Seasonal activity of savanna termites during and after severe drought

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As part of a broad programme to record the influence of severe drought on selected target populations, two taxa of termite were monitored over a 24-month period in the southern Kruger National Park, South Africa. Activity of harvester termites *Hodotermes mossambicus* reached highest levels during the drought, while macrotermitine *Allodontermes rhodesiensis* and *Microtermes* sp appear to favour less extreme levels of rainfall. The general impact of termites in the KNP is discussed and related to studies elsewhere in Africa.

Key words: drought, termites, savanna, *Hodotermes*, *Allodontermes*, *Microtermes*.

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Introduction

Termites are important elements of savanna ecosystems and their removal of plant biomass frequently rivals that of mammals (Wood & Sands 1978; Delany & Happold 1979; Josens 1983; Lamotte & Bourlière 1983; Deshmukh 1989). In the Kruger National Park (KNP) at least 22 genera of termites are known to occur (Coaton 1962), each with their own food and habitat requirements. They also respond differently to climatic conditions, with at least one species, *Hodotermes mossambicus* (Hagen), favourably influenced by drought conditions (Gouse 1985).

It is well known that in the summer rainfall areas of South Africa, including the KNP, cycles of approximately 10 years of above-average rainfall alternate with periods of similar duration of below-average rainfall (Tyson & Dyer 1978; Gertenbach 1980; Tyson 1986). Vegetational changes resulting from such climatic cycles are known to significantly affect vertebrate populations (e.g. Whyte 1985), while equivalent changes are also known for a wide range of insects (e.g. locusts).

The 1980s decade was characterised by low rainfall and, following chronic drought conditions during 1990 and 1991, it became obvious during early-1992 that the ensuing months would probably be the most intense drought in the recorded history of southern Africa. The KNP Management therefore regarded this as a unique opportunity to record the impact of such a drought on selected indicator organisms, termites forming one of the groups targeted for monitoring. This was not intended to be an exhaustive, intensive study, but rather a low-key programme aimed at establishing certain baseline values against which the impact of future droughts could be gauged; it is in this context that the findings reported below should be viewed.

This paper reports on the activity of *Hodotermes mossambicus* (Hodotermitidae) and combined activity of *Microtermes* sp. and *Allodontermes rhodesiensis* (Sjöstedt) (Termitidae: Macrotermitinae) monitored at monthly intervals over a 24-month period commencing during the worst months of the 1992 drought.

Materials and Methods

Since this was an opportunistic study adjunct to the normal research programme, monitoring activities had to be kept at the simplest level and it was decided to concentrate on two groups which by the nature of their activities lend themselves to rapid and easy assessment.

The harvester termite *H. mossambicus* was selected because it occurs widespread and commonly throughout the KNP, is known to be beneficially affected by dry conditions, and it deposits easily-visible, pyramid-shaped dumps of soil and other waste material aboveground which are ideal indicators of colony activity. Such soil-dumps have also been used in other studies as a convenient means of tracking colony activity (e.g. Hartwig 1965; Nel & Hewitt 1969). Three routes totalling 25 km near Skukuza in Landscape Zone 4 'thickets of the Sabie and Crocodile rivers' (Gertenbach 1983) were travelled (average speed 15-20 km/hr) each month, and the number of harvester termite pyramids counted. These routes (Skukuza staff village to Narina hut, Narina hut to near tarred road, and "Fishing road" along Sabie River east of Skukuza) were chosen because they are infrequently-used and therefore subjected to minimal disturbance which may affect termite activity. To standardise and avoid under-counting during grass-covered wet season, only pyramids within the road or within 30 cm of the roadside were counted; for similar reasons of standardisation, the numerous irregularly-shaped soil mini-pyramids (10 - 20mm high) left by swarming reproductives during November or December each year were not counted.

Microtermes sp and *A. rhodesiensis* are also widespread and common, forming suitable indicator species because they leave conveniently-visible soil runways as evidence of their activity. A transect at a standardised site along the Fishing Road, 2 km east of Skukuza, was used each month to monitor combined activity of these species. Starting 10 m off the road, a game-path was followed. At every third step a one-square-metre area on the left side of the path was visually assessed for a) presence or absence of soil runways b) percentage area of the square-metre plot covered by termite runways and c) percentage area of the square-metre plot covered by vegetation (ground surface coverage, dead or growing), until one hundred such plots had been recorded. Vegetation in this study area comprised fairly open to moderately dense stands of mixed *Grewia bicolor* and *Dichrostachys cinerea*, while the dominant grasses were *Eragrostis rigidior*, both subspecies of *Aristida congesta* (*barbicollis* & *congesta*) and *Themeda triandra*.

Termite identifications were done by the Biosystematics Division, Plant Protection Research Institute, Pretoria.

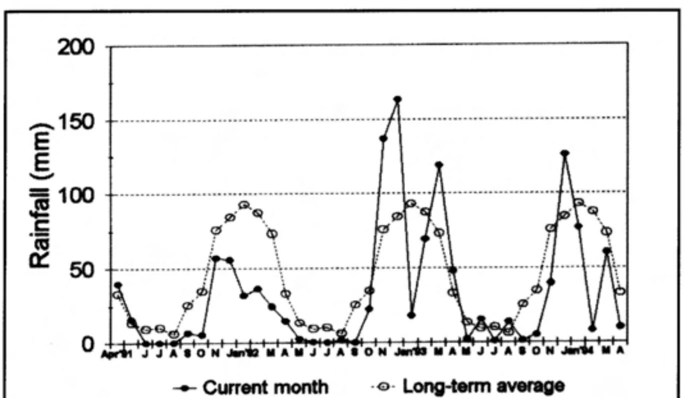

Fig.1. Monthly rainfall for Skukuza during the period April 1st 1991 to April 30th 1994 (filled circles), compared with the 74-year average rainfall for each month (open circles).

Fig. 2. Collective monthly counts of harvester termite (*Hodotermes mossambicus*) soil pyramids along three routes near Skukuza.

Results

Hodotermes mossambicus

Monthly rainfall before and during the monitoring period, as well as the long-term (74 years) average expected rainfall for each month for Skukuza are provided in Fig. 1. Cumulative counts of harvester termite pyramids along all 3 routes are presented in Fig. 2 (except for three months when the author was absent).

The highest count of termite mounds was in May 1992, at the onset of the cold season and immediately preceding the severest, final part of the drought. Counts made during the 1992 drought were higher (28%) than in equivalent months the following year, whereas collective pyramid counts in 1993 were lower (19%) than in equivalent months of 1994. Although there is no statistically valid correlation between mound counts and monthly rainfall, an intuitive trend does seem to exist: activity (as evidenced by the number of pyramids) was high during the early dry season (April–July), declined in the late dry season (August–September/October), experienced brief increases sometime during the early wet season (October–December) but mostly were at low levels during the months of high rainfall.

Microtermes sp / Allodontermes rhodesiensis

No consistent pattern is discernable when comparing the activity trends of these termites (Fig. 3a) against monthly rainfall (Fig. 1). During some months when there is a continuous increase in rainfall, termite activity declined (Oct.–Dec. 1992), whereas the next year during the same rainfall trend termite activity increased (Oct.–Dec. 1993); since monitoring was done randomly on only one day each month (not timed according to rain), the post-rainfall interval may be important and partly explain these anomalous results. Nevertheless, a higher percentage of plots showed termite activity during the drought months than equivalent months the following year, but the months immediately following the drought (November 1992–April 1993) had lower counts than equivalent months in the next season (Nov. 1993–Apr. 1994).

Figure 3b shows the average area of the plots covered by recently-constructed soil

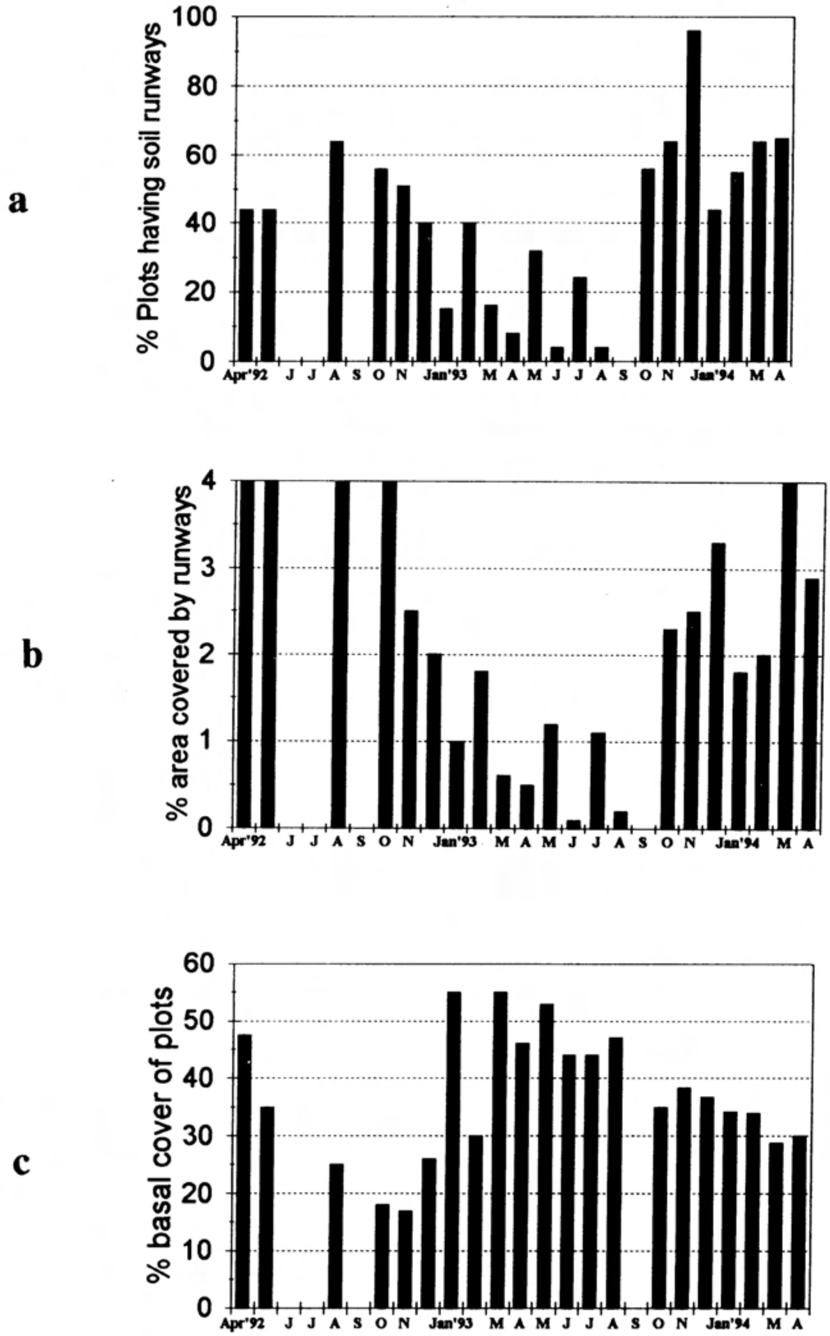

Fig.3. Monthly monitoring of plots frequented by *Allodontermes rhodesiensis* and *Microtermes* sp near Skukuza. (a) Percentage of plots having soil runways present. (b) Average area of each plot covered by soil runways. (c) Average vegetation cover of each plot.

runways, which is perhaps a better index of termite activity or abundance than the simple "Yes/No" answers upon which Fig. 3a is based. During the drought months an astonishingly consistent average of 4% of each sampling plot was covered by runways, but declined immediately with the onset of significant rain in November 1992. Average runway coverage persisted at below 2% during the wet season and continued thus throughout the dry winter months of 1993. With the arrival of the warm months of Spring (September/October 1993), but before the onset of the first significant rain of the wet season, activity (as measured by plot runway coverage) increased markedly and remained at elevated levels—although with some decline in January and February 1994—until in March 1994, after several months of below-average rainfall around Skukuza, plot coverage again reached 4% for the first time since October 1992.

The average basal cover (ground-level dead or live vegetation) in the monitoring plots is depicted in Fig. 3c. A clear pattern is visible; rapidly diminishing vegetation as the drought proceeded, reaching a minimum of 17% in November 1992. Good rain commencing in November 1992 resulted in a rapid flush of growth yielding average plot coverage of 55% by January 1993. Vegetation cover persisted at high levels (with some erratic troughs probably due to random sampling "error") until March 1993, followed by slow decline throughout the dry winter and even including the (sub-average) wet season of late 1993/early 1994, but never reaching the low levels achieved at the end of the 1992 drought.

Discussion

Hodotermes mossambicus

H. mossambicus is an underground-nesting termite forming extensive colonies throughout the drier savanna areas of the Afrotropical region (Coaton & Sheasby 1975). From a network of subterranean passages, it uses exit ports to forage aboveground, plugging these ports with moistened soil when not in use. Food consists of dry or green grass chewed into short lengths and carried below-ground to a series of interconnected storage chambers and hives between 10 cm and 7 m in depth (Coaton 1958; Hartwig 1965). Populations of this species are known to increase during dry years and, under such conditions, to compete seriously with mammalian grazers. During years of good rainfall they persist in patches where relatively dry conditions occur (Bissett & Macdonald 1974; Bissett 1981; Van der Linde *et al.* 1989).

Consumption of grass by *H. mossambicus* during certain years in Zululand may reach as much as 1.06 to 3.17 metric tons per hectare per year, while in the Orange Free State, light to moderate consumption is calculated to be 96 kg/ha which approximates 15% of total hay yield (Coaton 1958; Nel 1968). Elsewhere in the northern Orange Free State it was calculated to be 274 $kgha^{-1}yr^{-1}$ (Basson 1972). No estimates are available for consumption in the KNP, but I hold the opinion that although this species occurs commonly in many areas of the park; its consumption does not approach the combined intake of other above-ground foraging termites (Macrotermitinae), and that the extensive denudation visible during the drought in certain areas was caused by other termite species mentioned later in this paper.

Discussing various effects of the severe 1981-1983 drought in many parts of South Africa, Walker *et al.* (1987) refer to the situation in the KNP and state "...The decrease in grass during the drought was due not only to lack of growth and grazing by ungulates but also to harvester termites (*Hodotermes mossambicus*). There seemed to be an interaction between harvester termite damage and previous grazing history. In the winter of 1981, certain blocks were burnt according to the management plan. Large concentrations of wildebeest and zebra grazed the regrowth on these and, by late winter, harvester termites had removed the remaining grass, leaving only basal stubble. The worst affected were the base-rich soils. Blocks on the same soils that had not been burnt were much less affected by termites and still retained extensive stands of dry grass..." This is a somewhat misleading oversimplification and their statement that the termites involved were solely (or even mainly) *H. mossambicus* is erroneous. Those areas which were most noticeably affected by termites (most dramatically near Tshokwane and Lower Sabie but many places elsewhere) had not been burnt in the preceding two seasons, were heavily populated by Macrotermitinae and often showed no evidence of *H. mossambicus* (Braack *pers obs.*). The same phenomenon repeated itself during the 1991/92 drought and Macrotermitinae were again the main agents contributing to the denudation visible in certain areas of the basalt plains. Although the above-ground soil dumps of *H. mossambicus* were visible in many areas of the park and consumption by these termites must have been significant, they were not present in the areas near Tshokwane where denudation was complete and effected by Macrotermitinae. Nevertheless, it is well known that harvester termites preferentially colonise and utilise overgrazed or otherwise degraded areas of veld (Coaton 1958; Bissett & Macdonald 1974; Gouse 1985; Duncan & Hewitt 1989).

It is widely acknowledged that harvester termites alter their areas of occupation and foraging according to climatic conditions (Coaton 1958; Nel & Hewitt 1969; Coaton & Sheasby 1975; Gouse 1985), and that improvement in grass-layer leads to a reduction in activity (Coaton 1958; Hartwig 1965). The results reported here for *H. mossambicus* clearly indicate high levels of activity during the drought, but any clear pattern of correlation with rainfall will probably require a monitoring period well in excess of two years to reveal long-term population trends related to climate.

Allodontermes rhodesiensis/Microtermes sp

Both these groups of termites are "fungus growers" of the subfamily Macrotermitinae (Termitidae). They have subterranean nests but may occasionally be found opportunistically exploiting part of the above-ground mounds constructed by other Macrotermitinae. The nest system consists of a large number of cells scattered throughout the soil, each cell with a single fungus comb and connected to other cells by a maze of narrow tunnels. The termites forage below or aboveground for dead wood or leaf-litter, making protective soil runways (canopies) when venturing on the surface. Live young plants in suboptimal condition may also be susceptible to attack (Coaton 1981).

Although the *number* of plots showing termite activity (Fig. 3a) was relatively low during the drought period, the *average area* covered by termite runways (Fig. 3b) was highest during the drought. From these sustained high levels during the drought, termite runway coverage dropped steeply during the ensuing unusually wet season and subsequent dry season of 1993, but picked up sharply during the moderate rainfall of late 1993/early 1994. Buxton (1981) showed that in the Tsavo National Park of Kenya foraging was highest during the rainy seasons and declined to low levels during the long dry season. The data for the Kruger National Park do not clearly follow this pattern, but in general suggest that drier years (1992 & 1994) are more favourable to these macrotermitine termites than wetter years (1993). The data set is very small, however, and a much longer monitoring period is required to substantiate such a statement. It does, however, fit Buxton's (1981) similar conclusion that the importance (diversity/ abundance/consumption) of macrotermitinae declined with higher average annual rainfall.

Perhaps the most logically satisfying dataset of this study is represented in Fig. 3c, which portrays the decline in basal cover of the sampling plots in 1992, the high vegetation cover in the relatively wet 1993, with a slight decline in the somewhat drier 1994. Given the fairly dense cover of *Grewia* and *Dichrostachys* and the relatively low density of large herbivores in the monitoring area, termites were probably the greatest contributors to the rapid decline in basal cover from approximately 58% in April 1992 to 17% in November 1992, implying a consumption by these termites approaching 41% of available above-ground litter. This magnitude of consumption is well within the means of termites (Usher 1975; Collins 1977; Wood & Sands 1978; Buxton 1981).

General

The dynamics of a drought are of great importance to its impact on wildlife populations. For example, the relatively short, acute drought of 1982/83 resulted in massive die-off of impala and some other herbivore species, causing huge increases in populations of carrion-breeding blow-flies (Braack 1987). In contrast, the more severe, drawn-out, chronic drought culminating in the arid conditions of 1992 did not result in such a dramatic die-off of impala, nor a concommitant increase in blow-fly populations (Braack *unpublished data*). In the same way, droughts appear to affect termites differently too. One of my most vivid recollections – aside from the totally denuded areas near Tshokwane and Lower Sabie which were a feature of both droughts – of the 1982/83 drought was the very impressive extent to which macrotermitine termites had covered with soil runways the trunks and branches of mopane and other trees in large areas of the northern KNP. Although again evident in 1992, it did not approximate the extent reached in 1982/83. The impression one is left with is that drought initially favours macrotermitine termites due to the high level of fresh litter and plant material, but if the drought persists it eventually also negatively impacts upon the termites. Certainly, the data available for the termite populations monitored during this study show that the relationship between rainfall and population level is not a straightforward one and that other factors (length of drought, severity of drought, temperatures, initial start-up termite population, etc) almost certainly influence population response and complicate interpretation.

Although the sampling plots near Skukuza yielded only *Allodontermes rhodesiensis* and *Microtermes* sp, in some other areas where termite impact was obvious and severe the termite populations differed. Between Tshokwane and Mazithi Dam where all grass and forbs were completely stripped within a few months – leaving only trees and bare earth – *Ancistrotermes latinotus* (Holmgren) and *Odontotermes* sp (Macrotermitinae) were the principal species involved. The northern mopaneveld and riverine woodland had high levels of soil runways made by these two groups of termites, with *A. latinotus* particularly abundant in the riparian forest of Pafuri. *A. latinotus* is also a fungus-growing underground nester and is one of the most important species of termites in the eastern Transvaal (Coaton & Sheasby 1975b). Termites of this species were recovered from finger-like soil runways covering recently-fallen leaves and twigs, below broad sheet runways along trunks of trees, below loose bark and also in runways within and covering drying elephant dung. While *Odontotermes* were usually encountered below broad runways covering twigs and leaves on the ground or in runways going up trees, samples taken from sheet-runways covering heavily eaten portions of green lawns during April 1992 were also identified as *Odontotermes*. Of practical importance is the finding by Buxton (1981) that macrotermitine termites in Tsavo do not feed on decomposing wood, but only attack fairly recent litter. Lepage *et al.* (1993) showed that in shrub savanna where a choice of feeding substrates is available, *Ancistrotermes* and *Microtermes* vary their diet according to season.

Although subjective impressions gained during unusual conditions, such as the 1982 and 1992 droughts in Kruger, do allude to the importance of termites, published results on rates of consumption are available. These show that even under more normal, average conditions termites consume significant amounts of vegetation. Some of these findings are listed in Table 1.

The figures in Table 1 become more significant if coupled—where such data are available—with plant production figures. In northern Kenya, Bagine (1989) found that (out of a primary plant production of 488 $gm^{-2}a^{-1}$) termites consumed 50% of grass litter and 4% of woody litter. In the Kenyan Tsavo National Park which is broadly comparable to the Kruger National Park in both rainfall and general vegetation structure, 90% of dead wood decomposition is mediated by termites (Buxton 1981). Equally significantly, Coe (1977) calculated that termites were removing up to 8.7×10^3 kg of animal faeces (largely elephant) per km^2 from the surface of the ground in Tsavo (East) National Park.

Table 1

Biomass and Consumption of various savanna organisms

Taxon	Biomass	Consumption	Locality	Source
Macrotermitinae	6.39 g/m^2	139.9 $gm^{-2}yr^{-1}$	Nigerian savanna	Wood & Sands 1978
Macrotermitinae	0.72 g/m^2	15.8 $gm^{-2}yr^{-1}$	Senegal savanna	Wood & Sands 1978
Macrotermitinae		28.1 $gm^{-2}yr^{-1}$	Tsavo,Kenya	Buxton 1981
Macrotermitinae	4.9 kg/ha	1000 $kgha^{-1}yr^{-1}$	Lamto savanna Ivory Coast	Lamotte 1975
All termites	9.8 kg/ha	920 $kJm^{-2}yr^{-1}$	Nylsvley (Burkea)	Gandar 1982
All termites	1.6 kg/ha	179 $kJm^{-2}yr^{-1}$	Nylsvley (Acacia)	Gandar 1982
Ants		1.7 kg/ha	Nylsvley	Gandar 1982
Grasshoppers	2.28 kg/ha	599 $kJm^{-2}yr^{-1}$	Nylsvley (Acacia)	Gandar 1982
Grasshoppers	275-1060 g/ha	69.6 $kgha^{-1}yr^{-1}$	Lamto, Ivory Coast	Lamotte 1975
Ungulates	12.3-17.5 g/m^2		Tanzania (high density game reserve)	Wood & Sands 1978

The consumption of plant material by termites should not result in significant competitive interaction with herbivorous vertebrates during most months of the year, but is likely to become significant and even severe in the dry season of some years. In an average rainfall year herbivorous vertebrates will forage on growing leaves or grass during the wet season, selecting senescing material still moderately plentiful during the early dry season, but probably for at least two or three months before the onset of the rainy season such herbivores will compete directly with termites for grass-stubble or plant litter at ground level.

The high density of termites in the KNP, and their impact which is so abundantly visible during pronounced dry periods, indicate that these termites are highly effective competitors with vertebrates for food. Managers of wildlife areas traditionally tend to ignore invertebrates during consideration of management options and such views are short-sighted. To use termites as only one example, considered ecologically they are far more efficient in converting plant material into live biomass (production efficiency) (Wood & Sands 1978; Lamotte & Bourliére 1983; Deshmukh 1989), largely due to the metabolic cost of thermoregulation in mammals. Termites are far more effective in returning nutrients to the soil. Mound-building macrotermitinae may also shift surprisingly large volumes of soil (8 100 $kg ha^{-1} yr^{-1}$) not just in building mounds but also in soil-runways for foraging. They facilitate penetration of rainwater into the soil via extensive networks of galleries, by especially underground nesters (Josens 1983). We would do well to heed the words of Lamotte & Bourliére (1983): *The most conspicuous savanna herbivores are the ungulates, wild and/or domestic, the former being particularly numerous in Africa. However spectacular their numbers and standing crops may be, they do not necessarily play the leading role in energy transfer or nutrient cycling within the savanna ecosystem.*

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