The influence of fire on rodent abundance at the N'washitshumbe enclosure site, Kruger National Park, South Africa[†]

D.N. MacFadyen[1,2*], N.L. Avenant[3,4], M. van der Merwe[1] & G.J. Bredenkamp[2]

[1]*Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, 0002 South Africa*
[2]*Department of Plant Sciences, University of Pretoria, Pretoria, 0002 South Africa*
[3]*Department of Mammalogy, National Museum, Bloemfontein, 9300 South Africa*
[4]*Centre for Environmental Management, University of the Free State, Bloemfontein, 9300 South Africa*

The relative population numbers of rodents were studied in nine habitats in and outside the N'washitshumbe enclosure site, Kruger National Park, before and after burning the firebreaks that surround the enclosure. Trap success was exceptionally high, and the field work is suspected to have coincided with a *Mastomys* population explosion. This genus dominated the small mammal communities before and after the burn, and never disappeared from the burnt patches. Its numbers also did not crash directly after the burn, as have been reported in most other studies. Movement from the burnt areas was observed, which may have had a significant impact on the numbers of rodents caught both inside the enclosure and in the more natural areas outside. Our study suggests that fire can be investigated as a tool to keep rodent densities down in areas where they are nuisance animals, especially when used in conjunction with models that forecast outbreaks of *Mastomys*. It also emphasizes the value of long-term studies informing management strategies for animal damage control and biodiversity and ecosystem conservation.

Key words: small mammal communities, fire, *Mastomys*, indicator species, animal damage control, biodiversity, ecosystem conservation.

INTRODUCTION

Small mammals constitute an important, but poorly studied, component of the northern plains of the Kruger National Park (KNP) (MacFadyen 2007). As burrowers and consumers they impact on the resource of grazing ecosystems, and as prey they support a diversity of predator species. While the evolution of southern African small mammal communities with fire as a natural disturbance factor and important component has been debated (Cook 1959; Beck & Vogl 1972; Kern 1981; Swanepoel 1981; Rowe-Rowe & Lowry 1982; Avenant 2000; Salvatori *et al.* 2001), and the succession of species and species composition related to vegetation and ecological values (see Ferreira & Van Aarde 2000, 1999; Avenant & Cavallini 2007; Avenant *et al.* 2008), the indirect impact of fire on predators, through the impact on small mammal prey, has not been considered. Also, where the effect of burning on vegetation has been well

studied (e.g. Tansley 1935; Hopkins 1965; Kucera & Koelling 1964), the effects on mammals are less well documented (Yarnell *et al.* 2007). The influence of fire on African small-mammal populations has been studied in the Drakensberg montane grasslands (Rowe-Rowe & Lowry 1982), Zululand thornveld (Bowland & Perrin 1988), South African mixed bushveld (Yarnell *et al.* 2007), central South African grasslands (Avenant & Schulze 2011), Swaziland grasslands (Monadjem & Perrin 1998), tropical grassland (Cheeseman & Delany 1979; Delany 1964, Neal 1970), the South African lowveld of the Kruger National Park (Kern 1981), desert grassland (Christian 1977) and the Maasai Mara (Salvatori *et al.* 2001). While Ferreira & Van Aarde (1997, 1999) and Avenant & Schulze (2011) have alluded to the fact that small mammal community composition change with time and succession, Monadjem (1997) and Ferreira & Van Aarde (2000) mentioned the importance of pockets or patches of areas in different stages of succession for maintaining the diversity of small mammal species.

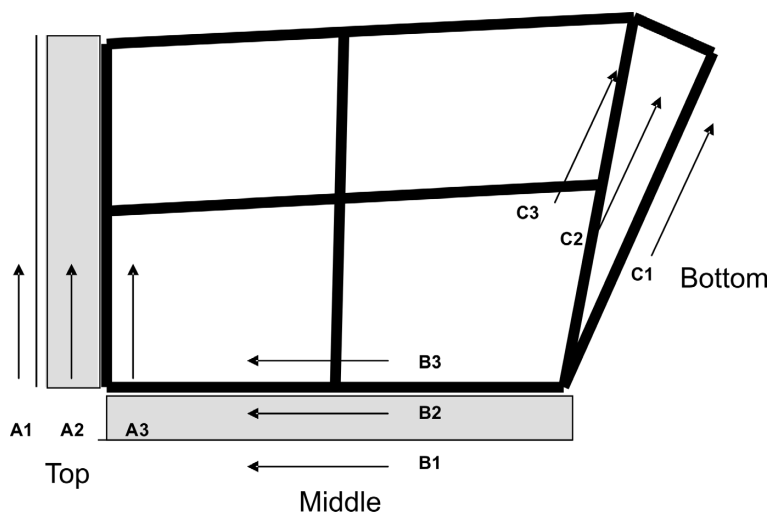The N'washitshumbe enclosure site was estab-

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Fig. 1. Illustration of the N'washitshumbe enclosure site and placement of three small mammal transects in each of three grid areas, A, B and C. Grey shading indicates firebreak areas.

lished in the late 1960s to allow intensive scientific research on rare ungulate species, as well as acting as a breeding nucleus for the augmentation of free-ranging roan antelope (*Hippotragus equinus*) herds (Joubert 1976). Its surrounding landscape is actively managed by burning annual surrounding firebreaks that effectively limit unplanned fire on the inside of the enclosure. This paper investigates the short-term effect of fire on small mammal population densities inside the firebreak and tests the hypothesis that fire-induced changes in the immediate environment affect their numbers and community structure instantaneously – with possible 'enormous' impact on the predators that feed on them. With the firebreak being in the middle, and directly adjacent to, natural veld and a long-term exclusion plot, the burn's impact on both these areas could also be investigated. The relatively undisturbed ecosystem of the KNP represents the ideal study area as these habitats, small mammal communities and predators have been largely unaffected by humans.

METHODS

The study was conducted at the 302 ha N'washitshumbe roan enclosure (22°43′–22°59′S & 31°12′–31°22′E) situated in the northern plains of the KNP, Limpopo Province, South Africa. This fenced area excludes all large predators and herbivores. The general area receives between 350 and 450 mm rain per year (Braack 1983), and the landscape is classified as Basaltic Plains with *Colophospermum mopane* shrub savanna (Solomon *et al.*

1999). Seasonally flooded depressions, referred to as vleis, drain these plains. The upland areas of the plains are dominated by *Mopane/Combretum* woodland while grasses dominate the low-lying, seasonally inundated vlei. The vegetation within the enclosure is more thickly overgrown than on the outside.

Researchers in the KNP have for many years instigated the long-term study of burning vegetation with the establishment of burning plots and firebreaks in the major vegetation units of the Park for research purposes (Brynard 1964; Enslin *et al.* 2000). The N'washitshumbe enclosure was built in 1968 for the exclusive breeding of endangered species (Joubert 1976). It is protected from fire by a network of firebreaks directly outside the enclosure, as well as controlled rotational burning inside the enclosure. These firebreaks are approximately 100 m wide and are burned in July of each year. Inside the enclosure the vegetation structure is regularly monitored and the habitat is managed through occasional rotational block burns (Levick 2001). In this case it contained substantial amounts of moribund grass and was considered in postclimax condition (MacFadyen 2007). The vegetation outside is burnt on average every four years (Trollope *et al.* 1998); in this specific case no fire outside the enclosure have impacted the small mammals on our trapping grids during at least the three years before the start of our study.

Three grids, each comprising three fixed transect lines of 30 Sherman traps each, were placed around the enclosure (Fig. 1). The transect lines

within each grid were spaced 100 m apart and the traps on each line 10 m apart. Trap stations were fixed for the duration of the study, and traps were checked and re-baited daily. On each visit trapping was conducted over two successive 24-hour periods. Small mammal data (» captures at point localities) were recorded at specific intervals from April 2004 to April 2005: in relation to the fire, about nine weeks before (April 2004), four weeks before (May 2004), two weeks after (July 2004), five weeks after (August 2004), 25 weeks after (December 2004) and 40 weeks after (April 2005). All captures were recorded by toe clipping (American Society of Mammalogists 1998) and marked using the 1-2-4-7 toe-clipping system (DeBlase & Martin 1981).

Grids (see Fig. 1) were designated according to slope: top (grid A), middle (grid B) and lower (grid C). Transect lines A3 and B3 were inside the enclosure while A2 and B2 were in the fire burn directly outside the enclosure. Lines A1 and B1 were outside the fire burns in the open, 'natural' veld. Two transect lines in grid C (C1-outside enclosure and C2-inside enclosure) were in a vlei wetland and the third (C3) in a sodic (highly mineralized) area inside the enclosure. During 2004 the areas A2, B2 and C1 were burnt on 4 July 2004. The evidence of partially burnt grass at the N'washitshumbe enclosure site gave evidence that this was a cool burn. Firebreaks were not burnt in 2003 due to low biomass, and in 2005 the firebreaks were burned only after completion of this study. Transects A1, A3, B1, B3 and C2 were all at least 50 m from the firebreak.

Because both *M. coucha* and *M. natalensis* occur in the area (Venturi *et al.* 2004), and it is impossible to distinguish between them using external characteristics, all multi-mammate mice trapped during this study will be referred to as *Mastomys* spp. This 'species' was expected in relatively high numbers in the burnt areas as it has been reported to numerically dominate the terrestrial small mammal fauna in recently disturbed areas (see Meester *et al.* 1979; Bronner *et al.* 1988; Linn 1991; Rowe-Rowe 1995; Leirs *et al.* 1996; Monadjem 1997; Ferreira & Van Aarde 2000; Caro 2001; Avenant 2011).

The term 'veld' refers to the South African name for an area that is mostly covered with natural vegetation. 'Trap night' was used to describe one trap that was set for a 24 h period (following Rowe-Rowe & Lowry 1982), and trap success (or percentage success) is the number of rodents captured/100 trap nights. Taking into account the

relatively short trap periods, the actual number of individuals caught was taken as indication of relative population size; no calculation of density estimates was possible. Recaptures on the same transect and during the same trap session were excluded when calculating total numbers, but taken into account when calculating trap success. To exclude the variations in daily trap success, the relative population size within and between habitats was also compared using the number of individuals trapped per day.

Normality of data was checked with the Shapiro-Wilk's *W*-test. Statistical analyses (all ANOVAS) were performed with Statistica for Windows (Statsoft Inc., 1995), and the 95% level ($P < 0.05$) was regarded as statistically significant for all tests. The maximum distance a rodent has been observed to move was determined by calculating the longest distance between all traps in which the specific individual was trapped.

RESULTS

Trap success during this study was very high (overall mean 39.3 ± 24.3, but ≥50 on 61% of all transects during the high density period April to August; mean trap success then 53.2 ± 16.9) (Table 1). Overall (all transects and sessions considered) *Mastomys* contributed 79.0 ± 31.3 % to the small mammal captures, *Gerbilliscus leucogaster* 14.1 ± 28.1, *Saccostomus campestris* $6.2 \pm 11.6\%$, *Aethomys chrysophilus* $0.1 \pm 0.5\%$ and *Lemniscomys rosalia* 0.5 ± 2.6. No differences could be found in small mammal species composition between the 'natural' veld and that on the inside of the enclosure: within similar grids (» habitats), A1 had three species (*Mastomys* spp., *S. campestris, T. leucogaster*) and A3 had the same three species plus one individual of *A. chrysophilus*; B1 and B3 both also had the same three species (*Mastomys* spp., *S. campestris, T. leucogaster*), and again with no indication that there could be any difference in composition.

Mean overall rodent numbers were at their highest two weeks after the burn, and then decreased significantly to December 2004, April 2005 (Table 1; $F_{5,48} = 21.537$, $P < 0.0001$). At the individual transects, however, the pattern differed from that of the mean. Where densities increased from April 2004 to July 2004 and then dropped to April 2005 in the 'natural' veld (outside the firebreak), densities inside the firebreak increased up to August 2004 (*c.* 5 weeks after the burn) before dropping to the lowest densities, also in April 2005. Inside the enclosure the density

Table 1. Number of rodent individuals trapped, percentage contribution (in brackets) and trap success for the entire small mammal community on nine transects at the N'washitshumbe enclosure site, Kruger National Park, 2004–2005.

| Trap session	Transect	*Aethomys chrysophilus*	*Lemniscomys rosalia*	*Mastomys* spp.	*Saccostomus campestris*	*Gerbilliscus leucogaster*	Trap success
April 2004	A1	0	0	26 (74.29)	6 (17.14)	3 (8.57)	58.3
	A2	0	0	29 (90.63)	3 (9.38)	0	53.3
	A3	0	0	18 (85.71)	1 (4.76)	2 (9.52)	35.0
	B1	0	0	29 (87.88)	3 (9.09)	1 (3.03)	55.0
	B2	0	0	32 (91.43)	3 (8.57)	0	58.3
	B3	0	0	21 (91.30)	1 (4.35)	1 (4.35)	38.3
	C1	0	0	22 (88.00)	2 (8.00)	1 (4.00)	41.7
	C2	0	0	21(100)	0	0	35.0
	C3	0	0	23 (92.00)	2 (8.00)	0	41.7
May 2004	A1	0	0	28 (96.55)	0	1 (3.45)	48.3
	A2	0	1 (2.78)	34 (94.44)	1 (2.78)	0	60.0
	A3	0	0	37 (97.37)	0	1 (2.63)	63.3
	B1	0	0	36 (97.30)	0	1 (2.70)	61.7
	B2	0	0	43 (100)	0	0	71.7
	B3	1 (2.63)	0	35 (92.11)	1 (2.63)	1 (2.63)	63.3
	C1	1 (2.94)	0	33 (97.06)	0	0	56.7
	C2	0	0	24 (100)	0	0	40.0
	C3	0	0	14 (100)	0	0	23.3
July 2004	A1	0	0	46 (97.87)	0	1 (2.13)	78.3
	A2	0	2 (9.09)	19 (86.36)	1 (4.55)	0	36.7
	A3	0	0	45 (100)	0	0	75.0
	B1	0	0	59 (100)	0	0	98.3
	B2	0	0	42 (97.67)	1 (2.33)	0	71.7
	B3	0	0	28 (93.33)	1 (3.33)	1 (3.33)	50.0
	C1	0	0	31 (93.94)	1 (3.03)	1 (3.03)	55.0
	C2	0	0	20 (100)	0	0	33.3
	C3	0	0	18 (81.82)	2 (9.09)	2 (9.09)	36.7
August 2004	A1	0	0	31 (93.94)	1 (3.03)	1 (3.03)	55.0
	A2	0	0	36 (100)	0	0	53.3
	A3	0	0	29 (100)	0	0	48.3
	B1	0	0	42 (95.45)	2 (4.55)	0	73.3
	B2	0	0	42 (97.67)	1 (2.33)	0	71.7
	B3	0	0	35 (94.59)	2 (5.41)	0	61.7
	C1	0	0	36 (97.30)	0	1 (2.70)	61.7
	C2	0	0	18 (100)	0	0	30.0
	C3	0	0	9 (75)	1 (8.33)	2 (16.67)	20.0
December 2004	A1	0	0	5 (100)	0	0	8.3
	A2	0	0	7 (63.64)	3 (27.27)	1 (9.09)	18.3
	A3	0	0	2 (50.00)	0	2 (50.00)	6.7
	B1	0	0	5 (41.67)	2 (16.67)	5 (41.67)	20.0
	B2	0	0	11 (73.33)	4 (26.67)	0	25.0
	B3	0	0	6 (75.00)	1 (12.50)	1 (12.50)	13.3
	C1	0	0	5 (71.43)	0	2 (28.57)	11.7
	C2	0	0	4 (100)	0	0	6.7
	C3	0	0	0	3 (60.00)	2 (40.00)	8.3
April 2005	A1	0	0	5 (100)	0	0	8.3
	A2	0	0	0	0	4 (100)	6.7
	A3	0	0	2 (22.22)	0	7 (77.78)	15.0
	B1	0	0	0	1 (11.11)	8 (88.89)	15.0
	B2	0	0	8 (88.89)	1 (11.11)	0	15.0
	B3	0	0	0	0	2 (100)	3.3
	C1	0	0	1 (16.67)	3 (50.00)	2 (33.33)	10.0
	C2	0	1 (16.67)	5 (83.33)	0	0	10.0
	C3	0	0	0	0	3 (100)	5.0
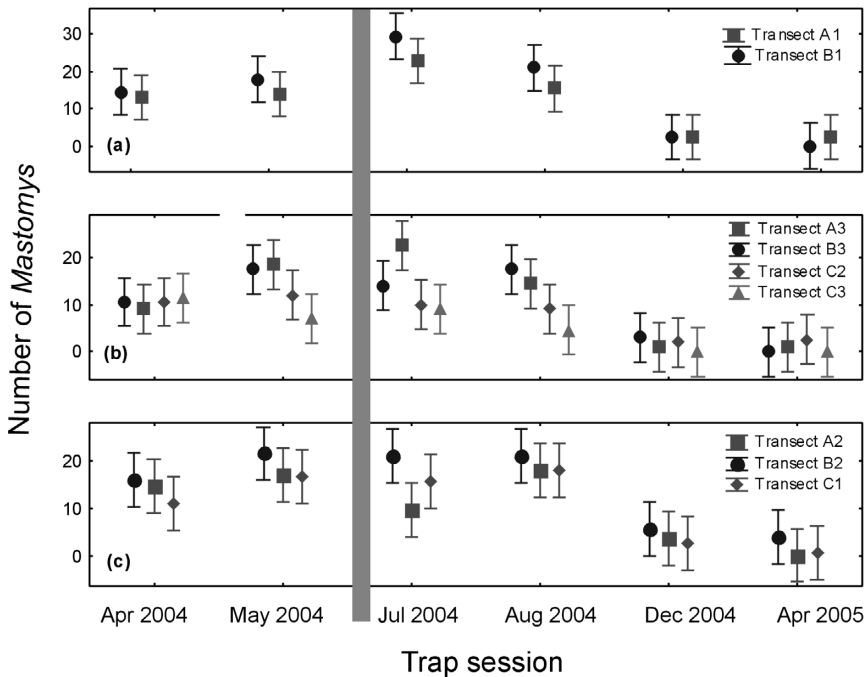
Fig. 2. The mean number of *Mastomys* specimens trapped per day during six trap sessions on transects (**a**) in natural veld, (**b**) inside the N'washitshumbe enclosure and (**c**) in the firebreak that surrounds the N'washitshumbe enclosure, the Kruger National Park. The bars present the 95% confidence limits; vertical grey bar presents the time of the fire.

patterns were different again, being highest on transects B3 and C2 just before the fire (in May) and on transect A3 two weeks after the fire (in July). To exclude possible inter-specific competition differences that may impact the results, the effect of fire on rodent numbers should in this case better be described for one species. Here *Mastomys* act as a convenient taxon, completely dominating trap success on all transects during the period April to August 2004.

Overall *Mastomys* numbers captured and trap success follow a trend similar to that of the mean number of all rodents (see above; Table 1). On the 'natural' transects A1 and B1, significant differences ($P < 0.05$) were also detected between trap sessions, with densities increasing from April to July 2004, after which it decreased to the following summer (December 2004) and autumn (April 2005) (Table 1; Fig. 2). No difference could be found in the number of *Mastomys* caught between these habitats, with much similar fluctuations observed on these transects.

Inside the enclosure (transects A3, B3, C2 and C3) the *Mastomys* numbers differed significantly between habitats during the trap sessions when densities were highest (May, July and August 2004;

$P < 0.05$) (Fig. 2b), with differences most obvious between the top habitat A3 (highest numbers) and the lowest ones, C2 and C3. *Mastomys* numbers also fluctuated differently in the different habitats: where highest numbers on transect A3 were reached during July, B3 and C2 already reached highest trappings in May and August 2004, C2 in May, and C3 in April (2004). Similar to the two transects in the 'natural' veld, *Mastomys* numbers inside the enclosure were lowest in December 2004 and April 2005.

In the firebreak the *Mastomys* number curves in each of the three habitats (Grids A, B and C) differed from that in the 'natural' veld in that no peak was found in July 2004 (Fig. 2c). Instead numbers remained high, and even slightly increased, until August. The firebreak transect in Grid B also had a different species composition than in the 'natural' veld, with transect B2 housing two species and B1 three (Table 1). A similar observation was made in Grid A, where the species differed between the natural veld (*Mastomys* spp., *S. campestris* and *T. leucogaster*) and the firebreak transect (*Mastomys* spp., *S. campestris* and *Lemniscomys rosalia*); the first *T. leucogaster* individual was trapped at the latter transect only 25 weeks after

the burn. In both these grids, however, *Mastomys* made similar relative contributions to the total community structure. The only period when significant differences in *Mastomys* (and small mammal) numbers were observed was two weeks after the fire (during the July 2004 session), when numbers were lower in the firebreak (Fig. 2). After this, population size became similar again as numbers dropped in the 'natural' veld but stayed unchanged in the firebreak. In both the December 2004 and April 2005 trap sessions *Mastomys* numbers were, similar to the period before the burn, slightly higher within the firebreak (*P* 0.05).

During the six trap sessions, spanning 12 months, 252 individuals were trapped more than once. Individuals were re-trapped over periods from successive days (= re-trapped the night immediately after first capture) to 12 months [e.g. *Mastomys* no. 474 (trapped in April 2004 on transect C3 and in April 2005 on A3); *Mastomys* no. 454 (trapped five times, in April, August and December 2004 and in April 2005 – and always on transect A3]. The maximum and mean maximum distances moved, were >500 m and 81 ± 121 m, respectively. A total of 197 individuals were always re-trapped on the same transect (maximum distance moved 200 m; mean = 33 ± 38 m), 55 on more than one transect (maximum distance moved >500 m; mean = 253 ± 153 m), and 27 individuals were trapped on more than one grid (maximum distance moved >500 m; mean = 314 ± 128 m).

In total, 10 specimens were observed to have moved into the firebreak in the nine-week period before the fire, and only four in the 40-week period after the fire. In comparison, six individuals have moved out of the firebreak before the fire, and 18 immediately (= within five weeks) after the fire (11 in the 'natural' veld and seven inside the enclosure, re-trapped in July and August). Focusing on the enclosures, four individuals were found to move out, and 10 moved in; 70% of the latter moved from the firebreak immediately after the fire.

DISCUSSION

The July 2004 firebreak burn could well have been at a peak of a *Mastomys* spp. population explosion as this species completely dominated the small mammal numbers on all grids and transects, and trap success was abnormally high; e.g. trap success recorded by: Rowe-Rowe & Lowry (1982) was <20%, Rowe-Rowe (1995) <30%, Monadjem &

Perrin (1998) <5%, Salvatori *et al.* (2001) <2%, Fitzherbert *et al.* (2006) <15%, Yarnell *et al.* (2007) 10.5%, Datiko *et al.* (2007) <20%, Avenant (2011) <11%. At one or other stage during the months following August 2004 there was a great decrease in *Mastomys* numbers because, when the site was visited during December 2004, *Mastomys* numbers had dropped significantly. Even as late as April 2005 their numbers had not recovered.

The seasonal pattern observed, with *Mastomys* densities reaching a peak in winter (as observed in the 'natural' veld), are nevertheless considered as the normal natural fluctuation in the KNP (De Wit 1972; Kern 1977; see also Yarnell *et al.* 2007 for mixed bushveld).

During the present study the two-night trapping method was set to report on differences and changes in relative densities, and not to test for species richness, other indicator species, or to describe community structure (see Avenant & Cavallini 2007). Its purpose was to note how *Mastomys* reacted to the fire (compared to the 'natural' veld). This species is also regarded as a good indicator of habitat integrity, whose domination in the small mammal community is associated with recent disturbance, or the sudden improvement after severe conditions (see Avenant 2011). It is also considered a non-trap-shy species, commonly being trapped the first night after traps were laid out in a habitat where they are present (National Museum, Bloemfontein, records; Avenant, unpubl. data). The *Mastomys* group has a wide distribution in Africa (*M. natalensis* in southern, east and central-west Africa, and *M. coucha* in southern Africa – Duff & Lawson 2004; Skinner & Chimimba 2005), and the results of this study are applicable wherever the group is considered as a health risk, agricultural pest or indicator species (Avenant 2011).

As the burn happened before the 'natural' density peak, densities inside the firebreak never climbed to the same heights. They nevertheless remained high and then dropped with the natural population. A second possibility may be that densities did indeed drop from a higher level at the time of the burn (the actual peak may not have been observed; also see the marked decrease on transect A2), but then stayed at a fairly high level, surviving on seeds, vegetation matter and insects (Watson 1987) raised another litter on the new shoots; and the new sub-adults could already, in the August trap session, have been part of the trappable population (Linn 1991). Immigration (not recorded here,

though) could also have contributed to the slight increase observed from July to August.

Importantly, although rodent numbers decreased in the firebreaks it never crashed (as was expected from previous work – see Cook 1959; Lawrence 1966; Neal 1970; Christian 1977; Cheeseman & Delany 1979; Kern 1981; Swanepoel 1981; Monadjem & Perrin 1998; Vieira 1999; Henriques *et al.* 2006; Avenant & Schulze 2011). Avenant & Schulze (2011) have found no direct mortalities immediately after the fire, and Lawrence (1966) presented evidence that animals that can escape down a burrow to a depth of a few inches will be safe from a burn; particularly from cool burns (such as this one) where fire burns along a narrow front which passes over any particular point, such as a burrow, in a very short space of time. It seems therefore that reported drastic post-burn reductions in small mammal numbers relate to removal of cover and, in the case of certain species, to emigration rather than to the increased influence of predators or direct mortality during the fire (see also Beck & Vogl 1972; Kern 1977).

In Kern (1977)'s study in the KNP small mammal populations drastically decreased two weeks after burning, and recovered four months after mid-winter burning when grass seeds had returned. In the present study, however, numbers remained high during at least a month after the burn, and then followed the natural decline to mid-summer (December 2004). In April 2005 (nine months after the fire) numbers were still low. According to Begg *et al.* (1981) a gradual fall in numbers later after a fire can be attributed to food shortages, increased predation or the lack of recruitment. In many southern African summer rainfall areas a combination of these factors typically leads to the general drop in rodent numbers from the end of the one growing season to the start of the next (Bronner *et al.* 1988) – as is expected to have happened here somewhere between August and December.

Our study suggests that fire can be investigated as a tool to keep rodent densities down in areas next to agricultural fields where they are a nuisance – especially when used in conjunction with models that forecast outbreaks of *Mastomys* (Leirs *et al.* 1996; Mwanjabe & Leirs 1997). A fire at the right time of year may exclude individuals, even if just the less fit adults (e.g. those from the younger and relatively old age classes), from reproductive activity for a while, with consequences on the exponential increase in numbers towards the time when sowing or harvesting the crop. Where such

reproductive activities can be stopped or postponed for a period of 23 days (the gestation period of *M. natalensis* – Johnston & Oliff 1954), for example, one generation, with their progeny, may be eliminated early on in the reproductive season.

Disturbance, such as fire, is regarded as a key ecological process, crucial for the conservation of *inter alia* plant and small mammal species diversity (Fraser 1990; Parr & Chown 2003). Mosaic burns, or the preservation of areas in different successional stages towards which individuals of fire-sensitive species can migrate and recolonize, is encouraged (see e.g. Rowe-Rowe 1995; Monadjem 1997; Carey & Wilson 2001). Other important factors for management of ecosystems, biodiversity or rodent numbers are the time and frequency of burning, and the combined effect of the previous year's rainfall and inhibition of vegetation recovery via grazing pressure (e.g. Vieira 1999; Yarnell *et al.* 2007). While a burn in the middle of the breeding season may temporarily halt the increase, a burn right at the beginning of the breeding season may delay onset of breeding activity, and fire at the end of the breeding season should contribute to a faster decline (or crash), especially in areas where seasons are more extreme (e.g. the highveld grassland) and where a sharp (*c.* 50%) drop from the end of the breeding season (end of the wet, warm period) to about the middle of the non-breeding season (cold, dry period) is observed on an annual basis (Bronner *et al.* 1988; Avenant 2011). The availability of food, e.g. after a good rainy season or in more temporal areas where one shower can still trigger new growth in the non-growing season, may also have an impact on how rodent populations and communities react after fire and should be born in mind when managing for a specific outcome. Understandably, when managing for ecosystem and biodiversity conservation such a management plan may differ drastically from one where the purpose is to manage for prey density/biomass or for animal damage control (see also Green & Taylor 1975). As such, the frequency, intensity and timing of burns are important factors to be kept in mind.

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