Loehle 1995).

Over the course of evolutionary time, interactions between hosts and parasitoids lead to innumerable morphological, behavioral, physiological, as well as ecological changes for the insect host (Vinson and Iwantsch 1980). These include behavioral changes such as behavioral fever, foraging, aggressive behavior, as well as various social interactions such as trophallaxis, grooming and social avoidance while physiological and ecological changes include influences on growth and development, reproduction, respiration, water balance, hemolymph solute as well as protein, and lipid content, host tissues, and habitat preference (Vinson and Iwantsch 1980, Thompson 1982, Moore 1983, Hegazi et al. 1988, Loehle 1995, Haspel et al. 2005, Roy et al. 2006, Libersat et al. 2009, Neoh and Lee 2010, 2011, Foo et al. 2011). Manipulation of the host is an unavoidable consequence of the exploitation of host tissues and resources by the parasitoid in their attempt to successfully complete development within the host (Poulin 1998). When the requirements of the parasitoid are not met, host changes are needed (Brodeur and Boivin 2004). These changes are often attributed to endophagous larval parasitoids (Vinson and Iwantsch 1980).

Macrotermes gilvus (Hagen) (Blattodea: Termitidae) is a common mound-building termite native to Southeast Asia (Roonwal 1970, Lee et al. 2007). Recently, the larvae of a new species of phorid fly *Misotermes mindeni* Disney and Neoh (Diptera: Phoridae) has been reported in Malaysia to parasitize *M. gilvus* fourth larval instars, major presoldiers, and major soldiers (Disney et al. 2009, Neoh and Lee 2010). This paper summarizes the studies on behavioral and physiological changes in the host *M. gilvus* induced by the endoparasitoid *M. mindeni*.

Behavioral Changes

Greater mutual grooming behavior of not-parasitized *M. gilvus* workers and major soldiers was observed in the presence of parasitized hosts (Foo et al. in preparation). The increase in the grooming frequency may be attributed to the workers attempting to prevent the unparasitized major soldiers from infestation by removing the fly eggs or larvae that latch directly on the termite cuticle. The presence of parasitized major soldiers also might raise alarm levels in the workers. On the other hand, host grooming behavior may also be advantageous for the parasitoid and it was proven that workers groom parasitized major soldiers of *M. gilvus* more than unparasitized ones (Foo et al. in preparation). The colony should generally have limited or no interest in looking after parasitized individuals as they will eventually die after the fly has emerged. Because workers groomed parasitized individuals more often than unparasitized ones, it would seem that parasitoids affected worker behavior via the demands of the parasitized nestmate to remove potential entomopathogens, which might be detrimental to the hosts and parasitoids' development and survival (Foo et al. in preparation).

An increase in feeding activity has been demonstrated in major soldiers of *M. gilvus* infested by *M. mindeni* (Foo et al. in preparation). The elevated feeding activity of the parasitized major soldiers is advantageous to both the parasitoid and host. The fly larva requires sufficient nutrients for development and the soldier requires food above what the parasitoid consumed. Further, the high food demands of the major soldiers due to parasitization might be the underlying mechanism that elicited the frequent trophallactic exchanges between workers and parasitized hosts (Foo et al. in preparation). The parasitized major soldiers were the ones that mediated the higher rates of trophallaxis from workers.

Physiological Changes

Foo et al. (2011) were the first to describe parasitoid-induced physiological changes in a termite host involving metabolic rate and water balance. Major soldiers of *M. gilvus* carrying the larval parasitoid *M. mindeni* have a higher respiratory metabolism than not-parasitized soldiers. This greater metabolic activity is important to either provide adequate energy for the larval parasitoid to complete its life cycle, is required by the host to recover from damage caused by the parasitoid, or is simply a reflection of the larger size of parasitized compared to not-parasitized soldiers. The higher metabolic rate of parasitized major soldiers may also be one reason that they congregate in outer chambers of the mound which provide better gas exchange than areas deeper in the mound.

The relative humidity of the peripheral zone is lower than in the inner zone of the mound. Hence, s physiological adaptations of the parasitized termites such as larger size, lower rates of water loss, higher tolerance to desiccation, and greater capacity to store metabolic water compared to not-parasitized individuals allow the hosts to better withstand this drier environment (Foo et al. 20011). In parasitized soldiers, the cuticle has a lower water content and the epidermis restricted water movement into the cuticle. This reduced cuticular water permeability resulted in lower rates of water loss (Foo et al. 2011). The authors concluded that these physiological adaptations would benefit the parasitoids, by promoting host survival and providing time for completion of parasitoid development before the host died under less favourable environmental conditions.

Conclusions

Behavioral and physiological changes in the host *M. gilvus* induced by the endoparasitoid *M. mindeni* can be the result of a defensive response of the host to protect themselves or colonies from infection or an adaptive modification of the hosts for the benefit of the endoparasitoids. However, when the modifications do not benefit either party, these changes may simply be pathological consequences of infection.

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