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Seasonal patterns in the activity and species richness of surface-foraging termites (Isoptera) at paper baits in a tropical Australian savanna

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Abstract: The species present, and the frequencies and intensities of termite attack on 600 paper baits exposed at the soil surface were compared over three seasonal exposures and between two savanna sites of contrasting vegetation structure in northern Australia. Eleven species were recorded, with *Microcerotermes nervosus* and *Schedorhinotermes actuosus* comprising 43% and 27% of collections respectively. The most commonly sampled species nest underground or build epigeal mounds and are known to feed on sound and decaying wood. Changes in species dominance occurred between seasons and the two forest types. In both vegetation types, the number of species active and the frequency of attack increased with the duration of bait exposure and decreased in the order: transitional > wet > dry. Bait consumption was greater in the site with higher canopy cover, and did not differ significantly between seasons. No direct relationships were noted between rainfall recorded at the sites and species richness, frequency and intensity of attack on baits. We recommend exposure of paper baits for at least 2 mo during the transitional period as the optimal protocol for sampling at the time of greatest activity and diversity of those species within the guild of wood-feeding species regularly attracted to paper baits.

Key Words: baiting, foraging activity, Isoptera, northern Australia, rainfall, savanna, seasonality, species richness, surface-foraging termites

INTRODUCTION

Termites are of key ecological and pedological importance in many tropical environments through both trophic and non-trophic effects, and exert a strong influence over ecosystem functioning (Bignell & Eggleton 2000, Jones 2000). Owing to their often-substantial local abundances and the broad diversity of their feeding habits, they play important roles in mediating breakdown processes at all stages of decomposition (Tayasu *et al*. 1998). They thereby contribute substantially to the regulation of nutrient recycling and energy flows in tropical forest and savanna systems (Jones 2000, Matsumoto & Abe 1979), and are major 'ecosystem engineers' in these environments. Through their non-trophic effects, termites play major roles in soil formation and maintenance (Lavelle 1997) and influence the distributions of the vegetation (Spain & McIvor 1988) and other biota (Lavelle 1996). Their activities may affect soil primary productivity and thereby influence communities of microorganisms, plants and wildlife (Lavelle 1996). The potential roles of termites are of particular importance in Australia because its soils are generally of low fertility, with notably low phosphorus concentrations (Norrish & Rosser 1983).

Despite their perceived importance, however, we have a poor understanding of the functional roles of different termite taxa in tropical ecosystems. Sampling difficulties are a major factor impeding such research. The sampling efficiency of termites is low, given their cryptic nature, relative inactivity, range of nesting habits and feeding strategies, and patchy distributions within and between habitats (Abensperg-Traun & De Boer 1990, Sands 1972). There is a lack of even basic natural-history information for most subterranean termite species (Dangerfield & Schuurman 2000). However, the development of effective termite sampling protocols is critical to understanding the relationships between termite diversity and ecosystem function, the impact of land management practices on these relationships, and, ultimately, what this means in terms of sustainable land use.

Subterranean termites are defined as those species gaining access to food via underground tunnels, and this definition includes a number of mound-building species (Abensperg-Traun & De Boer 1990). While they do not

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sample all species equally, an effective method for estimating the relative abundances of certain wood-feeding, surface-foraging termites is to analyse the species and activities of termites at baits exposed on the soil surface. Toilet-paper rolls are uniform in size and composition, and have been widely used in studies of territoriality and of the distributions and activities of these termites in North America (La Fage *et al.* 1973), Africa (Dangerfield & Schuurman 2000), and Australia (Abensperg-Traun 1993). Paper baits are a convenient technique for sampling wood-feeding, surface-active termites, but questions remain about their usefulness (e.g. Taylor *et al.* 1998). The aim of the present study was to assess the usefulness of paper baits in providing answers to the following questions:

(1) What are the ecological strategies of the termite species attracted to paper baits?
(2) How do relative species representation and richness differ between seasons?
(3) How do frequency and intensity of attack vary with the season and duration of exposure?
(4) From (2) and (3), what is the best time of year to sample, and optimum exposure period, for assessing the activity and diversity of the termite guild attracted to paper baits?

METHODS

Study site

Baiting was carried out in two adjacent, 1-ha plots (referred to as ‘closed’ and ‘open’) in tropical savanna at the CSIRO Tropical Ecosystems Research Centre (12°25′S, 130°53′E), near Darwin, northern Australia between April 1999 and March 2000. The vegetation of both plots was open forest (*sensu* Specht 1981) dominated by *Eucalyptus tetrodonta* F. Muell. and *E. miniata* Cunn. ex Schauer over a ground layer of annual and perennial grasses, primarily the annual grass *Sorghum extans* Lazarides. *Terminalia ferdinandiana* Exell and *Planchonia careya* (F. Muell.) Kunth dominated the mid-storey (4–10 m). The closed plot had greater upper canopy cover than the open plot (45% cover compared with 30%), a denser mid-stratum woody component (65% compared with 20%), but sparser grass understorey (40% cover compared with 80%). The species composition of these plots is characteristic of northern Australian tropical savannas (Wilson *et al.* 1990) although, at the time of the study, the closed and open plots had not been burned for 25 and 4 y respectively (since 1975 and 1997). This is unusual for northern Australian savannas, which on average are burnt every 1.5 y (Myers *et al.* 1998). It is therefore likely that the standing crop of litter on the soil surface was greater than that of more frequently burned sites. The soil was loamy sand derived from lateritized sedimentary parent materials (Myers *et al.* 1998) and is an oxisol, probably a ustox (Soil Survey Staff 1999).

The climate of the region is monsoonal, with highly seasonal rainfall and relatively constant high temperatures throughout the year. Mean annual rainfall at Darwin Airport (2 km from the study site), is 1715 mm, falling over an average of 111 rain days (Australian Bureau of Meteorology, URL: http://www.bom.gov.au/). Over 90% of the annual rainfall falls during the wet season (November to April), the timing and duration of which varies considerably from year to year (Williams *et al.* 1997). The average monthly maximum temperature is 31.9 °C with an average monthly minimum of 23.2 °C. The climatic characteristics of this region are further described in McDonald & McAlpine (1991). During the course of this study, daily rainfall was recorded on site by staff of the Tropical Ecosystems Research Centre.

The termites of the site are poorly known. Notable termite constructs include the epigeal mounds of *Nasutitermes longipennis, Coptotermes acinaciformis, Ephelotermes melachoma* and *Microcerotermes* species. Arboreal nests of *Nasutitermes graveolus* occur in a number of trees, with largely organic covered runways connecting these nests to the soil. Earthen runways and thin feeding covers are present on tree stems, over fallen wood and over grasses, although the species building these constructs are poorly known. A small number of *Mastotermes darwiniensis* colonies have also been noted in standing and fallen dead wood.

Experimental layout

Four 25 × 25-m subplots were established randomly within each of the two plots. Toilet-roll baits (10.5 cm diameter × 10 cm long, 500 sheet single-ply, unscented, bleached) were placed upright on the ground surface at the intersections (n = 25) of a central 5 × 5-m grid in each subplot. The toilet-paper rolls were reinforced at each end with a 24-mm-wide strip of packing tape to prevent unravelling (La Fage *et al.* 1973). Black polythene planter bags (2.5 litre, 240 mm) were placed over baits to prevent their disintegration during heavy rain and reduce animal interference. Litter present at the bait stations was brushed aside to ensure that the uncovered base of the bait was in contact with the soil surface. Baits were held in position with a short length of U-shaped steel wire, one half of which was inserted down the hollow centre of the roll, through the planter bag.

Sampling

Sampling was conducted during three seasons: 21 April–16 June 1999 (transitional period between wet and dry seasons), 10 August–5 October 1999 (dry season) and 11 January–7 March 2000 (wet season). During each sampling period, five of the 25 baits in each subplot were inspected at 2, 7, 14, 28 and 56 d after installation. Baits were lifted, examined for the presence of termites, assessed for degree of attack, and then replaced in their original positions. The five baits inspected at any given census were randomly selected from those baits that had not been previously examined. Examination of baits may disrupt termite foraging for some period because the anchoring wire and planter bag must be removed for inspection. The above sampling procedure was designed to obviate any possible confounding effect of bait disturbance on subsequent termite foraging activity. At the 7, 14, 28 and 56 d inspections, baits that had been examined during previous censuses (i.e. 5 baits at 7 d, 10 baits at 14 d, etc.) were re-examined for species collections only.

Surface-feeding termites forage within the toilet-roll baits and consume variable amounts of paper, leaving hollowed areas within the rolls (Nash *et al.* 1999). At each census, the frequency of termite occurrence was measured as the percentage of the five inspected baits in each subplot that had been attacked, indicated by the presence of termites or gallery material (Abensperg-Traun & Milewski 1995, Nash *et al.* 1999). The intensity of foraging activity was then measured indirectly, with baits assigned a score of one of six ‘Intensity of Attack’ (IA) rankings: 0 = no attack; 1 = 1–24% of bait consumed; 2 = 25–49% of bait consumed; 3 = 50–74% of bait consumed; 4 = 75–99% of bait consumed; 5 = bait completely consumed or replaced by gallery and/or faecal carton material.

Termite identifications

Soldier termites were collected when present, and identified using keys and descriptions from Hill (1942) and Miller (1991). A number of specimens were identified by Dr L. Miller, CSIRO Entomology, Canberra. Voucher specimens of all species are held at CSIRO’s Tropical Ecosystems Research Centre in Darwin.

Data analysis

We used two-way ANOVA to examine the effects of plot type and season on species richness. These analyses were conducted using the total numbers of species recorded over all baits (undisturbed plus re-checked), across all census days in each subplot and for each seasonal exposure.

Three-way ANOVA was used to assess the effects of plot type, season and duration of exposure on the frequency of occurrence of termites at the baits. The four subplots in each plot type were treated as blocks. Plot type, season and duration of exposure were the fixed factors and the response variable was the percentage attacked by termites of the five baits examined in each subplot at each census date. A lack of sufficient data precluded species-level analyses. Simple linear regressions were used to examine the nature of the relationships between exposure duration and the number of baits attacked for each season × plot type interaction.

For baits that had been attacked by termites (i.e. IA rating > 0), a non-orthogonal three-way ANOVA was used to test the effect of plot type, season and duration of exposure on the intensity of foraging activity. The response variable was the intensity of attack for each bait, at each census. To avoid statistical bias resulting from the high percentage (96%) of zero values, the analysis was conducted only on the results for baits exposed for 28 and 56 d. Data for the dry-season collections were excluded from this analysis for the same reason.

Simple linear regressions were also used to test for relationships between rainfall and mean species richness, percentage of baits attacked, intensities of attack. In examining these potential relationships, rainfall was expressed as that incident over the entire seasonal period, or as that of the 1–mo, 2-mo or 3-mo periods preceding the sampling dates.

For all analyses, standardized residuals were plotted against fitted values to assess homogeneity of variance. Least Significant Difference tests were used to identify differences between treatments when the seasonal effect was significant overall. All analyses were performed using Genstat 5 (Genstat 5 Committee 1997).

RESULTS

Of the 600 baits exposed during the study (25 baits per plot × 4 subplots per plot × 2 vegetation types × 3 seasons), 97 (16%) were attacked after 1 wk. Over the entire study 240 (40%) were attacked. A total of 219 collections of termites from 11 species and five genera were made, with soldiers present in 184 (84%) of these.

Species assemblages

Based on their frequencies of occurrence at baits, the 11 species collected formed three groups (Table 1): (1) the dominant species *Microcerotermes nervosus* (43% of records) and *Schedorhinotermes actuosus* (27% of records); (2) three species (*S. breinli, Heterotermes venustus* and *H. validus*) that each accounted for more than 5% of records, totalling 19% of observations; and (3) the remaining species that individually comprised < 5% of observations, totalling 10% of records. Three species (*Coptotermes acinaciformis*, *M. serratus* and *Nasutitermes graveolus*) were only recorded in the closed plot.

The relative contributions of the most common species differed between plots and between seasons. In the closed plot *M. nervosus* and *S. actuosus* accounted for 38% and 37% of records, respectively. In the open plot *S. actuosus* was less frequent (13%) than *M. nervosus* (51%), and

Table 1. Number of attacks mean (± 1 SE) on paper baits by all species during each season, and percentage representation within each season.

	Closed				Open			
Family/Species	Total	Transition	Dry	Wet	Total	Transition	Dry	Wet
Rhinotermitidae								
Schedorhinotermes actuosus (Hill)	40	29 (59 ± 11)	9 (40 ± 23)	2 (6 ± 2)	10	5 (13 ± 5)	1 (25 ± 15)	4 (15 ± 6)
Schedorhinotermes breinli (Hill)	12	4 (5 ± 5)	–	8 (21 ± 5)	1	–	–	1 (3 ± 2)
Heterotermes venustus (Hill)	1	1 (1 ± 1)	–	–	10	4 (24 ± 16)	2 (13 ± 8)	4 (13 ± 3)
Heterotermes validus Hill	3	2 (4 ± 4)	1 (25 ± 25)	–	8	4 (6 ± 6)	3 (8 ± 5)	1 (3 ± 2)
Coptotermes acinaciformis (Froggatt)*	2	–	1 (4 ± 4)	1 (4 ± 3)	0	–	–	–
Termitidae								
Microcerotermes nervosus Hill*	41	11 (19 ± 9)	2 (19 ± 12)	28 (65 ± 7)	39	13 (27 ± 12)	6 (17 ± 10)	20 (64 ± 6)
Microcerotermes serratus (Froggatt)*	3	2 (4 ± 2)	1 (13 ± 13)	–	0	–	–	–
Microcerotermes boreus Hill*	2	2 (4 ± 2)	–	–	1	1 (5 ± 5)	–	–
Nasutitermes eucalypti (Mjöberg)††	1	–	–	1 (4 ± 2)	6	4 (17 ± 10)	1 (6 ± 4)	1 (3 ± 2)
Nasutitermes longipennis (Hill)*	1	1 (1 ± 1)	–	–	2	1 (8 ± 8)	1 (6 ± 4)	–
Nasutitermes graveolus (Hill)**	1	1 (3 ± 3)	–	–	0	–	–	–
Total	107				77			

Unmarked species have subterranean nests; * species known to build epigeal mounds; ** species known to build arboreal nests; ††recorded from the mounds of other termites.

subdominant with *H. venustus* (13%). Within Group 2, *S. breinli* was most common in the closed plot with *H. venustus* and *H. validus* most common in the open plot.

During the transitional and dry seasons, *Schedorhinotermes actuosus* was recorded more frequently than *M. nervosus*. *Schedorhinotermes breinli* was only recorded during the wet and transitional seasons, with the other *Microcerotermes* species only recorded during the transitional and dry seasons. The two *Heterotermes* species were recorded during all seasons. *Heterotermes validus* (25%) and *M. serratus* (12.5%) were relatively more abundant in the closed plot during the dry season, when other species were poorly represented. *Heterotermes validus* was not recorded in the wet season. In the open plot during the dry season the relative contributions of *S. actuosus* (25%) and *Heterotermes validus* (8%) were greatest.

The different termite species attacked the baits in characteristic ways. Species of *Microcerotermes* (mainly *M. nervosus*) and *Heterotermes* entered baits through small holes in the base. Attacks by members of both genera were distributed throughout the baits with some concentration around their bases, while those of *Heterotermes* spp. were sometimes concentrated around the central core. Workings within the baits were lined with loose soil and black carton. Attacks by members of both these genera ceased well before exhaustion of the available resource.

Schedorhinotermes spp. attacked the baits voraciously from the base upwards and from the inside out. They encased baits with coarse, external soil coverings and the large chambers and galleries excavated were lined with black faecal carton. As the baits were consumed, the paper was replaced with soil and copious amounts of carton, leaving an outer shell; rolls therefore became heavier as attacks progressed. Members of this genus had the highest rate of attack of all genera in the current study. After 2 mo, 50–100% of all rolls had been consumed and in one instance 75–99% of one roll had been eaten after 14 d. The rate of attack by *S. actuosus* was greater than that of *S. breinli*. Unlike members of other genera, *Schedorhinotermes* spp. often continued to attack the baits until most or all had been consumed. Consumption tended to increase during the transitional period and was minimal during the dry season.

Species richness

Ten species were recorded during the transitional period, with seven and eight species recorded during the wet and dry seasons, respectively. In general, the number of species increased with bait exposure time. Between 28 and 56 d, the number of species recorded increased by one, two and three for the transitional, wet and dry seasons, respectively.

Over the entire study, all 11 species were recorded from the closed plot (range 5–7 at individual samplings) while eight species were found in the open plot (range 4–6). However, there was no significant effect of plot type on species richness (Table 2). Mean species richness varied significantly with season, with the strong seasonal effect mainly attributed to a significantly lower mean species richness value in the dry season (1.5 ± 0.2) compared with those for the transitional period (3.6 ± 0.4) and the wet (2.9 ± 0.3) season (Figure 1a).

The highest values for mean species richness, percentage of baits attacked and intensities of attack, all occurred during the transitional season. Therefore, no significant regression relationships between these values and various combinations of rainfall were found; nor was rainfall correlated with termite activity in any simple way.

Table 2. Summary of analysis of variances of termite species richness, and frequency and intensity of attack at paper baits from April 1999 to March 2000.

Source of variation	df	MS	F	P
Species richness				
Plot type	1	0.17	0.17	0.684
Season	2	9.29	9.56	0.001
Plot type × season	2	0.54	0.56	0.582
Error	18	0.97		
Frequency of attack				
Plot type	1	0.41	0.9	0.379
Season	2	7.91	19.2	< 0.001
Time since exposure	4	20.9	50.9	< 0.001
Plot type × season	2	1.11	2.70	0.073
Plot type × time	4	0.55	1.35	0.259
Season × time	8	3.52	8.57	< 0.001
Plot type × season × time	8	1.10	2.67	0.012
Error	84	0.41		
Intensity of attack				
Plot type	1	9.14	11.4	0.001
Season	1	0.28	0.35	0.560
Time since exposure	1	0.12	0.14	0.705
Plot type × season	1	0.28	0.36	0.550
Plot type × time	1	1.43	1.79	0.186
Season × time	1	0.71	0.89	0.350
Plot type × season × time	1	0.64	0.81	0.373
Error	64	0.80		

Frequency of attack

The frequency of termite attack on baits did not differ significantly between the closed (17% ± 3) and open (15% ± 3) plots (Table 2). However, frequency of attack varied significantly between seasons in the order: transitional (24% ± 5) > wet (18% ± 4) > dry (7% ± 2). For both plots, the mean percentage of baits attacked was significantly lower in the dry than in the other two seasons, but only in the closed plot was the mean percentage of baits attacked significantly higher in the transitional period compared with the wet season (Figure 1b).

Frequency of attack varied significantly with the duration of bait exposure (Table 2), increasing from 1% (± 1) at day 2 to 47% (± 6) at day 56. With the exception of the open plot in the dry season, the frequency of attack increased from 2–56 d in each plot in all seasons, as confirmed by significant ($P < 0.05$) linear regressions (Table 3). The rate at which baits exposed for longer periods experienced increased frequency of attack varied significantly with season (Table 2), in the order: transitional > wet > dry. A significant three-way interaction of plot type × season × day also reflected a slower increase in the frequency of attack in the open than in the closed plot during the transitional period. In the open plot, the transitional and wet periods showed similar increases in frequency of attack over time.

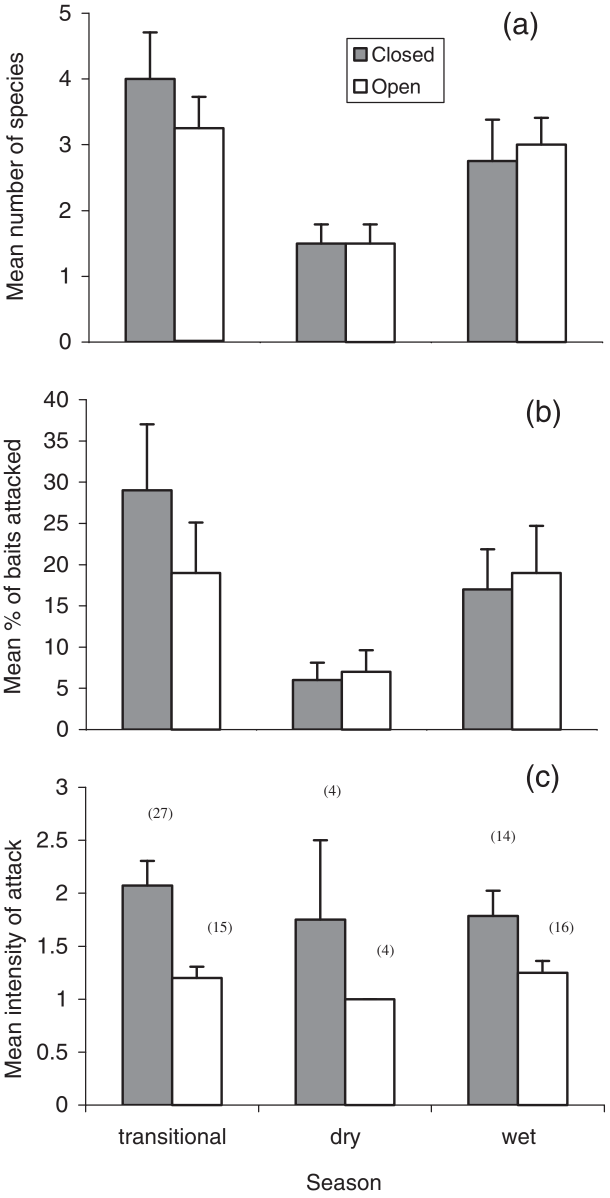

Figure 1. Mean (± 1 SE) (a) number of termite species, (b) percentages of baits attacked by termites and (c) intensity of attack recorded at paper baits (sample size for each treatment in parentheses), in the closed (shaded bars) and open (open bars) plot for the three sampling periods.

Intensity of attack

For most baits attacked, the extent of consumption remained generally low throughout the study, with 64% of the baits being less than 25% consumed. Only 6% had greater than 75% eaten and only one roll was completely consumed. Mean intensities of attack over the entire study were 1.9 ± 0.2 in the closed compared with 1.2 ± 0.1 in the open plot: both correspond to less than 25% of bait consumption. There was a significant effect of plot type on the intensity of feeding activity (Table 2), with consumption greater in the closed than open plot in all seasons (Figure 1c).

Bait consumption did not differ significantly between the seasons (Table 2) with overall mean scores (all sampling days) for the three seasons of 1.7 ± 0.2 (transitional),

Table 3. Regression statistics for relationships of the frequency of toilet-roll baits attacked by termites (F) versus day sampled (D) for each plot type × season treatment.

Response variable	Equation	df	F	P	r^2
Transitional					
Closed	$F = -0.370 + 0.085\ D$	18	149	<0.001	0.886
Open	$F = -0.250 + 0.056\ D$	18	37.6	<0.001	0.658
Dry					
Closed	$F = -0.012 + 0.015\ D$	18	11.1	<0.004	0.346
Open	–	18	1.43	0.247	0.022
Wet					
Closed	$F = -0.147 + 0.047\ D$	18	47.1	<0.001	0.708
Open	$F = -0.065 + 0.047\ D$	18	21.7	<0.001	0.521

1.5 ± 0.1 (wet) and 1.4 ± 0.2 (dry). In general, the amount of bait consumed increased with bait exposure time (day 2, IA = 1.0 ± 0.0). However, there was no significant difference in the overall intensity of attack between days 28 (1.6 ± 0.2) and 56 (1.6 ± 0.2). No significant interaction effects were found in analysis of the intensity of termite attack.

DISCUSSION

Assemblage structure and ecological strategies

The species most commonly found at the baits, *M. nervosus* builds small epigeal mounds often over dead stumps and roots or against the stems of dead or living trees. This species feeds on living, dead and partly decayed wood and woody litter (Braithwaite *et al.* 1988). Both *Schedorhinotermes* species nest in the soil or in wood buried in the soil (Miller 1987); they are reported to feed on the dead and partly decayed wood of a range of species and to cause considerable economic damage (Gay & Calaby 1970). *Schedorhinotermes breinli* has been found in the stems of shrubs and trees and in the nests of other termites (Hill 1942). Both *M. nervosus* and *S. actuosus* are very widely distributed in tropical Australia (Watson & Abbey 1993).

The two *Heterotermes* species collected during the present study have been reported to feed on a wide range of dead and partly decomposed woody materials, also including herbaceous materials (Gay & Calaby 1970). *Heterotermes venustus* has been reported to feed on decayed litter and soil (Braithwaite *et al.* 1988).

Of the less commonly collected species, *M. boreus* builds small epigeal mounds while *M. serratus* may build epigeal mounds or nest underground, often in contact with woody materials. Both species feed on dead and partly decayed wood and litter while *M. serratus* is recorded as feeding on decayed litter and soil (Braithwaite *et al.* 1988). *Nasutitermes longipennis* is highly polyphagous, and is recorded as eating sound and rotten wood, grass and surface vegetable debris; it builds small epigeal mounds but sometimes nests in the mounds of other termites (Gay & Calaby 1970). *Nasutitermes graveolus* builds carton nests in arboreal locations although it maintains contact with the ground where it feeds on weathered wood, bark and other debris (Gay & Calaby 1970). *Nasutitermes eucalypti* has been recorded from the mounds of other termite species and from the faeces of cattle and horses (Ferrar & Watson 1970); it is also recorded as feeding on decayed litter and soil (Braithwaite *et al.* 1988). *Coptotermes acinaciformis* is widely distributed throughout mainland Australia and, in the tropics, builds large mounds often associated with the bases of trees. It feeds on living, dead and decomposing wood. It is a major source of economic damage, both as a pest of living trees and as a species that attacks built structures.

Baiting studies conducted at other locations in tropical Australia have revealed the presence of the above and related species. At Weipa (12°38′S, 141°53′E) (Spain, unpubl. data) and at Gove (12°17′S, 136°51′E) (D. A. Hinz, unpubl. data), species of *Heterotermes, Microcerotermes* and *Schedorhinotermes* dominated the collections from paper baits exposed in both native forest areas and in areas rehabilitated to native forest species after bauxite mining. Species of the same genera were taken at baits exposed on rehabilitated bauxite processing wastes at Gove (D.A. Hinz, unpubl. data).

Stable C and N isotope studies have confirmed the feeding habits of a number of the above species. *Coptotermes acinaciformis, M. boreus, M. nervosus, S. actuosus* and *S. breinli* all have δ^{13}C values unequivocally in the C3 range and therefore derive their C from woody species (Spain & Reddell 1996, Tayasu *et al.* 1998). Similarly, all these species fall into the wood-feeding category, as defined by their δ^{15}N values (Tayasu *et al.* 1998). The highly polyphagous species *N. longipennis* may derive its tissue C from both C3 and C4 sources (Spain & Reddell 1996). The δ^{15}N values of the tissues of this species indicate that it feeds on little-decomposed wood (Tayasu *et al.* 1998).

Species richness

Eleven species were recorded from the baits of which two, *M. nervosus* and *S. actuosus*, comprised more than 70% of records. Braithwaite *et al.* (1988) found between 17 and 20 species that feed on fresh and decomposing wood and leaf litter in monsoon forest, open forest and woodland savanna environments in northern Australia. Abensperg-Traun (1993) reported 11 species at baits compared with 18 associated with the logs of *Eucalyptus capillosa* in a Western Australian environment. Baits of different types also attracted different numbers of species.

Termite species richness did not differ significantly between the two plots, suggesting that the greater structural complexity of vegetation and the more humid and even environment of the closed plot are of little consequence to those species regularly attracted to baits. This contrasts with the findings of Braithwaite *et al.* (1988) who found a significant negative correlation between termite species richness (as richness of dead wood, decayed wood and litter-feeding species) and projected foliage cover. These authors also found significant negative correlations between the species richness of decayed wood and litter feeders and harvesters with the depth of the litter layers. These correlations suggest that lower species richness might have been expected in the plot with the more closed vegetation structure. However, the sampling method used here is different from those of Braithwaite *et al.* (1988) and reflects activity rather than total species richness.

A strong seasonal effect was apparent in the present study, with fewer species active in the dry season. This compares with the reduced activity and species richness found by Abensperg-Traun (1991) during the dry summer and winter of his Mediterranean-climate study area. No seasonal effect was found by Braithwaite *et al.* (1988) on species richness.

The lack of a simple relationship between rainfall and termite activity and species richness should perhaps not be surprising. Extremely heavy rainfall during the monsoonal season causes surface flooding and saturates the soil for considerable periods and this must suppress termite activity. In southern Cameroon, Dibog *et al.* (1998) also found negative correlations between rainfall in the days preceding sampling with termite abundance and species richness. Reduced termite activity has also been reported for dry periods in Australia (Abensperg-Traun 1993) and elsewhere. It therefore seems probable that the moist but not saturated soil conditions of the transitional period are likely to be the most suitable for surface-active termites.

Frequency and intensity of attack

There was a strong linear relationship between the duration of bait exposure and the incidence of termite attack. In addition, there was a strong seasonal effect with the frequency of attack being lowest during the dry season and higher at other times, notably during the transitional season. Frequency of attack during the transitional and wet seasons did not differ in the open plot suggesting a more rapid drying of the surface after heavy rainfall.

There were no significant differences between the seasons in intensity of attack although the most intense attacks on the baits occurred at all seasons in the plot with the more closed vegetation structure. This may be due to the greater representation of *S. actuosus* at the baits in this plot. No significant increases in intensity of attack on the baits occurred after 28 d. It is possible baits declined in their attractiveness to termites due to sustained fungal activity (Lenz 1994).

Concluding remarks

The results of this study indicate that paper baits were most successful in sampling a limited suite of subterranean species feeding on relatively fresh and slightly decayed wood. The species found in the present study represent only a subset of the termites present on the site. *Mastotermes darwiniensis* occurs at the study site but was not recorded at the baits although it has been taken at paper baits elsewhere in the area (Spain & Reddell 1996). *Heterotermes vagus* also occurs at the site but was not found at the baits. Most other species that occur on the site are unlikely to have been attracted to the baits because they feed largely on finely triturated litter, harvest dead grasses or because they are soil:wood interface or humus feeders (e.g. *Ephelotermes melachoma*) and feed on more highly decomposed materials (Tayasu *et al.* 1998). It is also probable that some of the species rarely collected at baits – for example, *N. longipennis* and *C. acinaciformis* – were under-represented in relation to their presence at the site simply because they are only weakly attracted to paper baits (see, for example, Abensperg-Traun 1993). Other species such as *N. eucalypti* may simply be using the baits as shelter.

Changes in species dominance did occur between seasons and the two forest types. The numbers of species active, and frequency of termite attack, was greatest during the transitional period. Frequency and intensity of attack also increased with the duration of bait exposure. Based on the overall results, we recommend the exposure and regular inspection of paper baits for 2 mo during the transitional period (from wet to dry seasons); this appears to be the optimum sampling protocol for assessing the diversity and activity of this component of the termite assemblage. Different sampling methods (and bait types) are likely to increase the total number of species recorded at these sites, as may exposure of the toilet roll-baits beyond 56 d. Consequently, toilet-roll baits may be best used in conjunction with other suitable sampling methods, as part of an integrated sampling strategy where the aim is to detect the widest range of termite species in a given area. However, depending on the aims of the study, seasonal differences in relative species representation may also be of importance.

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