Distribution and density of termite mounds in the northern Kruger National Park, with specific reference to those constructed by *Macrotermes* Holmgren (Isoptera: Termitidae)

V.W. Meyer[1*], L.E.O. Braack[2], H.C. Biggs[2] & C. Ebersohn[1]

[1]*Department of Nature Conservation, Technikon Pretoria, Private Bag X680, Pretoria, 0001 South Africa*
[2]*Scientific Services, Kruger National Park, Private Bag X402, Skukuza, 1350 South Africa*

At least ten 2 ha belt-transects were surveyed in each of the 20 northern landscape zones of the Kruger National Park. Termite mounds were recorded and activity within the termitaria was determined. Approximately 1.1 million active mounds occur in the northern KNP (approximately 47 % of all mounds in the area), with an average density of 1.1 active mounds/ha. The main mound-building genera were *Macrotermes* Holmgren (accounting for 62.4 % of all active mounds), *Cubitermes* Wasmann (29.8 %), *Amitermes* Silvestri (4.3 %), *Odontotermes* Holmgren (2.1 %) and *Trinervitermes* Holmgren (1.4 %). *Macrotermes* had an average mound density of 0.73/ha, with *M. natalensis* (Haviland) and *M. ukuzii* Fuller comprising the dominant species at densities of 0.27 and 0.25 mounds/ha respectively. *Macrotermes* preferred sandy, granitic soils to basaltic clay, while undulating topography was preferred to concave flood plains. The spatial distribution of both active and inactive mounds of all termite species was aggregated.

Key words: termite mounds, Isoptera, Termitidae, Macrotermitinae, *Macrotermes, M. natalensis, M. ukuzii,* Termitinae, *Cubitermes,* Kruger National Park.

INTRODUCTION

Twenty two genera of termites have been recorded in the Kruger National Park (KNP), which covers almost two million hectares of South Africa (Coaton 1962). The mound-building genera include *Macrotermes* Holmgren, *Cubitermes* Wasmann, *Amitermes* Silvestri, *Odontotermes* Holmgren and *Trinervitermes* Holmgren.

Southern African termites were taxonomically well surveyed during the National Survey of Isoptera (1955–1982) conducted by W.G.H. Coaton and J.L. Sheasby (Plant Protection Research Institute). The distribution of southern African termites was reviewed by Ruelle (1978), while that of *Macrotermes* was documented by Ruelle *et al.* (1975).

Coaton (1962) conducted a taxonomic study of termites in the KNP, with some reference to their geographical distribution, while Van der Schijff (1965) studied the occurrence of *Macrotermes* mounds in relation to plant communities. Despite the high diversity of termites in the KNP (Coaton 1962; Muller *et al.* 1997), relatively few ecological studies have been conducted. Braack (1995) investigated seasonal and drought responses of non-mound-building termites in the southern KNP.

As termites are pivotal in nutrient cycling, we embarked on a project to establish quantitative baseline data for future reference and monitoring. Traditional management policies tend to focus on mammal populations owing to their high visibility, tourism value and the potential of some to significantly influence local environments when over or under-populated. This makes it difficult to formulate invertebrate management policies. For instance, the effect of fire regimes on the Isoptera (and hence on other ecosystem components) cannot be assessed without the appropriate distribution and density estimates.

To determine and quantify the distribution and density of mound-building termites, we surveyed the northern parts of the KNP because of the abundance and conspicuousness of mounds in that area. By using the landscapes classified by Gertenbach (1983) as *a priori* functional units, we attempted to determine possible reasons (*i.e.* preferences) for *Macrotermes* abundance in certain areas. The purpose of our study was to determine the distribution and mound density of *Macrotermes* species, in particular, in the northern KNP.

*To whom correspondence should be addressed: PO Box 1969, Wingate Park, 0153 South Africa.
E-mail: VictorMeyer@iname.com

MATERIAL AND METHODS

Study area

The northern KNP is the area comprising about 981 000 ha north of the Olifants River, between latitudes 22.32S and 24.04S (Meyer 1997). This area is characterized by mopane veld with a mean annual rainfall of 494 mm, and an elevation ranging from 300 to 450 m (Acocks 1988; Dent *et al.* 1987). In this study, we used Gertenbach's (1983) landscape classification of the KNP, which is based on differing associations of geomorphology, soils, vegetation patterns, fauna and climate.

Sampling procedure

At least 10 belt-transects of 1 km by 20 m (*i.e.* 2 ha strips) were surveyed in each of the 20 northern landscape zones (Gertenbach 1983), during 1995. Approximate localities of transects were determined by mapping before entering a landscape area so as to avoid bias. The main criteria applied for transect placement were as follows: (i) accessibility from roads and firebreaks, (ii) an even and wide spread across each landscape zone and, (iii) no bias towards any particular landscape zone (equivalent number of transects in each zone, independent of its area). Transects started approximately 30 m from roads to exclude the possibility of disturbed veld conditions, since roadside banks were sometimes preferred sites for mounds (Pomeroy 1977). Positional fixes at the start and completion of each transect were recorded with a Global Positioning System (GPS) receiver for geo-referencing purposes.

The total number of mounds within each transect was recorded. No minimum size limitation was applied (Pomeroy 1977, 1978), and small and even obscure, vegetation-covered mounds were carefully sought. Each mound's termite activity was confirmed by exposing its interior.

Termite specimens were collected from active mounds for identification. More than a third of the samples were deposited in the National Collection of Insects, ARC-Plant Protection Research Institute, as a reference series and for identification by V.M. Uys. Identification was also facilitated by published keys (*e.g.* Harris 1971; Coaton & Sheasby 1972; Ruelle 1989).

The number of active mounds in the entire study area was estimated by weighting mound numbers in the different landscapes according to the proportion of the area each landscape occupied. For comparison, a non-weighted procedure was also carried out. Mound density was estimated for each landscape zone using the formula $d = {}^{n}/_{s}$, where n = number of mounds sampled and s = area sampled (Meyer 1997).

Statistical procedures

The effect of landscape on mound density was assessed by the Kruskal-Wallis one-way ANOVA (analysis of variance by ranks), followed by the Dunn multiple-comparison analysis (Zar 1996). Bonferroni adjustment to significance levels (Johnson & Wichern 1992) was applied if multiple testing was carried out, even partially on the same data. The Dunn analysis makes provision for experimental groups (*i.e.* 20 landscapes) with unequal sample sizes to be compared. All testing was carried out at a confidence interval (C.I.) of 95 % ($\alpha = 0.05$).

The most important landscape attributes (Gertenbach 1983) relative to termite distribution (*i.e.* geomorphology and soil) were considered when interpreting differences in mound density between landscapes. For clarity (Fig. 1), landscapes were classified into large geological groupings (granitic, basaltic and other rock beds) by the use of Geological Survey (1981, 1985) maps, and the classifications of Gertenbach (1983) and Venter (1990). Other rock types (Fig. 1) may yield soils from sand to clay.

The method of Odum (1971) for determining spatial patterns of distribution, referred to as 'dispersion', was used to compare the variance of the mound counts between different landscape zones to the mean. The variance equals the mean for random (normal) distribution, but is greater than the mean for clumped (aggregated) distribution and smaller than the mean for a uniform or regular (overdispersed) pattern.

RESULTS

Density estimates of termite mounds

Using a weighted procedure, it was estimated that approximately 1.1 million active mounds occur in the northern KNP (approximately 47 % of all mounds), with almost 720 000 being those of *Macrotermes.* By contrast, the non-weighted procedure estimated about 1.2 million active mounds including 724 000 *Macrotermes* mounds.

The densities of active mounds of different species of termites are reflected in Table 1. A total

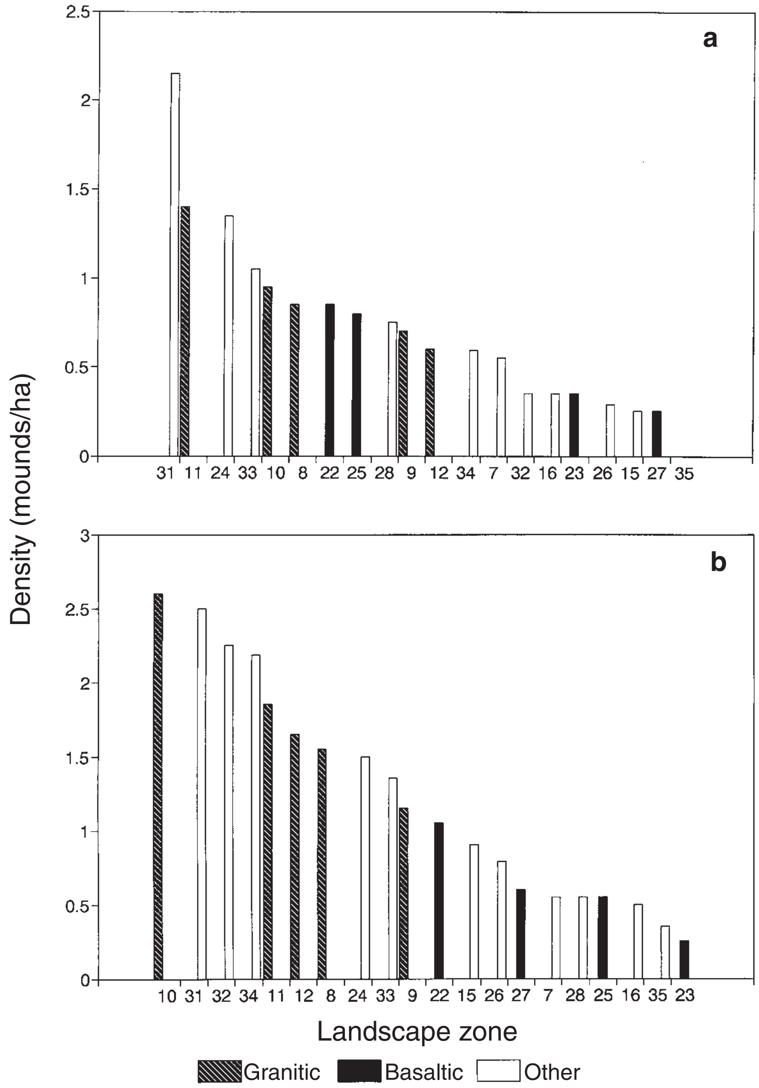

Fig. 1. Density of active (**a**) and inactive (**b**) mounds of *Macrotermes* in different landscapes of the northern Kruger National Park.

density of 1.11 active mounds/ha (111/km^2) for all mound-building termites was calculated. *Macrotermes* had an estimated density of 0.73 active mounds/ha (73/km^2), and the most abundant (dominant) species were *Macrotermes natalensis* (Haviland) at 0.27 mounds/ha (27/km^2) and *Macrotermes ukuzii* Fuller at 0.25 (25/km^2) mounds/ha.

Mound density and distribution of *Macrotermes*

The Kruskal-Wallis tests revealed significant differences in mound counts between the landscapes for both active ($P < 0.01$; $k = 20$; $n = 206$) and inactive ($P < 0.001$; $k = 20$; $n = 206$) *Macrotermes* mounds. The subsequent Dunn analyses revealed significant differences in mound density between individual landscapes (Table 2). The landscape attributes of zones where differences were noted provided some explanations for these differences (Table 2).

Considering active *Macrotermes* mounds, it appears that the undulating topography, with lithosols on koppies, of landscape zones 24 and 31 is preferred by these termites to the concave flood

Table 1. Estimated density of active mounds of different termite species in the northern Kruger National Park.

Species	Mound density (per ha)
Macrotermes natalensis (Haviland) (Macrotermitinae)	0.27
Macrotermes ukuzii Fuller (Macrotermitinae)	0.25
Macrotermes michaelseni (Sjöstedt) (Macrotermitinae)	0.12
Macrotermes falciger (Gerstäcker) (Macrotermitinae)	0.027
Macrotermes sp. (Macrotermitinae)	0.075
Cubitermes spp. (Termitinae)	0.33
Amitermes spp. (Termitinae)	0.051
Odontotermes prob. *latericius* (Haviland) (Macrotermitinae)	0.015
Odontotermes sp. (Macrotermitinae)	0.010
Trinervitermes dispar (Sjöstedt) (Nasutitermitinae)	0.015
Trinervitermes trinervoides (Sjöstedt) (Nasutitermitinae)	0.0024

Table 2. Comparisons of *Macrotermes* mound densities between landscape zones, with emphasis on those where significant differences were shown. Landscape attributes (Gertenbach 1983) are included for explanation of these differences.

Mound density	Landscape comparisons	
	Landscape attributes of zones with higher counts	Landscape attributes of zones with lower counts
Active mounds		
24 and 31 higher than 35	Undulating topography	Concave flood plains
	Lithosols on koppies	Brackish soils with white, surface salt deposits
Inactive mounds		
10 higher than 7, 16, 23 and 35	Moderately steep slopes	Flat to concave with vleis or flood plains; bottomlands and plateaus or alternatively steep slopes
32 higher than 23 and 35	Flat	Concave with vleis or flood plains
	Quaternary sand	Basalt with dolerite or alluvium
31 higher than 23 and 35	Strongly undulating (mountain range)	Flat to concave with vleis or flood plains
	Rhyolite	Basalt with dolerite or alluvium

plains, with brackish soils and salt deposits, of zone 35 ($P < 0.05$) (Fig. 1a, Table 2). Landscape zone 31 had the highest occurrence of active mounds, but zone 11 did not have significantly higher mound abundance than the lower ranking zones (Fig. 1a). This area has substantially less clay than landscape 24 and is more undulating (Gertenbach 1983). However, there were no significant differences in mound densities between these two landscapes and both supported high densities compared to the other 18 landscapes (Fig. 1a).

With regard to inactive *Macrotermes* mounds, it is difficult to find common attributes for landscapes 10, 32 and 31, where the mound densities were significantly higher than those of landscapes 23 and 35 (Fig. 1b, Table 2). However, it appears that *Macrotermes* mounds are unlikely to occur on concave flood plains or vleis, or on basalt (with dolerite) or alluvium ($P < 0.05$).

Landscape zone 23 (Mopane Shrubveld on Basalt), having high clay soils (Gertenbach 1983), supports very few termite mounds, compared with the landscapes to the west (being mainly on granitic rock beds with sandy soils) which are highly populated (Figs 1, 2). It appears that active mounds are uncommon on the basaltic landscapes

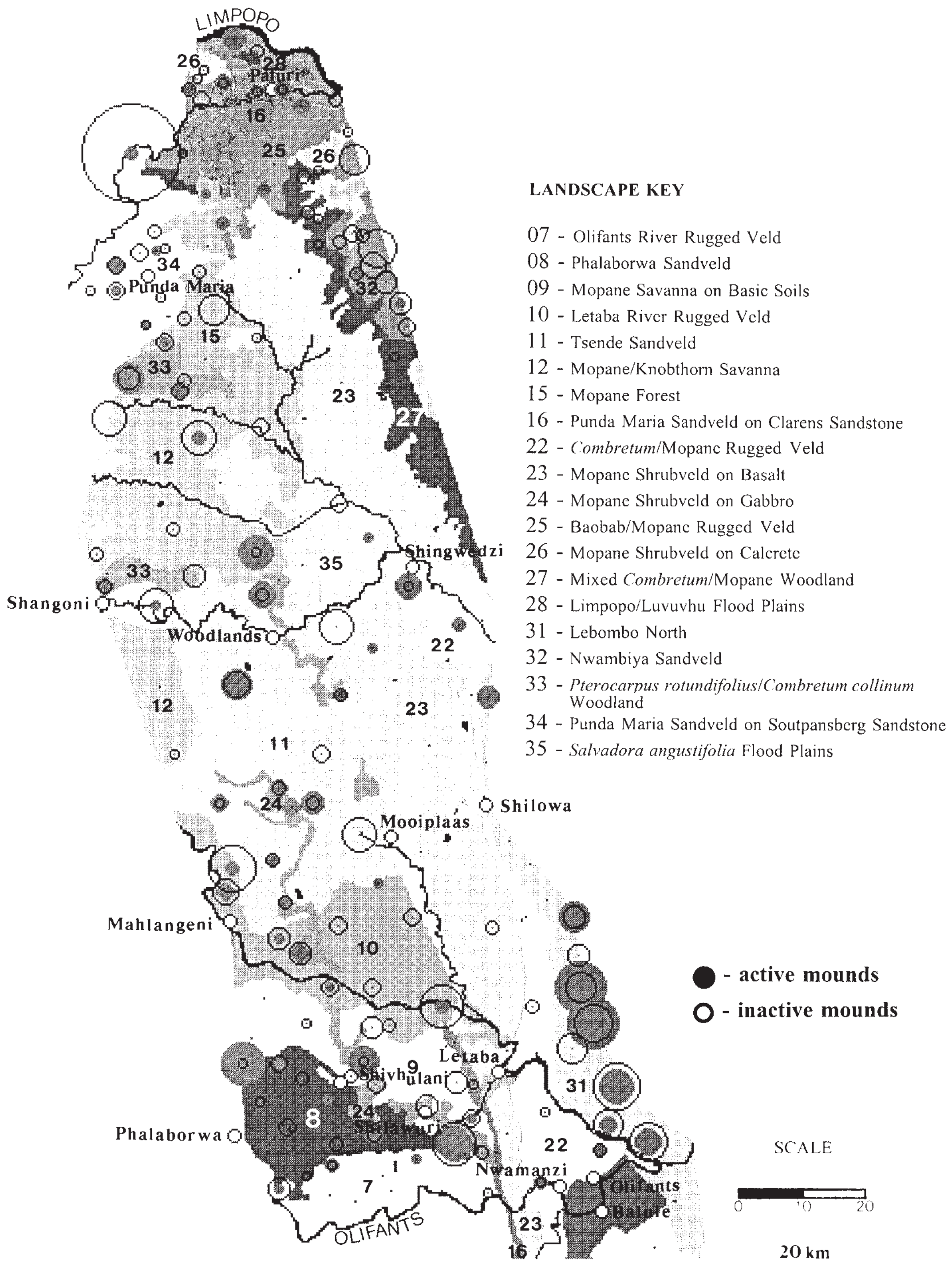

Fig. 2. Distribution and abundance of *Macrotermes* mounds, overlaid on landscapes of the northern Kruger National Park (based on transect plots). (The bigger the disc/circle, the larger the depicted abundance.)

(zones 23, 25 and 22) (Fig. 1a). Densities of inactive mounds (Fig. 1b) provided even stronger evidence of preferences for granitic zones over the basaltic areas.

Active mounds of *Macrotermes* are present in high numbers on the Lebombo Mountains, as well as around Shilawuri, Shivhulani, Malopeni, Mahlangeni and throughout the Woodlands region (Fig. 2). Areas of high inactive mound densities in landscape zones 10 (Letaba River Rugged Veld) and 31 (Lebombo North) are also indicated (Fig. 2).

Spatial distribution pattern of termite mound populations

The spatial distribution of active mounds ($\overline{X}$ = 2.36; s^2 = 24.0083) and inactive mounds ($\overline{X}$ = 2.68; s^2 = 9.8286) of all termites in the northern KNP is clumped, as their variances are greater than the means. This was also true of both active ($\overline{X}$ = 1.48; s^2 = 4.7482) and inactive ($\overline{X}$ = 2.50; s^2 = 7.9683) mounds of *Macrotermes.*

Although active mounds of both *M. natalensis* ($\overline{X}$ = 0.54; s^2 = 2.5229) and *M. ukuzii* ($\overline{X}$ = 0.49; s^2 = 1.4023) have a clumped distribution, in *M. ukuzii* the variance approaches the mean more closely, suggesting a distribution tending towards normality.

DISCUSSION

There are 6 % fewer active mounds (47 % of all mounds) in the northern KNP than inactive termitaria. Because inactive mounds are indicators of historic termite density, they can enhance the results obtained from active mounds, that relate to current density, as is evident from this study.

Lepage (1974) reported approximately 0.5 mounds/ha for *Macrotermes subhyalinus* (Rambur) in Senegal. According to Pomeroy (1977), *Macrotermes* species (mainly *M. bellicosus* (Smeathman) and *M. subhyalinus*) have a density ranging from 1–4 mounds/ha in most parts of Uganda. Mound density for Macrotermitinae in Zambia was estimated at 3–5/ha (Trapnell *et al.* 1976). It therefore appears that mound densities of *Macrotermes* in East and Central Africa are higher than in the northern KNP (0.73/ha), but lower in West Africa.

Macrotermes mounds tend to be more abundant on sandy soils, whereas they are less abundant and smaller on basaltic and doleritic soils (Van der Schijff 1965). These observations are mostly consistent with the results of this study (Fig. 1). However, it is unclear to what extent the granitic and undulating factors in landscapes contribute to these patterns.

Montmorillonite (three-layer clay), which is present in the soils of the basaltic landscape 23 (Gertenbach 1983), can absorb water molecules into the interlayers and so expand, effectively reducing water transmission rates and contributing to waterlogging. This may explain the low density of *Macrotermes* mounds recorded in this landscape. However, other high clay soils might have a structure that allows improved water transmission (Holt, pers. comm.), making them more suitable for supporting mounds. Indeed, active and inactive *Macrotermes* mound numbers for landscape zone 24 (Mopane Shrubveld on Gabbro) are high to relatively high (Fig. 1a,b). Soils of this landscape have large amounts of clay (Gertenbach 1983) which are permeable, without a tendency to be waterlogged (Venter, pers. comm.).

Termites need clay to bind sand particles when constructing mounds (Coaton & Sheasby 1972; Josens 1983). Pomeroy (1978) found that mound density was determined by clay content in soils at a depth of 1 m, while Bodot (1967) reported that *M. natalensis* uses clay, largely from the moist subsoil, for mound construction. Coarse-textured soils containing little silt and clay are unsuitable for mound construction. Soils that develop deep, wide cracks when dry (*e.g.* vertisols and other soils with high swell/shrink properties (active clays), such as montmorillonite of zone 23) are also unsuitable because of structural instability caused by expansion and contraction during inundation and desiccation. However, in soils of low activity clays, the suitability for mound construction generally increases with increasing clay content (Gertenbach 1983; Lal 1987; Soil Classification Working Group 1991; Venter, pers. comm.).

The present study showed that those landscapes with koppies or elevation characteristics have higher numbers of mounds. The eastern parts, especially zone 23, have little or no drainage, in contrast to the western granitic landscapes that are usually well-drained. This topographical factor may explain the low termite abundance on the eastern basaltic plains. Increased drainage may thus have a positive influence on termite mound density in the northern KNP. In Botswana, Schuurman & Dangerfield (1997) found that *Macrotermes michaelseni* (Sjöstedt) colonies could only tolerate very short periods of inundation. No active mounds of any termite genus were found on the *Salvadora* Flood plains (landscape 35), again suggesting low tolerances to inundation. Nkunika (1986) found that species diversity of termites in Zambia decreased from woodland to flood plain habitats, due to periodic flooding disturbance.

The strongly undulating mountain ridge of the Lebombo North (landscape 31) supports high mound densities (Fig. 1). According to Venter (unpubl.), this landscape's crestal rhyolitic soils have an average clay content of approximately 17 %, qualifying them as sandy loam (Soil Classification Working Group 1991). The rhyolite of this area is similar in chemical composition to the granitic rock types of the west, except for weathering differences (Venter 1990). Mound densities on the western granites are also high. Although *Macrotermes* mounds are abundant in the rocky mountainous areas of the Lebombo North (zone 31) (Fig. 2), they are generally smaller than those in the western landscapes (Meyer, unpubl.) Mound size may thus be limited by a lack of soil, as most places in the Lebombos are classified as lithosols (Gertenbach 1983).

The spatial distribution of all termite mound populations was aggregated, which represents by far the most common pattern of spatial distribution (Odum 1971). Random distribution is relatively rare in nature and occurs where the environment is homogeneous and where many minor factors act together on the population. When a few major factors dominate, as is usually the case, there is a tendency to aggregate. Uniform distributions prevail when competition is severe or where there is positive antagonism, promoting even-spacing.

In the northern KNP, there was no evidence of severe competition during comparisons of both active and inactive mounds involving all termite colonies, colonies of *Macrotermes* only, or colonies of the two dominant species of *Macrotermes* (only active mounds). Studies in West Africa by Collins (1981) and Lepage (1984) revealed that mounds of *M. bellicosus* were distributed randomly, from which they concluded that intraspecific competition was not a key factor in regulating distribution. Studies by Eggleton *et al.* (1996) in Cameroon revealed that, in all cases, termite abundance was highly clumped. The tendency of mounds to be aggregated in the northern KNP therefore suggests that a few major factors (presumably topography, geology and soil) are dominant in regulating their distribution.

ACKNOWLEDGEMENTS

We thank the following persons for their assistance: V.M. Uys, J.E. Ruelle, F.J. Venter, J.A. Holt, C.C. Grant, N. Zambatis, C.V. Maré, C.A. Wood, P.C. Viljoen, N. Baloyi, A.K. Nkuna and M.R. Mashabane. The South African National Parks and Technikon Pretoria provided logistical support and V.M. Uys (ARC-Plant Protection Research Institute) identified the specimens. The Foundation for Research Development is acknowledged for funding, while Towmaster is thanked for donating front protection bars for the research vehicle and Pertec International for the loan of a GPS unit.

REFERENCES

ACOCKS, J.P.H. 1988. Veld types of South Africa. 3rd Edition. *Memoirs of the Botanical Survey of South Africa* **57**: 1–146.

BODOT, P. 1967. Études écologique des termites des savanes de Basse Côte d'Ivoire. *Insectes Sociaux* **14**: 229–258.

BRAACK, L.E.O. 1995. Seasonal activity of savanna termites during and after severe drought. *Koedoe* **38**: 73–82.

COATON, W.G.H. 1962. Survey of the termites of the Kruger National Park. *Koedoe* **5**: 144–156.

COATON, W.G.H. & SHEASBY, J.L. 1972. Preliminary report on a survey of the termites (Isoptera) of South West Africa. *Cimbebasia* **2**: 1–29.

COLLINS, N.M. 1981. Populations, age structure and survivorship of colonies of *Macrotermes bellicosus* (Isoptera: Macrotermitinae). *Journal of Animal Ecology* **50**: 293–311.

DENT, M.C., LYNCH, S.D. & SCHULZE, R.E. 1987. Mapping mean annual and other rainfall statistics over southern Africa. *W.R.C.-A.C.R.U. Report* 109/1/89; 27.

EGGLETON, P., BIGNELL, D.E., SANDS, W.A., MAWDSLEY, N.A., LAWTON, J.H., WOOD, T.G. & BIGNELL, N.C. 1996. The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of the Royal Society of London* (B)**351**: 51–68.

GEOLOGICAL SURVEY. 1981. *1: 250 000 – Geological Series: 2230 Messina.* Government Printer, Pretoria.

GEOLOGICAL SURVEY. 1985. *1: 250 000 – Geological Series: 2330 Tzaneen.* Government Printer, Pretoria.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* **26**: 9–121.

HARRIS, W.V. 1971. *Termites: Their Recognition and Control.* 2nd Edition. Longman, Harlow.

JOHNSON, R.A. & WICHERN, D.W. 1992. *Applied*

Multivariate Statistical Analysis. 3rd Edition. Prentice-Hall, Upper Saddle River.
JOSENS, G. 1983. The soil fauna of tropical savannas. III. The termites. In: Bourlière, F. (Ed.) *Ecosystems of the World 13: Tropical Savannas.* 505–524. Elsevier, Amsterdam.
LAL, R. 1987. *Tropical Ecology and Physical Edaphology.* Wiley, Chichester.
LEPAGE, M. 1974. Les Termites d'une savane sahélienne (Ferlo Septentrional, Sénégal): Peuplement, populations, consommation, rôle dans l'écosystéme. D.Sc. thesis, University Dijon, Dijon.
LEPAGE, M. 1984. Distribution, density and evolution of *Macrotermes bellicosus* nests (Isoptera: Macrotermitinae) in the north-east of Ivory Coast. *Journal of Animal Ecology* **53**: 107–117.
MEYER, V.W. 1997. Distribution and density of mound-building termites in the northern Kruger National Park. M.Tech. thesis, Technikon Pretoria, Pretoria.
MULLER, C., FREITAG, S., SCHOLTZ, C.H. & VAN JAARSVELD, A.S. 1997. Termite (Isoptera) distributions, endemism, species richness and priority conservation areas: consequences for land-use planning in South Africa. *African Entomology* **5**: 261–271.
NKUNIKA, P.O.Y. 1986. An ecological survey of the termites (Isoptera) of Lochnivar National Park, Zambia. *Journal of the Entomological Society of Southern Africa* **49**: 45–53.
ODUM, E.P. 1971. *Fundamentals of Ecology.* 3rd Edition. Saunders College Publishing, Philadelphia.
POMEROY, D.E. 1977. The distribution and abundance of large termite mounds in Uganda. *Journal of Applied Ecology* **14**: 465–475.
POMEROY, D.E. 1978. The abundance of large termite mounds in Uganda in relation to their environment. *Journal of Applied Ecology* **15**: 51–63.
RUELLE, J.E. 1978. Isoptera. In: Werger, M.J.A. & Van Bruggen, A.C. (Eds) *Biography and Ecology of Southern Africa.* 747–762. Junk, The Hague.
RUELLE, J.E. 1989. Isoptera. In: Scholtz, C.H. & Holm, E. (Eds) *Insects of Southern Africa.* 2nd Edition. 53–61. Butterworths, Durban.
RUELLE, J.E., COATON, W.G.H. & SHEASBY, J.L. 1975. National Survey of the Isoptera of southern Africa. 8. The genus *Macrotermes* Holmgren (Termitidae: Macrotermitinae). *Cimbebasia* (A)**3**: 73–94.
SCHUURMAN, G. & DANGERFIELD, J.M. 1997. Dispersion and abundance of *Macrotermes michaelseni* colonies: a limited role for intraspecific competition. *Journal of Tropical Ecology* **13**: 39–49.
SOIL CLASSIFICATION WORKING GROUP. 1991. Soil classification: a taxonomic system for South Africa. *Memoirs on the Agricultural Natural Resources of South Africa* **15**: 1–257.
TRAPNELL, C.G., FRIEND, M.T., CHAMBERLAIN, G.T. & BIRCH, H.F. 1976. The effects of fire and termites on a Zambian woodland soil. *Journal of Ecology* **64**: 577–588.
VAN DER SCHIJFF, H.P. 1965. Die invloed van termitaria op die plantegroei van die Nasionale Krugerwildtuin. *Tydskrif vir Natuurwetenskappe* **5**: 48–54.
VENTER, F.J. 1990. A classification of land for management planning in the Kruger National Park. Ph.D. thesis, University of South Africa, Pretoria.
ZAR, J.H. 1996. *Biostatistical Analysis.* 3rd Edition. Prentice-Hall, Upper Saddle River.

Accepted 4 November 1998