

Flight Activity of Two Sympatric Termite Species, *Macrotermes gilvus* and *Macrotermes carbonarius* (Termitidae: Macrotermitinae)

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ABSTRACT Flight activities of two sympatric termite species, *Macrotermes gilvus* (Hagen) and *Macrotermes carbonarius* (Hagen), were studied in Penang Island, Malaysia. Herein, we present the first documentation of chronological reproductive isolation of *M. gilvus* and *M. carbonarius*. 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. Swarming events of *M. gilvus* and *M. carbonarius* occurred under atmospheric pressures of 1,005–1,011 and 1,006–1,010 hPa, respectively. Most flights of *M. gilvus* occurred on days with rain, whereas *M. carbonarius* avoided rain. Flight activity of *M. gilvus* was correlated significantly with atmospheric pressure and rainfall. The threshold temperature and relative humidity of *M. gilvus* flights were between 23 and 26°C and 83 and 98% RH, respectively; *M. carbonarius* swarmed between 25 and 30°C and 72 and 83% RH, respectively. The flight activity of *M. gilvus* concentrated in the warmer and humid months with a monthly total rainfall of 228 mm. Both species swarmed at distinct times of day during the limited field observations: Flights of *M. gilvus* began between 0300 and 0430 hours (light intensity <1 Lx), and flights of *M. carbonarius* lasted for only 4–10 min between 1900 and 1910 hours (at dusk; light intensity: 20–200 Lx). Windless conditions were preferred for the flights of both species.

KEY WORDS *Macrotermes*, flight phenology, swarming, chronological reproductive isolation

The fungus-growing termite genus *Macrotermes* is widely distributed in Africa and in South and Southeast Asia (Roonwal 1969). Of the 45 described species of *Macrotermes*, *Macrotermes gilvus* (Hagen) and *Macrotermes carbonarius* (Hagen) are commonly found in Southeast Asia. *Macrotermes* species are infamous for their damage to field crops, such as sugar cane, and to wooden structures (Harris 1969, Roonwal 1969, Cowie et al. 1989). In addition, *M. gilvus* is gaining notoriety as a secondary structural pest that becomes active once the dominant *Coptotermes* species are suppressed or eliminated from buildings by baiting (Lee et al. 2007). Managing *Macrotermes* infestations is more complex than dealing with those of *Coptotermes* (Lee 2002, Lee et al. 2007).

Synchronized release of alates from parental colonies across a given area is the main strategy for colony foundation and species dispersion. The flight season varies with termite species and location. In temperate regions, flight activity usually is restricted to rainfall events within the warmer months; in the tropics, it coincides with the main rainy periods (Nutting 1969). Studies have indicated that the actual timing of the flights can be triggered by both abiotic factors (e.g., temperature, humidity, rainfall, light intensity, wind velocity, atmospheric pressure, and electrical properties in the atmosphere) and biotic

factors (e.g., pheromones, nutrients, colony size, predators). An individual factor might influence the decision for alates to fly, or certain combinations of factors might affect their flight activity (Brian 1965, Nutting 1969). In some cases, sympatric termite species that respond to the same sexual communication signals might exhibit disparate flight patterns, whereas simultaneous flight might be governed by species-specific pheromones to avoid confusion and cross-breeding (Peppuy et al. 2004).

Stationary traps are feasible tools for monitoring flight phenology of insect populations (Kaspari et al. 2001, Nansen et al. 2001). Counting trapped alates might provide information about alate flight patterns and the population's sex ratio (Henderson and Delaplane 1994) and about how successfully a species colonizes in a given region (Henderson 1996, Osbrink et al. 2008).

In this study, we investigated the importance of ecological factors in triggering flight in *M. gilvus* and *M. carbonarius*. We documented two reproductive isolating mechanisms for these two sympatric species: different flight strategies and different periods of flight. Under conditions of abundant termite species and space constraints, colony sexual caste production may be limited not only by food abundance (Korb and Linsenmair 2001) but also by the accessibility of resources by colony members. Both intraspecific and interspecific territoriality may regulate food availabil-

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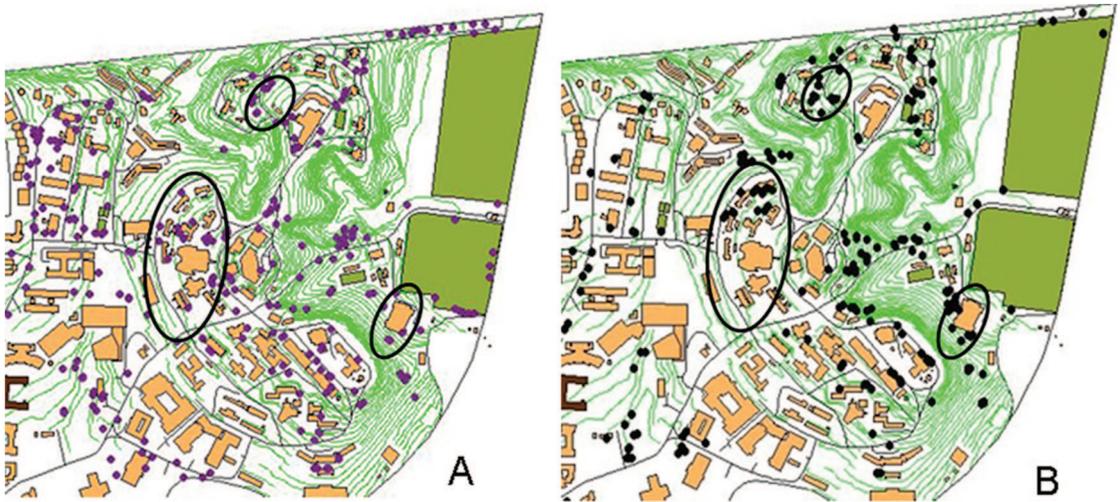


Fig. 1. Distribution of *M. gilvus* (A) and *M. carbonarius* (B) mounds at the USM Minden Campus. The purple squares represent *M. gilvus* mounds and the black squares indicate *M. carbonarius* mounds. Circles indicate field collection sites.

ity in a colony (Henderson 1996). This competition is even stronger during the period of alate production, because foraging activity peaks at this time (Schuurman 2006). Therefore, we considered our results supporting the above hypotheses with regards to factors that could influence the alate dispersal period.

Materials and Methods

Study Sites. The study was conducted on Penang Island, located on the northeastern coast of Peninsular Malaysia, between June 2007 and June 2008. Penang has an equatorial climate that is uniformly warm and humid throughout the year. Temperatures generally range from 29 to 35°C during the day and from 26 to 29°C at night. The mean annual rainfall of ≈2,670 mm is evenly distributed throughout the year, although September to November is considered to be the wettest period of the year (see <http://app2.nea.gov.sg/index.aspx>).

The study sites were located at the Minden Campus of Universiti Sains Malaysia (USM), Penang, Malaysia (5°21' N and 100°18' E). The campus encompasses an area of ≈100 ha. The density of termite mounds on the campus can exceed 8 mounds/ha. *M. gilvus* and *M. carbonarius* were the two most common mound-building termite species found on the campus, accounting for 43.7 and 32.4%, respectively, of the total termite mounds ($n = 978$) (Wong 2006).

Trapping of Termite Alates. Twenty-nine sticky traps (SELL Co., Jakarta, Indonesia), each measuring 28 by 19 cm, were hung on 36-W fluorescent lamps (Phillips, Bangkok, Thailand) with a light output of 2,600 lm that were located in three different areas of the campus (Fig. 1). Each sticky trap was positioned slightly below the lamp tube and suspended at ≈3 m above ground. Henderson (1996) found that numbers of trapped *Coptotermes formosanus* Shiraki alates showed no correlation with trap height. Our study sites were chosen based on areas known to have a high

density of termite mounds. The study sites were located between 300 and 500 m apart. Traps were checked daily (between 0900 and 1000 hours) to make sure no flight was missed out. The trapped alates on each trap were identified to species and pooled for all 29 traps daily. Sticky traps were replaced with new ones after each flight event.

Meteorological Data. Hourly temperature (°C), relative humidity (%), atmospheric pressure (hPa), and daily precipitation (mm) data were obtained from the Malaysian Meteorological Department (MMD) based on the recordings from the Bayan Lepas station (5°18' N and 100°16' E; altitude, 2.8 m), Penang Island, Malaysia (distance from study site = 8.5 km).

Data Analysis. The meteorological data (temperature, relative humidity, and atmospheric pressure) for the periods that best represented the flight activities for each species (based on observation: i.e., 0300–0500 hours for *M. gilvus* and 1900 hours for *M. carbonarius*) were used for analysis. This increased the reliability in assessing the relationship between day-to-day patterns of swarming and the environmental variables. Only days on which flight occurred were subjected to SPSS 11.0 spearman rho analysis (SPSS 2002). We assumed that the trap catch number was directly related to termite flight activity.

To reduce the bias that might be introduced by distribution and density-dependent factors, relative frequency (RF) of swarming events also was tested to analyze the relationship between number of swarming events per month and environmental variables. The RF was calculated using the following formula (Rebello and Martius 1994, Martius et al. 1996): $RF = E/T$, where E = number of swarming events per month and T = total number of swarming events in a year.

A three-dimensional scatter plot of RF to environmental factors was generated using SPSS SigmaPlot 8.02 (SPSS 2004). Data were smoothed and fitted to a mathematical function. SPSS 11.0 pearson correlation

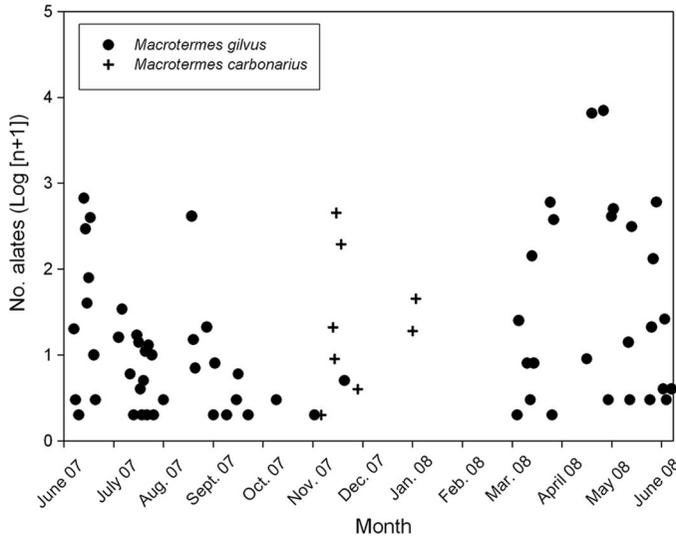


Fig. 2. Flight activity of the subterranean termites *M. gilvus* and *M. carbonarius* over a period of 12 mo. Data for trapped alates were transformed with $\log(n + 1)$.

analysis (SPSS 2002) was used to correlate RF and environmental factors.

Field Trip. We made routine field trips to selected areas of the Minden Campus. Dispersal flights of *M. gilvus* ($n = 4$) and *M. carbonarius* ($n = 2$) on different days were observed in April 2007 and November 2007, respectively. Environmental parameters were recorded hourly during observations. Temperature and wind speed were measured with a Thermo-Anemometer (AZ Instrument, Taichung, Taiwan). Relative humidity and light intensity were measured with a Whirling Psychrometer (G. H. ZEAL, London, United Kingdom) and a light meter (Sper Scientific, Taipei, Taiwan), respectively.

Collection of Sexual Caste Specimens. Mounds of *M. gilvus* ($n = 40$; height: 0.05–0.50 m; diameter: 0.60–1.80 m) and *M. carbonarius* ($n = 21$; height: 0.10–0.54

m; diameter: 0.65–1.90 m) were sampled over 2 yr between December 2006 and December 2008 to provide direct evidence on the presence of alates in one given colony over swarming period. The nymphs collected were preserved in 70% ethanol before morphometric analysis. To determine the nymphal stages, various parts of the termite were measured based on the description by Okot-Kotber (1981).

Results

Number of Alates and Period of Flight

Macrotermes gilvus. A total of 17,902 alates of *M. gilvus* were trapped (Fig. 2). The highest numbers trapped per day were recorded on 17 and 24 April 2008 and ranged from 6,500 to 7,000 alates, which accounted

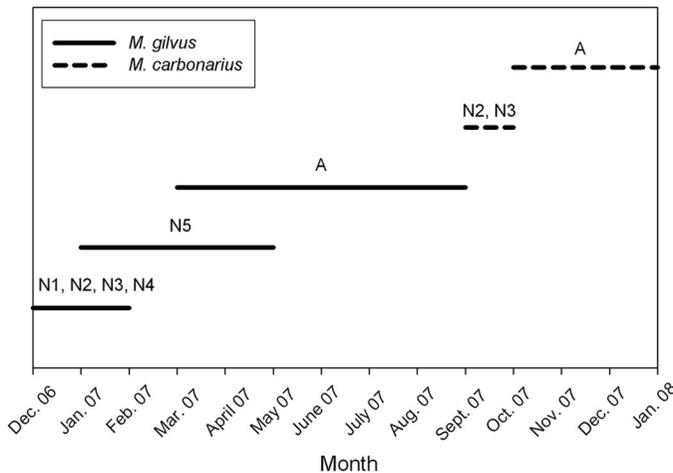


Fig. 3. Seasonal production of sexual castes in colonies of *M. gilvus* and *M. carbonarius*. N, nymphal stage; A, alate.

Table 1. Environmental conditions and flight time of *M. gilvus* and *M. carbonarius*

	Atmospheric pressure (hPa)	Temperature (°C)	Relative humidity (%)	Light intensity (Lx)	Flight time (hours)	Flight duration
<i>M. gilvus</i>	1,005–1,011	23–26	83–98	<1	0300–0430	1–2.5 h
<i>M. carbonarius</i>	1,006–1,010	25–30	72–85	20–200	1900–1910	4–10 min

Values are ranges.

for 75.4% of the total catch. The flight of *M. gilvus* was recorded over a notably long 7-mo period from March to September; the highest frequency of alates was released from June to July. High numbers of alates also were recorded between March and June. Small flights were observed from October to November.

Macrotermes carbonarius. A total of 736 alates of *M. carbonarius* were trapped during the study period (Fig. 2). The highest number caught per day was 449 alates (61.0% of the total catch) on 15 November 2007. Traps in close proximity to mounds tended to collect higher numbers of alates. Flights were confined to the months of November to January. Most flights occurred in November (the wettest month of the year), and sporadic flights took place between December and January. Generally, alates from both species were trapped in each location on flight days, indicating that swarms from different colonies were occurring simultaneously.

Seasonal Production of Sexual Castes

Macrotermes gilvus. Six of the 40 sampled between early December 2006 and January 2007 contained four nymphal stages (N1, N2, N3, and N4; Fig. 3). Between January and April, N5 was present simultaneously with N3 and N4 in five mounds. Seven nests contained alates from March to August.

Macrotermes carbonarius. In September, stages N2 and N3 were present in 1 of 21 colonies sampled (Fig. 3). Five nests were populated by alates in October and November.

Relationship of Flight Activity to Environmental Variables

Macrotermes gilvus. Most swarming events took place at atmospheric pressure of 1,008–1,009 hPa, $\chi^2(6, n = 64) = 32.906, P < 0.05$ (Table 1). Weak

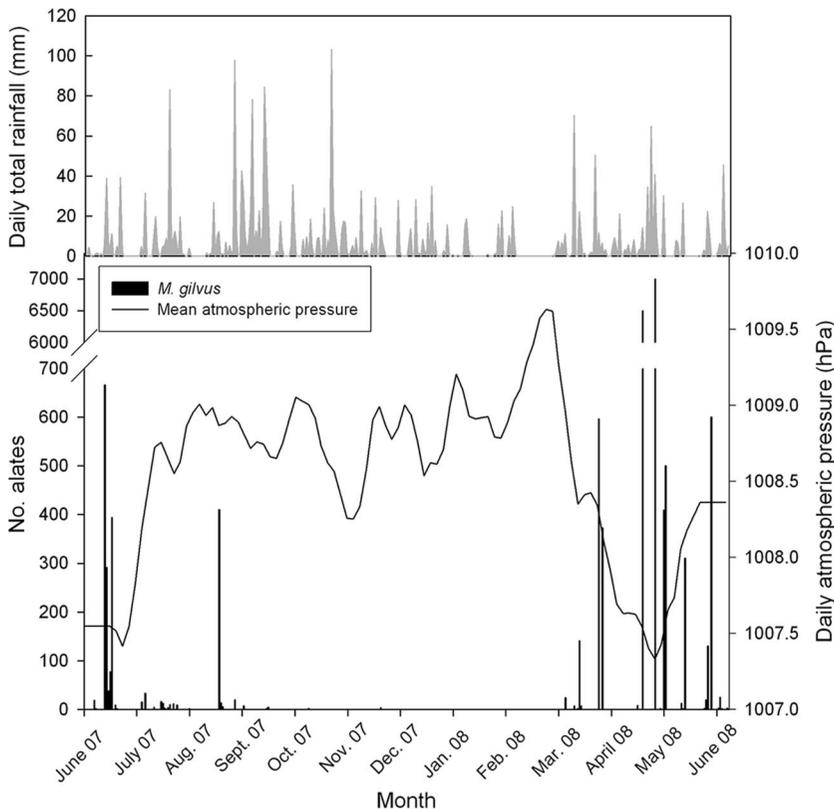


Fig. 4. Flight activity of *M. gilvus* in relation to daily atmospheric pressure and daily total rainfall. The environmental variable data were smoothed with a running average of 10% of the data set.

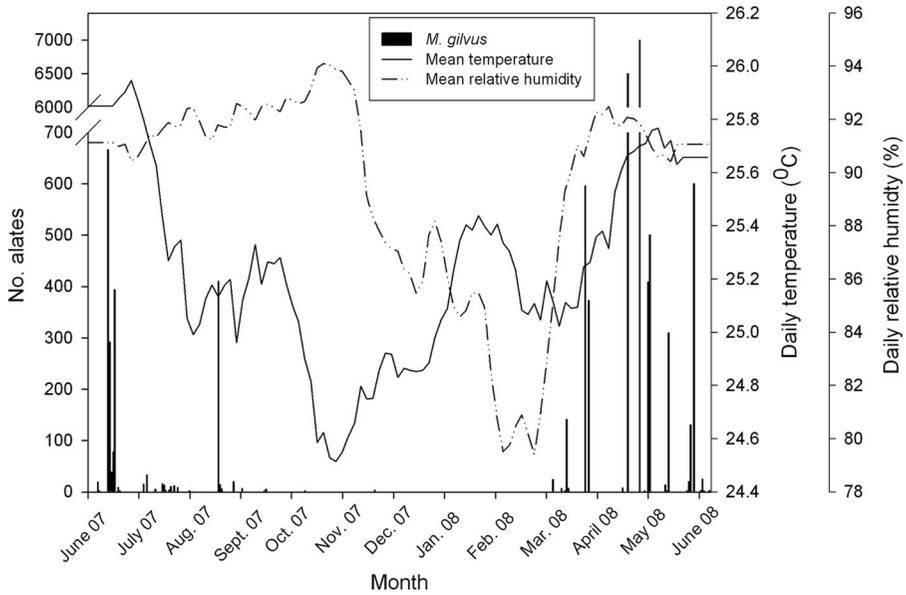


Fig. 5. Flight activity of *M. gilvus* in relation to daily temperature and daily relative humidity. The environmental variable data were smoothed with a running average of 10% of the data set.

correlation was detected between the number of trapped alates and atmospheric pressure ($r = -0.216, P < 0.05$). A transformed data with presence-absence (1-0) of rainfall recorded during the flight days was set. By looking at the incidence of rain on flight days, it was evident that most flights occurred on days with rain, $\chi^2 (1, n = 64) = 12.250, P < 0.05$ (Fig. 4); with temperature of 25°C, $\chi^2 (3, n = 64) = 21.125, P < 0.05$; and with high relative humidity ranging from 92 to 97%, $\chi^2 (13, n = 64) = 28.313, P < 0.05$ (Fig. 5). Progressive flights often occurred during 3–4 consecutive days of rain. Thus, rain was necessary to trigger swarming in *M. gilvus*, which is in accordance with field observations of swarming activity. Surprisingly, a total of 18 flight events occurred 1 or 2 days after the rain. The number of alates released was weakly but negatively correlated with rainfall ($r = -0.208, P < 0.05$).

Our field trip observations of the termite mounds showed that the first dispersal holes of *M. gilvus* could be observed at 2030 hours, especially after rain. Termites closed flight holes before alates were released under severe storm conditions or when predator pressure (e.g., frogs and ants attacked the termites that were stationed around the dispersal holes) was high. The flights normally took place between 0300 and 0430 hours, before dawn (light intensity: <1 Lx) and lasted for 1–2.5 h. Usually, flights were separated into multiple swarms (≥ 2). *M. gilvus* alates were capable of flying ≈ 100 m (unpublished data) under windless conditions.

Macrotermes carbonarius. This species avoided rain and swarmed preferentially during the dry days (Fig. 6). The alates appeared to be more tolerant of low relative humidity (Fig. 7), except in one case in which the alates swarmed at a high humidity condition (94% RH). No significant correlation was found between

the number of trapped alates and the environmental variables.

The first flight holes *M. carbonarius* could be observed around midday (1200 hours) under hot and dry conditions ($29 \pm 1^\circ\text{C}$ and $76 \pm 2\%$ RH) and mostly on days without rain. *M. carbonarius* flew at dusk between 1900 and 1910 hours (light intensity: 20–200 Lx) and flights lasted for 4–10 min. Only a single mass swarm was observed for each colony. Windless conditions were also favored for flights. The flight distance was ≈ 30 m (unpublished data). Birds usually attacked the alates once they dispersed from the parental colony.

Relative Frequency

Macrotermes gilvus. The highest RF of flight was 45.2% and occurred in July, during which a monthly total rainfall of 228 mm was recorded, followed by June with an RF of 38.5%. A monthly total rainfall of 88 mm was sufficient to trigger $\approx 30\%$ of flight events in May.

A significant positive correlation was detected between frequency of flight events and monthly mean temperature ($r = 0.662, P < 0.05$) and monthly mean relative humidity ($r = 0.517, P < 0.05$). RF was modeled using a Gaussian function to determine the effects of temperature and relative humidity on it. Warm and humid months were favored for flights (Fig. 8; $R^2 = 0.83$; SE of estimate = 0.08; $F = 8.82$; $P < 0.05$). The equation relating RF to temperature (T) and relative humidity is as follows:

$$\text{RF} = 0.39 e^{-0.5 \left[\frac{(\text{RH} - 91.20)}{1.41} \right]^2 - \left[\frac{(T - 25.64)}{0.47} \right]^2}$$

Modeling of the relationship between RF, T , and rainfall (R) also was conducted using a Lorentzian function. Flight events generally increased with the incre-

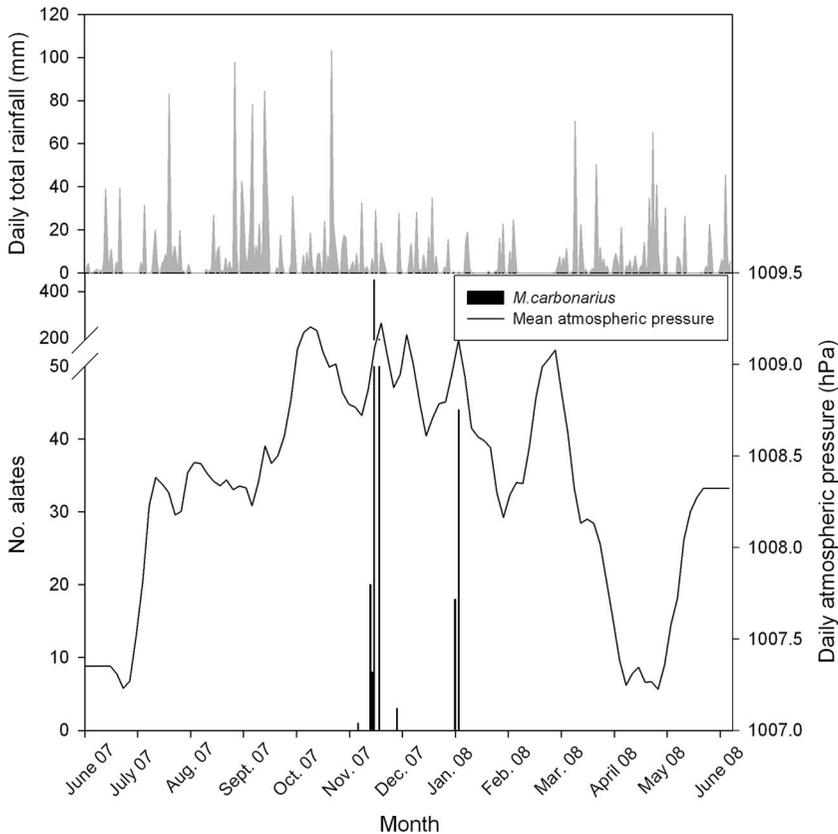


Fig. 6. Flight activity of *M. carbonarius* in relation to daily atmospheric pressure and daily total rainfall. The environmental variable data were smoothed with a running average of 10% of the data set.

ment of temperature under a monthly total rainfall of ≈ 200 mm (Fig. 9; $R^2 = 0.70$; SE of estimate = 0.11; $F = 4.02$; $P < 0.05$). The equation used was as follows:

$$RF = 4.43 / \{1 + [(R - 205.13) / 49.57]^2\} \{1 + [(T - 26.10) / -0.22]^2\}$$

Macrotermes carbonarius. Most flights, accounting for 75.0% RF, occurred in November, which had a monthly total rainfall of 146 mm.

Discussion

Nansen et al. (2001) reported that interpretation of trap catches of bostrichids (Coleoptera) is always complicated by several factors that may influence the magnitude of catches, for example, trap type, wind speed and direction, trap height, and weather conditions that may cause inconsistent results. In this study, we also experienced two extraordinarily high numbers of *M. gilvus* alates trapped in April 2007. These numbers might have been caused by a single bulk swarm of termites and by distance of the mound between the trapping sites (distribution-dependent factors); both factors have been highlighted by Henderson and Delaplane (1994) and Martius et al. (1996). Earlier data sets of termite flight activity were obtained by

varying data collection methods in the months and hours of the presumable flight period (Crosland et al. 1994, Henderson and Delaplane 1994, Henderson 1996, Costa-Leonardo and Barsotti 1998) or data collected at certain day intervals (Rebello and Martius 1994, Martius et al. 1996). The variability in methods caused inconsistent results. In this study, we conducted daily data collection and extracted meteorological data according to the time of flights. Thus, we can more accurately interpret our data.

The results of our study of flight phenologies of *M. gilvus* and *M. carbonarius* partially agreed with previous literature on the flights of other higher termites (Nutting 1969, Ruelle et al. 1975, Hu et al. 2007, Mitchell 2008). However, previous studies lacked empirical evidence of the relationship between flight activity and environmental factors (Martius et al. 1996, Martius 2003). In this study, we showed that the number of trapped alates was correlated with the environmental variables. With no seasonal distinction in the tropics, the flights of both species studied occurred under warm, humid, and a narrow range of weather conditions. Unlike in Penang, *Macrotermes natalensis* (Haviland) flew during a wide range of weather conditions in Africa (Mitchell 2008). *M. gilvus* and *M. carbonarius* alates flew over short distances without the aid of

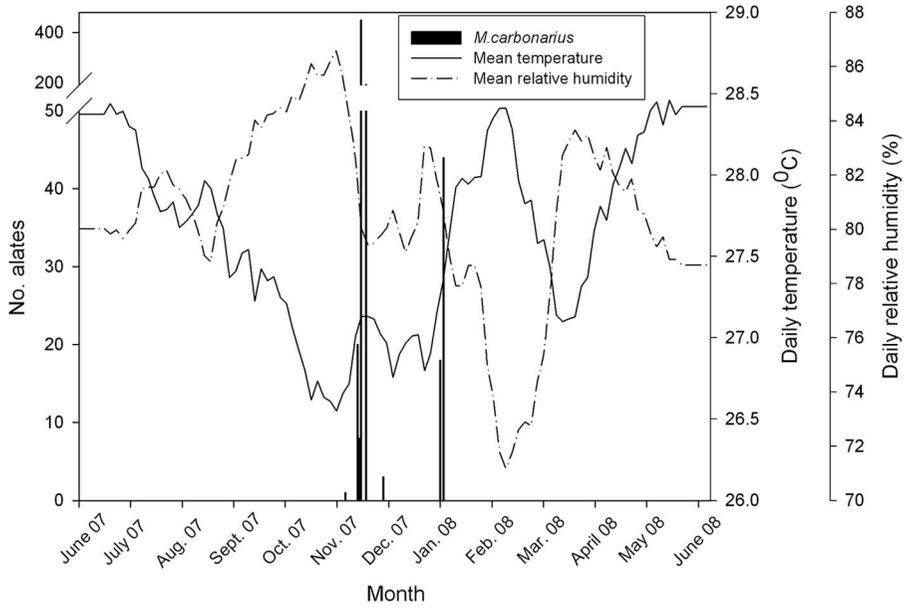


Fig. 7. Flight activity of *M. carbonarius* in relation to daily temperature and daily relative humidity. The environmental variable data were smoothed with a running average of 10% of the data set.

wind, thereby increasing their opportunities for post-flight pairing and inbreeding. However, in some species, alates flew under prevailing wind, e.g., *Amitermes emersoni* Light (Nutting 1969), *C. formosanus* (Messenger and Mullins 2005), and *Odontotermes formosanus* Shiraki (Hu et al. 2007).

Most subterranean termites swarm for a short flight period (William 1959, *Cubitermes* spp.; Sands 1965, *Trinervitermes* spp.; Ruelle et al. 1975; Darlington 1986; Mitchell 2008, *Macrotermes* spp.; Henderson and Delaplane 1994; Henderson 1996; Ferraz and Canello 2001, *Coptotermes* spp.). Interestingly, the flight ac-

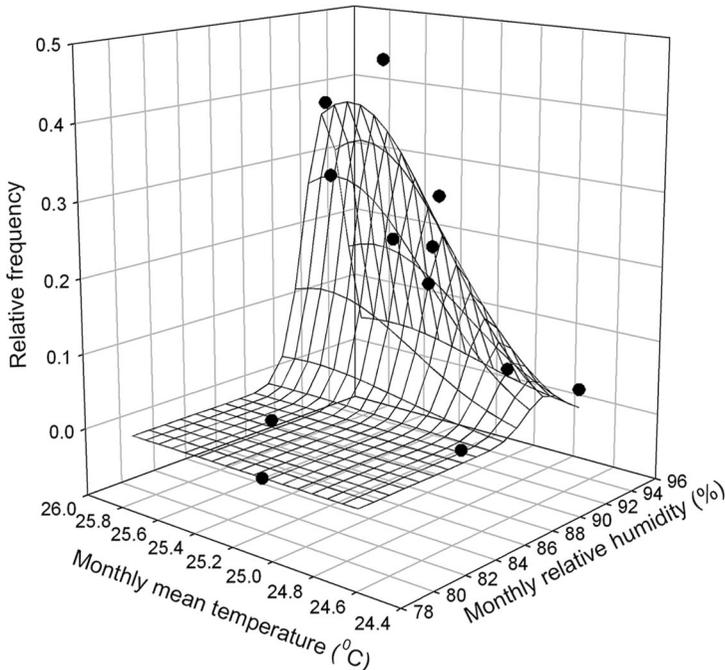


Fig. 8. Three-dimensional scatter plot with a fitted curve of the relative frequency of *M. gilvus* swarming events under combinations of temperature and relative humidity.

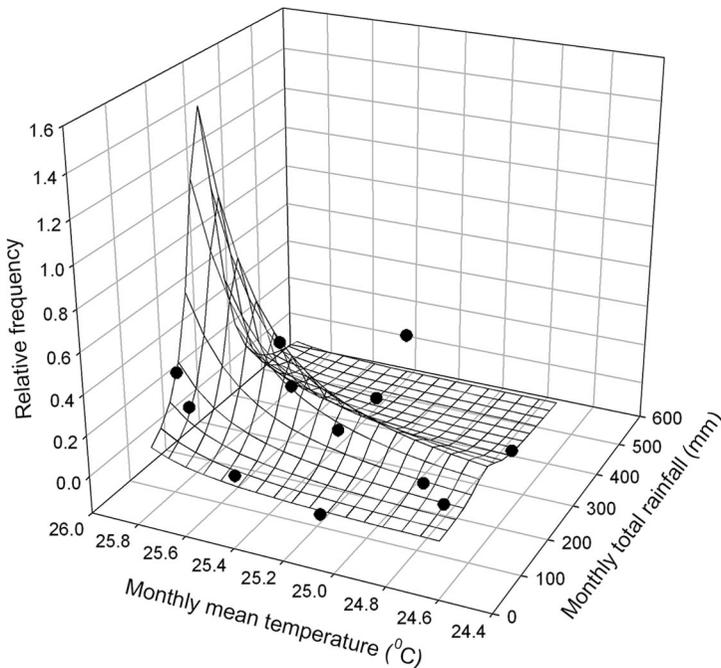


Fig. 9. Three-dimensional scatter plot with a fitted curve of the relative frequency of *M. gilvus* swarming event under combinations of temperature and rainfall.

tivity of *M. gilvus* occurred over a period of 7 mo, a fact that was further supported by the occurrence of alates in colonies for a lengthy period of time. A possible explanation for this long flight period is that dispersing sexual reproductive individuals remain in the parental colonies for months under unfavorable environmental conditions (Darlington 1986). Alternatively, perhaps this trait reflects the flight pattern of the subspecies (Haverty et al. 2003, *Reticulitermes* sp.). Both species also exhibit marked differences in their flight strategies. *M. gilvus* spreads its flights out over a long period before dawn (1–2.5 h) in the form of multiple swarms, thus receiving less attention from predators (Robinson 1996); in contrast, *M. carbonarius* flies for a shorter duration (4–10 min) but in massive number; this pattern might increase the possibility of finding a mate.

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 that precludes interbreeding. This phenomenon is not unique, because Darlington (1986) provided evidence of behavioral reproductive isolation between two *Macrotermes* species in Kenya. Viable pairs successfully formed in the laboratory from the cross-breeding of *Macrotermes michaelseni* (Sjöstedt) and *Macrotermes subhyalinus* (Rambur) (Lepage and Darlington 2000) and of *Reticulitermes grassei* Clément and *Reticulitermes santonensis* Feytaud (Clément 1979). Chronological reproductive isolation also was reported for *Cubitermes* sp. (William 1959), *Trinervitermes* sp. (Sands 1965), *Microtermes* sp. (Wood 1981), a hyme-

nopteran (honey bee [*Apis* sp.]) (Koeniger and Wijayagunasekera 1976), and some sympatric ant species (Hölldobler and Bartz 1985). Species-specific sexual communication signals were shown to mediate reproductive isolation between sympatric populations of different species whose flight activities occurred simultaneously (Hölldobler and Carlin 1987, Clément et al. 2001, Peppuy et al. 2004). However, to date, no information is available on pheromone-related reproductive isolation of the two sympatric *Macrotermes*.

The *M. gilvus* and *M. carbonarius* colonies studied herein were located between 4 and 150 m apart. Inoue et al. (2001) found that the total length of passages of *M. carbonarius* ranged from 33.8 to 112.8 m. Acda (2004) reported that foraging territories of *M. gilvus* covered an area of 350 m² and foraging distances were 16–48 m. Because both sympatric species share the same food resources and nesting strategies (Bignell and Eggleton 2000), competition between them is inevitable (Korb and Linsenmair 2001). The disparate flight periods and sexual castes production periods observed in this study suggest that little competition between both the species occurs. The situation creates a niche for colony founding and enables the both species to be successful inhabitants of the same region.

In conclusion, the results of this study showed that the disparate flight patterns exhibited by the two sympatric species act as a means of reproductive isolation. Moreover, environmental parameters are important determinants for flight initiation.

Acknowledgments

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