

Ecological adaptation success of the sympatric higher termites, *Macrotermes gilvus* and *Macrotermes carbonarius*

by

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Abstract

Macrotermes gilvus and *M. carbonarius* can form populous colonies in the same habitat. Encounters between termites from neighbouring colonies in areas of high mound density should be frequent. This phenomenon may pose the potential for conflict during foraging and interspecific hybridization that could result in reduced foraging efficiency and sexual caste infertility, respectively. Despite their sympatric distribution and ecological similarity, several mutual adaptive strategies were identified such as chronological reproductive isolation, lack of intraspecific aggression, and desiccation tolerance to preclude such adverse interactions. In addition, the population dynamic of *M. gilvus* and *M. carbonarius* in one given area could be considerably maintained owing to the potential of producing adultoids as replacement reproductive once a colony declines, and the decrease nest with the remaining valuable food source (fungus comb) which promotes intra-/inter specific re-colonization in the ready-made nest.

Key words: higher termite, reproductive isolation, reproductive acceptance, intraspecific aggression, desiccation tolerance.

Introduction

Fungus growing termites of the subfamily Macrotermitinae are widely distributed throughout the Paleotropics (Africa and Asia) but are not recorded from the Neotropics (i.e., Central and South America) and Australasia. The subfamily Macrotermitinae comprises approximately 330 species, covering 14 genera, and the genus *Macrotermes* alone contains 47 species (Kambhampati and Eggleton 2000).

The main four genera (i.e., *Hypotermes*, *Microtermes*, *Macrotermes*, *Odontotermes*) are predominantly distributed in Southeast Asia (Tho 1992). Aanen and Eggleton (2005) noted that *Macrotermes* originated in the African rain forest and later invaded savannahs, Asia and the Madagascar. Based on molecular divergence estimates, *Macrotermes* is believed to have dispersed to Asia in the early Tertiary, a period of humid climate and into savannahs during the Miocene (Brandl et al. 2007).

Ecological similarity of *Macrotermes gilvus* and *M. carbonarius* poses the potential for conflict between these sympatric species

Macrotermes gilvus (Hagen) and *M. carbonarius* (Hagen) are widely distributed in Southeast Asia, found mainly in Thailand, Cambodia, the Malay Peninsula and Borneo (Roonwal 1970). They usually present in lowland forests, it can also be found in agricultural and human dominated areas rural and suburban (i.e., parks and gardens) (Tho 1992). Both species build large subconical epigeal mound which can reach up 4 m in height and 5 m in diameter.

The density of termite mounds can exceed 8 mounds/ha and the distance between *M. gilvus* and *M. carbonarius* colonies can be as close as 4 m apart (Fig. 1). *M. carbonarius* usually forage for food on open ground, by constructing pavement tracks on the soil surface. Underground passage systems are connected with 4–10 major tracks with a total length between 33.8 and 112.8 m (Inoue et al. 2001). The foraging territories of *M. gilvus* can cover an area of 350 m² and foraging distances range from 16-48 m (Acda 2004). In all likelihood, their foraging territories could overlap. In addition, both sympatric species share the same food resources and nesting strategies, thus competition is inevitable. Korb and Linsenmair (2001) further supported that the distribution of older colonies of *Macrotermes bellicosus* (Smeathman) is influenced by intraspecific competition owing to limiting food sources.

The coexistence of sympatric species in one habitat may promote interspecific hybridization. For example, alates of *M. subhyalinus* and *M. michaelsoni* which are predominant in Kenya successfully formed mixed pairs under laboratory conditions (Lepage and Darlington 2000). However, the hybrids appeared to be infertile in most cases due to dysgenesis syndromes (Hägele 1999).

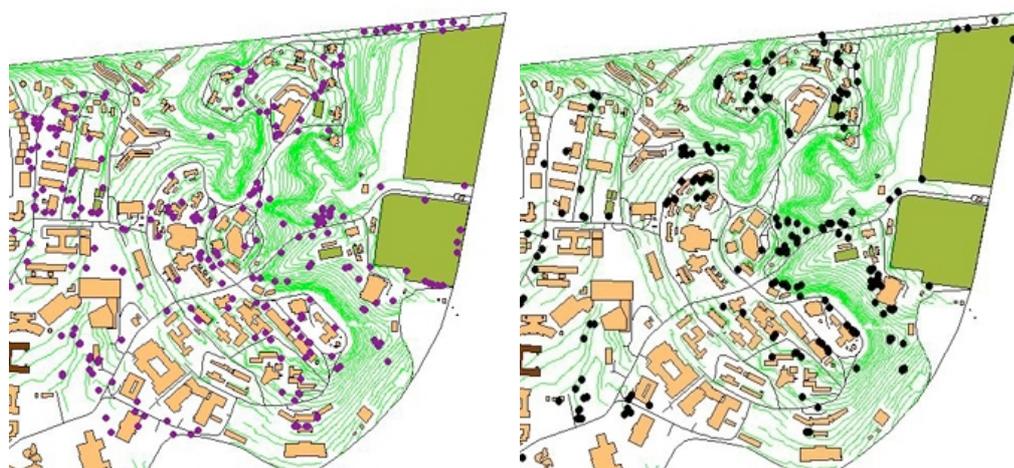


Fig. 1. Distribution of *M. gilvus* and *M. carbonarius* mounds at the USM Minden Campus. The distance between the *M. gilvus* (purple squares) and *M. carbonarius* (black squares) colonies can be as close as 4 m apart. This could pose possible conflict and interspecific hybridization among these sympatric species.

Strategies towards ecological success

Despite of the sibling relationship and ecological similarities between these termites, several mutual adaptive strategies were identified to ensure their separate ecological success.

Strategy 1: Chronological reproductive isolation.

Flights of *M. gilvus* were recorded over a remarkably long 7-mo period from March to September, whereas swarming of *M. carbonarius* took place from November to January (Fig. 2). The disparate flight periods and strategies exhibited by *M. gilvus* and *M. carbonarius* strongly indicate that reproductive isolation of these two sympatric termites is chronologically mediated. This might be an adaptive strategy that ensures successful colony foundation and precludes interbreeding.

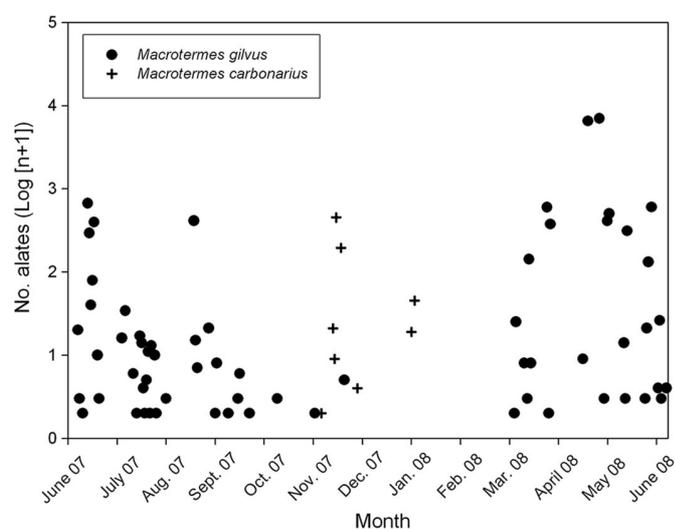


Fig. 2. Flight activity of the subterranean termites *M. gilvus* and *M. carbonarius* over a period of 12 mo. Data for trapped alates were transformed with $\log(n + 1)$ (Neoh and Lee 2009).

Strategy 2: Lack of intraspecific aggression.

Species of *Macrotermes* form very populous colonies. Encounters between termites from neighbouring colonies would be frequent in areas of high mound density as is the case for *M. carbonarius* and *M. gilvus* (Wong, 2006). If conditions are favourable for foraging, several congeneric colonies can often be found to forage simultaneously on the surface on widespread items of plant litter. However, workers of both *M. gilvus* and *M. carbonarius* exhibited limited intraspecific aggression (Neoh et al. 2012). This phenomenon avoids territorial fights among foraging groups that would be costly for both parties, due to loss of individuals and reduced foraging efficiency.

Strategy 3: Desiccation tolerance.

Despite both species showing no significant differences in calculated cuticular permeability, and percentage of total body water, they differed greatly in rate of water loss and surface area to volume ratio (Hu et al. 2012). This indicates that *M. carbonarius* with the higher body water content can tolerate water loss for a longer time period than *M. gilvus* before water loss reaches the critical point. This permits *M. carbonarius* to forage above ground and thus avoid direct competition for food with *M. gilvus* which forages underground.

Strategy 4: Reproductive replacement mechanism and re-colonization.

Population dynamics of *M. gilvus* and *M. carbonarius* colonies includes considerably static maintenance of populations in a given area. This is because a deceased colony can either be replaced via colony re-establishment by adultoids derived from alates or nymphs (Neoh et al. 2010), or re-colonization by a conspecific termite (Neoh et al. 2012).

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