



Chapter 4

Assessing the efficiency of termite sampling methods in southern African savannas

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Abstract

Although termites are of great importance in tropical and sub-tropical ecosystems across the globe, termite ecology is often constrained by sampling difficulties and a lack of sampling protocols in savannas. A comparison of two often used sampling methods, cellulose baits and active searching, was conducted across four savanna types situated along a rainfall gradient in South Africa during the wet season. The efficiency of sampling method varied with annual rainfall and a single method was not the best for all savanna types. In mesic savannas, active searching (an often neglected sampling method in savannas) was most effective at sampling termite diversity while baiting was more effective in arid savannas, although this method samples mostly wood feeding termites from feeding group II. Baiting also provides a better measure of termite activity than active searching. The type of study and feeding group needing to be targeted will determine which method is most appropriate, as well as the savanna site where sampling is to be conducted.

Keywords: active searching, baiting, feeding groups, invertebrate sampling, sampling protocols

Introduction

Termites (Blattodea: Termitidoidae) are considered key ecosystem engineers in tropical and sub-tropical systems. They are responsible for the redistribution of soil particles and alter the mineral and organic composition of soils, their hydrology, drainage (Jones et al., 1994; Konaté et al., 1999) and infiltration rates (Mando et al., 1996). Termites are also considered to be the dominant arthropod decomposer in tropical systems (Collins, 1981; Holt, 1987; Schuurman, 2005) and hence influence nutrient cycling and distribution (Holt & Coventry, 1990; Lepage et al., 1993). Their vast biomass alone makes them an important consideration in tropical and sub-tropical ecology (Josens, 1983); in African savannas they have been shown to have a comparable biomass to ungulates and mega-herbivores (Dangerfield et al., 1998). Termites are also a diverse and varied group comprising of several feeding groups, including wood feeders, grass harvesters and soil feeders which exert different ecological effects on ecosystems (Donovan et al., 2002; Josens, 1983).

However, despite their importance in tropical and subtropical systems, detailed knowledge on termites and their function in ecosystems is scarce, with even basic natural information lacking for many species (Dangerfield & Schuurman, 2000; Dawes-Gromadzki, 2003). This can largely be attributed to taxonomic and sampling difficulties. Although termites are often considered to be 'taxonomically tractable' (Brown, 1991), there are still major gaps in their taxonomy, particularly for southern hemisphere regions (Eggleton et al., 1996; Eggleton et al., 1995) and many genera are in need of revision (Eggleton, 1999; Uys, 2002). In order for taxonomists and ecologists to address these challenges, termites need to be sampled and herein lie more difficulties. Most termite species are cryptic in nature, being subterranean with a patchy distribution, resulting in many conventional insect sampling methods, such as pitfall trapping or sweep netting, being ineffective. A lack of standardised sampling protocols also causes difficulties, making comparisons between studies and ecosystems problematic (Dawes-Gromadzki, 2003), this is particularly true for savanna systems. Jones & Eggleton (2000) have designed a sampling protocol for tropical forests which is widely used (e.g. Donovan et al., 2002; Eggleton et al., 2002; Gathorne-Hardy et al., 2001), but its suitability for other

systems, particularly more arid ones such as savannas which have drier, harder soils, which make searching and digging difficult, is questionable.

Several studies have investigated termite sampling methods in savanna environments in an attempt to develop a standardised sampling protocol (e.g., (Dawes-Gromadzki, 2003; Zeidler et al., 2004), but as yet none are widely used. Baiting, especially with toilet paper rolls, is a commonly used and seemingly effective method (Le Fage et al., 1973), but is useful for a limited suite of termites only (mostly those which feed on wood) and also does not easily provide true abundance data because not all termites present can be sampled. Added to this is uncertainty regarding an optimal baiting system, such as the length of time baits should be in the field before checking, and whether they should be buried or simply placed on the substrate surface. Savannas are also highly variable environments when considering vegetation and abiotic variables (House et al., 2003) and sampling methods in one savanna system could well be inappropriate for another, given this variation. Prior to this study, however, the efficiency of sampling techniques focusing specifically on termites has not been compared between savanna types.

The aims of this study were to compare (i) the efficiency of different forms of baiting techniques, namely the position of cellulose baits, and time available for termite attack, and (ii) two commonly used termite sampling techniques: cellulose baits and active searching. Comparisons were made by assessing how well the techniques sampled termite diversity (richness, relative abundance and assemblage composition) and activity levels (frequency and intensity of attack). I evaluated these two techniques in savannas situated along a rainfall gradient of approximately 600 kilometers in South Africa, and thus were able to compare the efficiency of different methods in markedly different savanna systems. This is the first study on savanna termite sampling methods to be conducted on such a large spatial scale.

Methods

Study site

The study was conducted in four distinct savanna vegetation types situated along a rainfall gradient in two of South Africa's major reserves: Kruger National Park (KNP,

situated between 22° 25' and 25° 32' latitude south and 30° 50' and 32° 02' longitude east) and Hluhluwe-iMfolozi Park (HiP, situated between 28° 01' and 28° 25' latitude south and 32° 15' and 32° 26' longitude east). These parks are located in the eastern part of the country and have a sub-tropical climate with a distinct summer rainfall pattern.

The four savanna types consisted of Mopani woodland (Mopani area of the northern KNP), *Acacia* savanna (Satara area of the central KNP), *Terminalia* woodland (Pretoriuskop area of the southern KNP) and mesic *Acacia* savanna (Hluhluwe section of HiP). This study forms part of a larger study investigating the effects of long-term burning regimes on termites and accordingly sampling in KNP was carried out on a series of experimental burning plots (for more information on this burning trial see Biggs et al. 2003 and van Wilgen et al. 2007). Twelve replicated sampling plots (except for Hluhluwe where 11 plots were used) spaced 10 – 20 km apart were selected from within each of the four savanna habitats. These plots do, however, differ in their fire histories since they form part of a burning experiment, but together are considered representative of the habitat in question and a variety of its fire regimes. The total rainfall gradient represented by the four savanna types ranged from 450 mm (Mopani woodland in KNP) to 900 mm (mesic *Acacia* savanna in HiP) (see Appendix S1 of Chapter 3 for more information on the replicated sites in each of the four habitat types).

Termite sampling

Termites were sampled using two commonly used methods: cellulose baits and active searching. Sampling was conducted during the austral summer (wet season) from November 2008 to February 2009, which represents a time of peak termite activity (Dawes-Gromadzki & Spain, 2003). These methods were selected because, although commonly used, are often used in different systems (but see Zeidler et al. (2004) for a comparison): active searching in tropical forests (see e.g. Davies, 1997; Eggleton et al., 2002; Jones & Eggleton, 2000) and baiting in savannas (see e.g. Dawes-Gromadzki, 2003; Ferrar, 1982). Their relative efficiency in different savanna types has, so far, not been investigated.

Forty cellulose baits in the form of toilet paper rolls (500-sheet single-ply, unscented, unbleached - hereafter referred to as baits) were placed on each plot (see Le

Fage 1973), in a grid formation of five by eight baits, spaced five metres apart. In order to test differences in bait placement (position relative to the substrate and amount of time left in the field), half (twenty) of the baits were placed directly on the soil surface, any litter present was brushed aside to ensure direct contact was made with the soil and the base of the bait (Dawes-Gromadzki, 2003). These baits were wrapped around the middle with packaging tape to prevent unravelling and secured to the soil surface using an aluminium tent peg placed through the centre hole of each toilet roll. The other half of the baits (20) were buried below the soil surface to a depth of approximately 2 cm which ensured they were adequately covered with soil. Each line of eight baits consisted of four buried and four surface baits with the position of the baits alternated. Baits were checked for the presence of termites and assessed for termite attack after predetermined intervals of 5, 14, 28 and 56 days. At each of these time intervals, five surface and five buried baits were removed, and any termites present were sampled (at least ten of each caste where sampled when present to ensure a representative sample, Uys, 2002). The baits were then scored according to the intensity of attack (IA) using visual estimation. This involved giving each bait a score of one of six ratings as to how much of the bait had been consumed. Baits which were completely intact with no evidence of termite activity were assigned a value of 0, subsequent to this baits were scored according to the following scale: 1 = 1 – 25% consumed, 2 = 26 – 50% consumed, 3 = 51 – 75% consumed, 4 = 76 – 99% consumed and 5 = 99 – 100% consumed (Dawes-Gromadzki, 2003). Baits which had been disturbed by vertebrates or other factors (e.g. no longer in direct contact with the soil surface or completely destroyed) were excluded from analysis.

For the active searching, a modified version of the standardised belt transect method described by Jones & Eggleton (2000) was used. Two 50 by 2 metre transects were laid out on each plot, with each sub-divided into ten 5 by 2 metre blocks and each block searched for ten person minutes. During this time period the entire block was searched for termites; this included excavating soil and searching dead wood, termite nests and other microhabitats. Vegetation up to a height of one metre was searched, this included termite runways up tree trunks. This method was modified from that of Jones & Eggleton in that less time was spent searching in each block (ten minutes in my study compared to the standard sixty minutes), this was primarily because the Jones & Eggleton

method was designed for tropical forests which have a much higher termite diversity and density than semi-arid savannas and are also much easier to sample given the softer soils and more variable microhabitats. Additional logistical constraints prevented more time been spent searching each block. The transect was also divided into two 50 metre transects in order to limit any edge effects due to the small sizes of the plots sampled.

Termite Identifications

Termite samples were identified at the Natural History Museum, London, U.K., the University of Pretoria and the National Collection of Insects, Pretoria, South Africa. Specimens were identified to species where possible using soldier castes whenever available (when soldiers were not present, workers were used). Where this was not possible, morphospecies were used (e.g. for the genus *Odontotermes*), and where even this was problematic the specimens were treated as an aggregate for that specific genus (e.g. this occurred for the genera *Microtermes*, *Microcerotemes*, *Astalotermes* and others). With many termite genera in need of revision (Uys, 2002), it was considered a more conservative approach to treat many genera as an aggregate instead of risking the possibility of finding differences in community assemblages when species thought to be different were actually the same. Voucher specimens are lodged at the National Collection of Insects, Pretoria, South Africa.

Analyses

The efficiency of different forms of baiting were compared as well as how baiting performed compared to active searching seeing that termite ecologists are usually faced with this question when designing a sampling protocol. For comparisons of baiting techniques, a general linear model (GLM) was fitted to examine the effects of time (number of days in the field), bait position (surface or buried) and site (savanna habitat) on the frequency of termite attack and a separate GLM was fitted to test these effects on the number of species sampled (species richness). A generalised linear model with a Poisson distribution and log-link function was fitted to examine the effects of time (number of days in the field), bait position (surface or buried) and site (savanna habitat) on the intensity of termite attack. Data were first tested for overdispersion, but a

correction was not necessary. For all these analyses, plots of standardised residuals vs. fitted values were used to assess homogeneity of variance.

The efficiency of baiting compared with active searching was assessed by (i) how many species each method sampled in each savanna type (species richness), (ii) how the assemblages sampled differed and broadly, (iii) how each method compared in terms of the feeding groups sampled. For these comparisons, data from both surface and buried baits were combined because comparisons between these two methods have been performed above and the assemblages sampled (in terms of FG) are very similar, differences lie more in termite activity and abundance.

For species richness comparisons, student's t-tests were used to compare total number of species sampled by each method in each savanna. This was the total species richness for all bait checks combined. Assemblages sampled were compared using analysis of similarity (ANOSIM, Clarke & Warwick, 2001) in Primer v. 5.2 (Clarke & Gorley, 2001). Bray-Curtis similarity matrices of the data were constructed in order to assess overall compositional changes. The data were square root transformed before analysis (to weight common and rare species equally) (Clarke & Warwick, 2001). ANOSIM was used to test if there were significant differences in termite assemblage composition with sampling method. ANOSIM is a non-parametric permutation procedure applied to rank similarity matrices which underlie sample ordinations (Clarke & Warwick, 2001; Parr et al., 2004), in which a significant global R-statistic of close to one indicates distinct differences between the assemblages compared, this R-statistic can take on any value between -1 and 1.

The R-value itself is not unduly affected by the number of replicates in a sample, however, the significance level of this R-statistic is. This can result in a situation where the R-value is, for example, very low, which indicates that assemblages are barely separable, but this value may be significantly different from zero, perhaps leading to an interpretation that the assemblages in question are indeed different. However, this significance level is more a reflection of a high number of replicates or samples, and the R-value is of greater importance for interpretation (Clarke & Warwick, 2001; Parr et al., 2004). The opposite may also be true with an R-value being close to one.

The composition of the feeding groups sampled were compared descriptively in graphical form. Termites were classified into feeding groups based on the classification described by Donovan et al. (2001), which designates termites into four groups based on the humification of the feeding substrate. Group I comprises the lower termites which feed on dead wood and grass; group II is made up of Termitidae with a range of feeding habits which include dead wood, grass, leaf litter and micro-epiphytes; group III feed in the organic rich upper soil layers and are also Termitidae; and group IV contains the true soil-feeders which ingest mineral soil, again all Termitidae. Different termite feeding groups are considered to play different ecological roles and so an understanding of how different sampling methods affect the suite of termites collected is of importance.

Results

Termites from 18 genera and 5 subfamilies were collected during the study. Half of the species were from Feeding Group II, one third from Feeding Group III, 11 % from Feeding Group IV and 6 % from Feeding Group I (Table 3).

Cellulose baits

Mean number of species recorded at baits (species richness) varied significantly over time, with higher incidences of attack as time progressed at the more arid sites, species richness dropped off at the last bait check for both mesic sites ($F_{1, 376} = 74.72$, $P < 0.0001$; Fig. 1a). Across all sites, bait position had a significant effect on species richness ($F_{1, 376} = 17.30$, $P < 0.0001$). For days 1 – 28, species richness was greater at buried baits, but at the last bait check (56 days) species richness was similar for buried and surface baits (Fig. 1b). The effect of site on number of species sampled was also significant ($F_{3, 376} = 26.90$, $P < 0.0001$), which interacted significantly with position ($F_{3, 376} = 3.60$, $P < 0.05$). The highest species richness recorded was at Satara for all bait checks and the lowest was at Mopani for all bait checks except the last one, where Mopani had greater richness than both mesic sites (Fig. 1a).

Mean frequency of attack (FA) varied significantly over time, with higher incidences of attack as time progressed at all sites except Hlulhuwe ($F_{1, 376} = 194.99$, $P < 0.0001$; Fig. 1c). The drier sites (Mopani and Satara) showed markedly steeper increases

from 28 to 56 days (Fig. 1c). Across all sites, FA was also significantly greater at buried ($43.27 \pm \text{SE } 2.75 \%$) than surface ($27.96 \pm \text{SE } 2.50 \%$) baits ($F_{1, 376} = 28.80$, $P < 0.0001$). The effect of site on FA was also significant ($F_{3, 376} = 31.12$, $P < 0.0001$), but this interacted significantly with position ($F_{3, 376} = 7.17$, $P < 0.001$). The highest incidences of attack were at Satara for all bait checks (Fig. 1c).

There was a positive correlation between mean intensity of attack (IA) and time, which was significant (Table 1, Fig. 1d). At Mopani and Satara, there was a marked increase between days 28 and 56. Bait position also had a significant effect on IA (Table 1), with higher attack recorded at buried ($0.69 \pm \text{SE } 0.02$) than surface ($0.35 \pm \text{SE } 0.01$) baits. Site also had a significant effect on IA (Table 1, Fig. 1d), with higher attack levels at Satara than the other sites, which interacted significantly with position (Table 1).

Baits and active searching comparison

In contrast to the more arid sites where no significant differences in species richness sampled between methods were found, active searching compared to baits clearly sampled more species in Hluhluwe ($T_{20, 12} = 2.07$, $P = 0.0517$, Fig. 2) and significantly more in Pretoriuskop ($T_{22, 12} = 5.70$, $P < 0.0001$, Fig. 2).

Analysis of similarity (ANOSIM) revealed that the different sampling methods sampled different components of the overall termite assemblage as composition varied significantly being most pronounced at Mopani, followed by Pretoriuskop. They were somewhat distinct at Satara and fairly similar at Hluhluwe (Table 2).

A comparison of feeding groups (FG) sampled with each method in each savanna type separately shows that at the more arid sites (Mopani and Satara) FG composition does not differ much with sampling method (Fig. 3). However, at the mesic sites (Pretoriuskop and Hluhluwe), the FG sampled and relative contributions differ with sampling method; AS resulted in a wider range of feeding groups being sampled. At all sites, the baits sampled almost entirely FG II, although at the mesic sites some samples contained FG III. This is particularly pronounced at Pretoriuskop where FG III becomes more common and FG IV is recorded with AS only (Fig. 3).

Discussion

It is often assumed for termites that one particular sampling method is better suited to a specific habitat type or it is only tested within one form of this habitat. Generally active searching transects are thought appropriate for sampling in tropical forested areas (Jones & Eggleton, 2000) and baiting methods for drier areas such as deserts (Taylor et al., 1998) and savannas (Dawes-Gromadzki, 2003). However, my results show that the efficiency of each method and baiting technique in sampling the termite fauna differed significantly between savanna types; one method was not the most appropriate or effective for all habitats.

Baiting techniques

In terms of the baiting technique, there were profound differences in termite diversity and activity levels recorded between the arid and mesic savanna sites. Although overall species richness increased significantly over time at all sites, the difference between the 3rd and 4th censuses is of consequence (Fig. 1a). My results suggest that the temporal scale of a baiting protocol is of importance and should be modified according to the savanna type being sampled and not only the presentation or type of bait used (for bait type comparisons see Dawes-Gromadzki (2003) and Taylor et al. (1998)). At the arid sites, the number of species sampled, intensity of attack and frequency of attack, increased substantially between the 3rd and 4th censuses, which contrasts to that of the mesic sites which show a decrease or levelling off between these censuses. In northern Australia over this same time scale (8 weeks), Dawes-Gromadzki (2003) also found a decrease in species richness sampled (although attack levels increased), but these changes may have been more related to seasonality, in contrast to my study which was conducted within one season (wet) only. At the mesic sites in my study (particularly Hlulhuwe), fungus was found growing on many baits at the last census which may repel termites (Abensperg-Traun, 1993; Dawes-Gromadzki, 2003) and could explain why activity and richness recorded decreased. This would imply that in more mesic savannas, there is no benefit to leaving baits in the field for extensive periods of time (at least not as long as 56 days). In contrast, in arid environments a longer time period may be necessary to adequately sample the termite assemblages. Although not reflected in the analysis,

however, at the 4th census period baits were occasionally completely consumed with no termites present. This can occur where termite activity levels are very high (e.g. in Satara in the present study), and is an important consideration when selecting the optimal temporal scale for baiting.

My results indicate that bait position also plays an important role in baiting protocols. In contrast to studies in desert regions (e.g., (Ettershank et al., 1980; Taylor et al., 1998), but in agreement with savanna studies (e.g., (Dawes-Gromadzki, 2003), buried baits were more attractive to termites during the first three censuses. Dawes-Gromadzki (2003) suggested that savanna termites contrast to desert populations in that they do not use thermal shadows to locate surface baits (as suggested by Ettershank et al. (1980) for desert termites) due to higher levels of canopy cover (or grass biomass). My results support this idea, although the attractiveness of surface and buried baits did not differ at the last census (56 days) which is much earlier than in northern Australia (Dawes-Gromadzki, 2003). I suggest this could be due to lower levels of canopy cover, different feeding habits of African termites or higher levels of activity. It also implies that if there are no time constraints for a study, surface baits may be better to use as they are less labour intensive to establish, although they are more susceptible than buried baits to disturbances such as removal by people and animals.

Active searching in savannas

In the most arid savanna, termite diversity did not vary with sampling method (baiting or active searching). This suggests that if a termite species inventory is required it would make little difference which approach was used in arid savannas. This compares well with a previous study conducted in an arid Namibian environment, where species richness was similar with each sampling method, active searching and cellulose baits (Zeidler et al., 2004). However, if a measure of termite activity or relative abundance is necessary then baiting would be more appropriate as higher relative abundances of termites were sampled this way and signs of activity detected by active searching (e.g. tunnelling, sheeting) may only be evident immediately after termites have been active, which is likely to be soon after rainfall events. For savannas of intermediate rainfall, such as Satara, the assemblages seem very similar from the ANOSIM results, and it may seem

from these that either method would adequately sample the termite fauna present, however, 36 % of species sampled were only collected with active searching while only 1 species (7 %) was sampled with baiting alone. This would suggest that active searching should be considered when designing sampling protocols for even intermediate rainfall savannas.

For the mesic savannas, the success rate of each method was notably different, with active searching sampling a higher number of species and wider range of feeding groups. Previously, studies of savanna termites have not generally employed active searching (see e.g. Dawes-Gromadzki & Spain, 2003; Ferrar, 1982; Schuurman, 2005), citing sampling difficulties associated with harder soils and lower termite diversity (Dawes-Gromadzki, 2003). However we found that using active searching in these more mesic savannas can make a valuable contribution; if only baiting had been used a large proportion of the termite species present would not have been sampled. Indeed, none of the soil feeding termites would be represented and a new genus record for South Africa (*Aneneotermes*) would not have been recorded; this shows that although often neglected, active searching can play an important role in understanding termite communities of mesic savannas.

Synthesis and recommendations

My results show that sampling methods for termites need to be adjusted according to the characteristics of the study site (particularly rainfall), this being the case even within broad vegetation types. If a termite sampling protocol for savannas is to be established similar to that of Jones & Eggleton (2000) for tropical forests, this needs consideration. More method comparisons across a variety of savanna habitats would be welcomed in achieving this aim.

An optimal sampling design employed for savanna termites will also depend on which termite feeding groups are being targeted and whether diversity or only activity levels need to be assessed. If a study is aimed at diversity then the sampling methods need to target all feeding groups and a method, or composite methods, which sample as many species as possible should be implemented. However, if the study is related to other aspects of termite ecology, such as pest species which are mostly wood feeding termites

(Uys, 2002), a complete array of termite diversity need not be sampled. Here, baiting may well be more efficient as it samples this group more efficiently and gives an indication of termite activity, which would be beneficial for pest management strategies.

Other sampling methods such as mound density counts (e.g. Benzie, 1986; Traoré & Lepage, 2008; Trapnell et al., 1976), litter bags (e.g. Bocock, 1964; Ohiagu & Wood, 1979; Yamashita & Hiroshi, 1998) and other forms of baiting (e.g. Abensperg-Traun, 1993; Dawes-Gromadzki, 2003; Taylor et al., 1998) could also contribute to a sampling protocol. Although not assessed here, these can be valuable methods depending on the objectives of the study. While mound counts are often criticised for their limited scope and underestimation of diversity (Eggleton & Bignell, 1995), they can provide a quick and easy estimation of colony density, particularly if one specific species which builds charismatic mounds is the focus of a study. In addition mounds can be used in conjunction with remote sensing and related techniques to provide large scale estimates of termite distributions and densities. Litter bags also give an indication of termite activity levels and are focused on grass feeding termites, in contrast to the wood feeders targeted by cellulose baits. They can be useful in studies relating to decomposition and grass harvesting termites which are missed with baiting alone. Other forms of baiting such as wooden stakes (Abensperg-Traun, 1993; Dawes-Gromadzki, 2003) and dung (Taylor et al., 1998) have also been shown to be effective, although a disadvantage to using dung is that it is also consumed by other taxa which could possibly confound results.

These findings argue for more within-biome comparisons of termite sampling methods if a commonly used protocol is to be established. This is certainly the case for savannas and is likely to also hold true for other systems which show similar levels of variation. Advancement toward such protocols will enhance our presently limited understanding of termite ecology.

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Table 1: Results from a factorial generalized linear model (Poisson distribution, log-link function) comparing intensity of termite attack among time (number of days), position of bait (surface or buried) and savanna site. Scaled deviance for the model was 0.82. N = number of baits sampled, > significantly larger, < significantly smaller. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	N	df	X^2	Wald statistic	Effect
Time (days)	1641	1	509.79***	482.49	5<14<28<56
Position	1641	1	63.75***	61.23	buried>surface
Site	1641	3	153.49***	167.11	Satara>others
Position*Site	1641	3	8.53*	8.54	

Table 2: Analysis of similarity between two sampling methods used to sample termite assemblages (active searching and cellulose baits) for each savanna type. The R-statistic is a measure of similarity of assemblages, the closer this value is to 1, the more dissimilar assemblages are (Clarke & Warwick 2001). *P* is considered significant at the α -level of 0.05.

	R	P
Mopani	0.601	0.001
Satara	0.247	0.001
Pretoriuskop	0.498	0.001
Hluhluwe	0.201	0.008

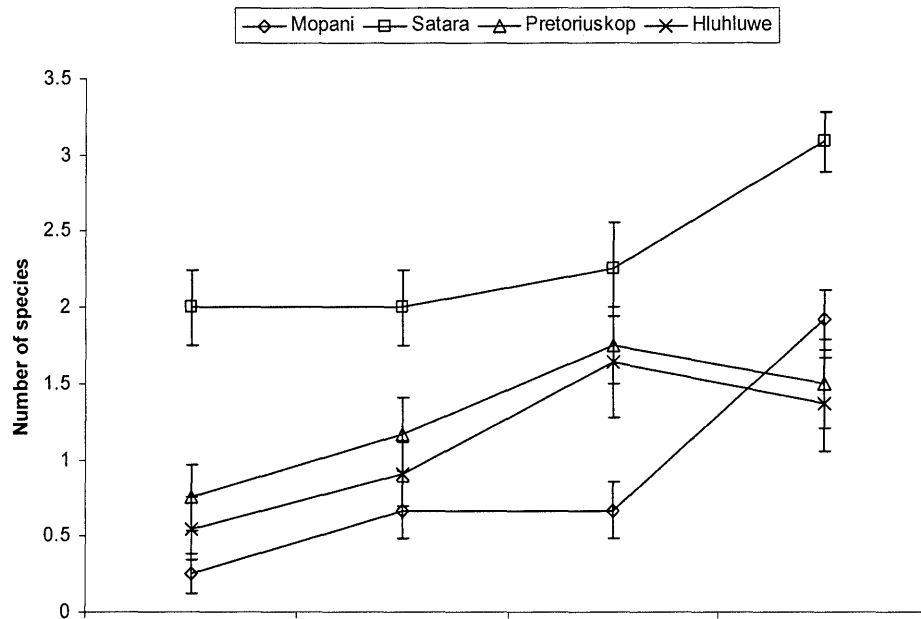
Table 3: Occurrence of termite species for each method at all 12 sites at each savanna habitat. For bait data, occurrence values are for all time checks. The Feeding Group for each species is also indicated. AS = active searching, SB = surface baits, BB = buried baits and FG = Feeding Group.

Termite species	Mopani			Satara			Pretoriuskop			Hluhluwe			FG
	AS	SB	BB	AS	SB	BB	AS	SB	BB	AS	SB	BB	
Hodotermitidae													
<i>Hodotermes mossambicus</i>	2	-	-	-	-	-	-	-	-	-	-	-	I
Termitidae													
Macrotermitinae													
<i>Allodotermes rhodesiensis</i>	2	-	-	16	7	9	3	6	4	20	8	4	II
<i>Ancistrotermes latinotus</i>	-	3	1	22	9	19	17	3	17	18	3	4	II
<i>Macrotermes michaelsoni</i>	4	1	11	3	9	16	-	-	-	1	-	-	II
<i>Macrotermes natalensis</i>	-	-	-	1	-	1	-	-	-	7	-	1	II
<i>Microtermes spp.</i>	7	36	66	34	44	86	46	39	38	31	27	28	II
<i>Odontotermes sp. 1</i>	-	-	-	-	-	1	3	-	-	3	-	-	II
<i>Odontotermes sp. 2</i>	-	-	-	3	-	1	1	1	-	17	5	5	II
<i>Odontotermes sp. 3</i>	2	-	1	18	4	7	-	-	-	1	2	2	II
Apicotermitinae													
<i>Adaiaphrotermes spp.</i>	-	-	-	-	-	-	7	-	-	10	-	-	III

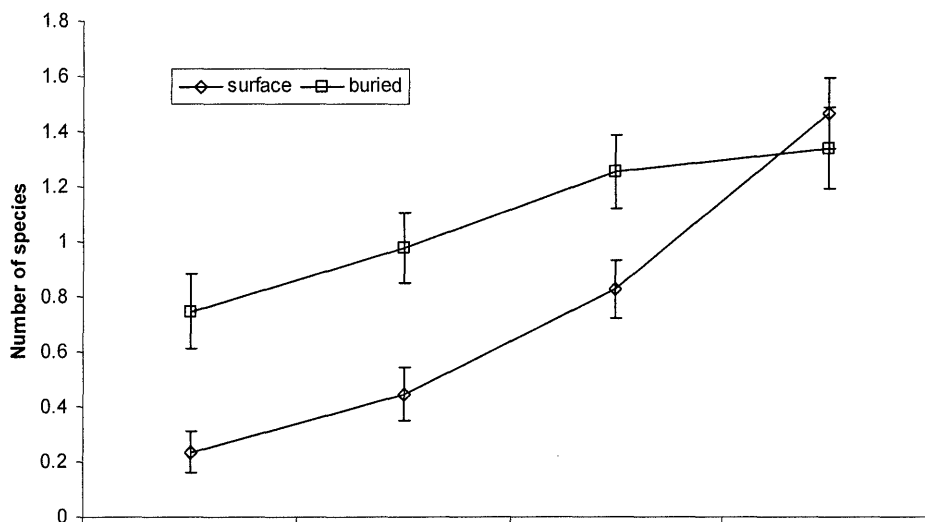


<i>Alyscotermes spp.</i>	-	-	-	-	-	-	7	-	-	1	-	-	III
<i>Anenteotermes spp.</i>	-	-	-	-	-	-	6	-	-	-	-	-	III
<i>Astalotermes spp.</i>	-	-	-	6	-	-	38	2	2	8	1	1	III
Termitinae													
<i>Amitermes hastatus</i>	-	-	-	1	-	-	-	-	-	-	-	-	II
<i>Amitermes messinae</i>	-	-	-	1	-	-	-	-	-	-	-	-	II
<i>Angulitermes spp.</i>	-	-	-	1	-	-	-	-	-	-	-	-	III
<i>Cubitermes spp.</i>	-	-	-	-	-	-	2	-	-	-	-	-	IV
<i>Lepidotermes spp.</i>	-	-	-	-	-	-	2	-	-	2	-	-	IV
<i>Microcerotermes spp.</i>	10	3	3	21	6	4	15	-	-	25	1	1	II
<i>Promirotermes spp.</i>	-	-	-	5	-	-	4	-	-	-	-	1	III
Nasutitermitinae													
<i>Trinervitermes trinervoides</i>	-	-	-	1	-	-	1	-	-	4	-	-	II
<i>Rhadinotermes coarctatus</i>	-	-	-	-	-	-	1	-	-	-	-	-	II

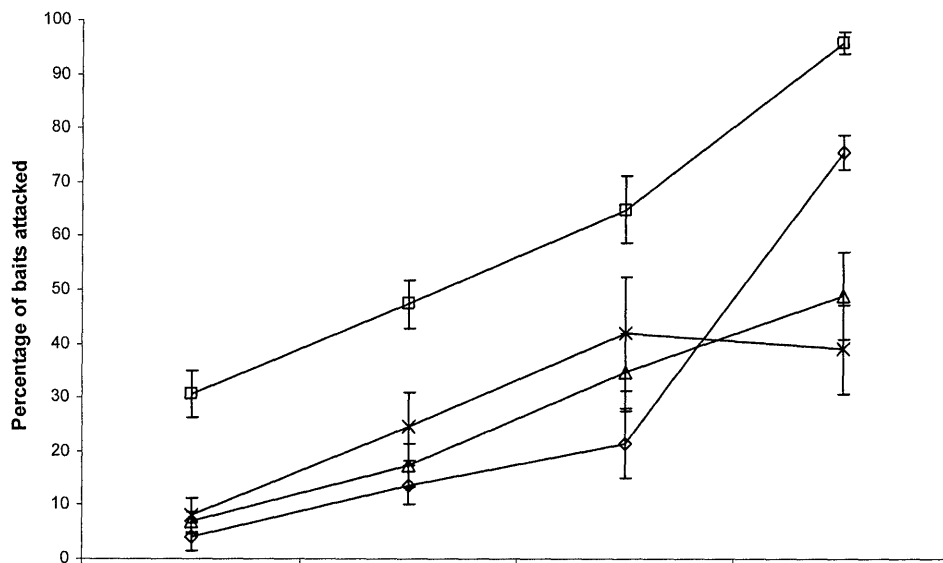
(a)



(b)



(c)



(d)

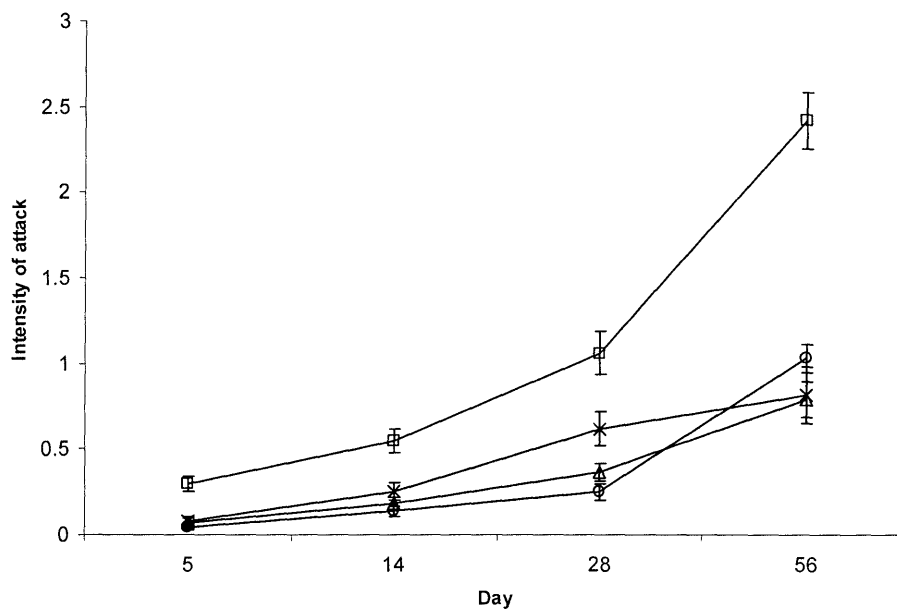


Fig. 1 Mean (\pm SE) (a) number of species recorded at baits, (b) number of species recorded at surface and buried baits, (c) intensity of attack on baits, and (d) percentage of baits attacked by termites at four censuses across four savanna sites

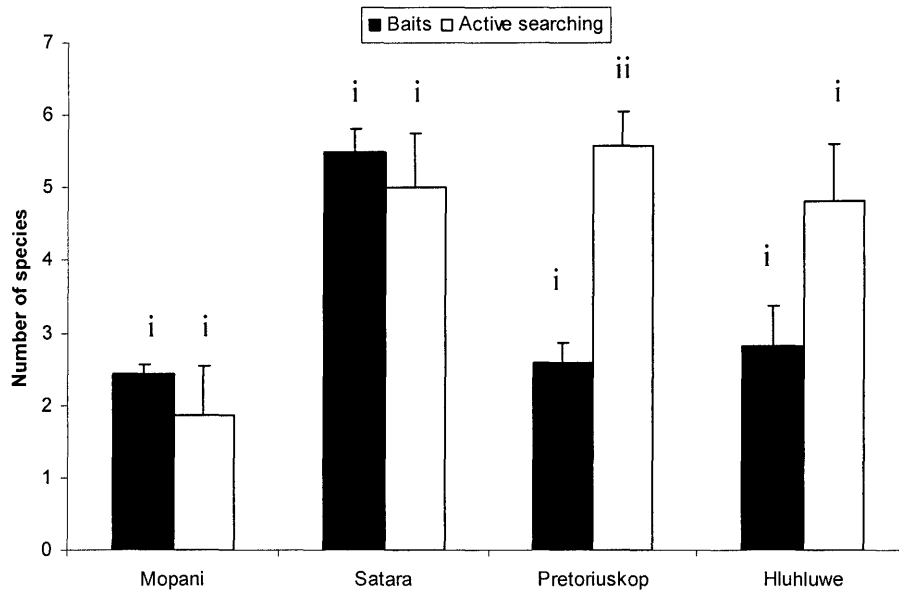


Figure 2: Overall mean (\pm SE) number of species recorded at baits and during active searching across four savanna types. Numerals denote significant differences within each savanna type.

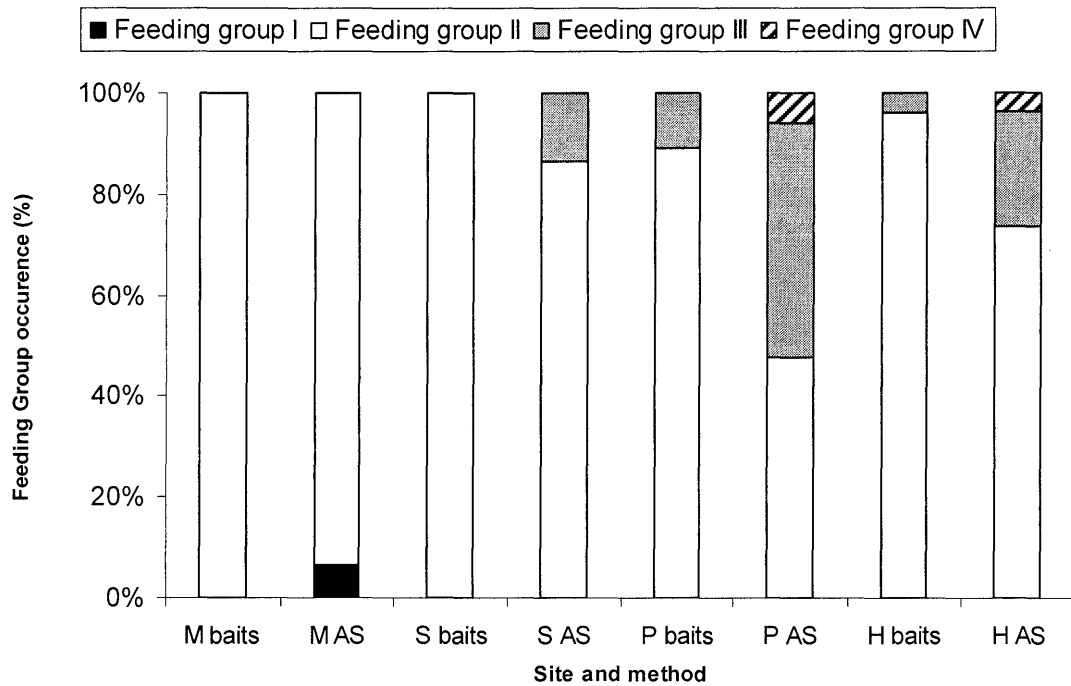


Figure 3: Feeding group composition of the termite assemblages sampled at each savanna site using baits and active searching. Feeding group I comprises the lower termites which feed on dead wood and grass; group II is made up of Termitidae with a range of feeding habits which include dead wood, grass, leaf litter and micro-epiphytes; group III feed in the organic rich upper soil layers and are also Termitidae; and group IV contains the true soil-feeders which ingest mineral soil, again all Termitidae. M = Mopani; S = Satara, P = Pretoriuskop, H = Hluhluwe, baits = cellulose baits, AS = active searching.

Chapter 5: Conclusions and recommendations

This thesis has addressed aspects of savanna termite ecology, a field of ecology which has been largely neglected relative to other taxa. In doing so, extensive termite sampling employing various methods has been undertaken, which is among the most comprehensive savanna termite sampling carried out to date for savannas across the globe. In addition to gathering information on effects of ecological patterns and processes on termites, a new genus record for South Africa, *Aneneotermes*, was recorded. Although comprehensive termite sampling has occurred elsewhere in the world (e.g. Eggleton *et al.* 1995, 1996), this is the first quantitative, systematic, repeatable and relatively complete sampling to be undertaken in multiple savanna habitats across several seasons.

As comprehensive as this sampling was, there are still other savanna habitats, even within Kruger National Park and Hluhluwe-iMfolozi Park, which have not been adequately sampled, for example the granite plains in the north of KNP where *Macrotermes* spp. mounds appear to occur at very high densities. In addition, the taxonomic constraints faced by termitologists, no doubt place further strain on our understanding of termite ecology, and if termite taxonomy were better resolved, surely higher levels of diversity would be recorded and an improved understanding of the underlying mechanisms responsible for spatial and temporal patterns of this diversity would be attained. The roles termites play in ecosystem functioning would also be better appreciated. Responses to burning regimes could well also be different if a finer scale analysis was possible highlighting the importance of multi-scale analyses in order to draw general conclusions from.

In terms of fire ecology and termites, much is still lacking in terms of empirical studies and broad conclusions cannot yet be drawn. In light of the results of this thesis, this becomes even clearer as termite communities along a rainfall gradient responded differently to fire. Findings prior to this thesis should therefore only be interpreted within the relevant savanna habitats sampled, and indeed within the termite suites sampled, as these are also shown here to respond differently to fire.

However, since fire is such a prevalent and important component of savanna ecosystems around the globe (Bond & Keeley 2005; Bond *et al.* 2005), studies

investigating its effects on diversity should be a priority. This is especially true in light of the current biodiversity crises (Abell 2002; Gilbert 2009; Olson *et al.* 2002) and the acknowledgement that the future survival of one species may be dependent on the survival of others; if species critical to ecosystem functioning become extinct or endangered, the implications for other taxa may be considerable (Koh *et al.* 2004; Pimm & Raven 2000). Potential mismanagement of fire in protected and non-protected areas could well lead to situations where diversity is threatened as a result of being susceptible to fire. Yet, in savanna systems of Africa and beyond, fire is used extensively as a management tool, often with a poor understanding of these potential repercussions.

Although effects of fire on vegetation are relatively well understood, this is not the case for fauna, especially invertebrates, which perpetuates the situation. This thesis aimed at addressing this shortfall to some extent, but runs the risk of standing alone if only a few other studies employing comprehensive sampling and carried out on long-term burning regimes are conducted. This highlights a current problem with fire ecology studies in that many of them are incomparable (see Parr & Chown 2003). If ecologists and conservation organisations are to better understand and manage savanna biodiversity, more comparable studies are necessary. This thesis suggests that this needs to take the form of studies focused on long-term burning regimes as indirect effects of fire are often more pronounced than direct effects. This is because many animals, particularly subterranean taxa such as termites, are often able to escape direct fire effects.

Using long-term burning regimes, this thesis found savanna termites overall to be highly resistant to fire. However, this level of resistance varied between markedly different savanna habitats, as did the termite communities present. This implies that studies which do investigate faunal responses to fire should be conducted in more than one habitat form, even within one dominant vegetation type or biome; conclusions from one form of habitat do not necessarily hold true for other areas. This has implications for more than just faunal studies, but also for more general ecology and indeed macroecological approaches.

Similar to the results related to variation in termite resistance, the efficiency of methods to sample termites showed significant differences when compared across savanna types. Consequently, studies (and especially sampling methods) need to be

comprehensive enough to encompass if not all, as many aspects of diversity as possible, particularly with regards to termites. Sampling method may also need to be adjusted according to the study site, one method which works well in one habitat may well be inappropriate for another.

Conservation implications

The maintenance of biodiversity in all its forms is one of the major goals of conservation bodies. Although in the past this goal has focused more on large, charismatic species, especially in southern Africa, the focus needs to shift to other taxa if the goal is to be met, including invertebrates (Parr & Chown 2003). In terms of conservation planning, vertebrates have also been favoured in the past as bioindicators to identify important areas for conservation and for tracking ecological change, with invertebrates often been ignored. However, it is important that invertebrates are included in this process, although this is often quite difficult to do because of insufficient knowledge of what is present and the distribution ranges of species. Invertebrates are proving, however, to be more reliable as bioindicators when data on distributions are available (McGeoch 1998; McGeoch & Chown 1998). Since fire is used as a management tool in southern African savanna reserves and elsewhere, it is important to have an understanding of the implications of different management forms for both the management of conservation areas and for future conservation planning. In lieu of this, several recommendations can be made from the findings of this thesis.

Firstly, termite communities showed large differences across savanna types, implying that ecologically, these systems function differently. Management approaches, whether fire policies or other issues, should therefore be modified according to different savanna habitats. One blanket approach to management in a large savanna park will not be appropriate for all areas; flexibility is necessary.

Second, because termite communities showed high levels of resistance to burning, managers can afford to focus attention on other taxa. Although not investigated fully, this seems to be the case for several other invertebrate groups. Ants for example have also shown high levels of both resistance and resilience in southern Africa (Parr *et al.* 2004), as have invertebrate groups in savanna systems elsewhere, such as springtails, flies,

mites, crickets, wasps, heteroptera, spiders, ants and grasshoppers in northern Australia (Andersen *et al.* 2005). This thesis does, however, provide support for the ‘stable’, ‘unstable’ approach to savanna systems suggested by Sankaran *et al.* (2005) with the implication that termites, and possibly other invertebrate groups, show more response to burning in mesic savannas; Parr *et al.* (2004) also found this to be true for ants. There is thus reason to suggest that in arid savannas, fire policies need not pay much attention to termites, but where burning occurs in mesic savannas, more care is necessary.

Finally, this thesis demonstrates that termite sampling should be adjusted according to savanna type. This is of relevance because efficient sampling of taxa is necessary in order to formulate species inventories and to understand ecological processes for better conservation efforts. This is particularly pertinent for termites, which are highly important taxa for ecosystem functioning and notoriously difficult to sample in savannas, with no widely applied sampling protocols yet developed. The findings of this thesis suggest a composite sampling protocol where possible, but where logistical constraints limit this, the savanna type being sampled needs to be considered when selecting for a specific sampling protocol.

Suggested future research directions

In order to further enhance understanding of both fire and termite ecology and improve efforts aimed at the conservation of biodiversity, the following are suggested future research directions:

- More comparable studies focused on fire ecology in Africa and around the globe are necessary. These should be focused on long-term burning regimes and, for termites, focus on the entire range of diversity.
- Studies comparing termite sampling methods in savanna systems would also be welcomed, especially studies comparing sampling efficiency across natural gradients such as vegetation changes.
- Turning it around, studies investigating the influence of termites on savanna ecology (e.g. decomposition processes and nutrient cycling) will

also be beneficial and help place this thesis in better context, as the implications of fire on termites will be better appreciated.

- Termites could also play a role in promoting or inhibiting fires and fire spread because of their foraging activities which remove dead grass and wood. Investigation of this would indeed contribute to fire and savanna ecology.
- Termite herbivore interactions were used in this thesis to explain some of the findings, yet they have been little tested. How termites, by concentrating nutrients, may effect herbivore distributions and how herbivores, by producing dung, may influence termite distribution and activity is also a research field worth exploring. (Eggleton *et al.* 1996)

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