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THE INFLUENCE OF FIRE ON POPULATIONS OF SMALL MAMMALS OF THE KRUGER NATIONAL PARK

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Abstract — A total of 16 000 trap-nights was employed over eleven months to examine the influence of burning on small mammal populations in two major veld-types of the Kruger National Park. Four burning treatments (control, annual August burning, triennial August and April burning) were examined in detail and the following parameters determined: small mammal species composition, population density, biomass and species diversity. The control treatment had a high, stable small mammal density, biomass and diversity; the annual burning treatment had a low diversity and was dominated by *Tatera leucogaster*. The triennial burning treatments showed a cycle of species composition from domination by *T. leucogaster* following burning, through domination by other rodent species to domination by *Crocidura hirta* at the end of the cycle. The distributions and movements of the small mammals can be explained in terms of cover and litter preferences.

Introduction

The occasional burning of vegetation is a natural ecological phenomenon, occurring most often as a result of lightning (Komarek 1964). With the advent of man the incidence of burning probably increased with its use by man for his own ends, for example, to drive game animals towards hunters, to induce game to immigrate into a certain area, and, more recently, for the production and maintenance of grazing. The result has been the widespread appearance of "fire-climaxes" in the vegetation (Tansley 1935). However, fires in the major vegetation biomes of forest and grassland are generically different (Daubenmire 1968) both in terms of actual fire processes and of the ecological effects. These are summarised by Ahlgren & Ahlgren (1960) for forest fires, and by Daubenmire (1968) for grassland fires. The emphasis of these summaries, and indeed of much of the available literature, is on the effects of burning on the vegetation (e.g. Kucera & Koelling 1964; Hopkins 1965), and by comparison the effects of fire on animals are less well documented. However, Bendell (1974) provides a good summary on the latter aspect. In the specific case of small mammals (defined here as being free-living small rodents and insectivores generally including animals up to 120 g — Delany 1974) the literature is very sparse, and most studies have been conducted in the United States of America, with few in

Africa (e.g. Neal 1970). Thus the Kruger National Park in South Africa represents an ideal setting for a study in the neglected field of the relationships between small mammals and fire.

In the past, the area that is now the Kruger National Park was subjected to much indiscriminate burning, probably since the advent of early man. Settlement by African tribes after the sixteenth century, and, in the first half of the nineteenth century, the arrival of European settlers heralded an increase in the incidence of burning, which continued almost unabated despite the proclamation of part of the area as the Sabie Game Reserve in 1902 (Brynard 1964). Even after the proclamation of the Kruger National Park in 1926 there was considerable accidental burning, mainly as a result of fires sweeping in from outside the Park, while the staff maintained a policy of burning annually those areas which escaped accidental burning. For a while around 1950 there was a period with no deliberate burning at all, but in 1954 a policy was introduced by the National Parks Board of burning any one area once every three years. At the same time the Board instigated a long-term study on the effects of burning on the vegetation, and experimental burning plots were established in the major veld-types of the Park for research purposes (Brynard 1964). The details of these plots are considered below under "Study Areas". It is sufficient to state here that most of the present study was conducted on these plots with a view to contributing to the National Parks Board's own research programme on the effects of veld burning, which, in the case of small mammals, had received virtually no attention in the past.

Study areas

The Kruger National Park covers an area of some 1 950 000 hectares in the eastern Transvaal lowveld, from latitude 22° 32′ to 25° 32′ South and from longitude 30° 50′ to 32° 02′ East. The topography and geology range from undulating hills of granitic origin, with dolerite intrusions, in the west, to the flat basaltic Lebombo plains in the eastern half, with the rhyolitic Lebombo Mountains forming the eastern boundary (Van Wyk 1971).

The area has a summer rainfall (October/November to March/April) with the peak between November and February, and mean annual rainfall varies with the exact area from 400 to 700 mm (Brynard 1964; Van Wyk 1971).

Zoogeographically the Park lies in the Southern Savanna biotic zone of Moreau (Davis 1962).

Van Wyk (1971) recognises six major veld-types in the Park:

1. *Terminalia-Dichrostachys* Savanna Woodland
2. *Combretum-Acacia* Woodland
3. *Acacia-Sclerocarya* Savanna Woodland
4. Shrub *Mopane* Savanna Plains
5. *Combretum-Mopane* Woodland
6. Sandveld Communities

The National Parks Board research on burning occurs mainly in the first four of these veld-types, in which formal experimental burning plots have been laid out.

Within each veld-type there are four duplicate series each comprised of fourteen plots subjected to fourteen different burning treatments. For the purposes of this study, work has been conducted in only two veld-types, the *Terminalia-Dichrostachys* veld centering on Pretoriuskop Rest Camp and the *Acacia-Sclerocarya* veld around Satara Rest Camp. That only two veld-types should be considered was necessitated if any one area was to be examined in any depth at all, and these particular two veld-types were chosen in consultation with the National Parks Board Chief Research Officer for the large differences in their respective plant communities.

The Pretoriuskop *Terminalia-Dichrostachys* veld occurs on brown, sandy-loam, granitic soils in an undulating area traversed by numerous streams, in the south-west section of the Park (Van Wyk 1971). The mean annual rainfall is 706 mm (Brynard 1964), and from the latter part of the nineteenth century to 1945 the area was subjected to annual autumn burning (Van Wyk 1971). The dominant tree species are *Dichrostachys cinerea* subsp. *nyassana* and *Terminalia sericea,* these contributing over fifty percent of the trees between them, and both tending to encroach. *Sclerocarya caffra, Parinari curatellifolia* and *Strychnos madagascarensis* are also important. The shrub layer is generally of little botanical importance, but includes *Maytenus senegalensis, Cassia petersiana* and *Xeromphis obovata.* The grass cover consists predominantly of sour grasses and is characterised by the tall, robust *Hyperthelia dissoluta.* Other "unpalatable" (Van Wyk 1971) species include *Elyonurus argenteus* (possibly the most abundant species), *Schizachyrium semiberbe* and *Loudetia simplex.* "Palatable" (Van Wyk 1971) species such as *Setaria flabellata, Heteropogon contortus, Digitaria* spp. and *Eragrostis* spp. are abundant, with stands of *Panicum maximum* under trees.

The Satara *Acacia-Sclerocarya* veld covers the basaltic Lebombo flats from the Crocodile to the Olifants Rivers, and is included in the "Arid Lowveld" of Acocks (1975). The mean annual rainfall is 550 mm (Brynard 1964). *Acacia nigrescens* and *Sclerocarya caffra* are the dominant trees scattered on broad, fairly open plains. Shrubs are represented by *Grewia* spp., *Securinega virosa* and *Dichrostachys cinerea* subsp. *cinerea.* The grasses are basically sweet, except that in the central parts the unpalatable (Brynard 1964) *Bothriochloa insculpta* has become dominant, or co-dominant with *Themeda triandra.* Also present are *Digitaria* spp., *Eragrostis* spp. and *Panicum* spp. The high incidence of *B. insculpta* can possibly be attributed to excessive burning and selective grazing (Brynard 1964; Van Wyk 1971).

Burning treatments

Only ten of the fourteen burning treatments were considered for examination, some by live- and some by snap-trapping, and are those which have been continuously applied since 1954. These treatments are:

a. Control (unburned)
b. Annual burn in August (end of Winter before rain)
c. Biennial burns in August, October (after first good rains), December (mid-Summer), and April (Autumn, about time of last rains)
d. Triennial burns in August, October, December and April.

Within each plant community one of the four duplicate series was chosen for examination using live-trapping methods. In the case of the Pretoriuskop area this was the Shabeni Series (since the visible differences between burning treatments appeared average compared with the other series, and because this series had remained free from significant accidental burns) and in the case of the Satara area the Satara Series (since it is the only one within easy access of the Rest Camp). On each of these two Series designated for live-trapping, four treatments were selected for actual study using live-traps; these were control, annual August burn, triennial August burn and triennial April burn. (Other treatments on these Series were examined by snap-trapping). The reasons for choosing these particular treatments were simple: the control treatment was essential to serve as a standard control, whilst the annual burn provided the maximum contrast in vegetation. The triennial August and April burn treatments were selected since both would be burned during 1976. (While the biennial August burn occurred in 1976, the biennial April burn had already taken place in 1975). Hence the effects of these pre- and post-Winter burns, which it was felt may reveal the greatest differences, if any, in effect of burning season on the small mammals, could be compared.

The slope and drainage of the four Pretoriuskop Shabeni Series plots on which live-trapping was conducted was as follows. All the plots have a slight west to east slope and are slightly east-facing. The predominant slope on the control treatment ran south to north and was north-facing, with no particular drainage pattern. The annual August treatment plot similarly slopes south to north but is south-facing, and again there is no particular drainage pattern. The triennial August treatment plot has a short north-facing slope and a long south-facing slope resulting in a very wet, almost vlei section in the dip. The triennial April treatment plot has a long south-facing slope with a flat section at the bottom which tends to a vlei-like condition.

The Satara live-trap plots were all relatively flat with little or no slope and consequently no significant drainage patterns.

All of the other six treatments under consideration on the Satara "live-trap" series, and many of the treatments on the three remaining series at Pretoriuskop (Numbi — ten treatments, Kamban — three treatments and Faai — two treatments) and also three treatments on the Nwanedzi Series of the Satara area were each sampled once (with the exception of one plot which was sampled twice) using snap-trapping techniques.

Each experimental plot is approximately 200 m x 400 m in size, covering an area of some 8 hectares.

Seasons and Plot Burning

Seasons were reckoned as follows: Autumn — March/April/May, Winter — June/July/August, Spring — September/October, early Summer — November/-December, mid-Summer — January.

The Pretoriuskop triennial April treatments were burned on 21st May 1976, the annual, biennial and triennial August treatments between the 7th and 16th September 1976, and the biennial and triennial October treatments between 25th and 27th October 1976. The Satara triennial April plots were burned on 26th May 1976 and the various August burns took place on the 25th and 26th August 1976.

Surrounding each series of experimental burning plots is a 20 to 30 m strip (firebreak) burned annually, with the surrounding tracts, which are divided into large blocks by firebreaks, being burned every three years on a rotational basis.

Materials and Methods

Live-trapping

Live-trapping was carried out on 10 m x 8 m grids using Sherman aluminium live-traps (230 mm x 90 mm x 80 mm) with 20 m spacing between traps. Twenty m spacing was adopted to cover as large an area as possible with the available traps, and in view of the experimental findings of De Wit (1972) that if anything 20 m spacing gave a higher capture rate than 10 m. Traps were placed in the most suitable looking site within 2 m of any particular trap-station. The traps were generally set in the late afternoon, and were left for six nights giving a total of 480 trap-nights per session. Traps were checked and reset as soon as possible after sunrise. After an early period of checking traps both in the mornings and in the afternoons it was decided to dispense with the afternoon check, since daylight captures were rare. Trap mortality was minimal, with the exception of the Winter trapping session on the Shabeni Series triennial August treatment, and it was not found necessary to provide elaborate shading for the traps.

Live-trapping was conducted in the Pretoriuskop area in late Summer/Autumn, Winter, Spring and early Summer 1976 and mid-Summer 1977, and in the Satara area only in Autumn and Winter 1976.

A 10 m x 8 m grid with 20 m spacing very conveniently occupied roughly half of a single plot. Where applicable, i.e. plots not burned in April/May 1976, it had been planned to alternately trap the different halves of each plot under consideration using live-trapping methods, in order to check on any local concentration differences in small mammal populations. However, after the Winter trapping sessions only one half of each plot was generally employed. From the point of view of being able to make firm deductions it might have been better to have used only one half of each plot throughout and thus to have avoided the introduction of an additional variable. The two halves of each plot and their respective grids were designated A and B.

Population densities per hectare were calculated for each species caught, for total rodents and total small mammals (with adjustments where necessary on the basis of the number of initial captures so that the sum of the individual species densities equalled the total small mammal density) using the Schumacher-Eschmeyer method (Overton & Davis 1969).

The Schumacher-Eschmeyer method was adopted as the sole method after an initial trial period during which the Schnabel and the Eberhardt methods (Overton & Davis 1969) were also employed. The Schumacher-Eschmeyer and the Schnabel methods both gave figures for population sizes which were close to the total number of individuals captured, i.e. appeared to make little allowance for the untrapped part of the population. The Eberhardt method results ranged on the whole from 1½ to 2 times those of the other two methods, and thus probably represented a better absolute assessment of population size. However, the method appeared to be over-sensitive to the recapture rate as opposed to the initial capture rate which is more closely followed by the other methods. Thus the Schumacher-Eschmeyer method was selected since it represented the more sophisticated method compared with that of Schnabel, and because, despite its suspect absolute accuracy, it was more consistent in what is a comparative rather than an absolute study of population sizes.

Species diversity was calculated using the following formula:

$$D = 1 - \sum \{ [n_i (n_i - 1)] / [N(N - 1)] \}$$

where D is species diversity, n_i is the number of individuals of one species caught during the trapping session, and N is the total number of individuals of all species caught during the trapping session (Pielou 1969).

A further indication of species diversity was obtained by an examination of the mean body weights of each species present at any trapping session, as utilised by Brown (1975). Since the sample sizes for individual species in any one trapping session were often very low, an average weight over the whole study period was calculated for each species.

Home ranges were calculated using the Exclusive Boundary Strip method of Stickel (1954), for those individuals with a minimum of three captures in different traps in any one trapping session.

Snap-trapping

Snap-trapping was conducted using four lines of traps, two of 10 Museum Specials alternating with two of 10 Victors. Again the spacing between traps and between lines was 20 m. Traps were left for three nights, giving a total of 120 trap-nights per session, and were checked in the early morning. Snap-trapping was conducted from March to November 1976.

The primary aim of snap-trapping was to examine food preferences and consequently the stomachs of trapped animals were removed and stored in 10 % formalin. Snap-trapping was also intended to clarify issues arising from the live-trapping results and to provide limited information on those burning treatments which could not be examined by live-trapping, and also to give information on reproduction. However, in accordance with National Parks Board policy on the removal of animal material for research purposes, snap-trapping was conducted on a limited scale only.

Bait

The bait used consisted of rolled oats, peanut butter, cane-sugar 'golden syrup' and sunflower oil, mixed very approximately as two volumes of oats to one of peanut butter with a tablespoon of syrup. Oil was added to give the desired consistency. It was generally found to be sufficient to rebait the live-traps on the third morning in winter, though a representative sample was always checked on the second morning and if necessary (i.e. if ant activity was high) all traps were rebaited then and again on the fourth morning. More frequent rebaiting was generally necessary during the summer months.

Cover

Cover was measured using a wheel-point method. The wheel was pushed up and down the trap lines 1 or 2 m from the actual line. For the live-trap grids this conveniently gave roughly 1 000 points. Each point was noted in the *Acacia-Sclerocarya* veld as being bare ground as a result of grazing or trampling, bare ground not as a result of animal activity, ground covered by *Bothriochloa insculpta,* ground covered by other grasses, or, ground covered by other than grass (e.g. fallen logs). In the *Terminalia-Dichrostachys* veld the structure was far too complex for subdivisions and merely 'Bare' or 'Covered' was recorded for each point. The criterion for rating as covered was taken, albeit subjectively, as being that a small mouse would be invisible to the observer if it was on the ground at that point. This is distinct from the botanist's criterion of basal cover where an actual rooted grass tuft must be struck to rate as a point of basal cover. Cover was measured during autumn and mid-summer i.e. before the grass began drying up or when cover had re-established itself after the winter. Hence the estimates tend to represent minimum bare ground and maximum cover.

Litter

Litter was estimated visually on the following five-point scale:

1. Very little, or no litter
2. Some litter, but no definite layer
3. Definite layer, but thin and patchy
4. Definite layer, thin and generally continuous
5. Definite layer, thick and generally continuous.

Litter was estimated at the same time as cover and hence the estimates tend towards maximum values.

Derivation of burn-related cycles and presentation of results

The results of this study have been presented so as to maintain an emphasis on the role of different burning treatments in determining the size and composition of small mammal populations. The study spanned only a year and started before the burning of most of the plots investigated, so the ends of most of the burn-related population cycles were seen first, followed by the effects of the actual burning and then only the initial stages of recovery. It was necessary, therefore, to infer whole population cycles, over three years in the case of the triennial burning treatments, from the limited stages examined. Hence for each burning treatment analysed by live-trapping an "inferred cycle", based on the direct observations available, was derived, and subsequently the principles which dictate the patterns were deduced.

Table 1

Population densities (numbers/ha) of individual species, total rodents and total small mammals, and percentage trap success for the Control and Annual August burning treatments on the Shabeni Series in the Terminalia-Dichrostachys *veld during four or five live-trapping sessions on each plot from autumn 1976 to mid-summer 1977*

SEASON/ DATE	BURNING TREATMENT								
	CONTROL				ANNUAL AUGUST				
	AUTUMN 1st Wk April	WINTER 2nd Wk July	SPRING 3rd Wk Oct.	MID SUMMER 2nd Wk Jan.	AUTUMN 3rd Wk April	WINTER 1st Wk July	SPRING 4th Wk Sept.[1]	EARLY SUMMER 3rd Wk Nov.	MID SUMMER 3rd Wk Jan.
GRID	A	B	B	B	A	B	A	B	B
Aethomys chrysophilus	1,27	3,24	2,56	1,01	0,62	—	—	—	—
Mus minutoides	—	—	—	—	—	0,31	—	0,60	1,63
Lemniscomys griselda	2,43	2,78	1,48	4,01	—	1,66	—	—	—
Otomys angoniensis	—	—	—	—	—	—	—	—	—
Praomys natalensis	1,52	1,59	—	—	1,29	0,31	—	—	—
Saccostomus campestris	0,62	0,31	0,63	0,64	1,70	—	—	0,31	—
Steatomys pratensis	0,62	—	0,93	—	0,62	—	—	—	—
Tatera leucogaster	1,24	5,82	3,47	2,63	5,39	4,27	0,62	2,16	2,54
TOTAL RODENTS	7,70	13,74	9,07	8,29	9,54	6,55	0,62	3,07	4,17
Crocidura hirta	3,95	0,31	0,62	0,31	—	—	—	—	—
TOTAL SMALL MAMMALS	11,65	14,05	9,69	8,60	9,54	6,55	0,62	3,07	4,17
% Trap Success	16,5	27,1	16,3	11,5	9,3	11,9	1,3	4,0	8,3

1= Burned 7-16/9/76

Results and Discussion

Population densities and species composition of small mammals on different burning treatments in the Terminalia-Dichrostachys *veld*

a. *Annual August burning treatment*

(See Tables 1 and 3)

The outstanding aspects of the annual August burning treatment as indicated by live-trapping on the Shabeni Series are the domination by *Tatera leucogaster* throughout the year-long cycle and the total absence of *Crocidura hirta.*

Two weeks after burning the small mammal population consisted entirely of *T. leucogaster;* the density was extremely low (0,62 animals/ha) and represented a decrease of 91% from the winter, pre-burn small mammal density, and of 86% from the pre-burn *T. leucogaster* density. There was ample green food material in the new growth of grass shoots at this time, even though there was heavy grazing by zebra, wildebeest and impala. In early summer, some two months after the burn, with a continued new growth of grass but still no seed heads, *T. leucogaster* density had increased to 2,16 animals/ha with a 19% contribution to the total density from *Mus minutoides*.

This species had increased to 39% of the total population while *T. leucogaster* had decreased to 61% by mid-summer (January, when grasses were seeding profusely) with the total small mammal population rising from the post-burn low of 0,62 to 4,17 animals/ha. By autumn of the inferred cycle, small-scale immigration, mainly of adult animals, had taken place, the migrant species being *Aethomys chrysophilus, Praomys natalensis, Steatomys pratensis* and *Saccostomus campestris* (though there may have been a small, resident population of this last species). This, combined with a doubling of the *T. leucogaster* population as a result of breeding and immigration, produced a peak in small mammal population density of 9,45 animals/ha. However, numbers fell during winter, in the case of some species back to zero, but *Lemniscomys griselda* appeared for the first time at this late stage in the cycle.

Obviously the details of this inferred cycle are subject to possible local concentration differences between grids A and B on the different halves of the plot. However, the broad pattern of *T. leucogaster* domination, plus the absence, or virtual absence of *C. hirta* is borne out by the snap-trapping results.

b. *Triennial August burning treatment*

(See Tables 2 and 3)

Deduction of the burn-related cycle is by no means as easy for the triennial August burning treatment as it is for the annual August treatment. However, spring trapping four weeks after the burn (when new grass growth was abundant but heavily grazed) indicated a small mammal population with a density 45% of that occurring prior to the burn. Much of this decrease is attributable to the disappearance (at least partly seasonal) of a sizeable (3,94 animals/ha) *C. hirta* population, since post-burn rodent population was a high 76% of the pre-burn figure. The dominant species were *S. pratensis* (40% of total population) and *S. campestris* (32%) and both probably represented permanent resident populations. By mid-summer, four

Table 2

Population densities (numbers/ha) for individual species, total rodents and total small mammals, and percentage trap success for the Triennial August burning and Triennial April burning treatments on the Shabeni Series (Terminalia-Dichrostachys veld) *during four or five live-trapping sessions on each plot, from autumn 1976 to mid-summer 1977*

SEASON/ DATE	BURNING TREATMENT								
	TRIENNIAL AUGUST				TRIENNIAL APRIL				
	AUTUMN 4th Wk April	WINTER 2nd Wk Aug.	SPRING 2nd Wk Oct.[1]	MID SUMMER 1st Wk Jan.	AUTUMN 4th Wk March	WINTER 1st Wk June[2]	SPRING 1st Wk Oct.	EARLY SUMMER 1st Wk Dec.	MID SUMMER 4th Wk Jan.
GRID	A	B	B	B	A	A	A	A	A
Aethomys chrysophilus	0,31	0,31	0,31	—	3,26	0,58	0,93	0,30	0,32
Mus minutoides	—	0,93	0,31	0,63	—	—	—	0,30	0,32
Lemniscomys griselda	0,93	2,29	—	—	—	—	—	—	0,63
Otomys angoniensis	—	0,31	—	—	0,31	—	—	—	—
Praomys natalensis	0,31	1,25	0,63	0,31	1,44	1,29	0,93	—	—
Saccostomus campestris	1,73	0,31	1,43	—	1,29	—	—	0,30	1,61
Steatomys pratensis	1,71	0,31	1,74	4,67	—	—	0,62	0,90	2,31
Tatera leucogaster	0,31	—	—	2,11	—	—	0,62	2,52	2,07
TOTAL RODENTS	5,30	5,81	4,42	7,83	6,30	1,87	3,10	4,32	7,26
Crocidura hirta	16,02	3,94	—	—	3,15	—	—	—	—
TOTAL SMALL MAMMALS	21,32	9,75	4,42	7,83	9,45	1,87	3,10	4,32	7,26
% Trap Success	14,8	10,7	5,75	6,8	12,3	4,0	5,4	7,3	10,5

1 = Burned 7-16/9/76, 2 = Burned 21/5/76

Table 3

Number of captures and percentage trap success from snap-trapping of different burning treatments on the four experimental series in the Terminalia-Dichrostachys *veld from March to November 1976*

BURNING TREATMENT	CONTROL	ANNUAL AUGUST	ANNUAL AUGUST	ANNUAL[1] AUGUST	ANNUAL[1] AUGUST	BIENNIAL AUGUST	BIENNIAL[1] AUGUST	BIENNIAL OCTOBER	BIENNIAL DECEMBER	BIENNIAL APRIL	TRIENNIAL[2] AUGUST	TRIENNIAL[1] AUGUST	TRIENNIAL OCTOBER	TRIENNIAL DECEMBER	TRIENNIAL APRIL	TRIENNIAL APRIL	TRIENNIAL[3] APRIL	TOTAL
SERIES	N	F	N	K	F	N	S	N	N	N	N	K	N	N	F	N	K	—
DATE (1976)	8/7	19/3	17/4	23/9	14/11	20/4	26/9	4/6	7/6	1/6	23/4	11/10	14/7	11/7	27/3	28/4	29/9	—
Aethomys chrysophilus	1	—	—	4	—	1	—	1	3	—	—	—	—	1	1	—	—	12
Dendromus mystacalis	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	2
Mus minutoides	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	2
Lemniscomys griselda	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	—	—	3
Praomys natalensis	1	—	—	—	—	2	—	4	1	1	5	—	—	—	—	3	—	17
Saccostomus campestris	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	4
Steatomys pratensis	—	—	6	—	1	1	—	—	—	—	3	—	—	—	2	2	—	15
Tatera leucogaster	1	11	3	5	7	1	1	—	3	—	—	—	—	—	3	—	—	34
TOTAL RODENTS	2	12	9	9	8	7	1	5	8	1	8	—	3	3	6	7	2	89
Crocidura hirta	—	—	1	—	—	—	—	1	—	—	—	—	—	1	—	3	—	6
TOTAL SMALL MAMMALS	2	12	10	9	8	7	1	6	8	1	8	—	3	4	6	10	2	95
% Trap Success	1,7	10,0	8,3	7,5	6,7	5,8	0,8	5,0	6,7	0,8	5,0	0,0	2,5	3,3	5,0	8,3	1,7	4,7

F = Faai, N = Numbi, K = Kamban, S = Shabeni

1 = Burned 7-16/9/76, 2 = Run for 4 nights, 3 = Burned 21/5/76

months after burning, with all grasses in seed, the small mammal population had increased from 4,42 to 7,83 animals/ha mainly owing to a rise in the *S. pratensis* population from 1,74 to 4,67 animals/ha (some of this undoubtedly from immigration — one specimen had been captured and marked over nine months earlier on a different plot) and the immigration of *T. leucogaster*. Their percentage contributions to total small mammal population were 60% and 28% respectively. Some two to two-and-a-half years later in the inferred cycle the total rodent population had fallen by over 25% and the species composition had significantly altered. *Tatera leucogaster* had all but disappeared while *S. pratensis* population density had returned to a value of around 1,7 animals/ha. *Saccostomus campestris, P. natalensis* and *L. griselda* (which contributed up to 24% of the total small mammal population) accounted for most of the rest of the rodent population. However, the small mammal population at this stage of the inferred cycle is dominated by *C. hirta,* as seen in the extraordinarily high density of 16,02 animals/ha recorded in autumn 1976. One can assume that between mid-summer of the first year after the burn and the autumn of the third year, rodents in general, and *T. leucogaster* in particular, decline in importance while *C. hirta* becomes prominent to produce the situation described above.

Otomys angoniensis was recorded once in winter, this plot having vlei-like conditions in parts at the end of the rainy season.

c. *Triennial April burning treatment*

(See Tables 2 and 3)

Live-trapping two weeks after burning, when there was a small amount of new grass growth, revealed a population comprising 69% *P. natalensis* and 31% *A. chrysophilus,* with a total density of 1,87 animals/ha, 20% of the pre-burn rodent density. By spring the total population had increased by approximately two-thirds to 3,10 animals/ha as a result of limited *T. leucogaster* immigration and probable *S. pratensis* immigration. In early summer, *P. natalensis* was absent and *A. chrysophilus* had become insignificant. *Steatomys pratensis* was important (21% contribution) and *T. leucogaster* was dominant (58%, population density 2,52 animals/ha). This large-scale *T. leucogaster* influx, by adult animals, coincided with the seeding of most of the grass species. By mid-summer, eight months after burning, rodent population density had reached 7,26 animals/ha. *Steatomys pratensis, T. leucogaster* and *S. campestris* were dominant with percentage contributions of 32%, 28%, and 22% respectively, and *Lemniscomys griselda* was recorded for the first time on this plot. By a little over two years later in the inferred cycle, however, *T. leucogaster* and *S. pratensis* were absent and the dominant rodent species was *A. chrysophilus,* supported by *P. natalensis* and *S. campestris,* with total rodent density little changed. *Crocidura hirta* contributed 33% of a total small mammal population of 9,45 animals/ha. The absence in the latter stages of the cycle of *L. griselda* and *S. pratensis* is in contrast with their important contribution at the same stage of the cycle on the triennial August burning treatment.

Otomys angoniensis was recorded once in the wettest section of the plot.

The results from snap-trapping do not significantly alter the picture, though the presence of *T. leucogaster* on the equivalent Faai Series plot shortly before burning is at first sight surprising. (However, this particular plot had relatively little litter and cover compared with other triennial burning treatments, the significance of which will be seen later).

d. *Control Treatment*

(See Tables 1 and 3)

The control treatment, as expected, shows a relatively stable species composition and small mammal population density throughout the year.

In autumn 1976 the rodent population density was higher by 1,40 to 2,40 animals/ha than on either of the triennial burning treatments but was lower than on the annual burning treatment. The dominant small mammal species was *c. hirta* (34% contribution), supported by *L. griselda, P. natalensis, A. chrysophilus* and *T. leucogaster.* By winter, *C. hirta* had all but vanished (probably a seasonal decline; c.f. the similar decline on the triennial August burning treatment) and *T. leucogaster* had become dominant (41%) with the rodent population increasing from 7,70 to 13,74 animals/ha. To what extent this increase may represent a local concentration difference between grids A and B on the two halves of the plot is hard to say. Breeding seems unlikely to be the sole explanation since the proportion of juveniles in autumn was low and in winter there were no juveniles at all. There were no visible differences in habitat between the two halves of the plot and immigration must therefore be considered as a possible explanation. Immigration could perhaps have been stimulated by burning that occurred in the vicinity in early winter or by the longer survival of green vegetation material and damp conditions in general in an area of relatively increased shade. Bellier (1967) found in a study in the Ivory Coast that at the end of the dry season many rodents moved temporarily into patches of unburned savanna located on damper grounds or at the edge of the forest, and that such areas played an important role as seasonal refugia.

By spring, the total population desnity had decreased to 9,69 animals/ha, and by mid-summer, when grasses were seeding and the first juveniles were being trapped, population density had further fallen to 8,29 animals/ha. This, when other burning treatments were showing marked population increases, is difficult to explain. *Lemniscomys griselda* was the dominant species in mid-summer, supported by *T. leucogaster.*

Mus minutoides was conspicuously absent from this treatment throughout the year.

Obviously one of the anticipated functions of the control treatment in this study was to indicate the seasonal variation which could be expected to occur under "normal" conditions as opposed to variations resulting more directly from burning. However, the winter rodent population is so markedly high as to suggest that immigration may have occurred, possibly from surrounding burned areas (see Conclusions), and this of course relates to the particular treatment (i.e. lack of burning). Hence, as an index of purely seasonal variation these results must be treated with caution. It must be noted, though, that the population densities at the other three seasons (autumn, spring and mid-summer) are very similar and that throughout the study the species composition is relatively stable.

To summarise, total small mammal density is generally higher on the control treatment than elsewhere, but this is by no means universally or even markedly so. Species richness is relatively stable on the control treatment, from five to seven species being recorded at different times. Both triennial burning treatments prior to, or long after burning have a species richness comparable to the control treatment, but the annual burning treatment shows a reduced richness.

With regard to individual species, *C. hirta* appears to decline in winter — a similar situation is recorded by De Wit (1972), but the densities in his study were low in comparison to those found in this study — and *P. natalensis* had generally declined by spring, when food supply was at its lowest. Both Smithers (1975) and Swanepoel (1972) note that in times of food shortage *P. natalensis* gave way to other species.

The control treatment is generally dominated by *T. leucogaster,* supported by *L. griselda* and *A. chrysophilus,* with seasonal domination by *C. hirta.* The annual August burning treatment is always markedly dominated by *T. leucogaster,* supported by *L. griselda* at the end of the cycle only. *Crocidura hirta* is conspicuously absent. The triennial burning treatments are invaded by *T. leucogaster* and *S. pratensis* in the months following burning, but by the latter stages of the burn-related cycle *T. leucogaster* has disappeared and *S. pratensis* has declined. *Crocidura hirta* is dominant then with local variation in the importance of the supporting species which include *L. griselda, A. chrysophilus, P. natalensis, S. campestris* and *S. pratensis.*

There are obviously many factors which influence the habitat preferences of small mammals — vegetation and food supply, soil-type, cover, litter and so on — but unfortunately little is known in detail of the ecology of individual small mammal species. While no doubt all habitat parameters could profitably be considered in order to explain the observed distributions described above, only those relating very directly to burning treatment will be discussed since the distributions are so obviously dictated at least in a substantial part by the burning regime.

The species composition of the grasses on the different burning treatments might be thought to offer some explanation of small mammal distribution. However, this seems unlikely as with one exception the differences between treatments are not very marked. The exception is the very high incidence of the pioneer grass *Digitaria pentzii* on the annual August burning treatment, and at first sight this might be thought to offer an attractive explanation for the marked domination of the small mammal fauna by *T. leucogaster* on this treatment. However, after the annual burning treatment the main permanent stronghold of *T. leucogaster* is the control treatment which has a very low incidence of *D. pentzii* in comparison with the unprotected areas. While this grass species may indeed have an influencing role, it would appear to be a very secondary one.

Similarly the tree and shrub components of the vegetation are probably not important. The control treatment averages 3003 trees/morgen (3568/ha) while the treatments subjected to burning vary from 1718 trees/morgen (2041/ha) for the triennial August treatment to 1976 trees/morgen (2348/ha) for the annual August treatment (Van Wyk 1971). This probably has little major effect beyond that already mentioned, namely delaying the drying of the soil and grasses in winter on the control treatment by virtue of increased shade.

When one comes to considering cover and litter there are obvious relationships with small mammal distribution, and three main conclusions emerge:

1. *Tatera leucogaster* is largely restricted to areas of relatively low percentage cover and little litter,
2. *Crocidura hirta* prefers areas with high percentage cover and a thick litter layer,
3. Rodents, with the exception of *T. leucogaster,* probably prefer areas with a good (70-90%) but not excessive (over 90%) cover but without a very thick, impeding litter layer.

Consider first the distribution of *T. leucogaster* as indicated by live-trapping on the Shabeni Series. This species, a large, long-legged gerbil equipped for rapid movement, is strikingly dominant throughout the year-long cycle on the annual August burning treatment where maximum cover at the end of autumn was only 63%. Four months after burning, in mid-summer, cover was only 29%. There was always little or no litter.

At the end of their respective cycles the triennial burning treatments have a very dense cover, 97% for the August treatment and 85% for the April treatment, and have large amounts of litter. *Tatera leucogaster* was virtually absent from these treatments at this time. However, in the months following burning *T. leucogaster* immigrated onto the triennial burning treatments which then had a very sparse cover (about 30%), similar to the annual August treatment, and had little or no litter.

The control treatment is the main *T. leucogaster* stronghold after the annual burning treatment and has a relatively low amount of litter compared with the triennial burning treatments prior to burning and also has a percentage cover not much more than the maximum encountered on the annual burning treatment, but again much lower than the pre-burn values from the triennial burning treatments. The low cover and litter values on the control treatment compared with those on the trienially burned treatments may be due to the elimination or alteration of the detritus fauna as a result of burning on these latter treatments. On the control treatment break down of litter probably matches accumulation. Daubenmire (1968) suggests that increased shade on unburned areas results in damper conditions suitable for microbial decay; burning removes shade and the drier conditions which follow are unsuitable for microbial activity.

The comparable snap-trapping results were of some value. Again the annual burning treatments show *T. leucogaster* to be dominant; litter quantities are always low and the one cover measurement from the relevant Numbi Series plot is only 55%. Of the other treatments on the Numbi Series, only the biennial December treatment shows any major contribution by *T. leucogaster* and both the litter and cover estimates for this treatment were lower than any others on the Series with the exception of the annual August burning treatment. As previously mentioned, the triennial April burning treatment on the Faai Series had relatively little cover and litter compared with the situation generally found on the triennial burning treatments, and *T. leucogaster* accounted for half of the captures.

It seems, therefore, that *T. leucogaster* flourishes in areas where percentage cover is less than 70% and that once cover becomes too dense (i.e. over 70%) and there is sufficient litter to form a definite surface layer this species declines. (It must be noted that there is a positive relationship between the amount of cover and the amount of litter).

Crocidura hirta appears to have completely opposite requirements to *T. leucogaster*. It is absent when live-trapping the low-cover, low-litter annual burning treatment and flourishes in the pre-burn conditions encountered on the triennial burning treatments, i.e. a very high percentage of cover associated with relatively large quantities of litter. The control treatment, with its good but not excessive cover and some litter, seems to provide an adequate though not an optimum environment.

The situation as regards other small mammal species is clouded and there are various apparent contradictions. However, some results considered below, though not as conclusive as those pertaining to *T. leucogaster* and *C. hirta,* do suggest a preference on the part of most of the rodents for good cover (70-90%) without excessive litter (visual estimate 3-4, or less). Several species move onto the annual burning treatment only late in the cycle when cover is near its maximum. Live-trapping shows *A. chrysophilus* to occur most on the control treatment and on the triennial April treatment prior to burning, but to occur at much lower densities on the extremes of cover and litter density found on the annual and triennial August burning treatments. Total rodent population densities for the triennial burning treatments prior to burning are lower than those on both the control and annual burning treatments, suggesting the negative influence of litter.

Species such as *A. chrysophilus, L. griselda, P. natalensis, S. campestris* and *S. pratensis* appear, though, to be fairly ubiquitous and to have habitat preferences, in so far as litter and cover are concerned, which are not as rigid as those demonstrated by *T. leucogaster* and *C. hirta.*

The apparent post-burn immigration of *S. pratensis* onto the triennial burning treatments following burning may appear at first sight to relate to cover and litter. However, this species is relatively unimportant on the annual burning treatment, which has low cover and low litter throughout the year, and makes the greatest contribution to the total rodent population on the triennial August burning treatment in autumn 1976 when this plot had very high litter and cover values. Its post-burn success may, therefore, relate to reduced resident competition.

Population densities and species composition of small mammals on different burning treatments in the Acacia-Sclerocarya *veld*

(See Tables 4 and 5)

By comparison with the Pretoriuskop *Terminalia-Dichrostachys* veld the *Acacia-Sclerocarya* veld at Satara has an impoverished small mammal fauna, and with only four rodent species recorded during live-trapping, the distribution patterns which emerge are more clear-cut. *Tatera leucogaster* is confined to the annual burning treatment, as indicated by both live- and snap-trapping. *Crocidura hirta* was found in low numbers on several treatments, notably the triennial August treatment, and

Table 4

Population densities (numbers/ha) for individual species, total rodents and total small mammals, and percentage trap success, for four burning treatments on the Satara Series (Acacia-Sclerocarya *veld) during live-trapping in autumn and winter 1976*

SEASON/ DATE	BURNING TREATMENT							
	CONTROL		ANNUAL AUGUST		TRIENNIAL AUGUST		TRIENNIAL APRIL	
	AUTUMN 1st Wk May	WINTER 1st Wk July	AUTUMN 2nd Wk May	WINTER 4th Wk July	AUTUMN 3rd Wk May	WINTER 3rd Wk July	AUTUMN 2nd Wk April	WINTER 3rd Wk June[1]
GRID	A	B	A	B	A	B	A	A
Lemniscomys griselda	0,94	3,05	2,81	0,31	—	—	1,43	—
Praomys natalensis	3,49	4,37	0,31	1,12	—	—	0,31	—
Saccostomus campestris	—	—	—	0,62	0,31	—	—	—
Tatera leucogaster	—	—	1,56	2,07	—	—	—	—
TOTAL RODENTS	4,43	7,42	4,68	4,21	0,31	—	1,74	—
Crocidura hirta	0,62	—	—	—	0,62	—	—	—
TOTAL SMALL MAMMALS	5,05	7,42	4,68	4,21	0,93	—	1,74	—
% Trap Success	7,5	9,2	8,5	9,6	1,0	0,0	3,2	0,0

1 = Burned 26/5/76

was not recorded on the annual burning treatment. *Elephantulus brachyrhynchus* was found on the annual burning treatment of the Nwanedzi Series. The most common species were *L. griselda* and *P. natalensis*. The latter dominated the control plot in the live-trapping analyses (59% in winter and 69% in autumn) but the former was dominant in the single snap-trapping analysis. Considered over both autumn and winter trapping sessions, neither was dominant over the other on the annual August burning treatments. Both live- and snap-trapping suggested that *L. griselda* was the more important species on the trienially burned treatments, but

Table 5

Number of captures and percentage trap success from snap-trapping of experimental burning plots on two Series in the Acacia-Sclerocarya *veld from May to July 1976*

BURNING TREATMENT	CONTROL	ANNUAL AUGUST	BIENNIAL AUGUST	BIENNIAL OCTOBER	BIENNIAL DECEMBER	BIENNIAL APRIL	TRIENNIAL AUGUST	TRIENNIAL OCTOBER	TRIENNIAL DECEMBER	TOTAL
SERIES	N	N	S	S	S	S	N	S	S	—
DATE (1976)	16/6	19/6	6/5	15/5	9/5	12/5	1/7	21/5	18/5	—
Dendromus mystacalis	1	—	—	—	—	—	—	—	1	2
Lemniscomys griselda	4	2	—	5	—	1	3	1	—	16
Praomys natalensis	—	2	—	2	5	3	—	—	—	12
Saccostomus campestris	—	2	—	—	—	—	—	—	—	2
Tatera leucogaster	—	4	—	—	—	—	—	—	—	4
TOTAL RODENTS	5	10	—	7	5	4	3	1	1	36
Crocidura hirta	—	—	—	2	1	—	—	—	2	5
Elephantulus brachyrhyncus		3	—	—	—	—	—	—	—	3
TOTAL SMALL MAMMALS	5	13	—	9	6	4	3	1	3	44
% Trap Success	4,2	10,8	0,0	7,5	5,0	3,3	2,5	0,8	2,5	4,2

N = Nwanedzi   S = Satara

snap-trapping showed that *P. natalensis* was prevalent on the bienially burned treatments.

The population densities calculated from live-trapping results show the control treatment to have the highest population of small mammals (5,05 and 7,42 animals/ha in autumn and winter respectively), followed by the annual burning treatment (4,68 and 4,21 animals/ha). However, the triennially burned treatments had extremely low densities in comparison, and this is reinforced by the snap-trapping results where the triennial burning treatments returned the lowest catches.

As with the Pretoriuskop area, these distributions can be satisfactorily related to cover and litter. Percentage cover on the *T. leucogaster*-supporting annual burning treatment was 59%, and the values for the other treatments, none of which supported *T. leucogaster,* ranged from 71% to 93%. There was little or no litter on the annual burning treatments. The fact that the relatively large elephant shrew, *E. brachyrhynchus,* was only ever recorded on an annual burning treatment may relate to cover and litter as the smaller shrew, *C. hirta,* was recorded on several treatments, but not on the annual burning treatment. *Crocidura hirta* made its greatest percentage contributions to the total populations on the triennial burning treatments which had the highest cover and litter estimates. While *L. griselda* and *P. natalensis,* both relatively ubiquitous species, appear less affected by cover and litter, it is apparent that the former is more tolerant than the latter of the thicker cover and litter at the end of the cycle on the triennial burning treatments as opposed to the biennial treatments. Both species are most successful on the control treatment, which has a high degree of cover, but, compared with the triennial burning treatments, relatively little litter. The inference from the Pretoriuskop results that very thick litter and very dense cover may have a negative influence on rodent numbers is given added weight by the low population densities occurring on the triennial burning treatments in the Satara area.

Biomass and species diversity

In the case of the *Terminalia-Dichrostachys* veld the values for biomass on the four treatments subjected to live-trapping (Fig. 1) were relatively similar in autumn, which can be considered as the optimum time of year in terms of food availability. However, on the control treatment the small mammal biomass nearly doubled between autumn and winter, with the reverse happening on the annual and triennial burning treatments. This dramatic increase in biomass on the control treatment also lends weight to the possibility, mentioned above, that immigration onto this treatment occurred in winter. After winter the biomass on the control treatment fell but still remained high. Burning caused a severe drop in biomass, especially on the triennial April and annual August burning treatments, but all three burned treatments recovered well by the mid-summer after burning, so much so that the biomasses in the autumn following burning could well be expected to equal those recorded in the autumn prior to burning.

Biomasses of small mammals on different treatments in the *Acacia-Sclerocarya* veld were low in comparison, with the values for the triennial burning treatments being particularly low. As in the *Terminalia-Dichrostachys* veld, winter produced the reverse effects on biomass for the control and annual August treatments, the former rising from the autumn value, the latter falling.

Species diversity of small mammals on the control treatment in the *Terminalia-Dichrostachys* veld (Fig. 2) remained relatively stable compared with the other treatments, and was consistently high. In contrast, the annual August burning treatment consistently displayed a low species diversity, particularly in winter and after

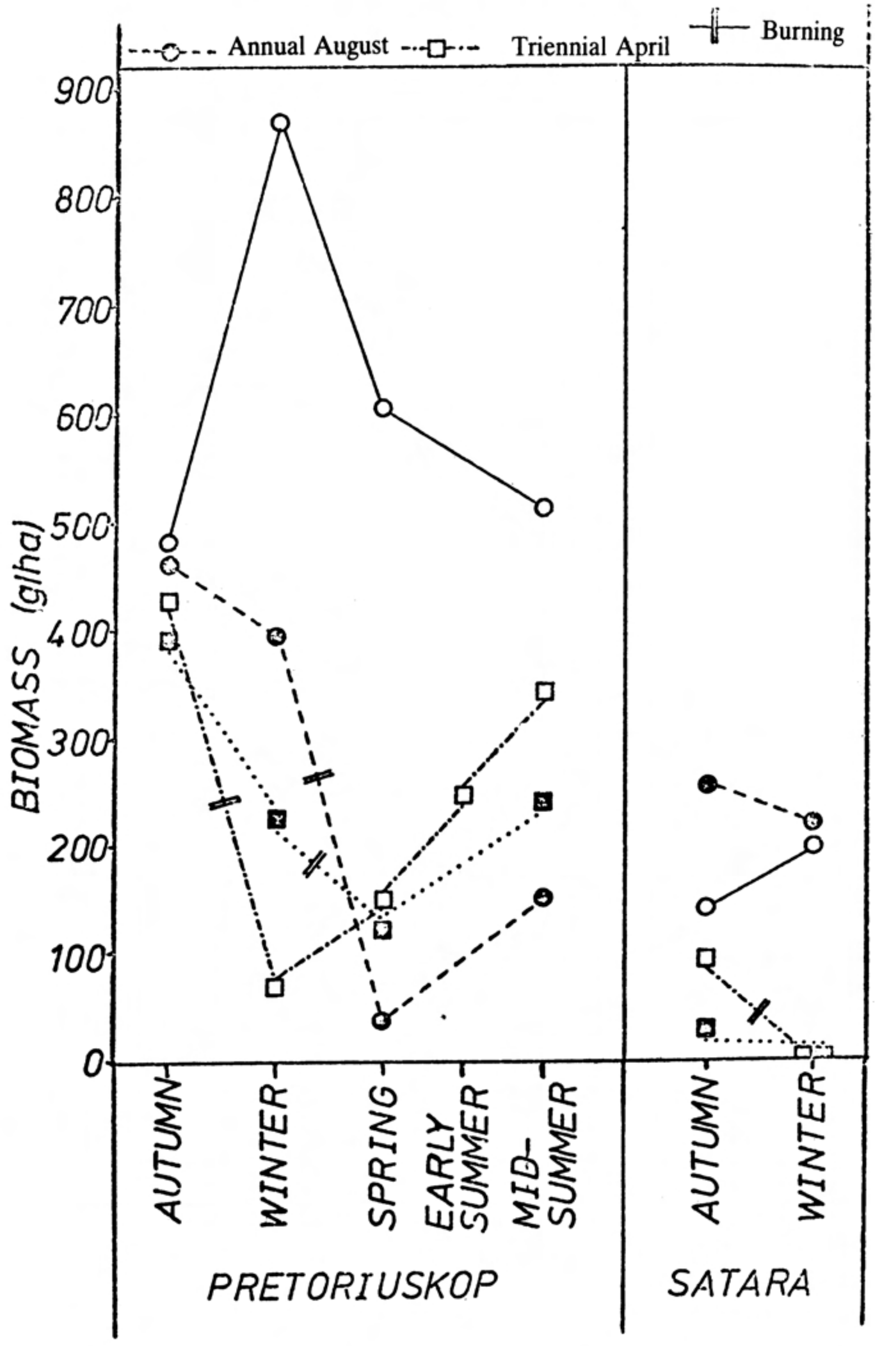

Fig. 1. Biomass (g/ha) of small mammals on four burning treatments in the Pretoriuskop and Satara veld-types from autumn 1976 to mid-summer 1977.

burning. Diversity on the triennial burning treatments did not follow a consistent pattern: the April treatment diversity decreased after burning, whereas that of the August treatment increased. However, from spring to mid-summer after burning, both treatments had high species diversities in comparison with the annual August treatment, the actual values being reasonably similar to the control treatment values.

In his study of desert rodents, Brown (1975) found that the most diverse communities consisted of five to six species which showed a remarkably regular spacing of body size, and that as diversity decreased the differential in size between pairs of coexisting species tended to increase. Also, decreases in species diversity were accomplished by the elimination of the small and medium-size species. The body weights of the different species recorded in live-trapping sessions during the present study are presented in Fig. 3. In general the species diversities in this study are well reflected in the species body size spacings, as Brown (1975) also found. The control treatment *(Terminalia-Dichrostachys* veld) had a very regular spacing of species falling into different weight classes and a consistently high species diversity; the highest diversity corresponds with the most regular distribution of body weights in autumn. The low species diversities for the annual burning treatment are mirrored in the body size spacing, and again both approaches demonstrate the highest diversity for this treatment in autumn. The same correlation between species diversity and body size spacing is also found on the triennial burning treatments, and particularly on the April burning treatment in autumn, before the burn, and in mid-summer, following the burn.

In the *Acacia-Sclerocarya* veld species diversity (Fig. 2) on the control treatment is, in contrast to the Pretoriuskop situation, lower than on the annual August treatment, and again this is mirrored by the body weight spacings (Fig. 3). The triennial April burning treatment diversity is particularly low, but that for the triennial August treatment is very high (perhaps a mathematical anomaly arising from the fact that only three individuals were trapped on this plot).

Overall, species diversity on the control treatment is relatively high and relatively stable, and that of the annual treatment relatively low, the situation one would expect in the two treatments which suffer the least and the greatest disturbance by burning respectively. The triennial burning treatment diversities fluctuate far more, but particularly following burning are generally high.

General comparison of the small mammal faunas of the Pretoriuskop and Satara veld-types

(See Tables 1-5, and Figs. 1-3)

The small mammal fauna of the Satara *Acacia-Sclerocarya* veld is comparatively impoverished in terms of species richness, species diversity, population density and biomass. Five rodent species were recorded, of which only two, *P. natalensis* and *L. griselda,* were at all common, and between them these two species contributed almost 80% of the live-trap catch and 63% of the snap-trap catch. *Elephantulus brachyrhynchus* was recorded on one plot but was never trapped in the *Terminalia-Dichrostachys* veld. Pienaar (1964) notes, in addition to the species recorded in this

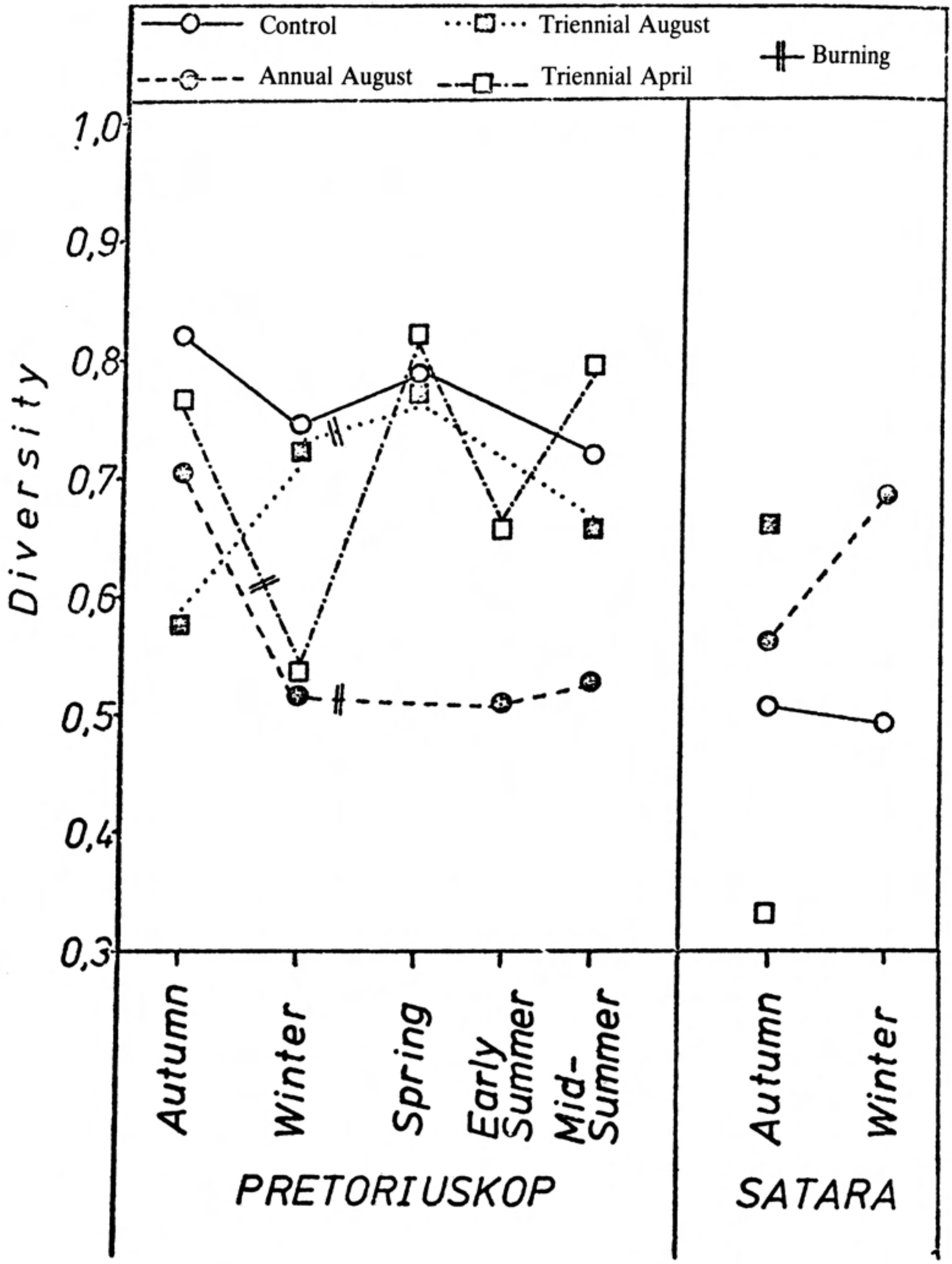

Fig. 2. Species diversity of small mammals on four burning treatments in the Pretoriuskop and Satara veld-types from autumn 1976 to mid-summer 1977 (formula from Pielou 1969).

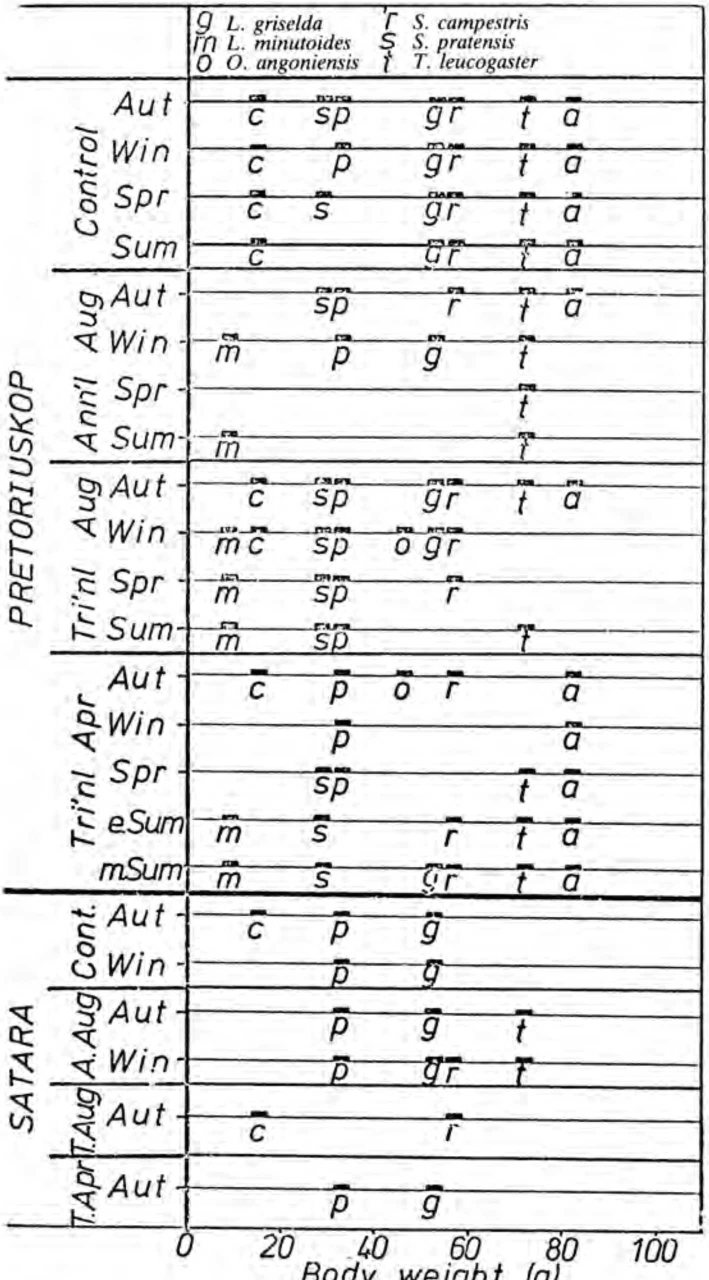

Fig. 3. Body weight distribution of small mammal species on four burning treatments in the Pretoriuskop and Satara veld-types from autumn 1976 to mid-summer 1977 (after Brown 1975).

study, *A. chrysophilus* as definitely occurring in the *Acacia-Sclerocarya* veld of the central region of the Park. With the exception of *E. brachyrhyncus,* both Pienaar (1964) and Coetzee (1963) noted the presence of all these species found in the *Acacia-Sclerocarya* veld, plus *S. pratensis* and *Aethomys namaquensis,* in *Acacia-Combretum* mosaics bordering the central region.

The more complex *Terminalia-Dichrostachys* veld fauna has six relatively common species, *A. chrysophilus, L. griselda, P. natalensis, S. campestris, S. pratensis* and *T. leucogaster. Crocidura hirta* was the only insectivore trapped, and *Dendromus mystacalis, O. angoniensis* and *L. minutoides* were recorded in low numbers in this area, but of these three rodent species only *D. mystacalis* was recorded in the Satara area. Pienaar (1964) notes the presence of *Dasymys incomtus, Dendromus melanotis, Suncus* sp. and *E. brachyrhynchus* in the *Terminalia-Dichrostachys* veld in addition to the species recorded in this study, with both Pienaar (1964) and Coetzee (1963) also recording *A. namaquensis* and *Graphiurus murinus.*

Total population densities on corresponding burning treatments were much lower in the *Acacia-Sclerocarya* veld; e.g. on the control treatment total densities ranged from 5,05 to 7,42 animals/ha in the Satara area compared to 8,60 to 14,05 animals/ha (maximum and minimum values) in the Pretoriuskop area on the annual August burning treatment prior to burning in the Satara area densities ranged from 4,21 in winter to 4,68 animals/ha in autumn, while in the Pretoriuskop area the figures were 6,55 in winter and 9,54 animals/ha in autumn. Similarly biomass was much lower in the *Acacia-Sclerocarya* veld than on the corresponding burning treatments in the *Terminalia-Dichrostachys* veld.

The comparative simplicity and paucity of the small mammal fauna of the *Acacia-Sclerocarya* veld is probably a reflection of the uniformity of this veld-type compared with the *Terminalia-Dichrostachys* veld. On only one plot in the Satara area was the percentage cover from *Bothriochloa insculpta* less than 50%. The high proportion of this grass species, which gives a dense, uniform, knee-height cover, along with concentrations of *Themeda triandra* and *Panicum maximum* around trees and bushes results in a limited foliage diversity and a structurally simple flora. By comparison, the *Terminalia-Dichrostachys* veld has many more important grass species; a general lack of any dominant species, and certainly no widespread domination of the type exhibited by *B. insculpta* and to a lesser extent by *T. trianda* in the *Acacia-Sclerocarya* veld.

Home range in relation to burning treatment

In general the records for individual species from each burning treatment are insufficient for an assessment of whether burning treatment affects home range, and only a few trends can be tentatively described.

In the *Terminalia-Dichrostachys* veld (Table 6), in the case of *T. leucogaster* there is a slight indication that home range on the annual August treatment may be greater than on the control treatment; the average home range for the whole study period on the annual August burning treatment is 2 220 m^2 whereas for the control treatment the figure is 1 900 m^2, i.e. 87% of the annual August burning treatment

Table 6

Home ranges (m²) for seven species of small mammals on different burning treatments in the Terminalia-Dichrostachys *veld (r = maximum-minimum range)*

Species	Burning Treatment	Season	Home Range (m^2)	n	r (m^2)
Aethomys chrysophilus	Control	Autumn	2 300	2	1 600
		Winter	1 500	2	600
	Tri'nl Apr.	Autumn	3 000	1	—
		Spring	2 200	1	—
Lemniscomys griselda	Control	Winter	3 330	3	3 400
		Spring	2 200	2	—
	Ann'l Aug.	Winter	2 800	1	—
	Tri'nl Aug.	Autumn	1 600	1	—
Praomys natalensis	Control	Autumn	2 400	2	2 400
		Winter	2 000	2	1 600
	Ann'l Aug.	Autumn	3 200	1	—
	Tri'nl Aug.	Autumn	1 800	1	—
	Tri'nl Aug.	Winter	1 530	3	600
Saccostomus campestris	Control	Autumn	1 200	1	—
	Ann'l Aug.	Autumn	2 000	1	—
	Tri'nl Apr.	Autumn	1 200	1	—
	Tri'nl Aug.	Autumn	2 800	1	—
Steatomys pratensis	Tri'nl Aug.	Autumn	1 200	1	—
	Tri'nl Apr.	Spring	1 200	1	—
Tatera leucogaster	Control	Autumn	1 800	1	—
		Winter	1 800	3	400
		Spring	3 200	1	—
		Mid-Sum.	1 400	2	400
	Ann'l Aug.	Autumn	3 600	1	—
		Winter	1 830	6	1 600
		Spring	4 400	1	—
		Mid-Sum.	1 600	2	400
	Tri'nl Apr.	Early Sum.	1 700	2	200
Crocidura hirta	Control	Autumn	3 930	3	4 000
	Tri'nl Aug	Autumn	1 400	2	400

figure. In the *Acacia-Sclerocarya* veld (Table 7) there is a slight indication that home range on the annual August treatment is larger than on the other treatments for several species.

Table 7

Home ranges (m^2) for four species of small mammals on different burning treatments in the Acacia-Sclerocarya *veld. (r = maximum-minimum range)*

Species	Burning Treatment	Season	Home Range (m^2)	n	r (m^2)
Lemniscomys griselda	Control	Winter	1 200	1	—
	Ann'l Aug.	Autumn	2 000	1	—
		Winter	2 000	1	—
Praomys natalensis	Control	Autumn	1 600	1	—
	Ann'l Aug.	Winter	2 900	2	200
Saccostomus campestris	Ann'l Aug.	Winter	2 400	1	—
	Tri'nl Aug.	Autumn	1 200	1	—
Tatera leucogaster	Ann'l Aug.	Autumn	6 000	1	—
		Winter	2 650	5	1 600

For a reasonable assessment of home range in relation to burning treatment, given the population densities recorded in this study, a truly massive trapping effort would probably be required; for example, something of the order of 200 traps left for 10 nights in each trapping session (i.e. 2 000 trap-nights per session as compared with 480 trap-nights per session in this study).

Food preferences

As with home range and reproduction, there is generally insufficient data from different burning treatments for any one species to evaluate the possible interaction between burning treatment and food taken (Table 8).

The classification of stomach contents into three categories, white and green plant material and insect material, represents the simplest possible analysis, but at the same time represents the most complex possible without requiring elaborate techniques and detailed knowledge of botany and of insect classification. White plant material includes seeds and stems, and green material includes leaves of trees, bushes, herbs and grasses.

The relatively low percentages of insect material in the stomachs of the two insectivores recorded, *C. hirta* and *E. brachyrhynchus,* is somewhat surprising, and

Table 8

The percentage composition of stomach contents for ten species of small mammals on different burning treatments in the Kruger National Park

Species	Veld Type 1	Burning Treatment	Time	n	White	Green	Insect
Aethomys chrysophilus	T-D	All	All	11	47	32	21
C. hirta	Both	All	All	7	58	2	40
Dendromus mystacalis	Both	All	All	3	60	18	22
Elephantulus brachyrhynchus	A-S	Annual August	Winter	3	20	30	50
Mus minutoides	T-D	Biennial December	Winter	1	80	2	18
Lemniscomys griselda	T-D	All	All	5	29	67	4
	A-S	All	All	11	50	48	2
Praomys natalensis	T-D	All	All	12	63	32	5
	A-S	All	All	10	79	3	18
Saccostomus campestris	T-D	All	All	7	67	15	18
	A-S	Annual August		2	90	10	0
Steatomys pratensis	T-D	All		11	83	4	13
Tatera leucogaster	T-D	Annual August	Pre-Burn	13	79	18	3
		Annual August	Post-Burn	11	34	43	23
		Others	Pre-Burn	6	56	41	3
	A-S	Annual August	Pre-Burn	4	32	67	1

1. T-D = *Terminalia-Dichrostachys* A-S = *Acacia-Sclerocarya*

the percentage of green material is high. The literature yields no records of stomach analyses of these species and hence comparison is not possible, but these insectivores are perhaps more omnivorous than previously suspected, supplementing a preferred insect diet with plant material in the same way that most rodent species obviously supplement their vegetation diet with insects.

Lemniscomys griselda includes the lowest proportion of insect material in its diet but the analyses from the other rodent species all included at least 10% of insect material in their diet at some time. Hanney (1965) found in the case of *A. chrysophilus* in Malawi that 35% of stomachs examined contained insect remains, 87% contained vegetable remains of which 50% included white material and 43% green material; this seems similar to the results from the present study. *Praomys natalensis* stomach contents show some variation between the two veld-types, with the proportion of insect material varying from 5% in the Pretoriuskop area to 18% in the Satara area. Hanney (1965) found that while white vegetable material was predominant, 31% of the stomachs contained insect material; and Delany (1964) found in Uganda that 92% of the stomachs he examined contained insect material, though generally only in small amounts. Again these findings seem similar to the Kruger Park results. All stomachs of both *S. campestris* and *S. pratensis* included mainly white plant material, though in the case of the former species Hanney (1965) recorded the occurrence of white material in only 39% of the stomachs analysed.

Once again the most interesting results come from *T. leucogaster*. In autumn and winter prior to burning in the *Terminalia-Dichrostachys* veld there appears to be a preference for white material on the annual burning treatment (79%) compared with the other burning treatments (56%), and the reverse is true of green material. This may reflect the greater availability of seeds on the annual burning treatment where, with no litter, fallen seed were easily found on the ground and often collected in depressions. Following burning there was a change in diet with green material becoming predominant. This undoubtedly reflects the situation that following burning there was little seed material available, and the major food supply was the new grass shoots. When dissected fresh, the stomachs of these animals exuded quite powerfully the characteristic smell of newly-mown grass. There was an increase of 20% in the amount of insect material in the stomachs collected after burning on the annual burning treatment as compared with those collected prior to burning. Whilst apparently preferring plant material, particularly white plant material when available, *T. ieucogaster* appears to supplement its diet to a considerable extent with insects when plant material is in relatively short supply.

To summarise, while most rodent stomachs contained insect material to a lesser or great extent, those of the two insectivore species contained surprisingly high amounts of plant material. *Tatera leucogaster* appears to change its diet in accordance with the prevailing food supply. It seems unlikely that burning treatment affects the distribution of small mammals in relation to their diet, but rather than the species resident on any particular treatment by virtue of its cover and litter characteristics are able to change their diet to suit the prevailing food supply.

The direct effects of burning

The biennial October burning treatment on the Shabeni Series in the *Terminalia-Dichrostachys* veld, which was burned on 26/10/1976, was specifically examined immediately before and after burning. The standard 10 x 8 live-trap grid was laid on the plot five nights before burning, was removed on the morning of 26/10/1976 and replaced later the same afternoon. In an effort to obtain the maximum possible catch after the burn, forty snap-traps were interspersed among the live-traps. Prior to burning the population densities per hectare and number of individuals captured were as follows:

A. chrysophilus 0,61/ha 2 individuals
L. minutoides 0,31/ha 1 individual
L. griselda 0,91/ha 3 individuals
S. campestris 0,93/ha 3 individuals
S. pratensis 0,90/ha 3 individuals

TOTAL 3,66/ha 12 individuals

Unfortunately two of the *S. campestris* individuals died in the live-traps on the last two nights before the burn, and so the known *S. campestris* population at the time of burning was one individual and the known total small mammal population was ten individuals.

The first night after burning there was no catch, the second night the one known *S. campestris* appeared in the live-traps and one marked *S. pratensis* appeared in the snap-traps. The known *S. campestris* individual reappeared in the live-traps on the third night, and the fourth night catch was zero. Thus the apparent immediate fall in rodent population was 80% with *L. griselda* and *A. chrysophilus* accounting for 50%.

Estimates of percentage fall in population following burning on other treatments are necessarily less accurate on account of the intervals between pre-burn trapping and burning, and between burning and post-burn trapping. However, on the Shabeni Series triennial April burning treatment, trapped two weeks after burning, the apparent decrease in population was 80%. For *C. hirta* the fall was 100% (part of which is probably attributable to a seasonal decline) while for rodents it was 70%, though *P. natalensis* fell by only 10%. *Saccostomus campestris,* present at a density of 1,29 animals/ha in autumn, was absent after the burn. The annual August burning treatment, again trapped two weeks after burning, showed a 91% population fall, 56% of which was attributable to *T. leucogaster*. No *L. griselda* were recorded (pre-burn density, 1,66 animals/ha). The triennial August burning treatment was trapped four weeks after burning and showed only a 23% decrease in rodent population but a 55% decrease in total small mammal population as a result of the fall in *C. hirta* density from 3,94 animal/ha to zero. *Lemniscomys griselda* also disappeared.

In the *Acacia-Sclerocarya* veld, the triennial April burning treatment was trapped three weeks after burning and the population was zero. Prior to burning the population density had been 1,74 animals/ha, 1,43 of which was contributed by *L. griselda,* the rest by *P. natalensis.*

With the exception of the Satara area triennial April burning treatment, all the burned plots were already producing fresh green shoots at the time of the trapping sessions mentioned above, and generally were being heavily grazed by the larger herbivores. Even the biennial October treatment was showing new grass shoots up to 10 cm long by the fourth morning after burning.

With falls in rodent population of between 23% and 91% in the weeks following burning it is not easy to see any common trends. *Lemniscomys griselda* appears to vacate burned areas, and *C. hirta* probably reacts similarly, though the situation is complicated by seasonal changes. Other species such as *S. campestris, S. pratensis* and *P. natalensis* appear relatively unaffected by burning. Neal (1970) found evidence that *Lemniscomys striatus* in Uganda emigrated from burned areas immediately after the burn, but though numbers were reduced this species remained one of the most common on the burned areas. Three other species, all largely diurnal, were drastically affected by the fire; no *Lophuromys sikapusi* or *Mylomys cunninghamei,* and only a few survivors of *Arvicanthis niloticus* were recorded after the burn. Cook (1959) recorded an "immediate post-burn crash" in rodent populations in both bush and grass following a fire in California, and Lawrence (1966) noted an immediate post-burn reduction in numbers following a chaparral fire in the Sierra Nevada foothills of California. Neither Cook nor Lawrence found any evidence of emigration from burned areas. Cook (1959) suggested that since seed food remained intact after the burn (though this was not the case in the present Kruger Park study) cover or lack of it was probably important in the initial post-burn decline, and Lawrence (1966) suggested that removal of the cover would expose the small mammal population to increased attack by predators. However, Neal (1970) discounted predation as being important since the fall in numbers was so rapid that a marked increase in the numbers of predators would be called for to account for it, and no such increase in small carnivores or raptors was noticed.

Lawrence (1966) presents evidence that there is unlikely to be any significant mortality during the actual fire since any animal that can escape down a burrow to a depth of a few inches would be safe. This is particularly so in an area such as the Kruger National Park where in general the fire burns along a narrow front which passes over any particular point such as a burrow in a very short space of time (1 to 2 minutes at the most). It seems therefore that the drastic post-burn reductions in small mammal numbers probably relate to removal of cover, and in the case of certain species to emigration, rather than to increased influence of predators or direct mortality during the fire.

Conclusions

From the present study, the following emerges:

a. Pretoriuskop area *(Terminalia-Dichrostachys* veld)

1. Annual burning — lowers species diversity and biomass, and maintains domination by *T. leucogaster* (by virtue of frequent removal of cover and litter);

2. Triennial burning — lowers biomass after burning, and produces post-burn conditions (low cover and litter) which favour *T. leucogaster*; but allows re-establishment of cover and litter over the three-year period, initially such that other rodent species become established, and finally to such a degree that litter build-up (possibly owing to elimination of detritus fauna and of damp conditions important for microbial decomposition of litter) favours *C. hirta* rather than rodents;

3. No burning (control) — maintains a high biomass and a stable, high species diversity, with cover and litter conditions which are adequate for most species of small mammals.

b. Satara area *(Acacia-Sclerocarya* veld)

1. Annual burning — promotes species diversity and biomass, and maintains low cover and litter conditions suitable for *T. leucogaster*;
2. Triennial burning — allows cover development and litter build-up which by the end of the three-year cycle exert a strong negative influence on rodent numbers and diversity;
3. No burning (control) — maintains a reasonably high biomass and high population densities of *L. griselda* and *P. natalensis*.

Hence, the burning regime with the least detrimental (or most beneficial) effects on small mammals appears to be that of not burning at all. Since small mammals are important as prey species for the smaller carnivores and some birds of prey, both a variety (i.e. diversity) and a high biomass is desirable. However, in a National Park other considerations (such as grazing for larger mammals and bush encroachment) must be borne in mind, and a management policy followed which caters as best as possible for a variety of animal and plant species. Assuming, therefore, that the three-year burn-related cycle of species composition found in this study on the small experimental burning plots also holds true for the large nature conservation blocks, and, given the fact that within any section a different third of the area will be burned each year, the rotational triennial burning policy of the National Parks Board would appear to be satisfactory for maintaining the small mammal species diversity, albeit to a certain extent at the cost of the highest population density. At the same time there should be enough areas of sufficient size which are never or rarely burned and which can, therefore, act as refugia, particularly in the Satara area.

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