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Source: Journal of Economic Entomology, 104(2):622-628. 2011.

Published By: Entomological Society of America

URL: <http://www.bioone.org/doi/full/10.1603/EC10346>

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Developmental Stages and Caste Composition of a Mature and Incipient Colony of the Drywood Termite, *Cryptotermes dudleyi* (Isoptera: Kalotermitidae)

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J. Econ. Entomol. 104(2): 622–628 (2011); DOI: 10.1603/EC10346

ABSTRACT The caste composition and sex ratio in a mature and an incipient colony of *Cryptotermes dudleyi* Banks (Isoptera: Kalotermitidae) was studied. Biometric descriptors of both immature and sexual castes were developed. Morphometric analysis revealed that there are four larval instars, a pseudergate, and three nymphal instars in the development of *C. dudleyi*. To differentiate between the fourth larval instars and the pseudergate, pronotal width and tibial length must be taken into account, because the head width overlaps between the two groups. The number of antennal segments increases in parallel with instar development. The mature colony was headed by a pair of physogastric nymphoid neotenic; the colony also contained multiple pairs of nonphysogastric de-alates and wing-torn alates. The majority of eggs and larvae were confined to galleries that connected to locations where nymphoid neotenic were found, whereas in general only pseudergates and nymphs were found together with de-alates and wing-torn alates. In contrast, the incipient colony contained only a pair of primary reproductives. Nymphs formed a major group in both mature and incipient colonies, as did pseudergates. The sex ratio of the mature colony was slightly but significantly biased in favor of females, whereas it was skewed toward males in the incipient colony. The data also suggested that the soldier caste was female skewed.

KEY WORDS *Cryptotermes*, sex determination, de-alates, nymphoid, sex ratio

Cryptotermes dudleyi Banks (Isoptera: Kalotermitidae) is the most widespread *Cryptotermes* species after *Cryptotermes brevis* (Walker). This species is believed to have originated from the Indo-Malayan region and was then introduced to the Neotropical, Australian, Papuan, Ethiopian, and Malagasy regions, possibly via human activities (Gay 1967). In Asia, the species is abundant in India, Sri Lanka, Bangladesh, Indonesia, the Philippines, Borneo, and Peninsular Malaysia. *C. dudleyi* is a common pest of timber (Roonwal 1970), and it is infamous for the damage to building structures in Sri Lanka and Brazil (Roonwal 1970, Constantino 2002). Chhotani (1970) and Scheffrahn and Krecek (1999) have described in detail the morphology of soldier and imago stages of *C. dudleyi*. *Cryptotermes* can be readily distinguished from the other two dominant genera in Southeast Asia (i.e., *Neotermes* and *Glyptotermes*) (Tho 1992) because its soldiers have a distinct vertical vertex at the front of the head. In addition, the anterior region of the pronotum has a saw-toothed appearance (Thapa 1977).

Like all members of the family Kalotermitidae, *Cryptotermes* species follow a central (linear) devel-

opmental pathway, which is characterized by seven successive molts leading from the first larval instar to the alate (Roisin 2000). However, development is highly flexible; after reaching the fourth larval instar stage, an individual may undergo a combination of progressive, stationary, or regressive molts to become a nymph, a neotenic reproductive, or a soldier (Roisin 2000) in response to environmental conditions (Korb and Lenz 2004) and colony-level conditions (Lenz et al. 1982, Luykx 1986). Indirectly, this flexibility may result in a caste composition shift and a sex ratio skew within a given colony (Luykx 1986, Maistrello et al. 2010).

Recently, we surveyed several buildings located in the coastal area of northern Peninsular Malaysia and found them to be heavily infested with *C. dudleyi*. Because limited information is available about this species, we opted to investigate the infestation in these buildings in greater detail. Here, we provide detailed biometric descriptors of both immature and sexual castes of *C. dudleyi*. We also collected all individuals from a mature and an incipient colony and analyzed them for colony composition and sex ratio. The significance of these findings on the management of drywood termites is discussed.

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Materials and Methods

Specimen Collection. One large *C. dudleyi* colony and one small *C. dudleyi* colony (hereafter designated as mature colony and incipient colony, respectively) were collected from wooden bunk beds in the student dormitories of the Centre for Marine and Coastal Studies, Universiti Sains Malaysia, located in Penang National Park, Telok Bahang, along the northwest coast of Penang Island (5° 28' N, 100° 11' E) in November 2009. The colonies were found infesting the bed base (180 by 90 by 1.5 cm) of the bunk beds in the dormitories. In both cases, the entire colony was preserved in 70% ethanol and brought back to the laboratory. The termites were identified using the keys of Tho (1992) and Scheffrahn and Krecek (1999).

Morphometric Measurements. In total, 128 individuals were randomly picked from the mature colony and measured. The termites were observed using an SZ61 stereomicroscope (Olympus, Tokyo, Japan) equipped with IC Imaging Standard, version 2.1 (The Imaging Source Europe GmbH, Bremen, Germany) and measured using Analysis Image Processing software (Soft Imaging System GmbH, Münster, Germany). Measurements were made of the following parts of the termite (Neoh and Lee 2009): head width, pronotal width, pronotal length, and hind tibial length. In addition, in nymphs, mesonotal and metanotal wing segments length were defined as the distances between the posterior margin of the mesonotum and metanotum to the tip of the wing bud, respectively. We also recorded the number of antennal segment present on each instar. We noted the fully developed antennal segments as well as the segments that were incompletely formed (especially in the active growth region) (e.g., eight segments with an incomplete segment were indicated by 8⁺) (see Neoh and Lee 2009).

Morphometric data were analyzed using discriminant analysis (SPSS, version 11.0, SPSS Inc., Chicago, IL) to assign a weight to each variable measured and to evaluate relationships among the groups with different development stages.

Caste Composition. All the samples of mature ($n = 3,893$) and incipient colony ($n = 56$) were classified into different stages based on the parameter measured in the current study.

Sex Determination. Sex determination was conducted based on the structures of the abdominal sternites (Fig. 1) as described in Luykx (1986). For each colony, all of the samples (mature colony, $n = 3,538$; incipient colony, $n = 51$) were sexed except for the first and second larval instars, for which the observed structure is indistinguishable. We tested the null hypothesis that the overall colony and different castes within a colony have equal sex ratios ($\varphi:\delta = 1:1$) by using the chi-square test (SPSS, version 11.0).

Results

Morphometric Study. Table 1 shows the measurements and the number of antennal segments of larvae (L1-L4), the pseudergate (Ps), and nymphs (N1-N3)

of *C. dudleyi*. The canonical discriminant function of the caste system shows two major directions of variability (Fig. 2). The first discriminant function, which accounted for 69.7% of the total variance (eigenvalue, 40.209), is highly correlated with head width. Thus, the head width represents a reliable parameter for distinguishing among the first four larval instars. However, relying solely on head width is insufficient for differentiating between groups L4 and Ps, because these two groups did not separate well in the discriminant graph (Fig. 2). Other parameters must be used to distinguish between these two groups. In fact, these groups are most heavily weighted on the width of the pronotum and the length of the hind tibia. In addition, L4 seems to be poorly pigmented and Ps is well sclerotized.

The second discriminant function, which accounted for 29.2% of the total variance (eigenvalue, 16.838), isolated nymphs into three groups. These groups can be differentiated from one another based on the pronotal length and the development of the wing buds.

Caste Composition. In total, 3,893 and 56 termite individuals were collected from the mature and incipient colonies, respectively. The mature colony was headed by a pair of neotenic (i.e., nymphoid neotenic derived from N2s). Nymphs were the major group among the termite individuals populating the mature colony; they accounted for 76.2% of the population (N1 = 16.7%, N2 = 55.8%, N3 = 3.7%). Larvae (L1 = 3.7%, L2 = 3.5%, L3 = 4.5%, L4 = 2.3%), pseudergates, and soldiers constituted 14.0, 7.0, and 2.0% of the population, respectively (Fig. 3). We also found 33 de-alates (alates that possess a pair of torn wings and have no wings) (0.8%) distributed in the wooden bunk bed.

The incipient colony was headed by a pair of primary reproductives. The incipient colony consisted of 42.6% pseudergates and 44.4% nymphs (N1). Only six L3s (11.1%) and one soldier (1.9%) were found in the colony (Fig. 3).

Sex Ratio. In general, the sex ratio in the mature colony was male biased ($\chi^2 [1, N = 3,538] = 7.602, P < 0.05$), whereas the incipient colony was skewed toward females ($\chi^2 [1, N = 51] = 5.667, P < 0.05$). However, the sex ratio varied among the specific castes in the mature colony. For example, an excess number of males was present among the second nymphal instars ($\chi^2 [1, N = 2,190] = 14.795, P < 0.05$) and pseudergates ($\chi^2 [1, N = 251] = 9.566, P < 0.05$). In contrast, the soldier caste was female skewed ($\chi^2 [1, N = 78] = 34.667, P < 0.05$) (Table 2).

Discussion

The general acceptability of using head width as a reliable variable for identification of termite instar stage (e.g., Roisin and Pasteels 1991, Neoh and Lee 2009) contrasts with the measurements made for L4s and pseudergates in the current study. We found that the head width measurement overlapped between the two groups. Thus, our data strongly suggest that ad-

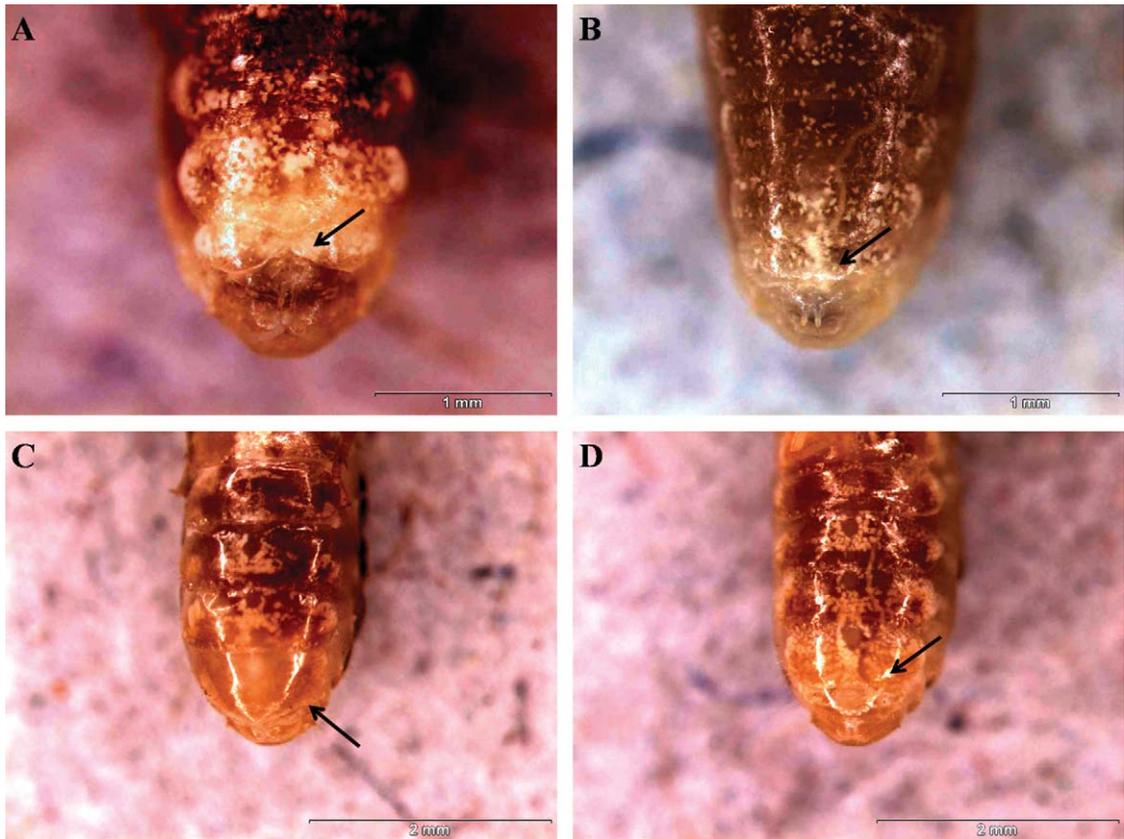


Fig. 1. Sex of members of various castes of *C. dudleyi* was determined based on the abdominal sternite structures (arrows). In the pseudergate, larvae, and nymphs, a notch is present at the posterior margin of the ninth abdominal sternite in females (A), whereas the posterior margin of the ninth abdominal sternite is smooth in males (B). In soldiers and reproductives, the seventh abdominal sternite is enlarged and enclosed the eighth and ninth sternite in females (C); in males (D), the seventh sternite is not enlarged and the eighth and ninth sternites are not enclosed. (Online figure in color.)

ditional variables (i.e., pronotal width and tibial length) must be taken into account to differentiate the two groups. We also found that the number of antennal segments increases in parallel with instar development (Table 1), and this relationship may prove to be a helpful tool to cross-check instar classification. However, the antennae of some specimens may be damaged due to agonistic interaction (Korb 2005), so this parameter must be used with caution.

To date, the classification of developing instars in the genus *Cryptotermes* has not been consistent. For example, *C. secundus* was assigned three larval stages and five nymphal stages throughout its developmental pathway (Korb and Katrantzis 2004, Korb et al. 2009). In contrast, Crosland et al. (2004) sorted *C. cavifrons* into four larval instars and three nymphal instars. Our current study and previous classifications of other drywood termite genera (e.g., *Neotermes papua* [Roi-

Table 1. Range and mean (in parentheses) of measurements of larval instars (L1–L3), pseudergate (Ps), and nymphs (N1–N3) of *C. dudleyi* (in millimeters)

	No. antennal segments	Max. head width	Pronotal width	Pronotal length	Mesonotal wing bud length	Metanotal wing bud length	Hind tibial length
L1 (n = 11)	6 ⁺ ,7 ⁺	0.38–0.59 (0.42)	0.36–0.46 (0.42)	0.13–0.17 (0.15)			0.17–0.26 (0.22)
L2 (n = 14)	7 ⁺ ,8 ⁺	0.60–0.80 (0.64)	0.50–0.63 (0.56)	0.18–0.23 (0.20)			0.28–0.34 (0.31)
L3 (n = 10)	8 ⁺ ,9 ⁺	0.81–0.90 (0.86)	0.69–0.74 (0.71)	0.26–0.34 (0.31)			0.35–0.45 (0.39)
L4 (n = 10)	9 ⁺ ,10 ⁺	0.93–1.11 (1.02)	0.75–0.90 (0.82)	0.35–0.41 (0.38)			0.45–0.57 (0.50)
Ps (n = 10)	9 ⁺ ,10 ⁺	1.03–1.15 (1.06)	0.87–1.00 (0.92)	0.39–0.49 (0.42)			0.59–0.70 (0.64)
N1 (n = 20)	10 ⁺ ,11 ⁺	0.96–1.24 (1.13)	0.79–1.24 (0.99)	0.33–0.82 (0.51)	0.07–0.20 (0.16)	0.04–0.19 (0.14)	0.46–0.77 (0.63)
N2 (n = 43)	11 ⁺ ,12 ⁺	1.07–1.31 (1.18)	0.93–1.19 (1.07)	0.41–0.69 (0.55)	0.21–0.40 (0.27)	0.21–0.41 (0.25)	0.45–0.83 (0.68)
N3 (n = 10)	12 ⁺ ,13 ⁺	1.11–1.23 (1.16)	1.03–1.14 (1.08)	0.44–0.61 (0.54)	0.65–0.88 (0.73)	0.65–0.92 (0.81)	0.56–0.88 (0.73)

n⁺, n segments and an incomplete formed of antenna.

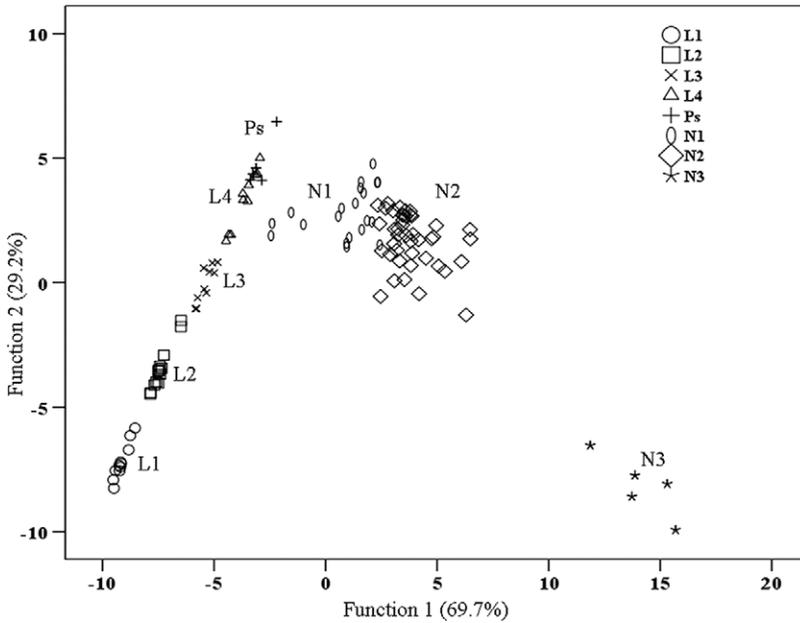


Fig. 2. Canonical discriminant functions of the castes of *C. dudleyi*.

sin and Pasteels 1991], *Incisitermes schwarzi* [Luykx 1986], and *Kaloterms flavicollis* [Maistrello et al. 2010]) agree with the latter classification.

In our study, the mature colony was headed by a pair of physogastric nymphoid neotenic. Multiple pairs of nonphysogastric de-alates and wing-torn alates were scattered in the wooden bunk bed from which the colony was collected. The majority of eggs and larvae were confined to the galleries that connected to locations where the nymphoid neotenic were found, whereas in most instances, only pseudergates and nymphs were found together with de-alates and wing-torn alates. In all likelihood, the de-

alates may have simply budded from the parental colony (that contained nymphoid neotenic) and started their own colony in the same piece of wood (see Roonwal 1970). López et al. (2006) explained this scenario as a result of the failure of alates to disperse for colony foundation and thus be retained in the parental colony.

The nymphs constituted the major group in the drywood termite colonies that we studied. This implies that nymphs are important in colony labor (e.g., proctodeal feeding and allogrooming) (Cabrera and Rust 1999, Crosland et al. 2004) and colony fitness. Pseudergates constituted the second major group in

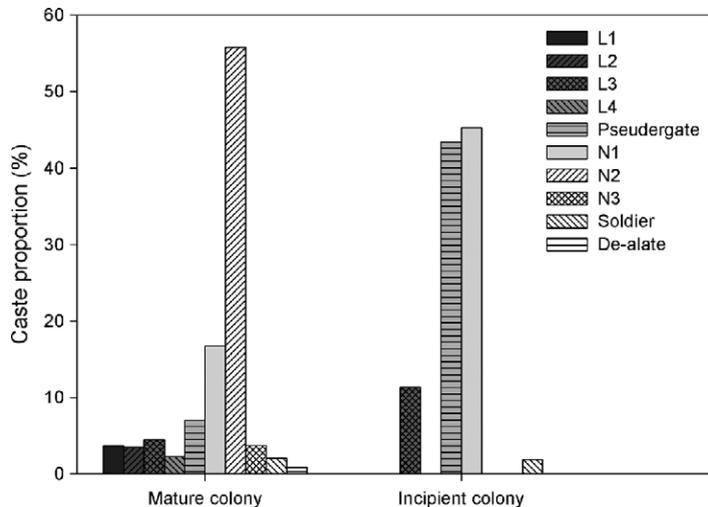


Fig. 3. Caste composition in a mature and an incipient colony of *C. dudleyi*.

Table 2. Sex ratio in castes of *C. dudleyi*

	♀:♂ ratio	
	Mature colony	Incipient colony
L3	1:1	1.5 ^a
L4	1:1	
Pseudergate	1:1.49 ^b	1:1.86
N1	1:1	1:1.67
N2	1.18:1 ^b	
N3	1.04:1	
De-alate	1.29:1	
Soldier	5:1 ^b	— ^c
Total	1.10:1 ^b	1:2 ^b

^a χ^2 test was not attempted because the assumption of size of expected frequencies was violated.

^b Sex ratio was significantly skewed from the expected ratio of 1:1 ($P < 0.05$; chi-square).

^c Sex ratio was not generated because only one female soldier was present in the incipient colony.

the colonies. Pseudergates rarely contribute to colony labor (e.g., brood care and colony maintenance) (Maistrello and Sbrenna 1996, Korb 2007) and only engage in tasks that are less costly. However, they play a major role in sexual caste differentiation (i.e., totipotency) (Korb 2007). Even so, caste composition in drywood termites may be variable throughout a period of time. Several alternative factors may account for the fluctuation: 1) Environmental condition. According to Korb and Katrantzis (2004), the number of helpers (immature castes) and dispersing termites (sexual castes) in a *C. secundus* colony is influenced by environmental conditions (e.g., food availability). The colony caste ratio shifted to dispersing castes during periods of food shortage or when the nest longevity decreased (Korb and Lenz 2004, Korb and Schmidinger 2004). Besides, in nature, all termites show annual fluctuations of nymphs and alates. For example, Maistrello et al. (2010) reported that the colony composition of *Kaloterms flavicollis* fluctuates seasonally. A large proportion of larvae (including eggs) were present in the colony during winter, but from spring to summer and autumn, numerous nymphs and alates were formed. 2) Colony-level condition. Fewer dispersing sexuals were produced in soldier-less colonies (Roux and Korb 2004). Also, in an inbred colony with high kin relatedness, the individuals preferred to remain as helpers rather than disperse from the parental colony (Korb and Schneider 2007). These situations may indirectly lead to caste composition fluctuation within a colony.

The sex ratio of the mature colony was significantly biased in favor of females. This finding is in contrast to reports about the lower termites *C. domesticus* (Muller and Korb 2008) and *Reticulitermes flavipes* (Dean and Gold 2004), which displayed an equal sex ratio. We also found that the pseudergate composition in the mature colony was biased toward males, whereas it was the opposite for the nymphs. Luykx (1986) reported that a sex ratio skew can be attributed to changes in the sex ratio within a certain caste. Thus, if there is a significant decrease in the number of female pseudergates in the colony, it will be balanced

by a significant excess of females among the nymphs. However, this assertion was disproved by Muller and Korb (2008), who found no correlation between the sex skew in soldiers and the sex ratio in other castes. Our data also demonstrate that the incipient colony was skewed toward males. The difference between the incipient and mature colonies probably reflects the underlying colony energy investment. Male progeny are less expensive compared with female progeny (Thorne 1983). Thus, in the incipient colony a male investment probably is favored because it would allow energy mainly to be channeled toward rearing the young and foraging for food. At present, we are unable to draw any firm conclusions, but we propose that sex ratio probably varies in response to the developmental phase of a given colony. Regardless, further studies are warranted.

In termites, the sex ratio of soldiers often is female biased (Dean and Gold 2004, Matsuura 2006, Muller and Korb 2008, Kitade et al. 2010). In the mature colony, the number of female soldiers present was five-fold higher than the number of male soldiers and one female soldier was found in the incipient colony. Matsuura (2006) used *Reticulitermes* as a model to study the sex allocation in soldiers and found that sexual size dimorphism and a size threshold for soldiers are linked to skewed sex ratios. This suggests that female soldiers, which have a larger head size, are favored in colony defense. However, this hypothesis does not fit our data because *Cryptotermes* does not show sexual size dimorphism. Muller and Korb (2008) later proved that both sexes of *C. secundus* differed significantly in passive behavior (i.e., being groomed). In this context, it was speculated that females that are more attractive (i.e., that are groomed more frequently) are predetermined to develop into soldiers, as soldier development is regulated endocrinologically via allogrooming (Korb et al. 2003, Korb et al. 2009).

Management strategies such as the use of heat, cold shock, microwaves, electrocution treatment and fumigation show promising outcomes (Lewis and Haverty 1996), but these measures are less applicable in treating infestation sites that encompasses larger areas (e.g., wood pillars and floors). Among the available strategies, chemical localized injection is still the most common approach used in drywood termite management program. The use of slow-acting insecticide (e.g., spinosad) that allows the toxicant to be transferred to other nestmates by poisoned individuals via grooming and eventually resulting in the elimination of the colony, is a preferred option (Ferster et al. 2001). Despite this, treatment with slow-acting toxicants sometimes gave inconsistent results. Woodrow et al. (2006) only recorded moderate mortality rate (≈ 50 –60%) on *Cryptotermes brevis* (Walker) in hard-wood shipping pallets treatment. The fragmented distribution of termites as recorded in our study may explain why there was high variability of success rate in the previous studies (Woodrow et al. 2006, Woodrow and Grace 2007). For example, in current study, we found that 33 de-alates/torn-wing alates (≈ 15 pairs

of potential reproductive) patchily spread in the single piece of wood bed bunk. If the toxicant failed to reach the isolated groups of termites, the remaining pairs of nonphysogastric de-alates/torn wing alates remain unaffected and commence breeding.

The condition is further complicated by the complex gallery system that challenges the effective penetration of toxicant from one gallery to another. Similar observation was made in our study and those that have been reported by Grace et al. (2009). The combinations of the patchy distribution of the insects and the extensive gallery systems have made management of drywood termites difficult. Such situation often leads to excessive use of toxicant due to multiple localized injections in the infested site. A low-toxic strategy such as the use of bait would be ideal. Previously, Indrayani et al. (2008) used a baiting strategy with hydramethylen bait toward *Incisitermes minor* (Hagen). However, this study only registered moderate success with 60–85% mortality rate due to bait avoidance response. More studies on the choice of bait toxicant, bait matrix and placement techniques are warranted and should be undertaken in future.

Acknowledgments

We thank K. H. Quah (formerly of Universiti Sains Malaysia) and B. T. Forschler (University of Georgia) for technical assistance and Khairun Yahaya (Center for Marine and Coastal Studies, Universiti Sains Malaysia) for permission to sample at the student dormitories. K.B.N. was supported under a postdoctoral fellowship from Universiti Sains Malaysia. The work reported here was partially funded by Dupont Professional Products, Wilmington, DE.

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Received 18 September 2010; accepted 16 January 2011.
