

---

# The importance of post-fire regrowth for sable antelope in a Southern African savanna

Francesca Parrini<sup>1\*</sup> and Norman Owen-Smith<sup>2</sup>

<sup>1</sup>*School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, 2050 Wits, South Africa* and <sup>2</sup>*Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, 2050 Wits, South Africa*

## Abstract

Burning is commonly used in savannas to stimulate grass regrowth for grazing ungulates. We recorded the relative use of burns occurring at different stages in the seasonal cycle, as well as in different regions of the landscape by two herds of sable. We also recorded behavioural measures of foraging efficiency and faecal nutrient contents as an indication of nutrient gains. Sable consistently concentrated their grazing on burned areas provided there was sufficient green regrowth during the dry season. In these circumstances they grazed for longer per feeding station, showed a slower step rate while foraging, and shorter between-patch moves, and a higher probability of encountering acceptable food per step taken while foraging than on unburnt areas. In the year when only a burn with insufficient regrowth was available, sable continued to forage in the area that had been burned during the previous year. Faecal crude protein was substantially higher at the end of the dry season in the year when burned areas were utilized. Accordingly early dry season fires can be important in helping sable bridge the nutritional limitations posed by the dry season, provided sufficient soil moisture remains to promote adequate grass regrowth.

*Key words:* burned grassland, faecal nitrogen, faecal phosphorus, fire management, foraging behaviour, *Hippotragus niger*

## Résumé

Les feux sont fréquemment utilisés dans les savanes pour stimuler la repousse des herbes consommées par les ongulés herbivores. Nous avons enregistré l'utilisation relative des aires brûlées à différents stades du cycle saisonnier, et dans

différentes régions du paysage, par deux hardes d'antilopes sable. Nous avons aussi enregistré des mesures comportementales de l'efficacité du nourrissage et le contenu en nutriments des matières fécales pour avoir une indication du gain en nutriments. Les antilopes sable concentraient leur pâturage de façon continue sur les aires brûlées pour autant que la repousse de verdure fût suffisante au cours de la saison sèche. Dans ce cas-là, elles paissaient plus longtemps par station de nourrissage, présentaient un nombre de pas plus faible en mangeant et se déplaçaient moins entre les arrêts, et la probabilité qu'elles rencontrent une nourriture acceptable par pas franchi en cherchant leur nourriture était plus grande que dans les zones non brûlées. L'année où ne fut disponible qu'une zone brûlée où la repousse était insuffisante, les antilopes ont continué à brouter dans la zone qui avait été brûlée l'année précédente. Le taux de protéines brutes des matières fécales était substantiellement plus haut à la fin de la saison sèche l'année où les zones brûlées ont été utilisées. En fonction de cela, on peut dire que les feux du début de la saison sèche peuvent être importants pour aider les antilopes sable à passer le cap des limites nutritionnelles imposées par la saison sèche, à condition qu'il reste suffisamment d'humidité dans le sol pour favoriser une repousse d'herbes adéquate.

---

## Introduction

Grassland burning is commonly used as a management tool to control the grass-woody plant balance in vegetation (Govender, Trollope & van Wilgen, 2006) and to alleviate nutritional stress among herbivores during the dry season when grasses become senescent (Hobbs & Spowart, 1984; Vemeire *et al.*, 2004). Fire removes accumulated dead material and stimulates the growth of new leaves of high

---

\*Correspondence: E-mail: Francesca.Parrini@wits.ac.za

nutritional value (Dörgeleh, 1999). However, the magnitude of the green regrowth depends on the amount of soil moisture remaining and hence on the timing of the fire in the seasonal cycle (van de Vijver, Poot & Prins, 1999). For most management objectives it is advised to ignite fires following the first rains initiating wet season regrowth (Van Wilgen *et al.*, 2004). However, burns at this time are of limited value to grazers because unburned grass also commences regrowth around the same time. Burns early in the dry season potentially shorten the period over which herbivores must survive on low quality grass, but if the green growth is not sustained the burned areas supply little or no forage until the subsequent wet season commences. A patch mosaic of burned and unburned grassland could be of greatest benefit, allowing herbivores to partition their grazing time between the high quality but limited amount of forage available on the burns and the more abundant but poorer quality grassland elsewhere (Brockett *et al.*, 2001; Vemeire *et al.*, 2004). Wild herbivores differ in the grazing conditions that they favour and hence in their relative use of burned areas, due to body size differences (Wilsey, 1996) and other factors (i.e. Gureja & Owen-Smith, 2002; Tomor & Owen-Smith, 2002; Hassan *et al.*, 2008). Furthermore, competition among grazing ungulates can arise for the limited quantity of green foliage available (Rowe-Rowe, 1982).

In our study area, the Kgaswane Mountain Reserve situated in the Magaliesberg range bordering the Highveld region of South Africa, fire policy is aimed firstly at promoting a dense grass cover during the wet season in order to sustain stream flow and water quality, and secondly at improving the nutritional value of the grassland for supporting wild ungulate populations (Nel, 2000). Among the species present is sable antelope (*Hippotragus niger*), a low density grazer highly valued by hunters and game ranchers with a restricted distribution in South Africa (Skinner, Smithers & Chimimba, 2005). This species has declined substantially in its abundance in South Africa's Kruger National Park in recent years (Ogutu & Owen-Smith, 2005), raising concerns about its conservation status in the region. Sable tend to be found in savanna regions with sandy soils where grasses are generally low in nutritional value. They reportedly rely on dry season burns to produce grass regrowth of sufficient quality to supply their nutritional requirements through the dry season months (Estes & Estes, 1974; Sekulic, 1981; Magome *et al.*, 2008). In contrast, sable made little or no use of burned areas in the Kruger National Park (Henley, 2005). Sable

favour relatively tall grass (Wilson & Hirst, 1977), and seem less adept at cropping grass shorter than 50 mm (Grobler, 1981). Burns may prove of little value if the grass regrowth remains below this level, as a result of inadequate soil moisture or competition from grazers better able to exploit short grass.

During our study, we fortuitously observed the contrasting conditions generated by fires occurring at different times of the seasonal cycle and in different regions of the landscape. In this paper we report (i) changes in grass height and greenness following burns; (ii) relative use of the burnt areas by two sable herds occupying adjoining home ranges; (iii) measures of the foraging efficiency of these animals on the burns (following Novellie, 1978) together with daily foraging time; and (iv) the diet quality as indexed by faecal crude protein and phosphorus levels.

## Materials and methods

### Study area

The Kgaswane Mountain Reserve (KMR) is situated at an altitude of 1250–1600 m a.s.l. in the North-West Province of South Africa (25°43' S, 27°11' E) and covers 4500 ha. Soils are derived mostly from quartzitic sandstone, and hence are deficient in nutrients (Carruthers, 2000).

Vegetation types include: (i) grassland found mostly on the northern slopes and central basin with *Brachiaria serрата*, *Eragrostis racemosa*, *Loudetia simplex*, *Schizachyrium sanguineum*, *Themeda triandra*, and *Trachypogon spicatus* the common grass species and scattered stands of *Protea caffra*, *Acacia caffra* and *Faurea saligna* trees; (ii) wetland grassland in the central alluvial basin and elsewhere including marshy areas supporting *Phragmites australis* reeds; (iii) open shrubland of *Englerophytum magaliesmontanum*, *Zanthoxylum capense*, *Ancylobotrys capensis* and *Tapiphyllum parvifolium* where *Diheteropogon amplexans*, *Themeda triandra* and *Melinis nerviglumis* are the common grass species; and (iv) open to closed woodland consisting of *Acacia caffra*, *Celtis africana*, *Combretum molle*, *Combretum zeyheri*, *Grewia occidentalis*, *Rhus leptodictya*, and *Ziziphus mucronata*, found mainly in the north eastern slopes and valleys, with *Themeda triandra*, *Setaria sphacelata*, *Heteropogon contortus*, *Panicum maximum* and *Setaria lindenberghiana* as the predominant grass species.

Rainfall averages 682 mm (CV 27% over 44 years). Most rain (88%) falls between October and March, defining

the wet season months. During the study period, the annual rainfall (July–June) was 645 mm in 2002–03 and 712 mm in 2003–04 but with the dry season component (39 mm in 2002 and 25 mm in 2003) below the long term average of 95 mm (CV 67%). Mean daily temperature ranges from 9.7°C in July–21.3°C in January.

Fire has been used as a management tool in the KMR since 1972, initially applied at the end of the growing season, following the first wet season rain. In 1994, this changed to early–mid dry season burns, in order to provide green regrowth to herbivores during the dry season. Burns cover on average 13.7% of the reserve each year with an interval of 8.2 years between successive fires in any one locality (Nel, 2000). During 2002, two management fires were ignited at the end of June, one covering 540 ha in and adjoining the central alluvial basin and the other covering 789 ha in the south-eastern section (Fig. 1). Also in June 2002, an accidental fire burned 110 ha of the northern high lying plateau. In 2003, a management burn covering 344 ha was ignited on slopes

south of the alluvial basin at the beginning of May, while an accidental fire in the second half of October burned about three-quarters of the reserve less than a week before the wet season rains started, without penetrating the central alluvial basin.

Two sable herds of about 30 females plus young each occurred in the reserve, with additional males making a total of about 70 individuals. The ‘grassland herd’ which occupied a range including the central alluvial basin will be distinguished from the ‘woodland herd’ which generally occurred in the slopes and valleys in the east. Other grazers included about 200 zebra (*Equus quagga burchellii*), 115 red hartebeest (*Alcephalus buselaphus*), 60 waterbuck (*Kobus ellipsiprymnus*), 70 impala (*Aepyceros melampus*), 30 springbok (*Antidorcas marsupialis*) and four roan antelope (*Hippotragus equinus*). Predators in the region included leopard (*Panthera pardus*), caracal (*Felis caracal*) and black-backed jackal (*Canis mesomelas*). Signs of leopard were last seen in 1997, while jackals had increased in numbers (R. Newbury, personal communication).

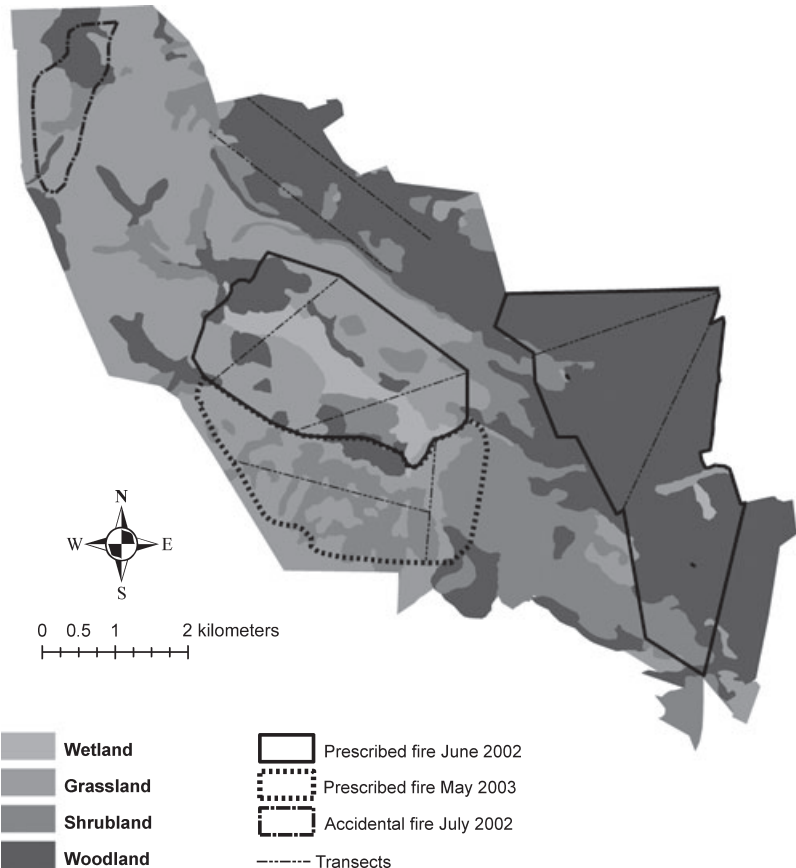


Fig 1 Map showing locations in the Kgaswane Mountain Reserve, in the North-West Province of South Africa, that were burned in the dry seasons of 2002 and 2003

### Data collection

During our study period the rain only fell at the end of October when all October data had already been collected and therefore we included the October data in the dry season, despite October being generally considered a wet season month. Observations were made during the late dry season of 2002 (August–October), the early wet season of 2002 (November–December), the complete dry season of 2003 (April–October) and early wet season of 2003 (November–December). For analysis, the dry season of 2003 was divided into early dry season (April–July) and late dry season (August–October) (Table 1).

To compare changes in grass height and greenness in burned and unburned areas, observations were made every 10 m along nine transects totalling 12 km in length on a monthly basis (Fig. 1). Height of the tallest grass leaf above ground was recorded in five categories: 0–50 mm, 51–100 mm, 101–200 mm, 201–400 mm, >401 mm. Greenness was visually estimated on unburned areas as the proportion of green leaves/total leaves and on new burnt areas as the proportion of green leaves/unit area, using Walker's (1976) eight-point scale: 0%, 1–10%, 11–25%, 26–50%, 51–75%, 76–90%, 91–99%, 100%.

When sable were seen, the area they occupied was recorded as either (i) unburned during the study period; (ii) burned in June 2002 (central); (iii) burned in June 2002 (eastern); (iv) burned in June 2002 (accidental); (v) burned in May 2003; or (vi) burned in October 2003 (Table 1). To estimate daily time spent foraging, one of the two herds of sable was observed from sunrise to sunset using the scan

sampling method (Altman, 1974) with 10 min intervals. Foraging was defined as standing or walking with head below the spine. To record measures of foraging efficiency, an adult focal animal was observed for 5–8 min, timing the period spent feeding and counting steps taken with head down. Steps taken with the head up were excluded. Bite rates (bites/min) were recorded separately during 1 min observation periods. These observations were restricted to the main foraging periods during the morning (sunrise – 9:00 am) or afternoon (sunset – 4:00 pm), and observations were not repeated on the same individual within an observation session. Fresh faecal samples were collected, air-dried and stored in sealed paper bags for later analysis. Samples from the same day were combined, yielding a total of 64 samples for the 'grassland herd' and 53 for the 'woodland herd'. Faecal samples were analysed for nitrogen and phosphorus as a proportion of dry matter using Kjeldahl digestion (Robbins, 1996). Nitrogen was converted to crude protein by multiplying by 6.25.

### Data analysis

From the number of herd sightings and the location of each sighting, the proportion of sightings in each burn type was calculated within each month ( $n = 368$  independent sightings) and corrected for the size of the area burnt. Changes in mean grass height and greenness were calculated from the midpoints of the categories assigned.

For each day, the hourly proportion of adult animals observed to be foraging was averaged to obtain the daily proportion of time spent foraging. Only days including all hours from sunrise to sunset were considered ( $n = 61$  days).

Records of foraging efficiency obtained from different focal animals during the same morning or afternoon session were pooled ( $n = 123$  afternoon or morning observation sessions). For each session, the following measures were calculated: (i) feeding time per feeding station (FTFS) – the time spent taking a sequence of bites without moving, a measure of the quantity of food on offer and time needed toprehend bites; (ii) step rate (SR) – the number of foraging steps taken divided by the total foraging time, a measure of foraging effort; (iii) log-survivor distribution of step-sets between feeding stations, indexing the probability of encountering food per step. The bite rate (BR) was recorded by dividing the total number of bites counted by observation period, as an additional measure of the effective food density. Because no differences in foraging measures and faecal crude protein

**Table 1** Schematic outline of the timing of the fires and rains in the Kgaswane Mountain Reserve during the study period. Location and size of the fires are also reported

Year	Season	Fires		Extent (ha)	Rain start
		Date	Location		
2002	Early dry	12 June	Alluvial basin	540	
		25 June	South-eastern section	789	
	Late dry Early wet				
2003	Early dry	10 May	North-facing slope	344	
	Late dry Early wet	17 October	Most of reserve	3300	25 October

content between the two herds were found (ANOVA, all  $P > 0.05$ ), data from these herds were combined.

For statistical analysis, FTFS, BR and SR were log transformed, while the proportion of the day spent foraging and faecal crude protein concentrations were arcsin transformed to conform to the normal distribution assumption for parametric tests. A *t*-test was performed to compare these measures between burned and nonburned areas within the same season, and a one-way ANOVA to compare them between areas burned at different times (Table. 2). Log-survivor plots of consecutive foraging steps were used to explore whether a consistent breakpoint between short and long step sets could be identified, distinguishing movements within patches with a high probability of food being found from movements between patches where food was less likely to be encountered (Tolkamp & Kyriazakis, 1999). To test whether the probability of food being obtained per step differed between seasons and burn type, the slopes before the breakpoint were tested for homogeneity using an *F*-test (Sokal & Rolf, 2000). All statistical tests were performed with SAS Enterprise Guide 3.0 (SAS Institute Inc., Cary, NC, USA) and the results are reported as mean  $\pm$  SE unless otherwise specified.

## Results

Following the burn in June 2002, grass had regrown to a height above 50 mm by August in both areas (Fig. 2).

Regrowth was much more rapid after the October 2003 burn and subsequent rain. In contrast, on the slopes burnt in the dry season 2003, grass height remained below 50 mm. Grass height in the areas that had been burned the previous year was below that in unburned grassland from August onwards, apparently as a result of grazing pressure, but still remained above 200 mm. The green leaf cover was considerably greater in burned than in unburned areas in 2002, but in 2003 the green leaf cover in the area burned in May remained just as low as that in areas not burned that year (Fig. 3).

Through the late dry season and early wet season in 2002 both sable herds were found foraging mostly in the areas burnt in June, with the grassland herd occupying the central burn and the woodland herd the eastern burn (Fig. 4). In 2003, neither herd used the area on the slopes that had been burned. During the late dry season the woodland herd shifted from the eastern area to the alluvial basin (central burn) that had been burned the previous year, to get higher quality food.

The proportion of the day spent foraging was lower during the early wet season than during the late dry season (ANOVA:  $F_{2,34} = 8.50$ ,  $P < 0.01$ , Table 2), but did not differ significantly between years (late dry season 2002 versus late dry season 2003,  $t_{22} = 1.07$ ,  $P = 0.29$ ).

During the late dry season, sable spent much less time per feeding station when foraging in recently burnt areas

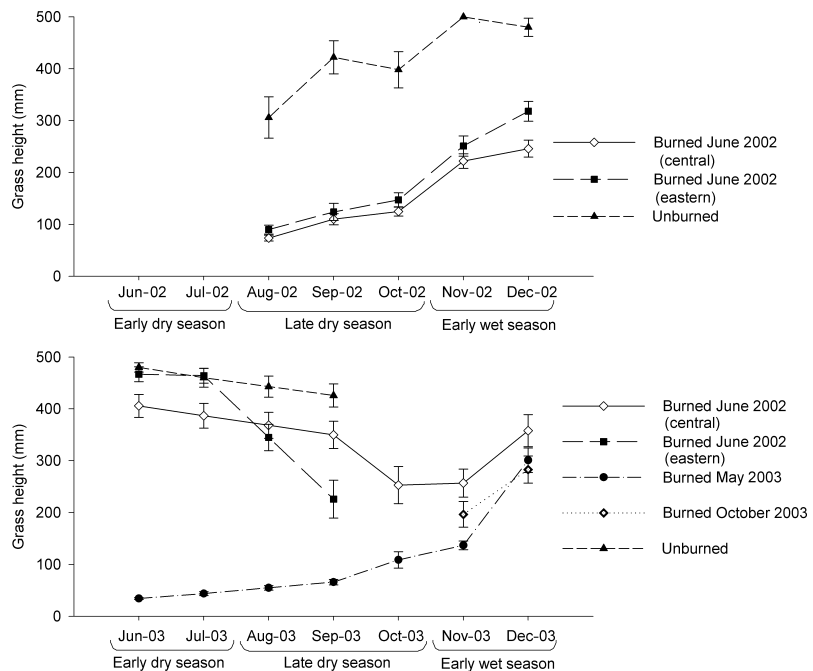


Fig 2 Grass leaf height trends comparing burned and unburned areas in (a) 2002 and (b) 2003 in the Kgaswane Mountain Reserve

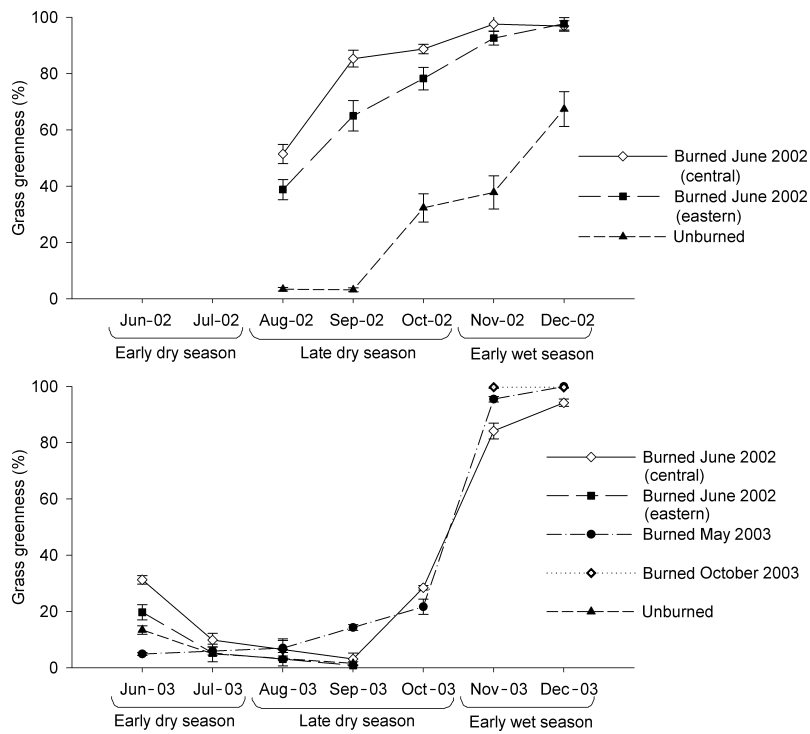


Fig 3 Greenness proportion of grass canopy cover (recently burned grassland) or among leaves (unburned grassland) in burned and unburned areas in (a) 2002 and (b) 2003 in the Kgaswane Mountain Reserve

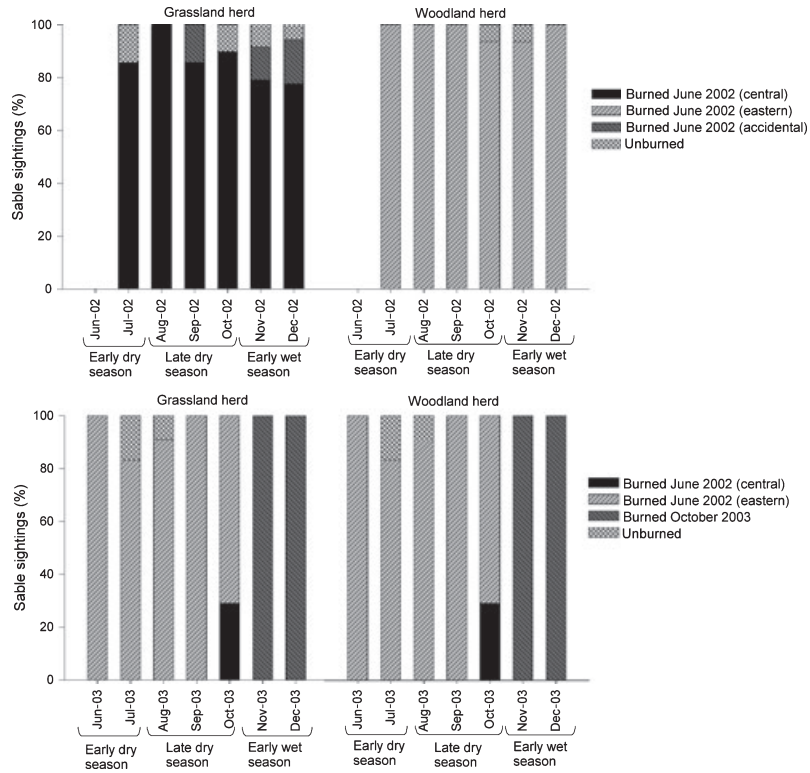


Fig 4 Monthly variation in the use of the areas burnt in (a) 2002 and (b) 2003 by the two herds of sable in the Kgaswane Mountain Reserve

**Table 2** Indices of foraging behaviour, time spent foraging, faecal crude protein ( $6.25 \times N$ ) and phosphorus during different times of the year and under different burn usage by sable antelope in the Kgaswane Mountain Reserve, South Africa. Means and SEs are in the original scale of measurement. Statistical tests between treatments are reported in the text

	Late dry season 2002 New early dry season burn	Early wet season 2002 Grown out early dry season burn	Late dry season 2003 Not burned within the year	Early wet season 2003 New early wet season burn
Daily foraging time (%)	55.4 ± 2.8	42.6 ± 2.1	51.5 ± 2.1	42.0 ± 2.8
Feeding time/feeding station (FTFS) (s)	7.0 ± 1.0	8.1 ± 1.1	12.7 ± 1.1	6.9 ± 1.0
Bites/min (BR)	41.1 ± 2.6	43.5 ± 1.9	40.6 ± 1.1	43.5 ± 1.9
Steps/min (SR)	13.9 ± 1.0	15.0 ± 1.4	10.1 ± 1.8	15.3 ± 0.8
Slope of log-survivor plot of step sequences <10 steps	0.13 ± 0.01	0.14 ± 0.01	0.10 ± 0.01	0.13 ± 0.01
Faecal crude protein (%)	10.1 ± 0.3	11.6 ± 0.1	7.4 ± 0.1	10.6 ± 0.3
Phosphorus (%)	0.29 ± 0.01	0.29 ± 0.01	0.24 ± 0.01	0.29 ± 0.01

in 2002 than when foraging in these same areas in 2003 after the grass had recovered (late dry season 2002 versus late dry season 2003,  $t_{45} = 4.14$ ,  $P < 0.01$ , Table 2). During the early wet season of both 2002 and 2003, feeding time per feeding station continued to remain low while sable were feeding in burned areas, despite the taller height reached by the grassland by that stage (late dry season 2002 versus early wet season 2002 versus early wet season 2002, ANOVA,  $F_{2,66} = 2.67$ ,  $P = 0.09$ ). Correspondingly, the step rate while foraging was somewhat higher when foraging in burned areas than when foraging in areas that had not been burned in that year ( $t_{45} = 3.79$ ,  $P < 0.01$ ). However, the bite rate did not differ significantly between the different burn treatments (ANOVA, BR:  $F_{2,66} = 1.92$ ,  $P = 0.16$ ). The probability of finding food per step seemed lower in burned areas than in unburned grassland ( $F_{1,12} = 15.84$ ,  $P < 0.05$ ).

Diet quality as indicated by faecal crude protein and phosphorus was substantially higher when the sable foraged in recently burned grassland than in 2003 when they grazed the area burned the previous year (CP:  $t_{38} = 9.0$ ,  $P < 0.01$ , P:  $t_{38} = 5.14$ ,  $P < 0.01$ , Table 2).

## Discussion

Both sable herds concentrated their grazing almost entirely in areas burned earlier in the dry season through the later dry season months in 2002. Although grass was shorter in height than in the surrounding unburned grassland, the burned areas retained green grass throughout the dry

season. This was the case for both the alluvial basin and the eastern area that included varying topography and where sable were observed grazing across the landscape (Parrini, 2006). In 2003, sable did not use the area burned in May, where regrowth was slow and green leaf cover remained low. Instead, they continued to forage in the areas that had been burned the previous year, until abundant green regrowth became available following the unplanned October 2003 fire. The northern aspect of the slopes where the May 2003 burn occurred would be drier, inhibiting regrowth, and soils poorer in nutrients, restricting forage quality, compared with the alluvial basin. Faecal crude protein dropped to slightly above 7% of dry mass, regarded as indicating marginal nutrition for a ruminant of this size (Robbins, 1996), and considerably lower than shown the previous year when the sable used grassland burned earlier in the dry season. Measures of foraging efficiency indicated that more grass was available to the sable when they were feeding in the areas burned the previous year than in areas that had not recently been burned. However, daily foraging time approached that recorded following earlier dry season fires where the quantity of forage on offer was low but the quality high. This suggests that sable increased their daily foraging time to compensate for the lower food quality in unburned areas and for reduced intake in recently burned areas, compared with the daily foraging times observed in the early wet seasons of the two years when both quality and quantity were high. Further evidence of nutritional stress at the end of the dry season in 2003 came from the range shift by the woodland herd into the alluvial basin, where grass

quantity or quality presumably remained somewhat better than in their usual eastern range.

In the Kruger National Park, where sable occur predominantly on sandy granitic soils in the west, poor grass regrowth could explain their lack of use of burned grassland (Henley 2005), especially in dry years. Here, faecal protein content ranged from 5.4% during the dry season to 7.5% in the wet season (Henley, 2005; Codron *et al.*, 2007). Similar studies on roan antelope, another low density species that has declined in the Kruger National Park (Harrington *et al.*, 1999), also found that the faecal nitrogen content was exceptionally low at the end of the dry season (September–October) in the absence of burnt areas (Dörgeleh, van Hoven & Rethman, 1998). In Pilanesberg National Park, the then thriving sable population had mean faecal protein content of 6.6% in the mid of the dry season (July), increasing to over 14% when they foraged on burns from September onwards (Magome *et al.*, 2008). This supports what we observed in the KMR, that the availability of recently burnt areas with grass at a suitable height increases the diet quality obtained by sable, and hence their likely survival through the dry season and reproductive success. On the 17–20 October 2003, when sable had gone through the dry season months without access to green regrowth on burns, the KMR experienced a cold spell and an accidental fire that left only small areas untouched. All the sable calves from that year died within less than one week of the cold spell, and 6% of the adult population died as well within the same period. This suggests that their nutritional status was inadequate to resist a sudden stress in the absence of areas recently burned during the dry season. Hence the declining population trend of sable in Kruger National Park could be partly a consequence of insufficient green regrowth on burned areas due to inadequate rainfall (Ogutu & Owen-Smith, 2005).

Fire can have a temporary homogenizing effect on the vegetation by replacing the mosaic of grazed and ungrazed patches in the grass sward by a more homogeneous sward of post-fire regrowth (Hobbs *et al.*, 1991; Archibald & Bond, 2004). However, one would expect to find an increased heterogeneity generated by the subsequent grazing pressure. This could hypothetically restrict the benefits of a burn as herbivores would have to increase the amount of time needed to find bites. Our data suggest that this did not happen in the KMR; the larger inter-patch step sets taken by sable and the observed smaller probability of terminating a step sequence in burned areas compared to all unburned areas suggest a more homogenous distribution of food in the burned sites independent of the time from the fire.

The reason why sable did not use the area that was burned on the slopes in 2003 appeared to be due to insufficient green leaf cover rather than inadequate grass height. To be beneficial to sable, not only the timing in the dry season, but also the position of the burn in the landscape, size, as well as the prior rainfall should be important considerations. Despite higher rainfall in the second year of our study, the burn located on north-facing and hence dry aspect did not attract the sable. The burn mosaic advocated by Brockett *et al.* (2001) should be sufficiently extensive so as to encompass topographic variation including areas with sufficient moisture to promote grass regrowth after the fire, and also to ensure that small patches do not become grazed down by other grazers competing with sable during the course of the dry season. Timing is also important because burns occurring too early in the dry season (i.e. April–May) may become grazed too short for sable before the start of the following dry season. The potential of dry season burned areas to generate adequate green regrowth to meet the needs of sable should be the prime consideration if the aim is to alleviate the nutritional shortfalls these animals would otherwise experience in the dry season and should be considered as a key management option for sable conservation. To be beneficial to sable, burns should ideally be timed to occur mid-way through the dry season, encompass landscape regions likely to support green regrowth during the dry season, and be sufficiently extensive to dilute competition from other grazers.

## Acknowledgements

The authors thank North West Parks Board staff at Kgaswane Mountain Reserve, in particular the late Richard Newbury, for the opportunity to undertake this project and the logistical support throughout the field work, the Nelspruit Laboratory of the Agricultural Research Council for chemical analysis, NRF and Platinum Mines for research founding. The authors wish to thank the following colleagues who read and gave valuable suggestions and comments on this paper: Prof. Shirley Hanrahan, Prof. Ed Witkowski, Dr Adrian Shrader and two anonymous reviewers.

## References

- ALTMAN, J. (1974) Observational study of behavior – sampling methods. *Behaviour*, **49**, 227–267.



- ARCHIBALD, S. & BOND, W.J. (2004) Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *Int. J. Wildland. Fire*, **13**, 377–385.
- BROCKETT, B.H., BIGGS, H.C. & VAN WILGEN, B.W. (2001) A patch mosaic burning system for conservation areas in Southern African savannas. *Int. J. Wildland. Fire*, **10**, 169–183.
- CARRUTHERS, V. (2000) *The Magaliesberg*. Protea Book House, Pretoria, South Africa.
- CODRON, D., LEE-THORPE, J.A., SPONHEIMER, M., CODRON, J., DE RUITER, D. & BRINK, J.S. (2007) Significance of diet type and diet quality for ecological diversity of African ungulates. *J. Anim. Ecol.* **76**, 526–537.
- DÖRGELOH, W.G., VAN HOVEN, W. & RETHMAN, N.F.G. (1998) Faecal analysis as an indicator of the nutritional status of the diet of roan antelope in South Africa. *S. Afr. J. Wildl. Res.* **28**, 16–21.
- DÖRGELOH, W.G. (1999) Chemical quality of the burnt and non-burnt grass layer in the Nylsvei Nature Reserve, South Africa. *Afr. J. Ecol.* **37**, 168–179.
- ESTES, R.D. & ESTES, R.K. (1974) The biology and conservation of the giant sable, *Hippotragus niger variani* Thomas 1916. *P. Acad. Natl. Sci. Phila.* **126**, 73–104.
- GOVENDER, N., TROLLOPE, W.S.W. & VAN WILGEN, B.W. (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity on savanna vegetation in South Africa. *J. Appl. Ecol.* **43**, 748–758.
- GROBLER, J.H. (1981) Feeding behavior of sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos national Park, Zimbabwe. *S. Afr. J. Zool.* **16**, 50–58.
- GUREJA, N. & OWEN-SMITH, N. (2002) Comparative use of burnt grassland by rare antelope species in a lowveld game ranch, South Africa. *S. Afr. J. Wildl. Res.* **32**, 31–38.
- HENLEY, S. (2005) *Habitat Dependency and Nutritional Ecology of Sable Antelope in Two Regions of the Kruger National Park*. Unpublished report, South African National Parks.
- HASSAN, S.N., RUSCH, G.M., HYTTEBORN, H., SKARPE, C. & KIKULA, I. (2008) Effects of fire on sward structure and grazing in western Serengeti, Tanzania. *Afr. J. Ecol.* **46**, 174–185.
- HOBBS, N.T. & SPOWART, R.A. (1984) Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. *J. Wildlife. Manage.* **48**, 551–560.
- HOBBS, N.T., SCHIMEL, D.S., OWENSBY, C.E. & OJIMA, D.S. (1991) Fire and Grazing in the Tallgrass Prairie – Contingent Effects on Nitrogen Budgets. *Ecology*, **72**, 1374–1382.
- MAGOME, H., CAIN, J.W.I., OWEN-SMITH, N. & HENLEY, S.R. (2008) Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa. *S. Afr. J. Wildl. Res.* **38**, 35–41.
- NEL, H.P. (2000) *Ecological Management Objectives and Monitoring Procedures for Rustenburg Nature Reserve, North West Province*, MSc Thesis, University of Pretoria, Pretoria, South Africa.
- NOVELLIE, P.A. (1978) Comparison of the foraging strategies of blesbok and springbok on the Transvaal highveld. *S. Afr. J. Wildl. Res.* **8**, 137–144.
- OGUTU, J.O. & OWEN-SMITH, N. (2005) Oscillations in large mammals populations: are they related to predation or rainfall? *Afr. J. Ecol.* **43**, 332–339.
- PARRINI, F. (2006) *Nutritional and Social Behaviour of Sable Antelope in a Magaliesberg Nature Reserve*, PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.
- ROBBINS, C.T. (1996) *Wildlife Feeding and Nutrition*. Academic Press, San Diego, California, USA.
- ROWE-ROWE, D.T. (1982) Influence of fire on antelope distribution and abundance in the Natal Drakensberg. *S. Afr. J. Wildl. Res.* **12**, 124–129.
- SEKULIC, R. (1981) Conservation of the sable, *Hippotragus niger roosvelti* in the Shimba Hills, Kenya. *Afr. J. Ecol.* **19**, 153–165.
- SKINNER, J.D., SMITHERS, R.H.N. & CHIMIMBA, C.T. (1990) *The Mammals of the Southern African Subregion*, 3rd edn. Cambridge University Press, Cambridge, UK.
- SOKAL, R.R. & ROHLF, F.J. (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*. Freeman & Co., New York.
- TOLKAMP, B.J. & KYRIAZAKIS, I.L.I.A. (1999) To split behaviour into bouts, log-transform the intervals. *Anim. Behav.* **57**, 807–817.
- TOMOR, B.M. & OWEN-SMITH, N. (2002) Comparative use of grass regrowth following burns by four ungulate species in the Nylsvey Nature Reserve, South Africa. *Afr. J. Ecol.* **40**, 201–204.
- VAN DE VIJVER, C.A.D.M., POOT, P. & PRINS, H.H.T. (1999) Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plat. Soil.* **214**, 173–185.
- VAN OUDTSHOORN, F. (1999) *Guide to Grasses of Southern Africa*. Briza Publications, Pretoria, South Africa.
- VAN WILGEN, B.W., GOVENDER, N., BIGGS, H.C., NTSALA, D. & FUNDA, X.N. (2004) Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conserv. Biol.* **18**, 1533–1540.
- VEMEIRE, L.T., MITCHELL, R.B., FUHLENDORF, S.D. & GILLEN, R.L. (2004) Patch burning effects on grazing distribution. *J. Range. Manage.* **57**, 248–252.
- WALKER, B.H. (1976) An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *S. Afr. J. Wildl. Res.* **6**, 1–32.
- WILSEY, B.J. (1996) Variation in use of green flushes following burns among African ungulate species: the importance of body size. *Afr. J. Ecol.* **34**, 32–38.
- WILSON, D.E. & HIRST, S.M. (1977) Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildlife. Monogr.* **54**, 14–107.

(Manuscript accepted 11 March 2009)

doi: 10.1111/j.1365-2028.2009.01143.x