

Caste Composition and Mound Size of the Subterranean Termite *Macrotermes gilvus* (Isoptera: Termitidae: Macrotermitinae)

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ABSTRACT The colony size and caste composition of different-sized *Macrotermes gilvus* (Hagen) (Isoptera: Termitidae: Macrotermitinae) mounds on Penang Island, Malaysia, were studied. The total number of termite individuals differed significantly among different-sized mounds. Small mounds contained $15,400 \pm 600$ ($n = 3$) individuals; medium mounds contained $33,500 \pm 2,400$ ($n = 3$) individuals; and large mounds contained $61,400 \pm 4,400$ ($n = 3$) individuals. Larvae constituted the largest proportion (42.60%) of the total population, followed by workers (42.19%), soldiers (14.16%), presoldiers (0.71%), and alates (0.34%). Population parameters (i.e., total population, total adult apterous caste, and total juvenile apterous caste) were positively and significantly correlated with mound size (e.g., mound height and mound diameter) and queen weight. Significant correlations also were found between mound parameters and queen weight. The sex ratio of alates was significantly skewed toward females in five of seven colonies. Of 44 colonies surveyed, 13.6% were polygynous and 11.4% were polyandrous. The degree of physogastry of female reproductives in polygynous colonies was lower than that in monogynous colonies. In contrast, there was no significant difference in the mean weight of male reproductives between monoandrous and polyandrous colonies.

KEY WORDS colony size, caste composition, *Macrotermes gilvus*, polyandry, polygyny

Shifting caste composition is widespread in most social insect species because it allows maintenance of colony stability. It is always linked with energy investment devoted to certain caste(s) in response to colony development (Lepage and Darlington 2000). In the colony developing phase, energy is channeled mainly into larval and worker production to increase the workforce for colony maintenance (e.g., brood caring) and construction (e.g., nest expansion and fungus-comb construction). In the colony reproductive phase, a trade-off occurs between the production of alates and soldiers for colony defense during dispersal activity and the production of workers for population growth. Population structure also fluctuates with ecological changes, such as seasonal changes and environmental stresses from competitors, predators, and lack of food resources (Forschler and Townsend 1996). For example, Lepage and Darlington (2000) reported that the proportion of *Macrotermes* spp. soldiers decreased in a dry environment, partly due to resource availability.

In some termite species, multiple functional female reproductives may coexist within a given colony (polygyny). In a polygynous colony, continuous egg pro-

duction by reproductives occurs. Such a situation is warranted in certain extreme circumstances, such as when the queen dies (Darlington 1985). Reproduction rate or egg-laying rate is greater and faster in polygynous colonies compared with monogynous colonies. This is particularly crucial for an incipient colony to ensure its survival (Thorne 1984, Brand et al. 2001). However, the number of reproductives may decline with time as conflicts occur between reproductives trying to gain dominance within a given colony (Neoh et al. 2010).

The fungus-growing termites of the subfamily Macrotermitinae are abundant in Africa and Asia (Roonwal 1970). *Macrotermes gilvus* (Hagen) (Isoptera: Termitidae: Macrotermitinae) is a mound-building termite usually present at the perimeters of buildings and structures; it rarely causes building structural damage, registering 6 and 2% of the total termite infestation in Malaysia and Thailand, respectively (Lee et al. 2007). However, in recent years, *M. gilvus* has gained notoriety as a secondary pest due to the prevalence of *M. gilvus* infestation in houses that have been treated for *Coptotermes* spp. (Rhinotermitidae) by using termite baits (Lee 2002, Lee et al. 2007). Unlike the lower termites, *M. gilvus* does not show much response to termite baits, and to date soil treatments with termiticides might be the only option for managing *M. gilvus* (Lee et al. 2007). The ineffectiveness of baiting sys-

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tems containing chitin synthesis inhibitors to work against *Macrotermes* may in part be due to the developmental pathway of *Macrotermes*, which differs from that of other termites: In *Macrotermes*, the molting process does not occur in the worker stage (Neoh and Lee 2009, Neoh et al. 2011). Thus, in all likelihood, the bait only affects larvae and not workers (Neoh et al. 2011). Detrimental effects of bait on a colony only are expectedly shown if large proportions of larvae or molting-castes are affected. However, little is known about colony size and caste composition of Southeast Asian *Macrotermes* spp. Thus, a fundamental study of *M. gilvus* colony structures is needed to better understand the effects of chitin synthesis inhibitor-based baits on *M. gilvus* colonies.

Colony sizes and caste composition of *Macrotermes* have been reported previously (Table 1). However, the comparability of previous data sets is debatable due to the varying methods used. In this study, we destructively sampled the nests by excavating the whole mound. Data collection based on complete nest excavation is laborious, but it is the most reliable. We also expanded the excavation areas to the termites' major foraging galleries near the nest. Using these data, we compared the colony size and caste composition of *M. gilvus* colonies from different-sized mounds. The relationships between mound parameters, population parameters, and reproductive parameters also were analyzed. The sex ratio of alates was determined based on data obtained from colony sampling and alate sampling during flight activity. Finally, frequency and percentages of polygyny and polyandry in nests of *M. gilvus* were investigated.

Materials and Methods

Termite Sampling. The sampling sites were located on Penang Island, which lies to the north of Peninsular Malaysia. Between December 2009 and December 2010, mounds of *M. gilvus* were sampled at the Minden campus of Universiti Sains Malaysia (USM; 5° 21' N, 100° 18' E). The mounds were classified as small (height, 1–20 cm; diameter, 1–50 cm), medium (height, 21–40 cm; diameter, 51–80 cm), and large (height, 41–60 cm; diameter, 81–120 cm). Three mounds from each category were dissected in this study. Mounds were excavated during morning when the termites were lull in foraging activity; most termites of *Macrotermes* species forage nocturnally (Inoue et al. 2001).

A circular trench was dug around the perimeter of the mound until termites and fungus combs were exposed, and the outer layer of the mound then was removed. The nest was carefully fragmented into manageable pieces. Nest materials and fungus combs that housed the termites were collected and transported back to the laboratory. To ensure the termites were wholly sampled, sampling was conducted over the course of several days. We also sampled from the main foraging galleries of the mound within a 1.4–2.2-m radius. *Macrotermes* construct subterranean foraging tube networks to forage outside their nest (Darlington 1982). In the laboratory, termites were separated from

Table 1. Summary of population size and caste composition of colonies of the genus *Macrotermes* from literature

<i>Macrotermes</i> species	Total pop size	Proportion of termite caste, %							Region	Reference
		Major soldier	Minor soldier	Major worker	Minor worker	Major presoldier	Minor presoldier	Larva		
<i>carbonarius</i>	8,7800 ± 6,900 (n = 4)	1.31	3.39	9.94	20.60	ND ^a	ND	64.76	West Malaysia	Matsumoto (1976)
<i>bellicosus</i>	3,57900 ± 5,4000 (n = 19)	0.65	0.96	10.08	29.53	ND	ND	58.77	Nigeria, West Africa	Collins (1981)
<i>subhyalinus</i>	1,161600 ± 2,24600 (n = 13)	1.18	2.17	21.25	34.34	0.07	0.24	40.75	Kenya, East Africa	Darlington (1990)
<i>michaelseni</i>	2,269600 ± 1,57400 (n = 22)	0.84	1.52	19.2	34.88	0.09	0.36	43.11	Kenya, East Africa	Darlington (1991)
<i>jeanneli</i>	7,77800 ± 2,82400 (n = 7)	1.64	1.59	15.55	24.55	0.21	0.55	55.90	Kenya, West Africa	Darlington et al. (1992)

^a ND, not determined.

nest materials by tapping mound materials onto trays. Termites in soil debris were handpicked with forceps. Termites were sorted into castes (i.e., larvae, major workers, minor workers, major soldiers, minor soldiers, major presoldiers, minor presoldiers, and alates). The sex of alates was determined based on the abdominal sternite structure: in females, the seventh sternite is enlarged and the eighth and ninth sternites are separated, whereas the opposite pattern is present in males (Weesner 1969).

Generally, the royal cell was located 0.25 m below ground level. The royal cells were opened to obtain the royal pair(s), and the number of queens and kings present in the colony was counted. The fresh weight of queens and kings was recorded within 30 min after collection by using an analytical balance (Sartorius AG, Göttingen, Germany).

Additional data from 35 nests examined between January 2007 and December 2009 were combined with the present data to evaluate the relationships between mound parameters and the frequency of polygyny and polyandry in *M. gilvus*. Additional data of light trap alates sampling from four colonies (Neoh and Lee 2008) examined between April 2007 and September 2007 also were combined with the present data to determine the sex ratio of alates.

Data Analysis. The percentages of each caste for different mound sizes and the fresh weight of reproductives from polygynous and monogynous colonies were subjected to square-root arcsine transformation. The transformed values then were analyzed using one-way analysis of variance (ANOVA); means were separated using Tukey's honestly significant difference (HSD) at $\alpha = 0.05$.

Pearson correlation analysis was used to evaluate the relationships between population parameters (i.e., total population, total adult apterous caste, and total juvenile apterous caste), mound size (i.e., mound height and mound diameter), and reproductive (i.e., queen and king) weight, as well as mound parameters and reproductive weight. The chi-square test was used to evaluate whether the sex ratio of alates deviated from 1:1.

Results and Discussion

Population Size. Table 2 shows the population size of *M. gilvus* colonies from different-sized mounds. The total number of termite individuals found in small mounds was $15,400 \pm 600$ (mean \pm SE; $n = 3$), in medium mounds was $33,500 \pm 2,400$ ($n = 3$), and in large mounds was $61,400 \pm 4,400$ ($n = 3$). The total number of termite individuals differed significantly among the three mound sizes ($F = 62.63$; $df = 2, 6$; $P < 0.001$). The population sizes found in this study were lower than those of *M. gilvus* studied in Philippines (0.25–0.46 million foraging individuals per colony) by using the mark–recapture method (Acda 2004). It is likely that the use of mark–recapture method in the latter study has overestimated the population. Evans et al. (1999) claimed that the assumption of the mark–recapture protocol were violated in both field and

Table 2. Characteristics of the nest population of *M. gilvus* from different-sized mounds

Mound size	Mound no.	Adult apterous caste pop (%)			Juvenile apterous caste pop (%)			Alate	Total pop
		Major soldier	Minor soldier	Major worker	Major presoldier	Minor presoldier	Larvae		
Small	1		2,559 (15.42)	3,085 (18.74)	5,099 (30.97)	3 (0.02)	164 (1)	164 (1)	16,462
	2	386 (2.53)	906 (5.94)	2,954 (19.38)	3,885 (25.48)	3 (0.02)	144 (0.94)	144 (0.94)	15,246
	3	295 (2.03)	877 (6.04%)	2,778 (19.14)	3,354 (23.11)	1 (0.01)	85 (0.59)	7121 (49.07)	14,511
Medium	Mean \pm SE	419 \pm 83 (2.69)	1,441 \pm 549 (9.13)	2,939 \pm 89 (19.09)	4,113 \pm 516 (26.52)	2 \pm 1 (0.02)	131 \pm 24 (0.84)	6,361 \pm 685 (41.70)	15,400 \pm 600
	4	297 (0.87)	2,628 (7.70)	6,639 (19.45)	7,460 (21.85)	5 (0.01)	144 (0.42)	16,965 (49.70)	34,138
	5	359 (0.96)	3,805 (10.20)	7,821 (20.97)	6,919 (18.55)	27 (0.07)	289 (0.77)	17,450 (46.79)	37,297
Large	6	820 (2.83)	2,331 (8.04)	4,989 (17.20)	6,028 (20.78)	6 (0.02)	192 (0.66)	14,638 (50.47)	29,004
	7	1,780 (2.59)	12,355 (17.96)	12,565 (18.26)	19,604 (28.50)	70 (0.10)	609 (0.89)	21,720 (31.57)	33,480 \pm 2,417
	8	1,562 (2.92)	5,320 (9.94)	6,079 (11.36)	11,684 (21.84)	4 (0.01)	211 (0.39)	28,237 (52.78)	68,798
Mean \pm SE of all mound types	9	1,610 (2.60)	8,410 (13.57)	11,540 (18.62)	17,126 (27.64)	20 (0.03)	375 (0.61)	22,880 (36.93)	53,499
	Mean \pm SE	1,651 \pm 66 (2.70)	8,695 \pm 2,036 (13.82)	10,061 \pm 2,013 (16.08)	16,138 \pm 2,339 (26.00)	31 \pm 20 (0.05)	398 \pm 115 (0.63)	24,279 \pm 2,007 (40.43)	61,419 \pm 4,425
	SE	854 \pm 207 (2.32)	4,352 \pm 1,270 (11.84)	6,494 \pm 1,205 (17.66)	9,018 \pm 1,952 (24.53)	15 \pm 7 (0.04)	246 \pm 54 (0.67)	1,5664 \pm 2,675 (42.60)	3,6768 \pm 6,851

Numbers in parentheses are caste proportions of total mound population.

Table 3. Regression equations associated with population parameters, mound parameters, and reproductive parameters

X	Pop parameter (y)		
	Total pop	Total adult apterous caste	Total juvenile apterous caste
Mound ht	$y = 1261x + 66, 0 < x < 60; r = 0.968^a$	$y = 775x - 1847, 3 < x < 60; r = 0.900^a$	$y = 480x + 1939, 0 < x < 60; r = 0.933^a$
Mound diam	$y = 586x - 4608, 20 < x < 120; r = 0.966^a$	$y = 354x - 4323, 20 < x < 120; r = 0.883^a$	$y = 229x - 261, 20 < x < 120; r = 0.955^a$
Queen wt	$y = 19806x - 4889, 0.5 < x < 3.5; r = 0.795^a$	$y = 13139x - 6917, 0.5 < x < 3.5; r = 0.797^a$	$y = 6622x + 1997, 0.5 < x < 3.5; r = 0.672^a$
King wt	$y = 1672737x - 76439, 0.05 < x < 0.08; r = 0.679^a$	$y = 1054215x - 50629, 0.05 < x < 0.08; r = 0.647$	$y = 620613x - 26077, 0.5 < x < 0.08; r = 0.638$
Queen wt	Mound ht $y = 4.67x + 19.21, 0.8 < x < 5.5; r = 0.389^a$	Mound diam $y = 6.25x + 68.05, 0.8 < x < 5.5; r = 0.212$	

^a A significant correlation was found at $\alpha = 0.05$.

laboratory test and could overestimate the population size as the studies found that the foraging population of *Coptotermes acinaciformis* (Froggatt) was 10-fold larger than the actual population in the nest by using direct counting. Matsumoto (1976) reported that populations of *Macrotermes carbonarius* (Hagen), a predominant species in Southeast Asia, consisted of $87,800 \pm 6,900$ ($n = 4$) individuals. *Macrotermes* spp. from Africa have larger population sizes compared with *Macrotermes* spp. from Southeast Asia (Table 1). For example, mounds of *Macrotermes subhyalinus* (Rambur) and *Macrotermes michaelseni* (Sjostedt) in Kenya were estimated to contain $1,161,600 \pm 224,600$ ($n = 13$) and $2,269,600 \pm 157,400$ ($n = 22$) termite individuals, respectively (Darlington 1990, 1991).

Colony Composition. Workers. In all but one of the mounds sampled, minor workers outnumbered major workers at a ratio of 1.4:1. Darlington (1990) also reported a minor: major worker ratio of 1.5:1 for *M. subhyalinus*. In contrast, *M. carbonarius* and *Macrotermes bellicosus* (Smeathman) colonies were reported to contain a ratio of 2.1:1 and 2.9:1, respectively (Matsumoto 1976, Collins 1981). Overall, workers constituted $\approx 42.19\%$ of the total population, and this value was the same regardless of mound size ($F = 1.076$; $df = 2, 6$; $P > 0.05$). Matsumoto (1976) found that workers only constituted $\approx 30.54\%$ of the total population of *M. carbonarius*. In contrast, the proportion of workers in *M. michaelseni* (54.08%) and *Macrotermes natalensis* (Haviland) (54.61%) populations was higher than that obtained in our study (Darlington 1991, Meyer et al. 2000).

Soldiers. In this study, minor soldiers outnumbered major soldiers by a 5.1:1 ratio. Rohrmann (1977) recorded a higher ratio of minor soldiers to major soldiers (12.1:1) in *Macrotermes ukuzii* (Fuller) colonies. In contrast, Meyer et al. (2000) found that *M. natalensis* colonies had more major soldiers than minor soldiers (2.5:1). In *Macrotermes jeanneli* (Grasse) colonies, the number of minor soldiers and major soldiers was almost equal (minor soldiers: major soldiers = 1.02:1) (Darlington et al. 1992). Overall, soldiers constituted $\approx 14.16\%$ of the total population in the current study. Noirot and Darlington (2000) reported that the proportion of soldiers in a population varies greatly

among species. For example, Meyer et al. (2000) reported that soldiers constituted $\approx 54.61\%$ of the total population of *M. natalensis*, whereas the proportion of soldiers in *M. bellicosus* and *M. jeanneli* populations was only 1.61 and 3.23%, respectively (Collins 1981, Darlington et al. 1992). Darlington (1990) found a higher proportion of soldiers in small mounds in *M. subhyalinus*. However, in our study no significant difference in soldier proportion was detected among the different-sized mounds ($F = 1.77$; $df = 2, 6$; $P > 0.05$). Presoldiers constituted $\approx 0.71\%$ of the total population.

Larvae. The mean percentage of larvae in smalls mound was $41.70 \pm 5.76\%$, in medium mounds the value was $48.99 \pm 1.12\%$, and in large mounds it was $40.43 \pm 6.37\%$. Proportions of larvae in different sized mound did not significantly differ ($F = 0.85$; $df = 2, 6$; $P > 0.05$). Overall, larvae constituted $\approx 42.60\%$ of the total population. This proportion was parallel to that reported for *M. michaelseni* (43.11%) (Darlington 1991). However, the proportion of larvae found in this study was lower than that of *M. gilvus* in Vietnam (51.13%) (Belyaeva and Tiunov 2010) and of *M. carbonarius* (64.76%) in West Malaysia and *M. bellicosus* (58.77%) in Nigeria (Matsumoto 1976, Collins 1981).

Alates. Overall, alates constituted $\approx 0.34\%$ of the total population. We found alates in three of the nine colonies sampled (Table 2).

Relationship Between Mound Parameters and Population Parameters. Height and diameter of mounds were significantly correlated with all of the population parameters measured (Table 3). These results agree with most previous studies (e.g., nest population of *M. michaelseni* was linearly related to mound dimensions) (Darlington and Dransfield 1987, Lepage and Darlington 2000). Mound size regulation is a significant adaptation to social life in an enclosed nest. It is crucial to promote microclimate stability in a termite nest as the number of termites in the population increases, and stability is maintained by enhancing gas diffusion and gas convection in the mound (Darlington and Dransfield 1987, Josens and Soki 2010).

Relationship Between Reproductive Weight and Population Parameters. The queen's weight was significantly correlated with all of the population param-

Table 4. Numbers and sex ratio of *M. gilvus* alates

Colony	<i>n</i>	Ratio (♂:♀)
5	627	1:1.31 ^a
7	95	1:1.02
8	402	1:1.48 ^a
F1	39	1:2.53 ^a
F2	1,054	1:3.62 ^a
F3	70	1:6.00 ^a
F4	312	1:0.88

Data for colonies F1–F4 were adopted from Neoh and Lee (2008).

^a Sex ratio was significantly skewed from the expected ratio of 1:1 ($P < 0.05$; χ^2 test).

eters studied (Table 3). Adams and Atkinson (2007) reported that the reproductive output of a female reproductive is strongly associated with the queen weight increment (i.e., the degree of physogastry). Roisin and Pasteels (1986b) found a correlation between mean egg-laying rate and mean weight of the queen in *Nasutitermes princeps* (Desneux). In the current study, the king's weight also was significantly, but weakly, correlated with total population size ($r = 0.675$, $P < 0.05$) (Table 3). The results indicate that the weights of female and male reproductives reflect colony age. This allows extrapolation of a colony's age based on mound dimensions and king and queen weight.

Relationship Between Reproductive Weight and Mound Parameters. Mound diameter was significantly, but weakly, correlated with queen weight ($r = 0.297$, $P < 0.05$) (Table 3). This result contrasts with study of *M. gilvus* conducted in Thailand (Inoue et al. 1997). No significant correlation between king weight and mound height ($r = 0.053$, $P = 0.737$) or mound diameter ($r = 0.030$, $P = 0.851$) was detected.

Sex Ratio of Alates. As a rule, the sex ratio is consistently equal in insects (Fisher 1930). However, if production of males and females incurs different costs, the sex ratio tends to deviate from 1:1. An asymmetric proportion of male and female alates is common in termite colonies (Nutting 1969), because rearing female alates is more energetically costly (Thorne 1983) as female alates tend to be larger than male alates; this is particularly true in *Macrotermes* (Neoh and Lee 2009). Thorne (1983) reported that the sex ratio was skewed toward male alates in *Nasutitermes corniger* (Motschulsky) colonies. Sexual size dimorphism also was reported in *Mastotermes darwiniensis* (Froggatt) colonies, where male alates weighed less than female alates. In that study, there was a slight but significantly higher ratio of male alates collected compared with the female alates (1.1:1) (Nalepa et al. 2001).

Based on previous studies, a male-skewed sex ratio was expected in this study. However, the sex ratios were significantly skewed toward female alates in five of seven colonies (Table 4). In termites, the phenomenon of a female-biased sex ratio is rare. However, it also was reported in *Coptotermes formosanus* (Shiraki), for which the sex ratio was significantly biased in favor of females (χ^2 (1, $n = 21,715$) = 55.42, $P < 0.001$) (Henderson and Delaplane 1994).

Polygyny, Polyandry, and Association With Fresh Weight of Reproductives. Of the 44 *M. gilvus* colonies surveyed, six were polygynous (13.6%) and five were polyandrous (11.4%). Monogynous colonies accounted for 86.4% of the total mounds sampled. In most instances, multiple kings were only present in polygynous colonies.

Polygyny is more common than polyandry in higher termites (Thorne 1984; Darlington 1987, 1988). For example, Darlington (1985) found that 23.3% of *M. michaelseni* nests had multiple queens, whereas only 5.3% of nests had multiple kings ($n = 361$). Similarly, in *Nasutitermes costalis* (Holmgren), all colonies sampled were polygynous (100%, $n = 14$), whereas only 71% of these colonies were polyandrous (Roisin and Pasteels 1986a). According to Hacker et al. (2005), in newly developed polygynous colonies, intraspecific aggression occurs between young queens up to the stage when they become physogastric. Such encounters might then cease due to immobility. In contrast, young kings remain mobile throughout their life span and may continue to compete with each other until only one survives.

There are two mechanisms by which polygyny can occur in *Macrotermes*: pleometrosis and reproductive replacement. In pleometrosis, it is possible that multiple pairs of alates commence breeding and cooperatively found the colony (Thorne 1984). This premise is supported by Hacker et al. (2005), who found that queens in a polygynous *M. michaelseni* colony were unrelated. Reproductive replacement generally occurs if the primary reproductives weaken or die. In *Macrotermes*, numerous replacement reproductives that originate from alates that are retained in the parental colonies (adultoids) are formed upon the death of primaries (Darlington 1985, Neoh et al. 2010). However, the number of replacement reproductives may decrease with time due to conflicts between reproductives (Neoh et al. 2010).

Figure 1 shows that the degree of physogastry of queens in monogynous colonies was highly variable compared with that in polygynous colonies, whereas queens in polygynous colonies were relatively constant in weight. Mean weight (\pm SD) of monogynous queens (2.3732 ± 1.0733 g) was significantly higher than that of polygynous queens (1.2978 ± 0.4296 g) ($F = 14.92$; $df = 1, 52$; $P < 0.01$). These results agree with observations of *M. michaelseni* made by Kaib et al. (2001). Results of other studies showed that the mean weight of female reproductives was inversely correlated with the number of female reproductives present in the royal cell (Thorne 1984; Roisin and Pasteels 1986a,b; Adams and Atkinson 2007). This phenomenon may occur because of competition between the royal pairs being attended by workers for food (Roisin and Pasteels 1986b, Kaib et al. 2001). Roisin and Pasteels (1986b) postulated that mean weight of queens depends on the extent of care provided by the worker caste. Roisin and Pasteels (1986a) also stated that inhibitory hormones in queens may play a role in impeding growth of other queens in the same royal cell.

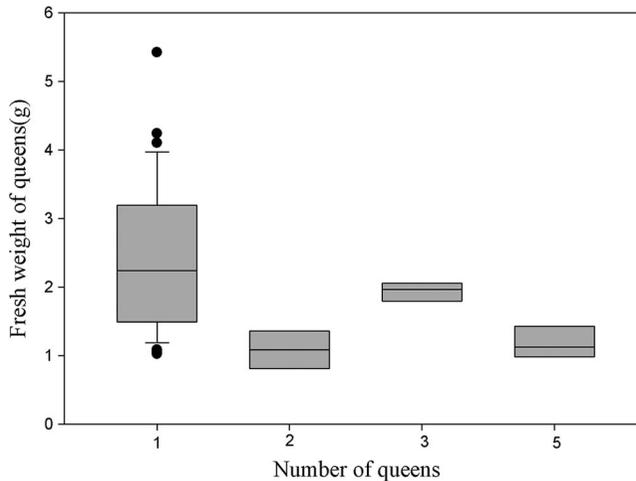


Fig. 1. Box and whisker plots of fresh weight of queens present in monogynous and polygynous colonies. Horizontal bars indicate median values, boxes show the lower and upper quartiles of the data sets, and outliers are represented by solid circles.

Mean weights of kings in monoandrous and polyandrous colonies did not differ significantly ($P > 0.05$). Mean weight of kings in monoandrous colonies was 0.0696 ± 0.0013 g ($n = 38$), and the mean weight of polyandrous kings was 0.0687 ± 0.0017 g ($n = 11$). This result is similar to that reported by Darlington (1985) for *M. michaelsoni*. This indicates that the development of male reproductive(s) is not affected by the presence of multiple reproductives in the royal cells.

In summary, the present results demonstrated the colony size across varying sizes of *M. gilvus* mound. Larva caste was the most abundant in number in the termite colony followed by those of the workers, soldiers, and presoldiers. We found that the mound parameters, reproductive weight, and the population size were interrelated. This suggests that those mound parameters could be surrogate in estimating one colony age. Interestingly, unlike most of the termite species, sex ratios of *M. gilvus* significantly skewed toward female alates. Evidently, this might increase the chance for males in finding females during swarming activity. Together with the existence of multiple reproductives in a colony (polygyny), this could be regarded as an adaptive strategy in ensuring colony foundation success.

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