NUTRITIONAL AND SOCIAL ECOLOGY OF THE SABLE ANTELOPE IN A MAGALIESBERG NATURE RESERVE

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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(Signature of candidate)

________24_______ day of __November_2006

ABSTRACT

This study focused on how changes in food availability during the dry season, influenced various aspects of sable (*Hippotragus niger nige*r) foraging and social ecology. The main purpose of this was to determine whether differences in their foraging ecology explained the reduction in population size compared to other more abundant herbivores (e.g. zebra, buffalos, hartebeest).

Contrary to expectation, sable did not limit their foraging to woodlands, but also fed in open grasslands, provided these retained green grass during the dry season. Wetlands were key resource areas during the dry season, but sable did not limit their feeding to these bottomland areas. They also fed on hill slopes and upper plateaus that had been burnt. During the study, sable were attracted to burnt areas despite the reduced grass availability. My study highlights how these burnt areas were important in alleviating nutritional deficiencies during the dry season.

At lower spatial levels, I looked at the factors that influenced the selection of feeding areas and plant species. Like other grazers, sable were attracted to green leaves but did not avoid brown leaves or stems. Grass species eaten were the same as those preferred by most domestic and wild grazers.

Surprisingly, adult males stayed with the breeding herds despite their different activity budgets. Unlike most other African grazers, sub adult sable males did not form bachelor groups. Instead, they stayed within the breeding herds the whole time and had a similar activity budget to females. As adult males moved with the breeding herds, I was able to examine the costs and benefits involved with such a

social structure. From this, I was able to relate my results to the bigger picture of factors influencing sexual segregation in ungulates.

In conclusion, sable utilised a wide variety of habitat types and adjusted their foraging behaviour to accommodate different seasonal situations. I was unable to find anything in their feeding ecology that could explain the continued decline in population size. Therefore, I suggest that future research needs to focus on other potential causes such as a higher susceptibility to predation and disease as compared to more abundant herbivore species.

For

My parents

Without whose support all of
this would have never been possible

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CHAPTER 1

General introduction

I designed this study as part of a project on sable antelope (*Hippotragus niger niger*), undertaken by the Centre for African Ecology at the University of the Witwatersrand. The aim of the project was to understand the ecology of the rare antelope species that are declining in the Kruger National Park (KNP).

THE NEED FOR THE STUDY

Sable antelope numbers have progressively declined in different parts of South Africa. In the KNP, sable have decreased from 2500 in 1986 to less than 500 in 1996 (KNP Ecological Aerial Surveys). Numbers of other rare grazing antelopes, particularly roan (*Hippotragus equinuus*) and tsessebe (*Damaliscus lunatus*), also declined (Harrington et al. 1999, Grant & Van der Walt 2000). A risk assessment model for the ungulate species in the KNP shows how sable could locally be at risk of extinction in the next 100 years (Nocholls et al. 1996). Reasons suggested for the decline include 1) increased predation by lions (*Panther leo*), whose numbers appear to have increased in the northern part of Kruger following an influx of zebra (*Equus burchelli*) and wildebeest (*Cannochaetes taurinus*), attracted by the provision of artificial water points (Harrington et al. 1999, Owen-Smith & Mills 2006), 2) decreased dry season rainfall (Ogutu & Owen-Smith 2003, Owen-Smith & Mills 2006). Different factors may possibly interact (Owen-Smith et al 2005, Owen-Smith & Mills 2006). It is likely that a reduction in dry season rainfall and an increase in temperature, with consequent increase in water evaporation (Ogutu & Owen-Smith 2003), may have reduced the availability of green foliage through the critical dry period. Such stressful conditions could be associated with increased susceptibility of ungulates to predation (Ogutu & Owen-Smith 2005, Owen-Smith et al. 2005).

The sable population in the KMR was of particular interest because it appeared to be doing well, in contrast to populations elsewhere. Moreover, the KMR does not have big carnivores, and the numbers of zebras (*Equus burchelli*) and waterbucks (*Kobus ellipsiprymnus*), potential competitors with sable, are controlled at levels where they do not adversely affect the performances of the sable population (Nel 2000).

What is it that makes sable more susceptible than other herbivores? Does sable foraging and social ecology differ from that of grazers that are more common, to the extent of making sable potentially more vulnerable than other species? Are certain age and sex classes more vulnerable than others are? In an attempt to answer these questions, my study aimed at identifying the factors influencing the foraging and social ecology of a population of sable antelope in the KMR. The specific objectives of the project were to:

1) Analyse sable use of space
2) Establish factors influencing sable selection for a) food patches and b) grass tufts
3) Determine the grass species preferred by sable
4) Determine foraging behaviour response to changes in a) food quality and b) food quantity
5) Identify the critical periods for nutrition

6) Compare foraging behaviour, synchronization of activities and nutritional status of different age and sex classes.

LITERATURE REVIEW

Factors influencing landscape region selection

The end of the dry season is a critical period for herbivores, when they have to select areas to mitigate the limitations of decreasing forage quality (Scoones 1995). Scoones (1995) coined the concept of 'key resource habitat type' for areas utilized by cattle during the dry season as a 'buffer' against the poor quality forage available. Key resources may include vegetation growing in areas were soil moisture is retained, unpalatable grasses or browse components for grazers (Owen-Smith 2002). Scoones (1995) found that cattle in the dry areas of southern Zimbabwe grazed in lower slope habitats (drainage line, riverine habitats) during the dry season. These small low-lying areas had higher herbaceous green biomass and higher available browse compared with larger upland areas (Scoones 1995). Topi (*Damaliscus lunatus*), buffalo (*Syncerus caffer*), zebra and roan all showed similar preferences for bottomland areas in the dry season (Duncan 1975, Bell 1984, Heitkönig 1993, Perrin & Taolo 1999) as did sable in the Pilanesberg NP (Magome 1991). Bell (1984) related the seasonal changes in the use catena regions to the different characteristic of grasses at the different catena levels. Short grasses, present on the upper level of the catena, were used during the wet season. Long grasses, present in the lower part of the catena, were selected in the dry season. Indeed, Scoones (1995) found the standing crop of the bottomland habitats to be significant higher than in the upland area during the dry season. Topi selected areas with the highest grass abundance during the dry season (Duncan 1975). Heitkönig (1993) attributed the preferential use of bottomlands during the dry season by roan antelope to the longer availability of green grass in these areas than in upper level areas.

Different species of herbivores show a different preference for open or closed vegetation types. Sable avoided the more open habitats, favoured by other grazers (white rhinoceros, *Ceratotherium simum*, wildebeest, and zebra) in the Pilanesberg National Park, South Africa (Borthwick 1986 in Magome 1991). Wilson and Hirst (1977) reported sable using habitat with woody canopy cover ranging from 15% in the Percy Fyfe Nature Reserve (South Africa) to 25% in the Matetsi area (Zimbabwe). They reported 20% woody canopy cover in the areas used by sable in the Rustenburg Nature Reserve (now the KMR).

An important element influencing habitat use is fire (Moe et al. 1990, Gureja & Owen-Smith 2002, Tomor & Owen-Smith 2002). Burning improves the nutritional quality of forage by stimulating the sprouting of new grasses (Hobbs & Spowart 1984, McNaughton 1985, Hobbs et al. 1991). In the Nylsvley Nature Reserve, the nitrogen content of the flood plain sward increased from about 1.7% to 2.5% after the sprouting of new green grass following the fires (Dörgeloh 1999). Protein concentration increased in the winter diets of mountain sheep and mule deer when feeding on burnt grassland and mountain shrub communities in Colorado, as compared to levels when feeding on non-burnt areas (Hobbs & Spowart 1984). In Kenya and Zimbabwe, sable grazed frequently on burnt areas after the rains (Sekulic 1981, Grobler 1981). In the Matopos National Park, Zimbabwe, sable grazed on burns when the height of grass was at least 60 mm

(Grobler 1981). When the grazing pressure from the others herbivores reduced the mean grass height to below 50 mm, sable started to feed on non-burnt areas. After the rains, when the mean height on the burns increased again to at least 60 mm, sable used again burnt areas. In contrast, Gureja (2001) did not observe much use of burns by sable compared with hartebeest, *Alcephalus buselaphus*, roan and tsessebe on a private farm in the Limpopo Province, South Africa. Magaliesberg soils are sandy and hence generally poor in nutrients, which is typical of the sourveld (Wilson & Hirst 1977). The grasses tend to be tall and stemmy: herbivores in this kind of environment are likely to have difficulties in extracting sufficient nutrients from their food supply (Bell 1984). The use of a burning regime is a possible management strategy to overcome the low nutrient availability during critical periods especially on these poor soils. In the Pilanesberg NP, sable used burnt areas towards the end of the dry season, from August onward, and in fact, the faecal protein level increased in September (Magome 1991).

Factors influencing forage selection

Species composition

In the course of the year the leaf to stem ratio, greenness and growth stage of the grasses change with consequent seasonal variation in grass quality (Owen-Smith 2002). As grass quality changes so does the plant species preference of grazing ungulates (O’Reagain & Schwarz 1995, Meissner et al. 1999).

Grasslands in good condition for supporting cattle contain a high proportion of perennial species (Tainton 1981) such as *Themeda triandra*, a high quality and high forage bulk grass. Sable in the Pilanesberg NP consumed *Themeda triandra* over the entire year (Magome 1991). *Themeda triandra* accounted for most of the sable diet in the Rustenburg Nature Reserve during the dry season (Wilson & Hirst 1977). No data are available for other parts of the year in Wilson & Hirst's study. *Panicum maximum*, which occurs mostly under the trees, was eaten only during the dry season by sable in the Matopos National Park, Zimbabwe (Grobler 1981). Sable in the PNP selected *Panicum maximum* the whole year, with a maximum at the beginning of the late wet season and a decrease over the course of the dry season (Magome 1991). However, the species that contributed most to the sable diet in the PNP was *Chrysopogon serrulatus* (Magome 1991). *Panicum maximum* was the second most selected grass and *Heteropogon contortus* was the third species (Magome 1991). *Heteropogon contortus* contributed in all seasons to the diet of the sable in Zimbabwe (Grobler 1981).

Grobler (1981) had only four observations out of 4000 in which sable were browsing. This was during the hot dry season. Wilson & Hirst (1977) did no report any sighting of browsing by sable. However, from the rumen content they found that dicotyledons accounted for 3% of the sable diet in the Rustenburg Nature Reserve during the dry season. Magome (1991) did not observe any browsing in the PNP, but all his results derived from direct observations.

Physical characteristics of the grasses

The physical properties and structure of the grass influences its acceptability (O'Reagain 1993). Grass selection by both cattle and sheep (*Ovis aries*) was negatively correlated with leaf length (O'Reagain & Mentis 1989). Grobler (1981) observed sable bites at heights between 40 mm and 140 mm, while in the Pilanesberg NP sable grazed over a broader height range of grass heights (100-300 mm, Magome 1991). Nevertheless, grass species were less favoured when they became tall (Magome 1991). Grobler (1981) attempted to explain the restricted feeding range of sable with hypothetical structural constraints and with the possible higher protein and lower fibre content of grasses shorter than 140 mm compared with grasses taller than 140 mm.

Sheep and cattle show a clear preference for green material as compared with dry material (O'Reagain 2001). For both zebra (Winkler 1992) and wildebeest (Wilmshurst et al. 1999), the plant species acceptance was mainly correlated with greenness. Sable preferred green leaves too (Grobler 1981, Magome 1991). Magome (1991) in fact explained sable preference for *Panicum maximum* during the late growing period with a selection for greenness: *Panicum maximum* grows underneath the trees and remains green for longer compared to other grasses.

Stems have a lower digestibility compared to the green fraction of the plant since they have a higher content of fibre than green leaves (Murray & Illius 1996). Selection for green leaves and avoidance of stems has been observed in sheep, cattle, bison (*Bison bison*) and topi (Duncan 1975, O'Reagain & Mentis 1988, O'Reagain 1993, O'Reagain 2001, Fortin et al. 2002). In both topi and bison the degree of selection against stems was lower in immature grasses and higher in mature grasses (Duncan 1975, Fortin et al. 2002). On the contrary, roan did take more stem-free bites on immature grasses than on brown grasses (55% vs. 19%, Heitkönig 1993). Magome (1991) explained the preference of sable for C*hrysopogon serrulatus* in the Pilanesberg NP with the preference for grasses with a high leaf/stem ratio. *C. serrulatus* was always the plant species with the highest leaf to stem ratio compared to other species (Magome, 1991).

Stems also indirectly affect grazers' accessibility to leaves. The acceptability of *Hyparrhenia hirta* by cattle declined rapidly as it became stemmy over the growing season (O'Reagain & Mentis 1989). This may explain the presence of *Hyparrhenia* spp. only during the wet season in the diet of sable in the Pilanesberg NP (Magome 1991).

Foraging behaviour

When foraging, herbivores need to decide whether to stay and feed in a food patch or whether to leave to look for another patch: the decision they are faced with depends on the forage quality, quantity and distribution and on their degree of selectivity (Novellie 1978, Owen-Smith 1979, Underwood 1983). The movement rate and the feeding time or bites per step have repeatedly been used as an indicator of the food distribution and availability (i.e. Novellie 1978, Owen-Smith 1979, Underwood 1983, Jiang & Hudson 1993, Bradbury et al. 1996, Fortin et al. 2002).

Foraging behaviour has been described as a spatial and temporal hierarchical process (Senft et al 1987, Bailey et al. 1996). At the bottom of the scale is the 'bite' (Underwood 1983, Laca & Ortega 1995, Bailey et al. 1996, Owen-Smith. 2002), followed by the 'feeding station', defined as the area that can be exploited by an herbivore without moving (Novellie 1978). The amount of time spent per feeding station depends upon the number of bites available there and the time necessary to look for and chew those bites. Reedbuck (*Redunca aurundinum*), impala (*Aepyceros melampus*), tsessebe, wildebeest and buffalo in the Kyle Recreational Park (Zimbabwe) were feeding for six to 12 seconds per feeding station (Underwood 1983). The feeding time per feeding station had a seasonal pattern, with a peak during the dry season, probably due to the longer amount of time needed to select the green leaves (Novellie 1978, Underwood 1983). A cluster of feeding stations describes a ‘food patch’ (Bailey et al. 1996). Owen-Smith and Novellie (1982) used the breakpoint in the log-survivor distribution of step sets of kudus (*Tragelaphus strepsiceros*) to determine the number of steps after which the probability of encountering a feeding station was low and hence the kudus could be considered in a different patch. The definition of food patch is however more difficult for grazing herbivores: Novellie (1978) did not found any breakpoint in the log-survivor curve of step sets for blesbok (*Damaliscus dorcas*) and springbok (*Antidorcas marsupialis*) and hence he considered a succession of more than two steps as indicating movement between different food patches. The number of feeding stations per patch tended to be greater in the wet season, suggesting a less patchy distribution of food than in the dry season (Novellie 1978, Underwood 1983).

Ungulates show different foraging behaviour on burnt and non-burnt areas (Novellie 1975, Tomor 1999). Both Novellie (1975) and Tomor (1999) reported greater mobility and less feeding time per feeding station by ungulates foraging on burns compared with unburned ranges. They explained it with the low biomass available on burnt areas and the low handling time due to quality uniformity of the forage (Novellie 1978, Underwood 1983). In fact, Heitkönig (1993) found that roan were taking more bites per minute (39 bites/min) on grass re-growing on firebreaks than elsewhere (25 bites/min) (Heitkönig 1993).

Most mammal herbivores change the amount of time they spend feeding during the day as the season progresses, in an attempt to maintain their energy requirements as quality and quantity of the available food changes. Most African ungulates appear to spend more daytime foraging during the dry season than during the wet season (i.e. giraffe (*Giraffa camelopardalis*), Pellew 1984; hartebeest, Ben-Shahar & Fairfall 1987; impala, Jarman & Jarman 1973; kudu, Owen-Smith 1979; roan, Heitkönig 1993; sable, Grobler 1981; springbok, Novellie 1978; waterbuck, Spinage 1968). However, topi and dik-dik (*Madoqua kirkii*) did not show a clear seasonal variation in time spent foraging (Duncan 1975, Manser & Brotherton 1995) and conflicting results exist for buffalo: an increase in foraging time in the dry season (Beekman & Prins 1989) or no seasonal variation (Stark 1986). Blesbok in contrast reduced foraging time in the dry season (Novellie 1978).

An increase in foraging time during the dry season has been attributed to an increase in selectivity (Beekman & Prins 1989, Novellie 1978), searching time (Pellew 1984), and a decrease in intake rate (Owen-Smith 1979) or a reduction in thermal stress (Berry et al. 1982, Ben-Shahar & Fairfall 1987).

Diet quality

Nutritional quality of grasses differs among grass species and varies seasonally as the ratio green leaf to dead material changes (O'Reagain & Schwarz 1995). The availability of both energy and protein declines as the forage matures and the cell wall lignifies (Meissner 1999). Nitrogen and macro-mineral content of grasses in the savanna are higher in summer than in the dry winter season, and fibre content is at its lowest at the onset of the wet season (Heitkönig 1993, Dörgeloh 1999). Therefore, herbivores may face diet quality deficiencies at some stage during the year (Owen-Smith 1982, Dörgeloh 1999). In fact, faecal crude protein levels were higher in summer than in winter for both roan in the Nylsvley Nature Reserve (Dörgeloh et al. 1998, Heitkönig 1993) and sable in the Pilanesberg NP (Magome 1991). The crude protein level in the sable faeces increased in August after they started to make use of burnt areas (Magome 1991). In both studies by Heitkönig and Dörgeloh the faecal crude protein values reported for the dry season were close to the minimum values (5-8%) necessary for maintenance in wild ruminants (Robbins 1996).

Protein content is not the only important determinant of diet quality; macro-minerals are also important (McDowell 1985, Robbins, 1996). Low mineral intake may lead to poor lactation limiting the ability of females to raise their offspring (McDowell 1985, Freeland & Coquenot 1990). For grazing livestock, particularly cattle, P deficiency appears to be the most important mineral limitation in tropical countries (McDowell 1985). Potassium deficiencies in wildlife are rare due to the very high K contents in growing plants, usually in excess of animal requirements (Robbins 1996). Even if its concentration is higher in summer and lower in winter (Dörgeloh 1999) it should never be a limiting factor (Robbins 1996, Dörgeloh et al. 1998). Sodium deficiency is on the contrary a frequent problem in grazing ruminants (Henry 1995). Limited availability of Na in certain areas may even restrict animal distribution and productivity (Robbins 1996). Na could be particularly limiting in winter, when its content in the grasses is at its lowest (Dörgeloh 1999).

The use of faecal nitrogen as an indicator of diet quality is widespread (e.g. Hobbs et al. 1981, Leslie et al. 1984, Hobbs 1987, Leslie et al. 1989). Because the use of only nitrogen gives biased results when an herbivore's diet is rich in tannins, the combination of faecal nitrogen and phosphorus is often preferred to predict the nutritional status of wild herbivores (e.g. Grant et al. 1995, Duncan et al. 1997, Wrench et al. 1997, Osborn et al. 1998).

Age and sex differences in daily time allocation

Females have additional nutritional demands compared to adult males, because of pregnancy and lactation and therefore in most ungulate species females forage for longer than males (Owen-Smith 1988). However, in the non-dimorphic oryx (*Oryx gazella*) and zebra, there was no significant sex difference in time spent grazing during the early wet season (Ruckstuhl & Neuhaus 2002). Males of non-dimorphic Camargue feral horses (*Equus caballus*), instead spent less time foraging than females as expected (Duncan 1980).

Males of most species spent more time walking than females: oryx, gerenuk (*Litocranius walleri*), bighorn sheep, giraffe, mouflon (*Ovis musinum*) and ibex (*Capra ibex ibex*) (Ruckstuhl & Neuhaus 2002). In bison (*Bison bison*), males took a lower number of steps per minute than females (Komers et al. 1993). On the contrary, bighorn sheep males and females had similar step rates (Ruckstuhl 1998).

Differences between calves and adults in time spent foraging were reported for muskoxen (Cote' et al. 1997), caribou (*Rangifer tarandus*, Boertje 1995, Oakes et al. 1992) and mouflon (Moncorps et al. 1997). Pre-weaning calves spent more time lying and standing and less time feeding than the other age-sex classes, as one would expect since they are still lactating. In Camargue wild horses, yearlings spent more time resting than adults (Duncan 1980) whereas Oakes et al. (1992) reported no difference in time spent foraging by adults and yearlings caribou.

Age and sex differences in diet quality

Age and sex influence the amount of energy needed and the mineral requirements of animals (McDowell 1985). Mature individuals have requirements for maintenance, while immature individuals and pregnant or lactating cows have additional needs (McDowell 1985). Male waterbuck had higher faecal crude protein levels than females during the hot dry season (18% vs. 14%), but not during the rains and the cold dry season (Thomlinson 1979). On the contrary, female white-tailed deer (*Odocoileus virginianus*) had significantly higher levels of faecal N than males all year round (Beir 1987). Faecal samples from males and females bighorn sheep had similar protein content (Ruckstuhl 1998).

STUDY AREA

The reserve was proclaimed with the name of Rustenburg Nature Reserve in 1967 (Nel 2000). It lies on the southern outskirts of Rustenburg, in the North-West Province of South Africa (25 43’ S, 27 11’ E, Fig. 1). At the time of the proclamation, the reserve covered an area of 2898 ha (Nel 2000). In the following years more land was acquired and nowadays the reserve is 4,257 ha wide. The name of the reserve was changed to Kgaswane Mountain Reserve in 2002. The reserve lies on the north-west end of the Magaliesberg low mountain range, and encloses a 17-km^2 catchment area. The Magaliesberg form a distinct climatic boundary between the savanna and the grassland biomes (Low & Rebelo 1996).

Two geomorphologically distinct regions characterize the reserve: a high-lying plateau and low-lying valleys (Coetzee 1975). The high-lying plateau contains a flat area of exposed quartzite, at an altitude of 1500–1600 m (Coetzee 1975). This plateau descends southwards into a basin of deep alluvial soil and marshland, forming the largest natural wetland of the Magaliesberg (Carruthers 1990). The wetland lies at an altitude of 1425–1440 m (Coetzee 1975). The second geomorphological region is a series of northwest to southwest valleys underlaid by diabase (Coetzee 1975). These valleys separate the larger part of the summit plateau from a chain of quartzite hills extending from the northern plateau to the southeast (Coetzee 1975). Altitudes of these valleys vary between 1250 and 1320 m (Coetzee 1975).

Deep and well-differentiated soils characterize the northern summit plateau (Nel 2000) dominated by grassland communities and evergreen *Protea caffra* woodlands (Coetzee 1975). The central basin has deep, very deep well-differentiated and black clayish soils (Nel 2000). The black clayish soils underlie the *Phragmites australis* reed bed, while deciduous *Acacia caffra* woodland and evergreen *Protea caffra* trees, occupy the northern corner of the basin (Coetzee 1975). Grassland communities, plus *Burkea africana* and *Protea caffra* woodlands (Coetzee 1975) cover the other parts of the basin. Shallow soils are present in the crests and upper slopes, medium-deep soils on the foothills and young soils in the bottomlands of the valleys. *Protea caffra* and *Acacia caffra* woodlands dominate the hills, separated by small areas of grassland communities (Nel 2000).

The reserve's boundaries include the upper catchment of the Waterkloofspruit (Carruthers 1990). The stream flows through a *Phragmites australis* reed marsh in the central basin area, drops over a 60 m high waterfall and flows further through the low-lying part to join the Hex River north of the reserve (Nel 2000). Several smaller streams, annual and perennial ones, also have their origin in the reserve (Carruthers 1990, Nel 2000).

When the reserve was proclaimed, it was fenced and stocked with a variety of game including 12 sable antelopes (Wilson 1975). The sable population increased very slowly initially (Fig. 1.2). The management of the reserve started systematic counts only in 1985. These counts indicate a period between 1990 and 1995 where the sable population stabilized between 36 and 42 animals, while from 1996 onwards, the growth of the population resumed at an increased rate. At the time of the study, besides sable (approximately 70 individuals in total) there were other mammal herbivores including zebra (200) and antelopes such eland *Tragelaphus oryx* (68), kudu (15+), mountain reedbuck *Redunca arundinum* (70+), impala (70), red hartebeest (115), roan (4), springbok (30) and waterbuck (60). Very small numbers of predators, including caracal (*Felis caracal*), aardwolf (*Protele cristatus*), black-backed jackal (*Canis mesomelas*) and leopard (*Panthera pardus*) also occurred. Signs of leopard were last seen in 1997, while the jackal population seems to have increased in number (R. Newbury, pers.comm.).

Fire has been used as a management tool in the KMR since 1975 (Nel 2000). Fire was mostly applied at the end of the growing season, after the first summer rains and immediately before spring growth. In 1994, early winter burns were implemented (Nel 2000). The rationale for applying late summer burns was to ensure green flush during winter. The idea is that green regrowth should help support animals through the dry season. The period between successive fires for the reserve is variable. Environmental factors such as rainfall, prolonged drought, herbivory and accidental fires have an impact on vegetation structure and composition and thus prevent a rigid and prescribed burning program (Nel 2000).

STUDY DESIGN AND THESIS OUTLINE

The study was undertaken in 2002 and 2003 and extended over two dry seasons (August-October 2002 and April-October 2003) and two transition periods to the wet season (November-December 2002 and November-December 2003). These are critical periods for African herbivores, since the availability of high quality food declines as the dry season progresses.

The park management ignited two block burns at the end of June 2002. These provided flushes of green grasses during the late dry season of the same year. In 2003, a block burn was put in on a north-facing slope at the beginning of May. This, however, did not result in green flushes and thus green grass was not available during the dry season in 2003. An accidental fire in late October 2003 burnt approximately three-quarters of the reserve, just before the rain started. The green flush from this fire thus provided herbivores with green grass throughout November and December. Therefore, without planning it, I had the opportunity to compare one dry season with burnt areas with one dry season without burns and ‘pre-rain’ burns with ‘post-rain’ burns and their effects on sable behaviour.

I used radio tracking to facilitate the localization of sable to do the field observations. Radio collars were placed on three adult females. Radio collaring was achieved by immobilizing the animals from a helicopter and was done after the annual counts in August 2002. I placed the collars on females of two different groups living in separate areas of the reserve. One group was living in the low-lying part of the reserve under typical woodland conditions, the other one was living in the central basin area and northern slopes, favouring, unusually for sable, open grassland and vlei. I will refer to the two groups as ‘woodland herd’ and ‘vlei herd’ respectively from now on. The use of such different areas by the two herds enabled me to test whether there were common factors influencing their behaviour despite the different habitat choices and if one group was better off than the other one, above all considering the unusual choice of habitat by the ‘vlei’ herd.

I approached sable using the homing-in technique, by car or by foot. I conducted all the observations from a parked vehicle or, whenever possible, from natural vantage points with the aid of a pair of 10x42 binoculars or a spotting scope.

First, I examined sable use of space (Chapter 2). This paper does not contribute much in terms of scientific knowledge, but it is fundamental in providing a base to all other papers. I calculated sable seasonal and annual home ranges and compared them with the available knowledge on sable use of space. I examined sable use of vegetation types. I tested whether the use of burnt areas influenced space and habitat use by the two herds, by comparing the dry season without green flushes and the dry season with green flushes.

Next (Chapter 3), I examined sable behaviour at smaller spatial resolutions than the landscape level. Herbivores usually feed only in certain food patches within the selected habitats. At an even smaller scale, within these food patches, they select for certain grasses and avoid others. I analysed how grass height, greenness and stemminess influenced sable selection at the two above-mentioned levels and compared the response of the two different herds. I tested if the two herds were selecting for different/similar features despite the different habitat preferences, to see to what extent sable were able to adapt to different habitat conditions by eventually changing their selection criteria. Moreover, I compared the results to the available knowledge about other grazers, to see to what extent sable differ from more common ungulate species and how these differences could help explain why sable are more vulnerable that other species. To record grass features at the food patch level and lower, I first identified foraging areas, defined as the area where sable were foraging between two consecutive resting bouts, and approached the area once sable had moved on. Within each foraging area, I located food patches through the presence of fresh dung, tracks and fresh bites. Within each food patch, I placed twelve 0.5 x 0.5 m quadrats and within them identified grazed and ungrazed tufts, and recorded measures of height, greenness and presence of stems.

Sable may differ from other grazers not just in their selection criteria but also in their choice of what to eat. Most herbivores shift and widen their diet as the dry season progresses and the preferred species availability declines. In addition, the use of burnt areas could influence the choice of what grass species are available. To analyse seasonal changes and the effect of the use of burnt areas in grass species use by sable (Chapter 4), I identified the species grazed within the quadrats placed in the food patches. However, at the end of the dry season, fresh bites were difficult to identify. Similarly, on new-burnt areas grasses were difficult to identify reliably by species. Therefore, because of the limitations encountered in recording eaten grasses in the field, I also used an alternative non-field based technique to assess the relative importance of different grass species throughout the year. I examined the epidermal fragments in the faeces with the microhistological technique outlined by Stewart (1967). This is a non-invasive technique used to provide informations on herbivore diet as an alternative to direct observations or rumen content analysis (e.g. Holechek et al. 1982, Monro 1982, Putman 1984, Hanley et al. 2001). The plant species are identified from epidermal features such as the shape of the silica bodies or the presence and form of hairs and papillae. To make these features visible, the leaves need to be treated with concentrated nitric acid to remove the mesophyll tissue (Monro 1982, Hanley et al. 2001). The main problem of this technique is the different digestibility and fragmentation of different species (Monro 1982, Holechek et al 1982). Nevertheless, previous studies have shown no effect of the digestion on the relative frequency of grass species in the faeces (McInnis et al. 1983). In fact, the different digestibility is mainly a problem for forbs, less for grasses (McInnis et al. 1983, Hanley et al. 2001). Another problem is that some grasses are difficult to separate at the species level (Holechek et al. 1982). Different species of *Eragrostis* for example are not identifiable at the species level, and need to be grouped together as a genus (Monroe 1982, Hanley et al. 2001). Despite these potential problems, the microhistological technique has been used as an indicator of diet in studies on roan (Perrin & Taolo, 1999), bison (Larter & Gates 1985), buffalo (Macandza & Owen-Smith 2004), feral horses (Lenarz 1985) and muskoxen (Oakes et al. 1992).

Herbivores behaviour reflects seasonal changes in grass quality and quantity. I used indices of foraging behaviour (Chapter 5) to test how sable adapted to changes in grass quality and quantity during a dry season without burnt areas and during a dry season with burnt areas available. I choose to record bite and step rates on focal animals (Altman 1974) and daily foraging time by scan sampling

(Altman 1974) as indices of foraging behaviour. I used a Psion Organizer II that had been programmed for a study on white rhinos for the observations on the focal animals (Shrader 2003, see Appendix I for the programme). I considered the nutritional status of sable as a measure of how well they adapted to the grass changes during the two dry seasons. I collected faecal samples (see above) and analysed them for nitrogen and phosphorus. I did not analyse faeces for potassium, since it never appears to be a limiting mineral in the diet of herbivores. Sodium is an important nutrient but it is not excreted with the faeces. Calcium is mainly excreted through the faeces (McDowell 1985) but its relation with dietary calcium is not known yet and therefore I did not analyse for it. Fibre content in the diet has also been used to evaluate the diet quality of herbivores, but because of budget constraints, I limited the analyses to nitrogen and phosphorus only. The near infrared spectroscopy (NIRS) has been successfully used instead of chemical analysis (Foley et al., 1998) but its costs were too high and therefore the samples have been analysed using conventional chemical analysis (Kjeldahl digestion) at the ARC Laboratory in Nelspruit.

Finally, I examined in more detail at the social structure of sable and the costs and benefits involved with it (Chapter 6). I analysed activity budgets, synchronization and social affiliation among age and sex classes in the bigger picture of the causes of segregation among ungulates (see Ruckstuhl and Neuhaus 2002 for an extensive review). I decided to look at this aspect since the potential causes of a species decline cannot be fully understood without taking into account the complex interactions between age and sex classes. Too often management decisions are made for a species as a whole, without considering that different segments of the populations may have different requirements. In sable, females live in groups with yearlings and juveniles. Sub-adult males are reported to form bachelor groups or alternatively to stay in the females' groups. Adult males are supposed to be territorial, but often follow the females' groups for most of the time, possibly with costs involved. I distinguished between adult males, sub adult males, adult females, yearlings, pre-weaning and post-weaning calves when doing the observations. I identified males by the tufted penile out growth behind the navel and by the horns, which are thicker than in females, and thicker and more curved when adult. I defined juveniles as the individuals born within the year (in February-March) and yearlings as the individuals born the previous year. I identified them by the horn length and shoulder's height in relation to females. As a measure of potential costs/benefits involved in the observed social structure, I originally planned to test for age and sex differences in nutrient status. Unfortunately, I was not able to collect an enough big sample size of faecal samples for each sex and age class and therefore left this comparison out from the final thesis.

At the end (Chapter 7) I summarised all the findings and linked each chapter in the bigger picture of sable ecology. I pointed out the main differences between sable and other grazers and how these differences can help understand why sable are rare. I pointed out which areas still need further research. I also considered what my study has achieved in terms of sable management. Too often scientific results are just seen as a theoretical exercise and not as practical information to be used in management and conservation plans.

I did not write the thesis in the traditional way, but as separate papers. I have written each chapter as a manuscript. To avoid repetitions in the references, I listed the references for all paper at the end of the thesis. Most papers/chapters although not published yet have been presented at national and international conferences:

Chapter 2: SAWMA symposium, Gaanzenkraal, Western Cape, South Africa, 21-23 September 2003.

Chapter 3 & 4: SAWMA symposium, Magoebaskloof Hotel, Limpopo Province, South Africa, 2-4 October 2005.

Chapter 5**:** SAWMA symposium, Kathu, Northern Cape, South Africa, 21-22 September 2004 & 4th Kruger National Park Networking Meeting, Skukuza, Kruger National Park, 13-17 March 2006

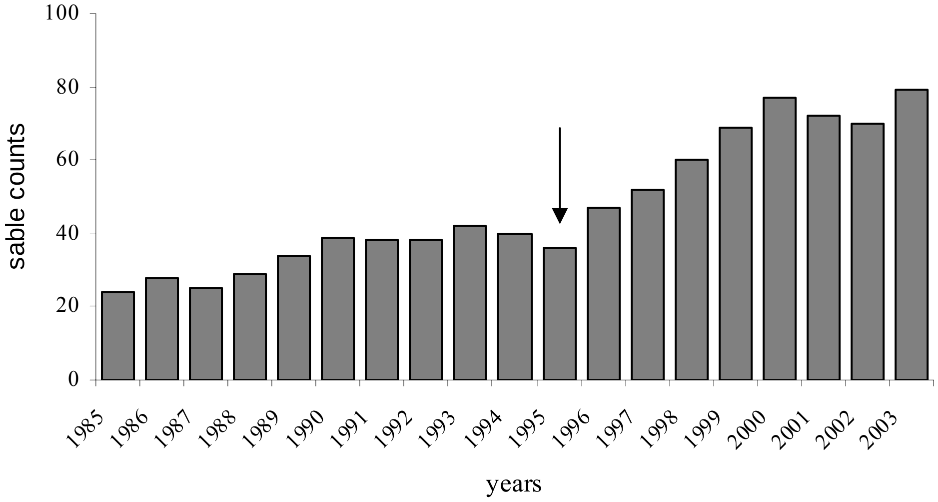
Chapter 6: ISBE2006, Tours, France, 23-29 July 2006.

FIGURE CAPTIONS

Fig. 1.1. Sable antelope counts in the KMR. In 1995 prescribed early winter fires started to be ignited, and sable numbers appeared to have gone up

Fig. 1.2. Study area: the Kgaswane Mountain Reserve (5000 ha), North-West Province, South Africa. A: high lying plateau (1500 – 1650 m); B: central alluvial basin (1425 – 1440 m); C: low lying eastern part (1250 – 1320 m).

Fig. 1.1


100
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sable counts
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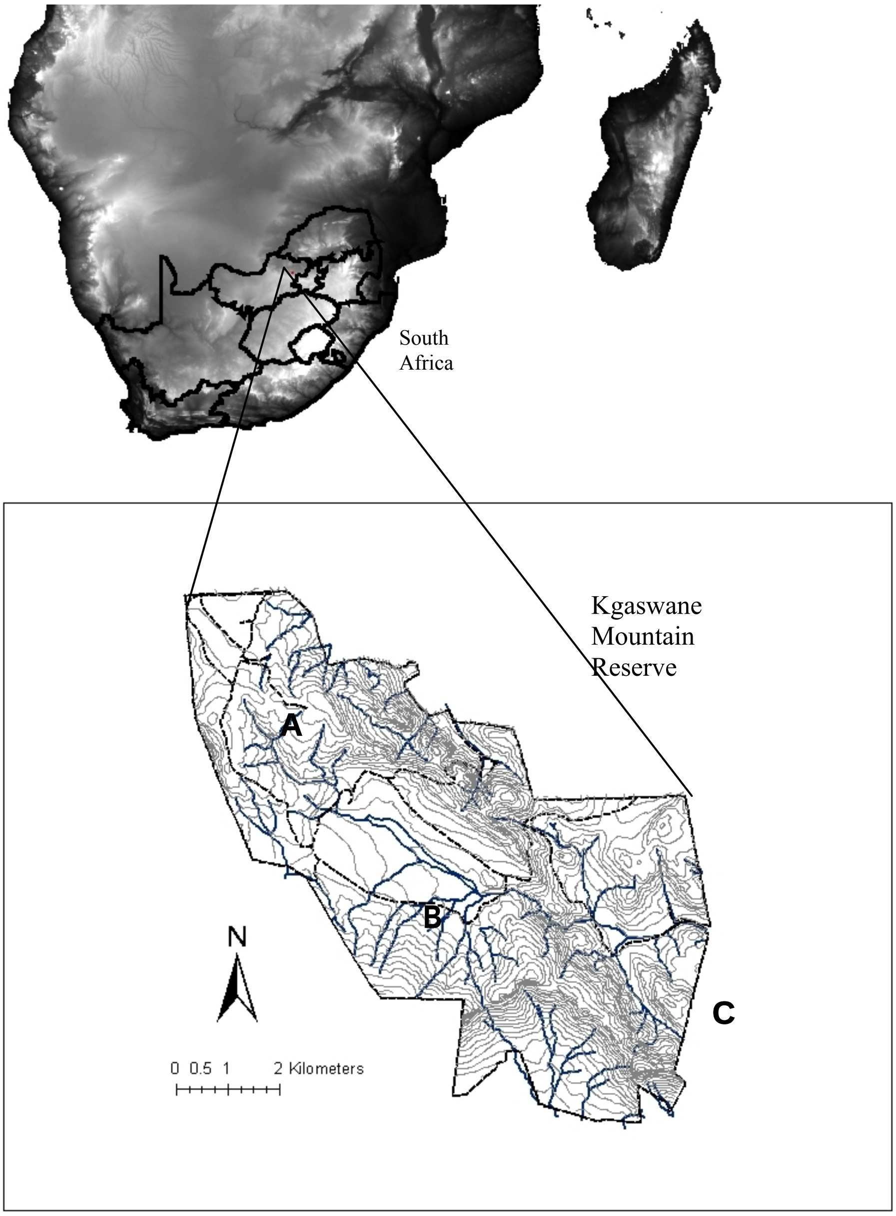
Fig. 1.2


South
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CHAPTER 2.

Spatial behaviour and habitat use by sable antelope in the Kgaswane Mountain Reserve, South Africa

Abstract

I analysed seasonal variation in the use of landscape regions by two herds of sable antelope (*Hippotragus niger*) in the Kgaswane Mountain Reserve. The landscape variables considered were catena position, burn history, tree canopy cover and presence of other ungulates. The home ranges of the two herds were similar to those reported in previous studies on sable. The two herds had a different use of space. The vlei herd expanded its range when using burnt areas. The woodland herd had a more conservative use of space when burnt areas were available, and expanded its range during the season with no burns available. The vlei area in the central part of the reserve was used in all periods by the vlei herd but only as a key resource at the end of the dry season by the woodland herd. Because of its concentrate use of the vlei area, the vlei herd was seen most of the times in areas with no trees. Both herds made extensive use of burnt areas when available despite the higher number of other grazers present in these areas as compared to unburnt ones. Apparently, in this reserve potential competition on burnt areas was not a limiting factor for sable, which were able to use burnt areas and the bottomland vlei area as key resources to bridge the limitations imposed by the dry season.

INTRODUCTION

It is important to understand the habitat requirements of a species during the ‘critical season’ i.e. the period when resources are limiting (Sinclair 1975, Riney 1982). In Southern Africa, the critical season is usually the dry season, when herbivores need to mitigate the limitations imposed upon them by the decrease in forage quality (Scoones 1995). During these critical periods, small sections of the landscape may make an important contribution to supporting herbivore populations (Scoones 1995, Illius & O’Connor 1999, 2000). The use of key resources during the dry season may be especially important for rare antelopes like sable antelope (*Hippotragus niger*) whose numbers have been declining over the last 30 years in the Kruger National Park, South Africa (Harrington et al 1999). Hypotheses that have been proposed to explain the species decline include the effect of prolonged dry conditions on food resources, the increased competition from other grazers (Harrington et al 1999) and increased predation (Owen-Smith & Mills 2006).

Past research has shown how the use of bottom lands, where greater soil moisture enables the retention of more green foliage, allows herbivores to limit the shortcomings of the dry season (e.g. Duncan 1975, Sinclair 1977, Knoop & Owen-Smith 2006). In the Pilanesberg National Park, sable antelope did indeed move to the bottom of valleys during the dry season (Magome 1991). The use of these low lying areas by sable may reduce to some extent grazing competition from Burchelli’s zebra (*Equus burchelli*) and blue wildebeest (*Cannochaetes taurinus*) which generally favour shorter upland grasslands, whereas topi

(*Damaliscus lunatus*), buffalo (*Syncerus caffer*) and roan (*Hippotragus equinuus*) appear to also preferring low-lying areas during the dry season (Duncan 1975, Macandza et al 2004, Knoop & Owen-Smith 2006).

Burning stimulates the growth of plants even during the dry season (Vesey-Fitzgerald 1971), providing forage of high quality (Dörgeloh 1999) thus supporting herbivores during the dry season (Moe et al. 1990, Grossman et al 1999). However, short grass grazers such as impala (*Aepyceros melampus*), wildebeest and tsessebe (*Damaliscus lunatus*) could keep grass regrowth on burns below the height at which species using taller grass, such as sable, can graze efficiently (Grobler 1981). In Kenya, Zimbabwe and Pilanesberg National Park in South Africa, sable grazed frequently on burnt areas (Sekulic 1981, Grobler 1981, Magome 1991), whereas Gureja & Owen-Smith (2002) did not observe much use of burns by sable compared with Lichtenstein's hartebeest (*Alcephalus lichtensteini*), roan antelope (*Hippotragus equinuus*) and tsessebe in the Madrid Game Ranch, Limpopo Province, South Africa.

Grazers also achieve ecological separation through different preference for open or closed vegetation types. Roan preferred open grassland (Bell 1984, Heitkönig 1993), as did white rhinoceros (*Ceratotherium simum*), wildebeest and zebra in the Pilanesberg National Park, South Africa (Borthwick 1986 in Magome 1991). Sable, on the contrary, avoided the more open habitats (Wilson & Hirst 1977, Magome 1991).

My study was conduced in the Kgaswane Mountain Reserve as part of a larger project on the foraging and social ecology of the sable population whose numbers appeared to be stable (Nell 2000). A 'vlei' area is included within the reserve boundaries and early winter burns were implemented each year. Therefore, the aim of this paper was 1) to assess the relative importance of the burnt grasslands and ‘vlei’ area for two herds of sable occupying distinct home ranges and 2) to report on differences in the landscape zones occupied by the two herds, during the critical dry season and transition period to the start of the wet season.

METHODS

Study area

I carried out the study during the dry season and the transition period to the wet season in 2002 and 2003, in the Kgaswane Mountain Reserve (KMR). This is a provincial nature reserve, fenced along all boundaries, which lies between the latitudes 25º 41’ and 25º 45’ S, and longitudes 27º 09’ and 27º 13’ and is approximately 4500 ha in extent. Topography is mountainous and altitude ranges from 1250 meters in the low-lying eastern parts, to 1600 meters above sea level on the high lying western summits. Vegetation types may be crudely classified as woodland, open-woodland, shrubland and grassland communities (see Nel 2000 for a detailed phytosociological classification of the reserve). A natural wetland exists in the reserve and several small annual and perennial streams have their origin on the reserve.

Mean annual rainfall was 791 mm (SD: ± 259 mm) over the last 30 years. Most of the rain (88%) falls from November to March, thus defining a wet and a dry season. Both the dry season and the wet season rainfall were below average during the study period (Table 2.1). The average daily temperature varies from

6.7°C to 21.7°C in winter, to 16.8°C to 30°C in summer (7-year record). During the study period, the summer of 2003 was hotter than average (Table 2.2).

Since 1994, early winter burns were implemented in the KMR. Two block burns were ignited at the end of June 2002 and provided green grass as soon as July (Fig. 2.1). One of the burnt areas was the central alluvial basin with the surrounding grassland and open-woodland communities, all bottomland and foothill areas. The other area was in the eastern part of the reserve, encompassing a larger variety of vegetation types, from woodland to grassland communities and from bottomland areas to hilltops. An accidental fire also occurred, in July 2002 that burnt part of the northern high lying plateau (Fig. 2.1). In 2003, a block burn was put in on a north-facing slope at the beginning of May (Fig. 2.1). However, the burnt areas did not flush, probably because of being on a north-facing slope. Thus, green grass was not available during the dry season in 2003. An accidental fire in late October 2003 burnt approximately three-quarters of the reserve, just before the rain started. The central basin was the only area that was completely saved from the fire.

The reserve hosted about 70 sable, divided in two herds: the ‘vlei herd’ and ‘woodland herd’ plus about 8 single adult males. Other grazers, potential competitors with sable, were zebra (200), impala (70), red hartebeest (115), and waterbuck, *Kobus ellipsiprymnus* (60). Only four roan antelope lived in the reserve at the time of the study. There were also about 70 impala and 30 springbok, which may have contributed to keep the grass height on burns under a suitable grazing height for sable.

Field data collection

The study attempted to associate sable distribution with defined habitat variables. Data collection spanned two dry seasons (April-October) and transition periods to the wet seasons (November-December), being the critical periods for herbivore nutrition in Southern Africa. The dry season was further divided into three periods, namely early dry (April-May), mid dry (June-August), late dry (September-October). Data collection thus proceeded from the end of August 2002 to the end of December 2002, and beginning of April 2003 to the end of December 2003. I plotted the position of each group of sable seen on a 125m x 125m grid, superimposed on a 1:10000 map. The reason for the use of a 125m x 125m grid was that such a grid was already in use in the Kgaswane Mountain Reserve. Besides the position, I recorded a number of landscape variables associated with the sable position (Table 2.3). I did not plot more than one sighting per morning and one per afternoon in one day. Observations were in total 313 for the 'vlei herd' and 304 for the 'woodland herd', divided as follows: late dry season 2002, vlei herd (n= 53), woodland herd (n= 61); transition period 2002, vlei herd (n= 48), woodland herd (n= 54); early dry season 2003, vlei herd (n=58), woodland herd (n=30); mid dry season 2003, vlei herd (n=61), woodland herd (n=68); late dry season 2003, vlei herd (n=51), woodland herd (n=46); transition period 2003, vlei herd (n=42), woodland herd (n=45).

During the dry season 2003, a group of sable moved away from the vlei herd and joined the woodland herd. Only during the final part of the dry season did the vlei sub-group join again with the vlei herd.

Data analysis

I transferred all sightings data to a Geographic Information System (GIS), ArcView (ESRI, California). I calculated home ranges with the program HRT9 for ArcView using two methods. I calculated minimum convex polygons (MCP – Hayne 1949, Harris et al. 1990) using 100% convention, in order to compare the results of the present study with previous studies that used MCP 100%. I also calculated adaptative kernel home ranges (Worton 1959, Harris et al. 1990, Kernohan et al. 1998) using both 50% and 95% conventions. In contrast to the MCP, which plots home ranges based on peripheral data points, kernel methods utilize information derived from the placement and density of interior data points. The 50% Adaptative kernel provides an estimate of a core use area ('core home range').

For each period, I calculated the number of sightings in each of the landscape categories. The frequency distribution of the sightings in the different categories is non-normal. One way to deal with this type of distribution is to use statistical techniques in which non-normal distribution can be specified. Hypothesis test applied to the Generalized Linear Model (GLZ) do not require normality of the response variable, nor do they require homogeneity of variances (Quinn & Keough 2002). GLZs are a widely used class of such models that can accommodate count, proportion and presence/absence response variables (e.g. Agresti 1996, McCullagh & Nelder 1989, Dobson 2002). Sightings data are appropriately analyzed as a Poisson random variable (Seavy et al 2005). Therefore, I used a GLZ with a Poisson error term and a log link function. The habitat variables specified in table 2.3, seasons and herd were the categorical predictors. I first tested for herd differences and when there was no significant difference I combined the data from the two herds. I then tested for seasonal influence on the use of the different habitats, considering one habitat variable at the time. I performed all analysis with STATISTICA 6.0 at 95% confidence level.

RESULTS

Home ranges

The vlei herd had larger seasonal home ranges than the woodland herd, except for the transition period 2002 and the late dry season in 2003 (Table 2.4). The core areas did follow a similar pattern, except during the mid dry season 2003 when the core areas were similar despite the ‘woodland herd’ home range being only about half of the ‘vlei herd’ home range (Table 2.4). At the end of the dry season in 2002, the vlei herd used two distinct ranges, one in the central basin and one on the northern plateau, while the woodland herd showed a more conservative use of space (Fig. 2.2). The vlei herd used a similar area again during the transition period, while the woodland herd more than doubled its range. By the start of the dry season in 2003, the vlei herd had abandoned the northern plateau, limiting its range to the central part of the reserve. During this period, the sub-unit of the vlei herd moved towards the northeastern section of the reserve (Fig.2.2). In the mid dry season of 2003, the woodland herd joined with the vlei sub-group (overlapping home range areas, Fig.2.2). Only during the final part of the dry season did the vlei sub-group join again with the vlei herd. The woodland herd also moved into the central basin at the end of the dry season (Fig. 2.2), but only used similar areas than the vlei herd, without ever joining. The extended movements of both the woodland herd and vlei-sub group during this period explain their large home ranges in this season. In the following transition period, the vlei herd moved again to the northern plateau as in the same season the previous year and the woodland herd went back to the eastern side of the reserve.

Habitat use

The use of areas with different canopy cover differed between the two sable herds (χ^2=132.2, d.f.=1, p<0.001). While the vlei herd was seen more often in area with no trees, the woodland herd was seen more often in wooded areas (Fig.2.3). There was no seasonal variation in the use of areas with different canopy cover by the vlei herd (χ^2=5.56, d.f.=5, p=0.35). The proportion of sightings in areas with no trees increased in the late dry season for the woodland herd (χ^2=14.64, d.f.=5, p=0.012) when they moved to the vlei area.

There was a difference in the use of burnt areas between the two herds (χ^2=4.4, d.f.=2, p=0.04), however the difference was not significant if one limits the comparison to 2002, when both herds concentrated almost entirely on recently burnt areas (χ^2=0.3 p=0.61). During the dry season in 2003, the proportion of sightings of the vlei herd in non-burnt areas was between 20% and 30%, starting from the early dry season, whereas the woodland herd only included unburnt areas from the mid dry season (Fig. 2.4). In the early dry season, the home range of the woodland herd was still completely included in the areas that were burnt the previous year. After the accidental fire at the end of October, probably because of the large extent of the fire, the woodland herd home range was all included in the burnt area, while the vlei herd was in part (25% of sightings) still seen on the vlei left untouched by the fire.

The use of different regions of the catena changed in the course of the year for both herds (χ^2=25.9, d.f.=5, p<0.001). The two groups did not show similar seasonal patterns (χ^2=5.8, d.f.=1, p<0.02), with the vlei herd on lower catena positions than the woodland herd (Fig. 2.5). More than 40% of the observations of the vlei herd were in bottomland areas, specifically the vlei and surrounding area in the central basin of the reserve. This proportion decreased in the early and mid dry season in 2003 when the vlei herd was often seen on the foothills and hill slopes bordering the central basin. The vlei herd moved higher up along the catena during the transition periods, although both bottomlands and upper slopes areas included in their home ranges were burnt. The woodland herd, on the contrary, only made extensive use of bottomlands at the end of the dry season in 2003 when it moved to the vlei. In all other seasons the only bottomland areas available in the woodland herd home ranges were those at the bottom of valleys, but sable were rarely seen there (Fig. 2.5). The woodland herd was instead observed on hill slopes, and as seen for the vlei herd, they moved higher up the catena during the transition period in 2002, but not in 2003 (Fig. 2.5).

In any one season, there was no difference in the numbers of times the two herds were grazing with other herbivores (χ^2=4.7, d.f=1, p=0.46), nor did season (χ^2=8.4, d.f.=5, p=0.14) or catena position have an influence on it (χ^2=8.6, d.f.=4, p=0.07), but burnt status had (χ^2=10.1, d.f.=2, p=0.006). There was a higher proportion of sightings with other herbivores at less than 100 m on recently burnt areas (30%) as compared to unburnt areas (11%).

DISCUSSION

Sable home ranges were not different to those reported for other sable populations and in a previous study in the Kgaswane Mountain Reserve (Table 2.5). The splitting of one sub-unit from one of the herds is not new in sable. Sekulic (1981) has observed it in the Shimba Hills, Kenya. In my study, the sub-group joined another herd.

I distinguished two different space use strategies in the KMR. The vlei herd tended to use larger home ranges when burnt areas were available while limiting itself to the vlei area in other periods. The woodland herd moved more during the dry season with no burns available than when burns were available. Both herds consistently used burnta eras when these were available. Burnt areas provide the animals with high quality grass during the dry season (Dörgeloh 1999). Therefore, a preference for burnt areas is not surprising and previously observed for sable in the Pilanesberg National Park and Loskop Dam Nature Reserve, in South Africa and in Rhodes Matopos National Park in Zimbabwe (Magome 1991, Wilson & Hirst 1977, Grobler 1981). However, Gureja and Owen-Smith (2002) did not observe sable using burnt areas. In the Kruger National Park, sable did not use burnt areas either in 2001-2002, despite the dry conditions of the study period (S Henley pers. comm.). Short grass grazers could keep grass regrowth on burns below the height at which sable can graze efficiently (Grobler 1981). However, in the KMR, both sable herds used burnt areas despite the higher grazing pressure from other species on burnt as compared to unburnt areas. Wilson & Hirst (1977) noted how burning can attract sable away from their usual localities. Sable used certain areas of the reserve, such as the northern high-lying plateau, only after these areas were burnt.

Both herds included unburnt areas in their home range during the second dry season, when no recent burn was available, and herbage quality on the burn of the previous year had declined to that on unburnt areas (unpubl. data). As mentioned above, the vlei herd had a more conservative use of space than the woodland herd in this dry season. The bottomland vlei had an important value as key resource area for the vlei herd. The other herd only moved to the vlei area at the end of the dry season while keeping to using hill slopes during most of the dry season. Similarly, Magome (1991) observed how sable moved to valley habitats during the dry season (April-September), without completely avoiding hillsides. He suggested that this was a consequence of the limited extent of greener valley habitats and increased competition in these areas. In the KMR, the woodland herd used wooded habitats on the hill slopes during the dry season and made extensive use of *Panicum maximum* (Chapter 4). However, the grazing competition was not higher on bottomlands than in other areas. Therefore, I suggest that the observed difference between the two herds was the consequence of two different responses facilitated by the different characteristics of the two areas the herds used. Only at the end of the dry season did the woodland herd move presumably out of its usual range to the vlei area. Use of open vlei grassland by sable, has been documented by Grobler (1981) in Zimbabwe and by Estes & Estes (1974) in Angola during the dry season.

In my study, the vlei is an important key resource area that burnt areas and the vlei were important key resource areas that helped sable survive through dry season. When burnt areas were not available, sable did limit themselves to the vlei or moved extensively in order to find suitable resources (e.g. *Panicum maximum*).

The reasons why sable not always use burnt areas, as evidenced by other studies, has not well been explored, but according to this study an early winter burning regime that provides burnt areas in the sable ranges is a useful management tool to help sable bridge the critical dry season. The two different spatial behaviours shown by the two herds in the one dry season with no burnt areas, suggests however that sable are able to adapt their behaviour depending on the characteristics of the area they live in. Both by using exclusively the vlei as key resource area or by moving over a wide range in order to find and exploit key resources sable adapted to the limitations of the dry season showing an unexpected behavioural plasticity.

FIGURE CAPTIONS

Fig.2.1. Map of block burns and accidental fire in the Kgaswane Mountain Reserve during the study period

Fig. 2.2. Map of sable seasonal home ranges in the Kgaswane Mountain Reserve. Green: vlei herd, Blue: woodland herd, Maroon-orange: vlei sub-group. Light colours: Kernel 95%, dark colours: Kernel 50%.

Fig. 2.3. Seasonal variation in proportion of sable sightings in areas differing in tree canopy cover.

Fig. 2.4.Seasonal variation in the use of burnt areas by the two herds of sable in the Kgaswane Mountain Reserve.

Fig. 2.5. Seasonal variation in the use of catena positions by the two herds of sable in the Kgaswane Mountain Reserve.

Table 2.1. Rainfall in the KMR: 30 years average and study period values

Season	Year	Rainfall (mm)
Wet	Average past 30 years	696
	November 2001-March 2002*	518
	November 2002-March 2003	606
	November– December 2003**	326
Dry	Average past 30 years	95
	April – October 2002	39
	April – October 2003	25

* wet season prior to start of the study
**beginning of wet season at the end of the study

Table 2.2. Average daily temperature in the KMR

Year	Coldest month	Warmest month
1990-2001	14.2 ºC	30 ºC
April 2002- March 2003	June (15.5ºC)	October (29.4ºC)
April 2003- March 2004	June (14.3ºC)	December (33.6ºC)

Table 2.3 Habitat variables associated with sable sightings

Habitat variables	Measured as:	Categories
Vegetation type	Woody canopy cover %	No trees 1-25% > 25%
Fire	Month of burning	Not burnt Burnt June 2002 Burnt May 2003 Burnt October 2003
Topography	Catena position	Bottomland Foothill Lower slope Mid slope Upper slope and hill top
Grazing competition	Grazers within 100 m	Yes No

Table 2.4 Sable home ranges in the Kgaswane Mountain Reserve, calculated using Kernel 95% and Kernel 50%. All values are in hectares.

	Kernel 95%			Kernel 50% (core areas)		
	'vlei herd'	**'woodland herd'**	**'vlei sub-group'**	**'vlei herd'**	**'woodland herd'**	**'vlei sub-group'**
Late dry 2002	1065 (N=53)	235 (N=61)	-	187	57	-
Transition 2002	587 (N=48)	614 (N=54)	-	119	166	-
Early dry 2003	749 (N=58)	384 (N=30)	672 (N=38)	138	81	135
Mid dry 2003	609 (N=61)	293 (N=68)	326 (N=48)	45	50	50
Late dry 2003	573 (N=51)	1030 (N=46)	1049 (N=40)	103	176	232
Transition 2003	1518 (N=42)	646 (N=45)	-	317	148	

Table 2.5. Mean annual home range size (MPC 100%) for sable in the Kgaswane Mountain Reserve compared to previous studies.

Study area	Study	Home range (Km²)
Kgaswane Mountain Reserve, SA (vlei herd)	Present study	19.1
Kgaswane Mountain Reserve, SA (woodland	Present study	15.6
Pilanesberg National Park, SA	Magome 1991	27.3
Percy Five Nature Reserve, SA	Wilson & Hirst 1977	7.5
Loskop Dam Nature Reserve, SA	Wilson & Hirst 1977	9.2
Rustenburg Nature Reserve, SA	Wilson & Hirst 1977	17.7
Sandveld Nature Reserve, SA	Jooste 2000	24.7
Shimba Hills Game Reserve, Kenya	Sekulic 1981	10-24

Fig.2.1

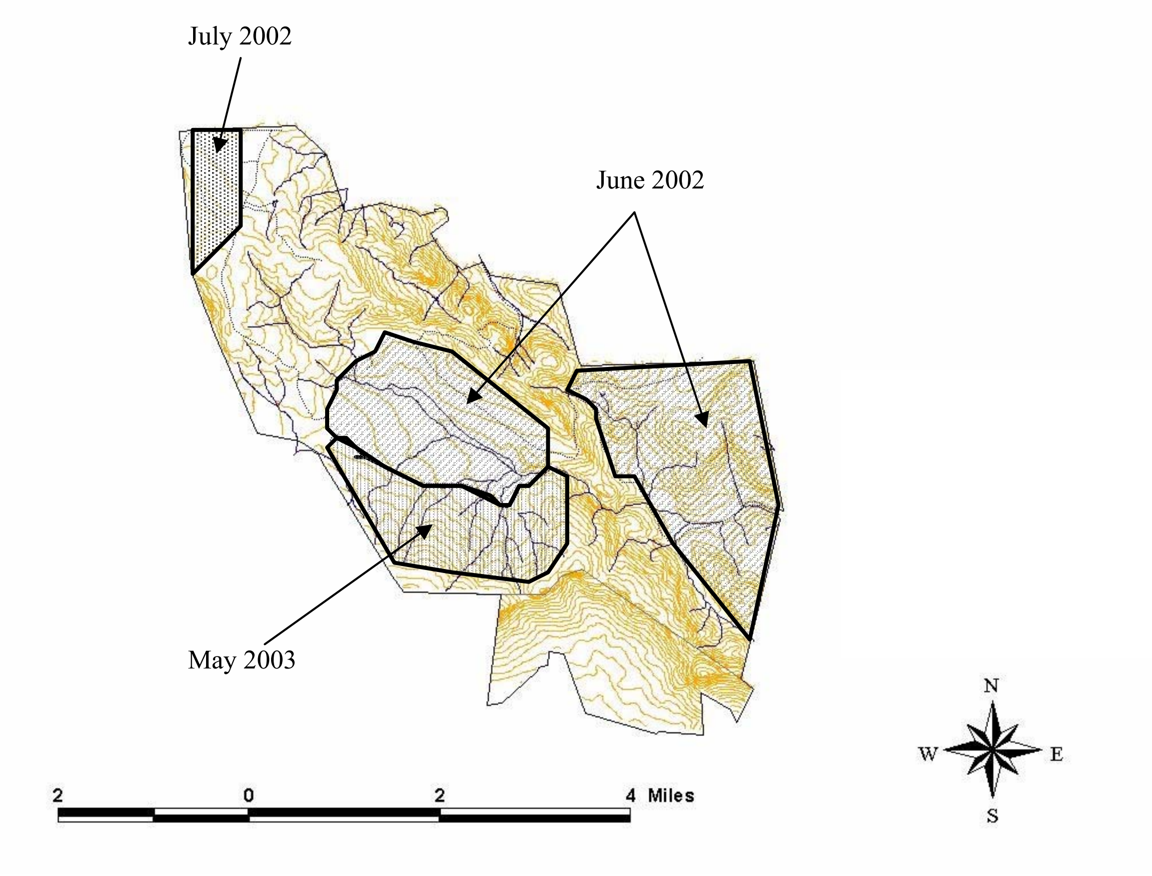
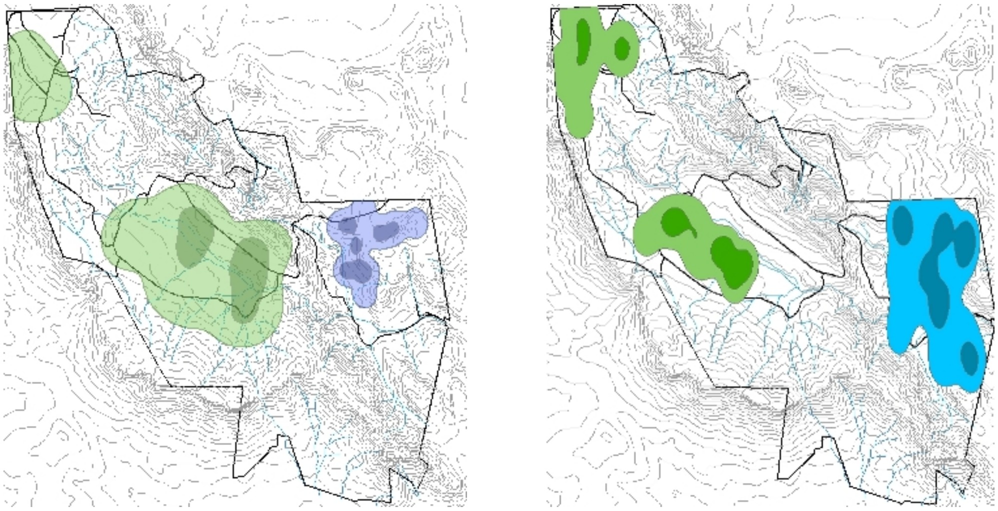
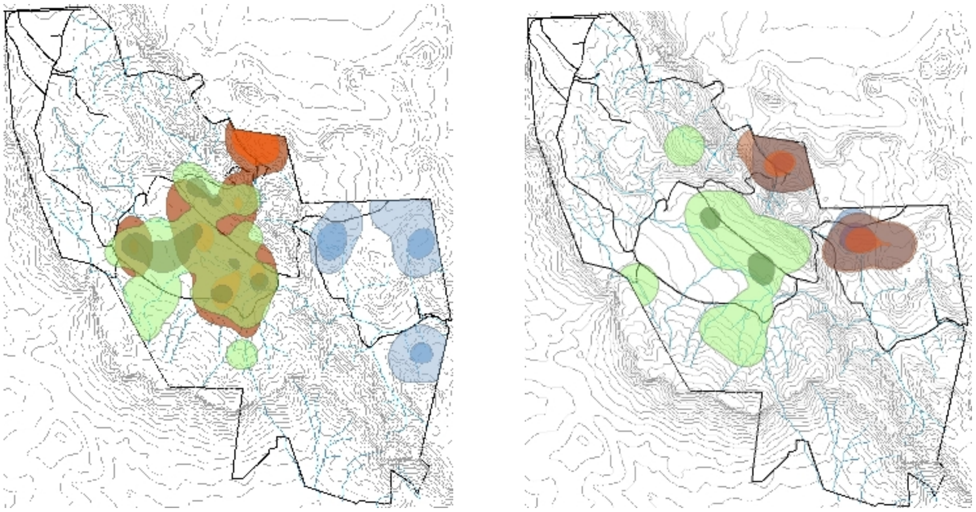


Fig. 2.2



Late dry season 2002

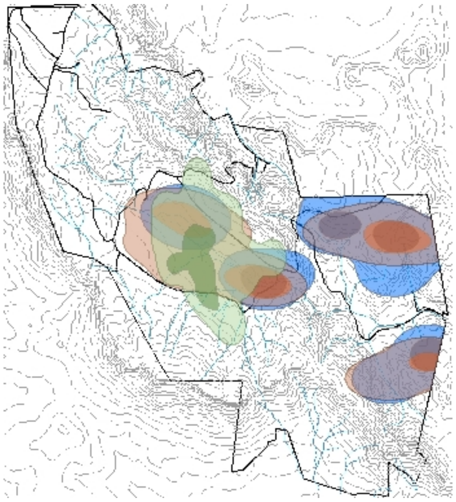
Transition period 2002



Early dry season 2003

Mid dry season 2003

Late dry season 2003



Transition period 2003

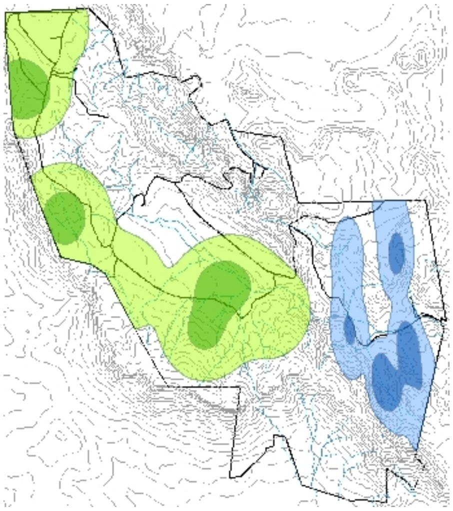
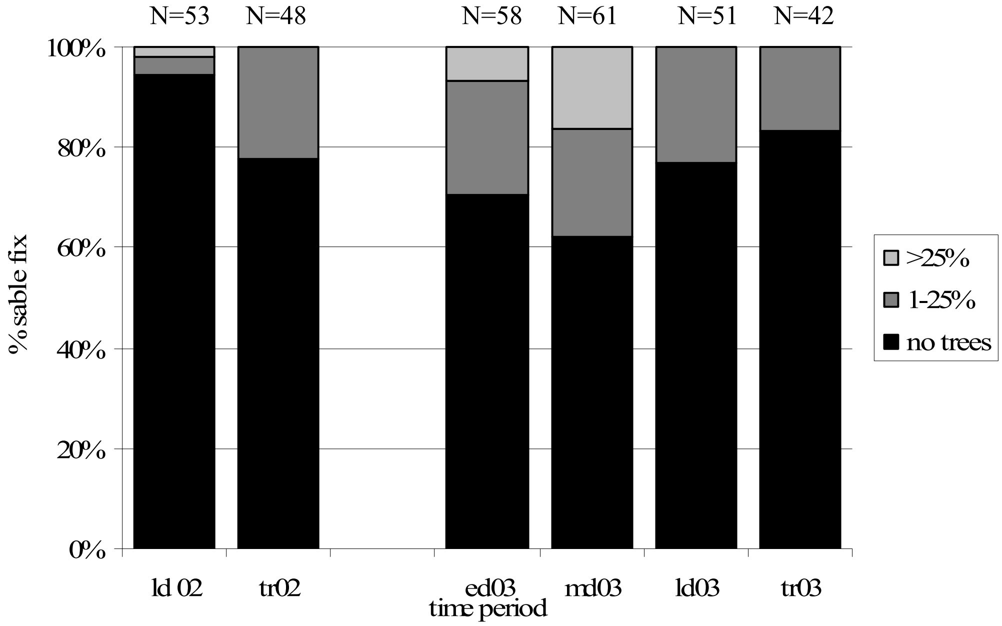


Fig. 2.3

Vlei herd



Woodland herd

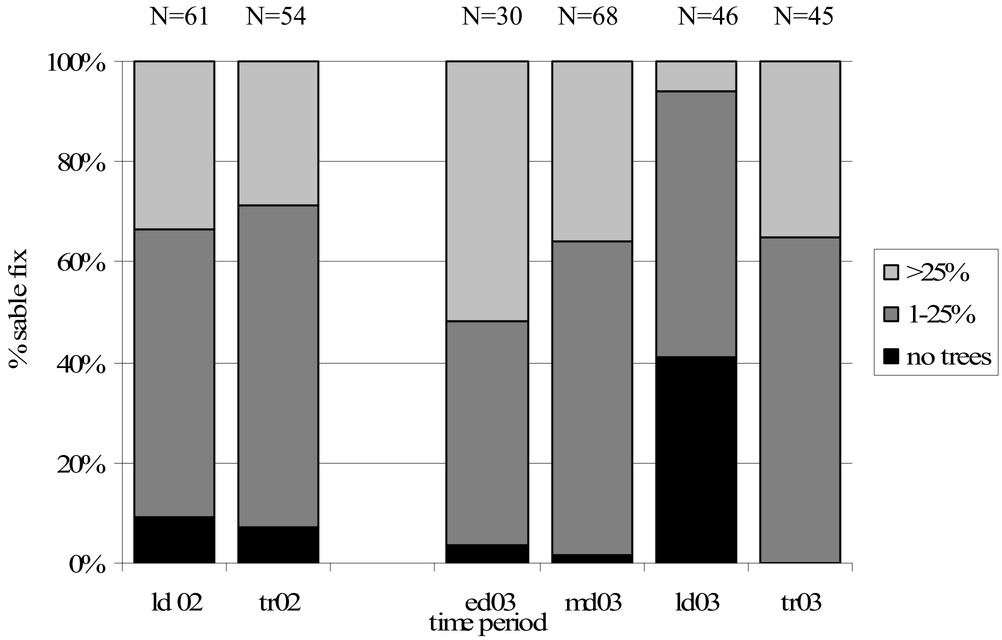
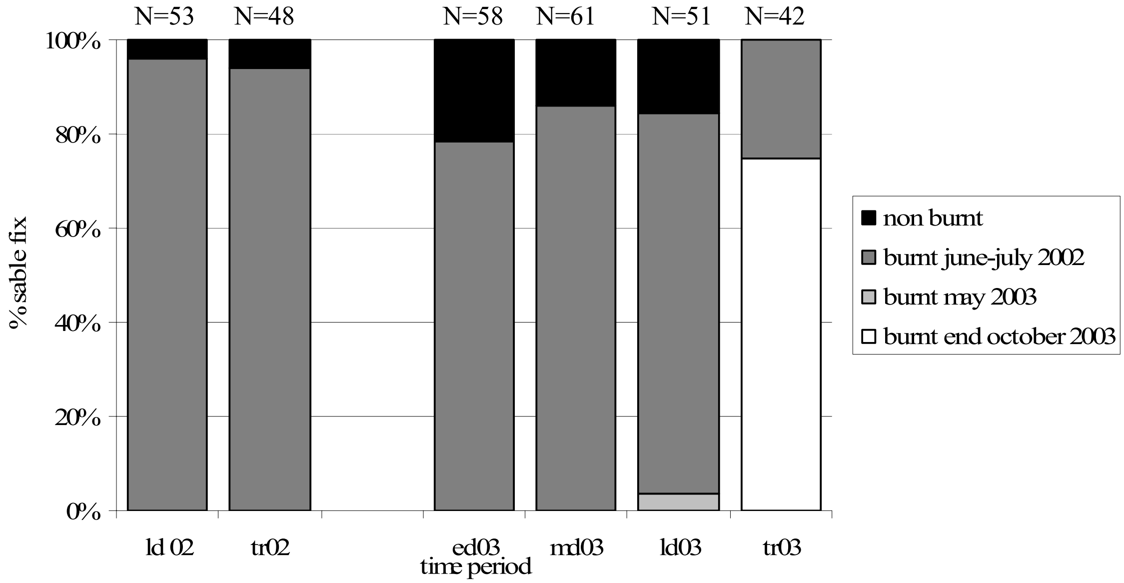


Fig. 2.4

Vlei herd



Woodland herd

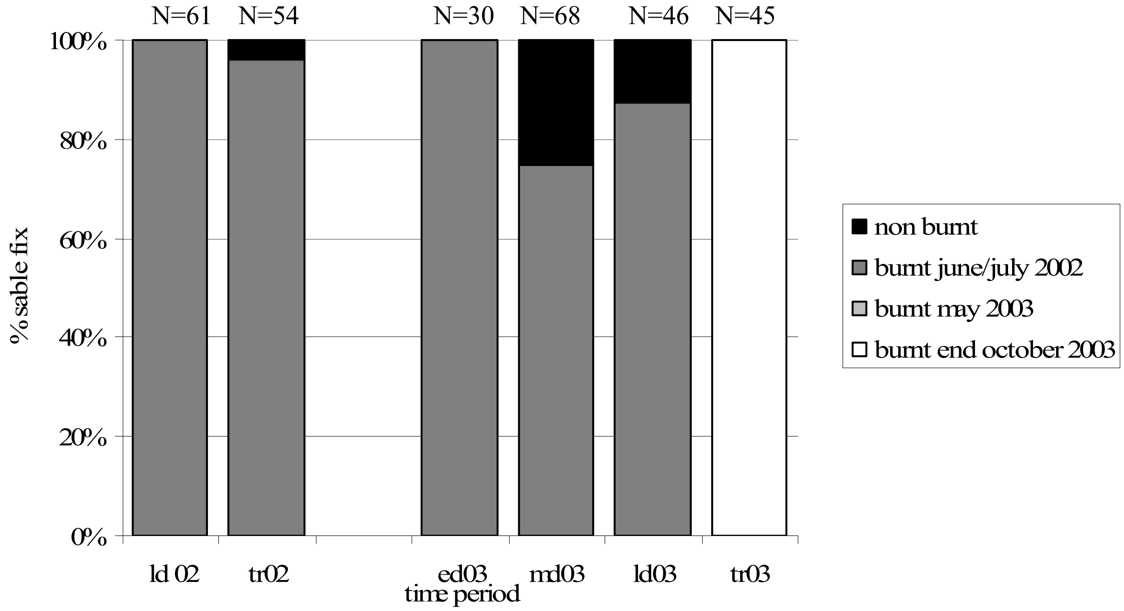
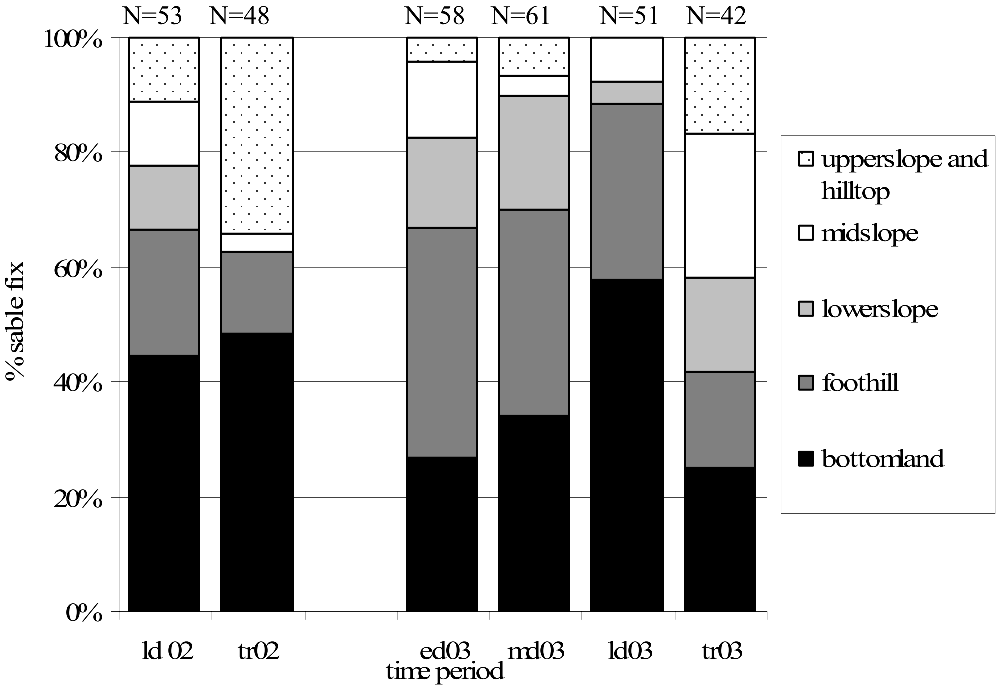
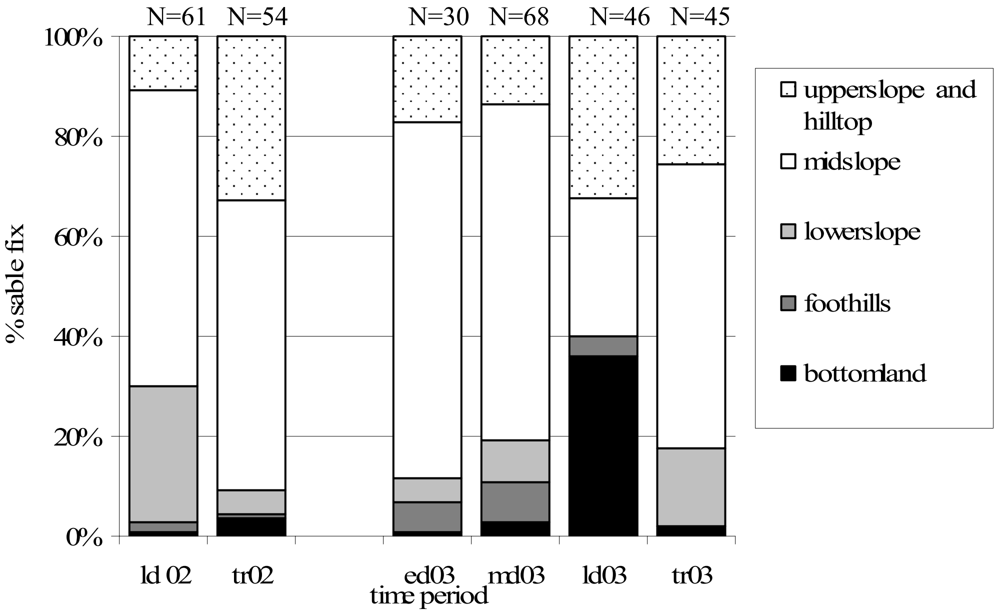


Fig. 2.5

Vlei herd



Woodland herd



CHAPTER 3.

Hierarchical food selection by sable antelope in the Kgaswane Mountain Reserve, South Africa.

Abstract

Prediction of animal distribution and resource use requires multi-scale consideration because animals can use different sets of selection criteria at different hierarchical levels. I investigated whether patterns of food selection by sable antelope (*Hippotragus niger*) in the Kgaswane Mountain Reserve, South Africa, followed different rules across multiple levels. I assumed that grass physical features alone did not explain sable choice of vegetation types at the landscape level, and therefore concentrated on how grass greenness, stemminess and height influenced sable choice of feeding patches within vegetation types and grass tufts within feeding patches. Previous studies reported sable preference for greener grasses, with few or no stems and of intermediate height, without specifying the spatial level at which the selection occurred. In the present study, sable selected for feeding patches that had the greenest grasses but did not avoid feeding patches with brown grasses. However, within feeding patches, selection against brown leaves occurred. Grass stemminess clearly influenced the choice of food patches, since sable always preferred patches with few stems. However, once in the food patch, sable did eat grass tufts in proportion to their availability independently of stemminess, avoiding only grasses with more than five stems. On burnt areas, sable were able to take advantage of the high quality food available, adapting their selection criteria to limit potential quantity limitations. The

present study shows how, at different hierarchical levels, sable are differently influenced by the same grass characteristics. Moreover, season and burn status appeared to play an important role in determining the degree of selection and the level at which the selection operated, showing how sable are potentially able to adapt to different conditions.

INTRODUCTION

Many studies addressing food selection have described what animals eat and where they feed as a hierarchical process (Jarman & Sinclair 1979, Bailey et al. 1996, O'Reagain 2001, Owen-Smith 2002). Within the landscape, herbivores select foraging areas and within these, feeding patches where plant communities might offer higher nutrient levels than surrounding sites (McNaughton 1985, Scoones 1995). Within feeding patches, grazers select for particular grass species (Meissner et al 1999). Grass height, greenness and stemminess are seasonally variable factors that clearly influence food choice by grazing ungulates (O'Reagain & Mentis 1989, Illius & Gordon 1992, Wilmshurst et al. 1999). Stems reduce accessibility to green leaves and have lower digestibility than green leaves, because of the high fibre content (Murray & Illius 1996). Therefore, grazers tend to avoid them (O'Reagain & Mentis 1988, O'Reagain 1993, O'Reagain 2001, Fortin et al. 2002). The degree of selection against stems tends to be lower in immature grasses and higher in mature grasses (Duncan 1975, Fortin 2002), although a study by Heitkönig (1993) showed how roan antelope (*Hippotragus equinuus*) increased their acceptance of stems as the dry season progressed. As leaves mature and grass height increases, structural carbohydrates increase and the protein content of the leaves decreases (Van Soest 1996). Consequently, grazers tend to select the greenest grasses (Winkler 1992, Wilmshurst et al. 1999, O'Reagain 2001) and to avoid the very tall ones (O'Reagain & Mentis 1989).

Some of the studies addressing how the level at which selection operates affects selection criteria conclude that animals use different criteria at the different levels (e.g. Senft et al. 1987, Fortin et al. 2003). Other studies report how animals may use same selection criteria across spatial levels (e.g. Ward & Saltz 1994, Hall & Mannan 1999).

The larger the spatial level the more important the role abiotic factors play in determining the selection criteria (Bailey et al. 1996). Since the purpose of this paper was to test the influence of grass features alone, I focused on the low levels of the spatial hierarchy, excluded the landscape level and tested how the grass features influenced sable choice of feeding patches within vegetation types and bites within feeding patches.

I undertook the study in the Kgaswane Mountain Reserve (KMR), in the Magaliesberg low mountain range. The reserve lies on sedimentary quartzite and soils in this area are sandy and hence poor in nutrients (Wilson & Hirst, 1977). The grasses are prevalently tall and stemmy. Herbivores in this kind of environment are likely to have difficulties in extracting sufficient nutrients from their food supply (Bell 1984). During the present study, which encompassed two dry seasons, the reserve management implemented early winter burns. The burnt areas produced new green grass during the first dry season but not during the second year. Consequently, sable consistently used burnt areas during the first dry season but not during the second one, enabling me to test for differences between burnt and non-burnt areas as well as seasonal differences. Based on the available knowledge on sable feeding ecology (Grobler 1981, Magome 1991) I expected sable to select medium-tall grasses, to prefer green leaves and to avoid stems. In this paper, I explore how sable adjusted their selection criteria and whether they used different criteria at different spatial levels. I did so by testing 1) how grass greenness, height and stemminess influenced sable selection for food patches within vegetation types and for single grass tufts within food patches, 2) how season and availability of burnt areas influenced the selection criteria.

METHODS

Study area

I conduced the study in the Kgaswane Mountain Reserve (KMR), in the North-West Province, South Africa (25º 41’- 25º 45’ S, 27º 09’- 27º 13’ E). The 4,257 ha reserve has an altitude ranging from 1250 m to 1600 m a.s.l.. It lies on the north-west end of the Magaliesberg low mountain range, which forms a climatic boundary between the savanna and the grassland biomes (Low & Rebelo 1996). The reserve encloses a 17-km² catchment area, characterised by *Phragmites australis* reed marsh, deciduous *Acacia caffra* woodland, evergreen *Protea caffra* trees and grassland communities. The other areas of the reserve include a summit plateau with grassland communities and evergreen *Protea caffra* woodlands, and hills dominated by *Protea caffra* and *Acacia caffra* woodlands.

The area is characterised by well-defined dry and wet seasons, and the rainfall was below the average of the last 30 years during the study period (see Chapter 2 for details). The dry season is a critical period for African ungulates: the low rainfall causes the quality of the food to decline during this part of the year. Therefore, I collected data over two years, and focused on the dry seasons and the transition periods to the wet season, from September to December 2002 and from April to December 2003.

KMR has adopted a policy of early winter burning (May-June) since 1994, to support animals through the dry season with the green flushes provided on the burns. During the study period, two block burns were ignited at the end of June 2002, one including the vlei and one in the wooded eastern part of the reserve. These provided flushes of green grass as soon as July and for the rest of the dry season. The following year, a block burn took place at the beginning of May 2003 on a north-facing slope. No grass regrowth occurred, despite the rain that followed. The burnt area was high lying with shallow soils and, most importantly, was north facing. The sun radiation thus facilitates water evaporation (Shevenell 1999). At the end of October 2003, an accidental fire occurred which burnt almost the whole of the reserve except for the vlei area. The start of the rains arrived at the right moment extinguishing the fire and making available green flushes over the entire burnt range only one week later.

Sable occurred in two groups inhabiting separate areas for most of the year. The ‘vlei herd’ lived in the central alluvial basin and northern slopes favouring open grassland and vlei. The ‘woodland herd’ was mostly seen in the low lying eastern part of the reserve in woodland and open woodland habitats, except from the end of the dry season in 2003 when it moved up to the vlei area.

Field data collection

I located and observed a pre-selected group in the early morning and again in the late afternoon, when sable were foraging. I approached the area where sable were foraging on foot once sable had moved on. Within the foraging area, I located feeding patches through the presence of fresh dung, tracks and fresh bites. Based on the vegetation type I identified a food patch as falling into one of the following categories: vlei, grassland, open-woodland (1-50 % tree canopy cover) and woodland (>50 % tree canopy cover). I further classified the food patches based on the last time the area where they occurred had been burnt: non-burnt, burnt June 2002, burnt May 2003, and burnt October 2003.

Within each patch, I placed twelve 0.5 x 0.5 m quadrats. When fresh footprints or/and signs of cropping identified a foraging path, I laid twelve quadrats every two meters starting from a random point along the path. If I could not identify signs of fresh bites inside the selected quadrats, but within 0.5m on either side, I flipped the quadrat one time in order to contain the cropped plants (sampling procedure A, Fig. 3.1). I recognized fresh bites from the tip of the broken leaves being lighter than the rest of the leaf. When unable to identify fresh bites, I laid the quadrats according to a 4x3 regular grid (sampling procedure B, Fig. 3.1). The reason for choosing a 0.25 m² quadrat was that it is the closest representation of a feeding station ('the area that an adult animal is able to reach by swinging its head without moving its feet' *sensu* Novellie 1978), which is the next spatial hierarchical level within the feeding patch. Within each quadrat, I identified grazed and ungrazed plants. I identified grazed tufts from signs of fresh bites. For each grass tuft in the quadrat, I recorded measures of height, greenness and presence of stems. I measured grass height as the height of the tallest basal leaf above ground and classified it into five categories: very short (0-50 mm), short (51-100 mm), medium (101-200 mm), medium-tall (201-400 mm) and tall (401+ mm). I classified the proportion of green leaves/total leaves according to the eight-point scale: 0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99%, 100% (Walker 1976). I counted the emergent culms per tuft and categorized them into four classes: zero stems, 1-2 stems, 3-4 stems and 5+ stems. For grazed tufts, I measured the characteristics of an ungrazed tuft close by to minimize bias due to the alteration of grass sward structure by sable grazing. From August until October 2003, I found it extremely difficult to identify signs of fresh cropping on the brown grasses. Therefore, I did not separate grazed and ungrazed tufts. During April and part of May 2003, I was not able to locate the 'woodland herd' on a regular basis and therefore did not collect enough data to document its behaviour in this period.

To measure the characteristics of the grasses available to sable in the different vegetation types, I recorded grass greenness, height and variation in stems per tuft along nine fixed transects (10 km of length in total) once a month. I located groups of three transects in three different areas of the reserve to cover the above-mentioned vegetation categories. Along each transect, I estimated the grass features every 20 m.

Data analysis

Based on rainfall pattern, I distinguished six periods: late dry 2002 (September-October); transition 2002 (November-December); early dry 2003 (April-May); mid dry 2003 (June-August); late dry 2003 (September-October); transition 2003 (November-December). Based on the different availability of burnt areas, I grouped the above-mentioned periods in two further categories when discussing the results: 'non-burnt areas' when burns did not flush (early, mid and dry season 2003); 'burnt areas' when sable made extensive use of green regrowth following the fires (late dry 2002, transition 2002 and transition 2003).

For 'non-burnt areas' for each period, I calculated the number of grasses in each of the greenness, height and steminess categories at the landscape level and tested for seasonal variation in the grass features available at this level. Seeing the categorical nature and non-normal distribution of the data, I applied a Generalized Linear Model (GLZ) with a Poisson error term and a log link function (McCullagh & Nelder 1989, Dobson 2002) with period, vegetation types and herd as categorical predictors. I tested for each grass feature separately. I combined the eight greenness categories in four broader ones: brown (0-10%), mainly brown (11-50%), mainly green (51-90%), very green (91-100%). Grass height and stems per tuft categories were those defined in the data collection section: five levels for height and four for stemminess. The effect of herd (‘vlei’ and ‘woodland’) was never significant, and I excluded it from the model. Vegetation type was non-significant only in the case of grass stemminess when I excluded it from the model. To test how the use of the grass features at the food patch and grass tuft level differed from their availability in each period, I applied a χ^2 test (Beyers et al. 1984). For ‘burnt areas’ I followed the same steps discussed for the ‘non-burnt areas’. However, I discussed the effect of the time from the fire instead of seasonal trends and focused only on grass height, which I considered a measure of grass regrowth following the fire. Both herd and vegetation type effects were non-significant and therefore I excluded them from the final model. I performed all analyses using STATISTICA 6.0 at 95% confidence level.

RESULTS

Greenness

In the vlei area the availability of green leaves at the landscape level changed during the dry season (GLZ, season*category effect: $\chi^2=46.9$, d.f.=6, $p<0.001$). Here, at the beginning of the dry season, ‘mainly green’ grasses were the most abundant ones, and decreased to mostly ‘very brown’ ones and only 1% ‘mainly green’ in the mid dry season (Fig. 3.2A). The greenness slightly increased at the end of the dry season when 5% of grasses were ‘mainly green’ and 61% ‘very brown’.

At the feeding patch level, the greenness differed from the landscape availability at the beginning of the dry season (landscape vs. feeding patches availability: Chi-

Square test: χ^2=4.50, d.f. = 3, p<0.04) but not during the mid dry season (overall availability vs. feeding patches availability: Chi-Square test: χ^2=0.03, d.f. =2, p=0.97). The difference was again significant at the end of the dry season (Overall availability vs. feeding patches availability: Chi-Square test: χ^2=4.6, d.f. =2, p<0.03). At the beginning of the dry season, I recorded a higher proportion of 'green' grasses than available in the landscape and in the mid dry season most grasses were 'very brown' and 'mostly brown' (Fig. 3.2A). At the end of the dry season the feeding patches were again greener than the overall availability, with more 'mainly green' grasses and less 'very brown' grasses (20% and 47%) than in the vegetation (5% and 61%).

At the level of food consumed, grass greenness differed from the feeding patches one at the start of the dry season (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=9.6 d.f. = 2, p=0.008) and in the mid dry season (Feeding patch availability vs. eaten grasses: Chi-Square test: χ^2=9.6, d.f. =2, p=0.08). In the early dry season, 'mainly brown' grasses were less represented than in the feeding patches and in the mid dry season, 'very brown' grasses were eaten less and the greenest categories (i.e. 'mainly brown', 'mainly green') were eaten more than expected from their feeding patch availability (Fig.3.4A).

For all the other vegetation types, the greenness of the available grasses declined from early to late dry season in absence of burns (GLZ, season*category effect: χ^2=132.5, d.f.=6, p<0.001). The 'mainly green' category for example decreased from 45% in the early dry season to 0% at the end of the dry season, while the 'very brown' category increased from 3% in the early dry to 55% in the mid dry and 97%

in the late dry season (Fig. 3.2B). At the feeding patch level greenness was different from the available grasses in the landscape at the beginning of the dry season (Overall availability vs. feeding patches availability: Chi-Square test: χ^2=30.1, d.f. =2, p<0.001) but not in the mid dry season (overall availability vs. feeding patches availability: Chi-Square test: χ^2=4.9, d.f. =2, p=0.10). As in the vlei the difference was again significant at the end of the dry season (overall availability vs. feeding patches availability: Chi-Square test: χ^2=12.6, d.f. =2, p<0.001). At the start of the dry season less 'mainly brown' grasses were recorded in the feeding patches (23%) than overall (52%) (Fig. 3.4B). At the end of the dry season 98% of all available grasses were 'very brown' but the proportion of 'very brown grasses decreased to 85% inside the feeding patches, where 15% of the grasses were 'mostly brown'.

At the food level I recorded more 'very green' grasses and less 'mainly brown' grasses than available in the feeding patches (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=9.3, d.f. =2, p<0.01). In the mid dry season, sable used 'mainly green' grasses more and 'very brown' grasses less than expected from their feeding patches availability (feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=45.8, d.f. =2, p<0.0001).

Stemminess

The number of stems per tuft varied as the dry season progressed (GLZ, season*category effect: χ^2=16.1, d.f.=6, p=0.013), with the 'no stems' class increasing from 4% to 21% and the '5+ stems' class decreasing from 52% to 38%

from early to late dry season (Fig.3.3). During the early dry season, the numbers of stems in the feeding patches were different from overall (Overall availability vs. feeding patches availability: Chi-Square test: χ^2=68.5, d.f. =3, p<0.001), There were higher proportions of 'no stems' and '1-2 stems' grasses and lower percentages of '3-5 stems' and '5+ stems' grasses in the feeding patches than in the vegetation types (Fig. 3.3). In the mid dry season the n feeding patches had a different number of stems than were overall (Overall availability vs. feeding patches availability: Chi-Square test: χ^2=108.6, d.f. =3, p<0.001) with a higher proportion of low stems classes than overall (Fig.3.3). At the end of the dry season, the difference between availability in the landscape and steminess of the grasses in the feeding patches was even more evident (overall availability vs. feeding patches availability: Chi-Square test: χ^2=108.8, d.f. =1, p<0.001) since sable completely avoided areas with grasses with more than two stems when choosing feeding sites (Fig.3.3).

In the early dry season there was no significant difference between number of stems of the grasses available in the feeding patches and the eaten grasses (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=7.2, d.f. =3, p>0.05), contrary to the mid dry season (feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=22.4, d.f. =3, p<0.001) when sable underutilized the '5+ stems' class at the food level (20% of the available grasses in the feeding patches, 8% of the accepted grasses)(Fig.3.3).

Grass height on non- burnt areas

The relative proportions of grasses in the different height categories varied seasonally both in the vlei (GLZ, season*category effect: χ^2=70.4, d.f.=6, p<0.001) and in the other vegetation types (GLZ, season*category effect: χ^2=44.7, d.f.=6, p<0.001).

In the vlei area, 'medium' and 'medium-tall' grasses available increased from the early to the late dry season (from 6% to 19% and 23% to 37% respectively) while 'tall' grasses decreased from 70% in the early dry season to 37% in the late dry season (Fig. 3.4A). At the start of the dry season sable selected feeding patches with grasses of different height than the grasses overall (overall availability vs. feeding patches availability: Chi-Square test: χ^2=54.3, d.f. =3, p<0.001), less 'tall' and more 'short' and 'medium' grasses than in the landscape (Fog.3.4A). In the mid-dry season, the difference between landscape and feeding patches was still significant (Overall availability vs. feeding patches availability: Chi-Square test: χ^2=9.7, d.f. =3, p<0.05). Probably because 'tall' grasses in the landscape were anyway less than in the previous period, sable did not select against them when choosing a feeding area (Fig. 3.4A). In this second part of the dry season, sable seemed to select for areas that had more 'tall' and less 'medium' grasses than in the previous season (47% vs. 36% and 13% vs. 24% respectively). At the end of the dry season, as overall height decreased, the height of the grasses recorded in the feeding patches did even more so (Overall availability vs. feeding patches availability: Chi-Square test: χ^2=16.9, d.f. =3, p<0.001). 'Short' and 'medium' grasses were present more than the overall availability, and 'medium-tall' and 'tall' grasses were less than overall (Fig.3.4A).

At the food level, there was no difference in grass height between landscape and feeding patches (feeding patches availability vs. eaten grasses: Chi-Square test: $\chi^2=1.5$, d.f. =2, $p>0.05$) but sable avoided the category 'short' grasses completely (Fig. 3.4A). Instead, in the mid dry season the grass sward height in the feeding patches selected by the sable was different from the overall availability (Overall availability vs. feeding patches availability: Chi-Square test: $\chi^2=16.9$, d.f. =3, $p<0.001$) and 'medium' grasses were underused and 'medium-tall' grasses used more than expected from their availability in the feeding patches (Fig. 3.4A).

In the other vegetation types, at the beginning of the dry season only 'medium-tall' (24%) and 'tall' (76%) grasses were available (Fig. 3.4B). At the end of the dry season, 'tall' grasses decreased to 44% and 'medium-tall' grasses increased to 36%; by the end of the dry season, 'medium' and 'short' grasses were also available in the landscape (17% and 3% respectively). Similar to what described for the vlei vegetation type, sable selected feeding patches with less 'tall' and more 'medium' grasses than overall (Overall availability vs. feeding patches availability: Chi-Square test: $\chi^2=19.2$, d.f. =2, $p<0.001$). At this level, tall grasses made up 55% of the recorded grasses and 'medium-tall' grasses 38% of the grasses available in the feeding patches (Fig. 3.4B). Differently from the vlei, sable selected against areas with 'tall' grasses in favour of areas with more 'medium' and 'medium-tall' grasses than overall when choosing feeding sites during the mid dry season (Overall availability vs. feeding patches availability: Chi-Square test: $\chi^2=21.2$, d.f. =3, $p<0.001$). Nevertheless, 'tall' grasses made up 47% of the recorded grasses, as in the feeding areas in the vlei (Fig. 3.4B).

At the food level, no selection towards any particular grass height occurred (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=4.0, d.f. =2, p>0.1): sable accepted all grass heights in proportion to their availability (Fig. 3.4B). Selection occurred in the mid dry season (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=22.0, d.f. =2, p<0.001) when sable ate less 'medium' (4% vs. 13%) and more 'medium-tall' grasses (43% vs. 37%) than available in the feeding patches (Fig. 3.4B).

Grass height on burnt areas

As expected the time from the fire and the timing of the fire (pre-/ post-rain fire) had a significant effect on the relative proportion of different grass height categories available in the burnt areas (GLZ, season*category effect: χ^2=17.6, d.f.=8, p<0.001). In a two months old winter burn (late dry season 2002), most grasses were 'short' and 'medium' (33% and 36% respectively) and only 19% were 'medium-tall'. Of the total grasses recorded, 11% were still 'short' (Fig. 3.5). In the same burnt areas after the rains (transition period 2002), the 'medium' category increased to 45% and the 'medium-tall' to 53%. On a post rain burn (transition period 2003), grass regrowth was much faster and most of the grasses I recorded were 'medium' (60%) and 30% were already 'medium-tall'. There were no 'very short' grasses and only 10% were 'short'.

In all these different situations, sable selected feeding patches with a majority of 'medium' grasses (Fig. 3.5). This means that during the dry season 2002 'very short' and ‘medium-tall’ grasses were underrepresented in the sable feeding patches (overall availability vs. feeding patches availability: Chi-Square test: χ^2=52.2, d.f. =3, p<0.001). During the transition period 2002 ‘medium-tall’ grasses were underrepresented (overall availability vs. feeding patches availability: Chi-Square test: χ^2=43.7, d.f. =2, p<0.001). Only in the transition period 2003 were sable feeding patches not different from the overall availability (overall availability vs. feeding patches availability: Chi-Square test: χ^2=2.7, d.f. =2, p>0.1). This difference was probably because the favoured ‘medium’ grasses by sable were highly available overall in the ‘post-rains burns’ so that sable did not have to actively select for them.

‘Medium’ grasses were also the most represented ones within eaten grasses, during both the dry season 2002 and the transition period 2002 (Fig. 3.5). In addition, during the late dry season of 2002, ‘short’ grasses were also eaten by sable, whereas ‘medium-tall’ grasses were completely avoided (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=29.3, d.f. =2, p<0.001). In the following transition period, sable ate the grasses in proportion to their availability, and therefore ‘medium-tall’ grasses were eaten too (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=0.38, d.f. =1, p>0.5). The following year on the post rain burn, the feeding patches differed from the overall availability (Feeding patches availability vs. eaten grasses: Chi-Square test: χ^2=10.9, d.f. =2, p<0.005) with ‘short’ grasses were eaten more and ‘medium-tall’ grasses less than expected from their availability in the feeding patches (Fig. 3.5).

DISCUSSION

Sable appeared to use different selection criteria at the two spatial levels considered, and these criteria were influenced by changing seasonal availability and by the use of burnt areas. Sable always favoured the greenest grasses available both at the feeding patch level and among grass tufts. However, the decrease in greenness available in the course of the dry season restricted them to feeding patches where more than 90% of the grasses were brown. Despite this, sable ate the greenest leaves available. Moreover, of the total grass eaten by sable, in any one period during the dry season, less than 25% had less than 10% of leaves green. Old leaves were more of a deterrent in the selection of grass tufts than feeding patches. Instead old leaves where a deterrent at the feeding patch level for roan in a study undertaken by Heitkönig & Owen-Smith (1998) in the Nylsvley Nature Reserve in South Africa. No data were available to show how sable adjusted their food choice at the very end of the dry season when almost all grasses in their patches had more than 90% of leaves brown.

Inside the feeding patch, sable only selected against grasses with more than five stems per tuft. At the patch level instead, sable always preferred areas with high proportion of grasses with less than two stems and at the end of the dry season completely avoided areas that had grasses with more than two stems per tuft. The apparent increase in stem avoidance at the feeding patch level as the dry season progressed coupled with the non-avoidance of stem behaviour inside feeding patches, suggests that sable may be tolerant of stems in habitats with intermediate to high nutrient levels. It appears that under the threshold of five stems per tuft, stem density is an effective deterrent only when most grasses available have brown leaves. Similarly, roan antelope tolerated stems when leaf quality was high, whereas when old leaves were prevalent they always selected for feeding areas where the lowest stem density tended to occur (Heitkönig & Owen-Smith 1998).

Sable adjusted their selection for grass height as the season progressed and grass become shorter from the early to the mid dry season so that the grass height in the feeding patches was similar during the whole dry season. For topi, the effect of seasonal changes in habitat selection was to maintain the animals in grasslands of roughly the same grass quantity throughout the year (Duncan 1975). Could it be the same with sable? Sable did feed in areas where as much as 90% of the grasses were taller than 200 mm. Fifty percent of the grasses were even taller than 400mm. Magome (1991) reported that sable preferred grasses between 100 and 300 mm and avoided grasses taller than that in the Pilanesberg National Park. Topi, when feeding on grasses with more that 20% of green leaves, always selected for species that had relatively long leaves and for the tallest plants (Duncan 1975). If this is the case with sable, they should avoid tall grasses at least at the end of the dry season when most grasses are brown. Unfortunately, the lack of data on the grasses eaten at the end of the dry season leaves this question unresolved.

On burnt areas, the new green leaves provide food of high quality, but of low quantity (Hobbs & Spowart 1984). Quantity, measured in this study as the height of the grass regrowth, is influenced by the timing, amount of rain and by grazing, and can be an important limitation for animals feeding on burns. In fact, on short grass burns sable avoided the shorter grasses and only grazed on grasses of medium height.

On post rain burns, where more medium and tall grass was available, sable grazed on short grasses as well. By being able to include more taller grasses into their diet, sable were likely to be able to get enough quantity of food without being selective against short grasses as they were in the pre-rain burns.

In general, the factors governing sward selection by sable appear similar to those influencing other grazing ungulates (Duncan 1975, Murray & Brown 1993, Heitkönig & Owen-Smith 1998, Wilmshurst et al. 1999). Nevertheless, sable appear to be tolerant of stemmy grasses, and brown leaves act as a strong deterrent mainly at the grass level. The stem tolerance suggests that sable may discriminate better at the plant part level than other ruminant species or might be able to eat the stems despite their lower digestibility. The evident preference for green grasses on burns despite the potential limiting quantity, suggests that sable are able to adapt to limited quantities of high quality food.

FIGURE CAPTIONS

Fig.3.1. Sampling pattern adopted at each feeding site. A: 0.5 x 0.5 m quadrats were laid down along sable foraging paths. If there were no signs of fresh bites inside the selected quadrats, but there were signs within 0.5 m on either side, the quadrat was flipped one time in order to contain the cropped plants. B: When unable to identify fresh bites, the quadrats were laid according to a 4x3 regular grid.

Fig.3.2. Percentage of grass tufts recorded in each greenness category available in the landscape, present in the food patches and for eaten grasses on non-burnt areas during the dry season of 2003. No data on eaten grasses were available for the late dry season. A) vlei, B) other vegetation types

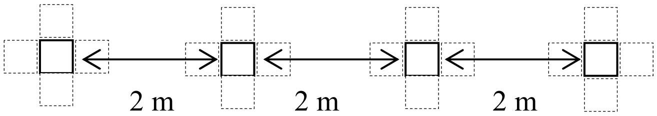
Fig.3.3. Percentage of grasses with different number of stems per tuft recorded during the dry season at the three levels of selection.

Fig.3.4. Percentage of grasses in each height category recorded on non-burnt areas during the dry season 2003 (from top to bottom) at the different levels of selection (from left to right). A) vlei, B) other vegetation types.

Fig.3.5. Percentage of grasses in each height category recorded on burnt areas at the different levels of selection (from left to right).

Fig. 3.1

Sampling procedure A



Sampling procedure B

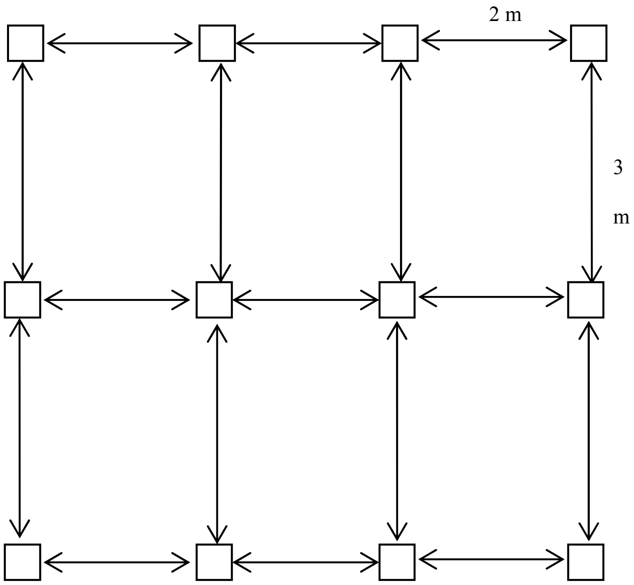


Fig. 3.2A **Vlei**

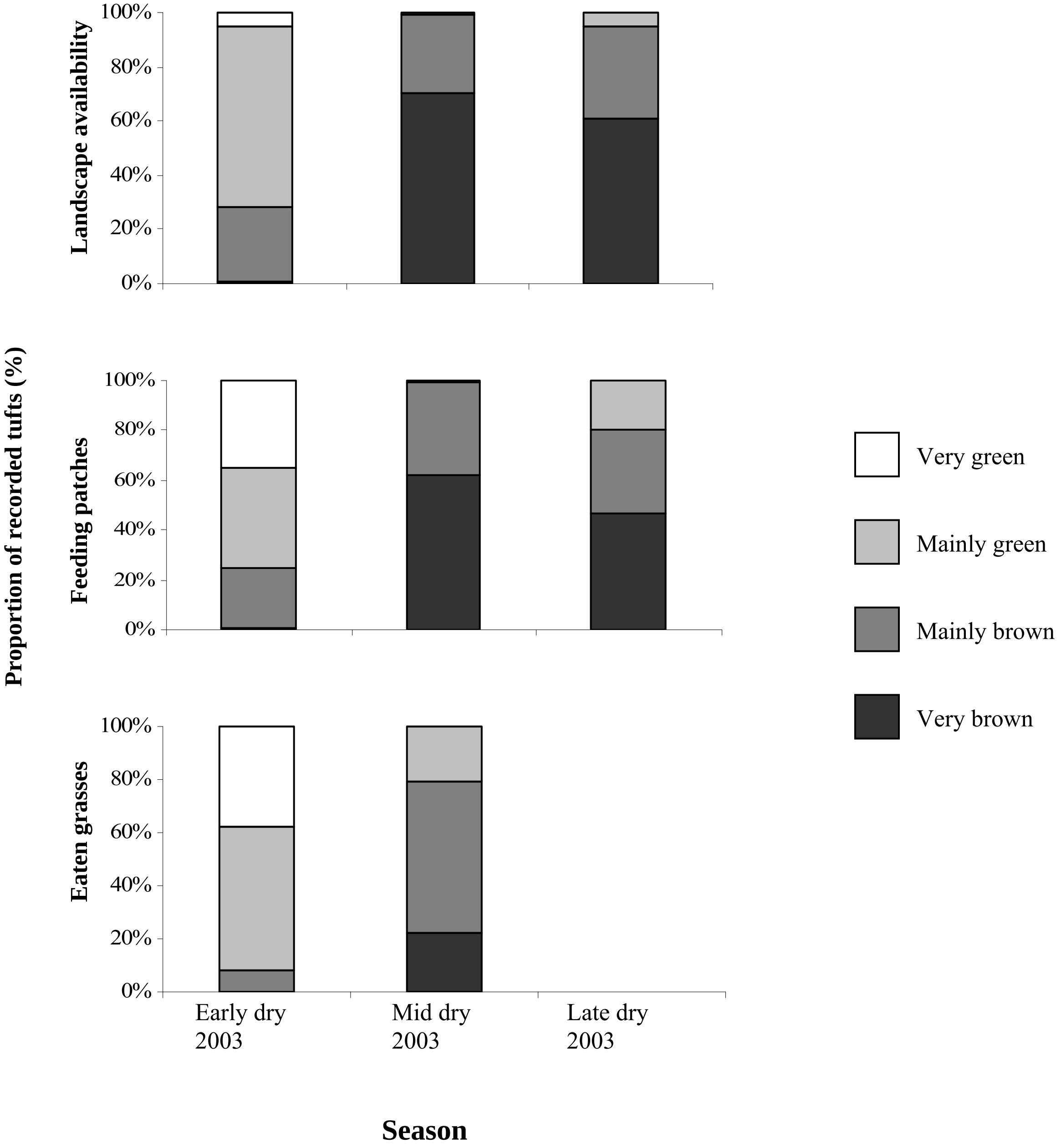

100%
80%
60%
40%
20%
0%
Landscape availability
Feeding patches
Eaten grasses
Proportion of recorded tufts (%)
Early dry 2003
Mid dry 2003
Late dry 2003
Season
Very green
Mainly green
Mainly brown
Very brown

Fig. 3.2 B **Other grassland and woodland**

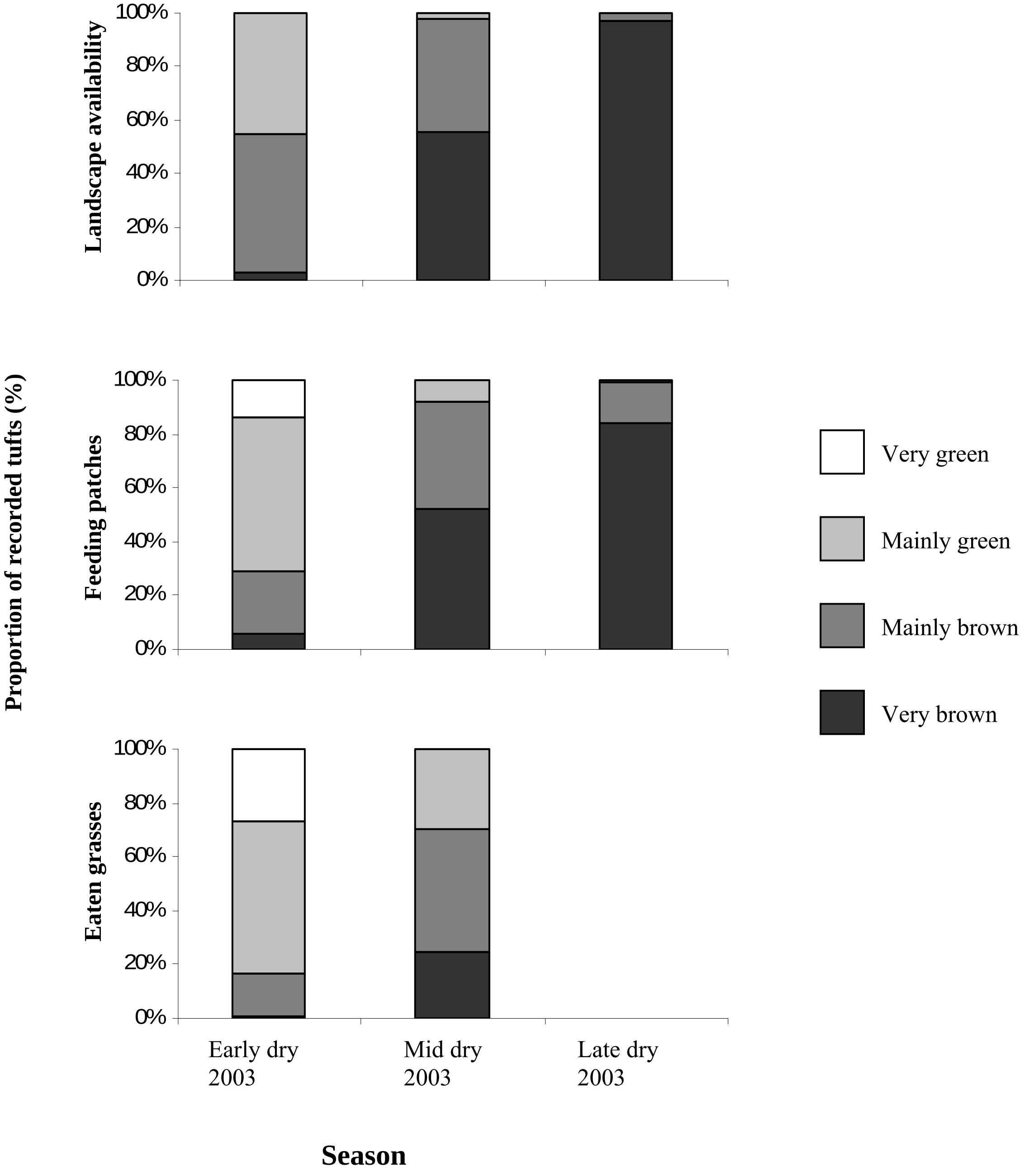


Fig. 3.3 **All vegetation types**

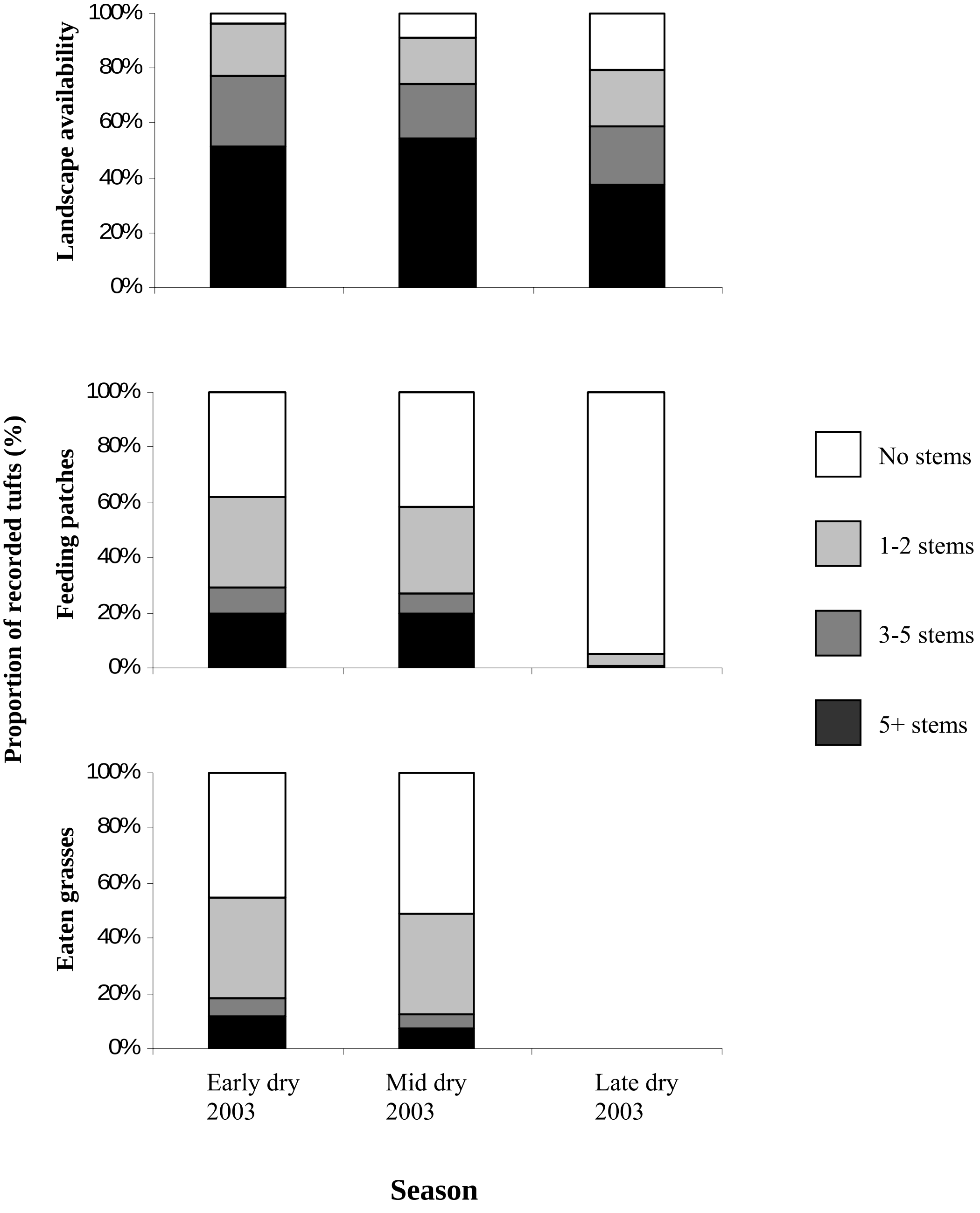


Fig. 3.4A **vlei**

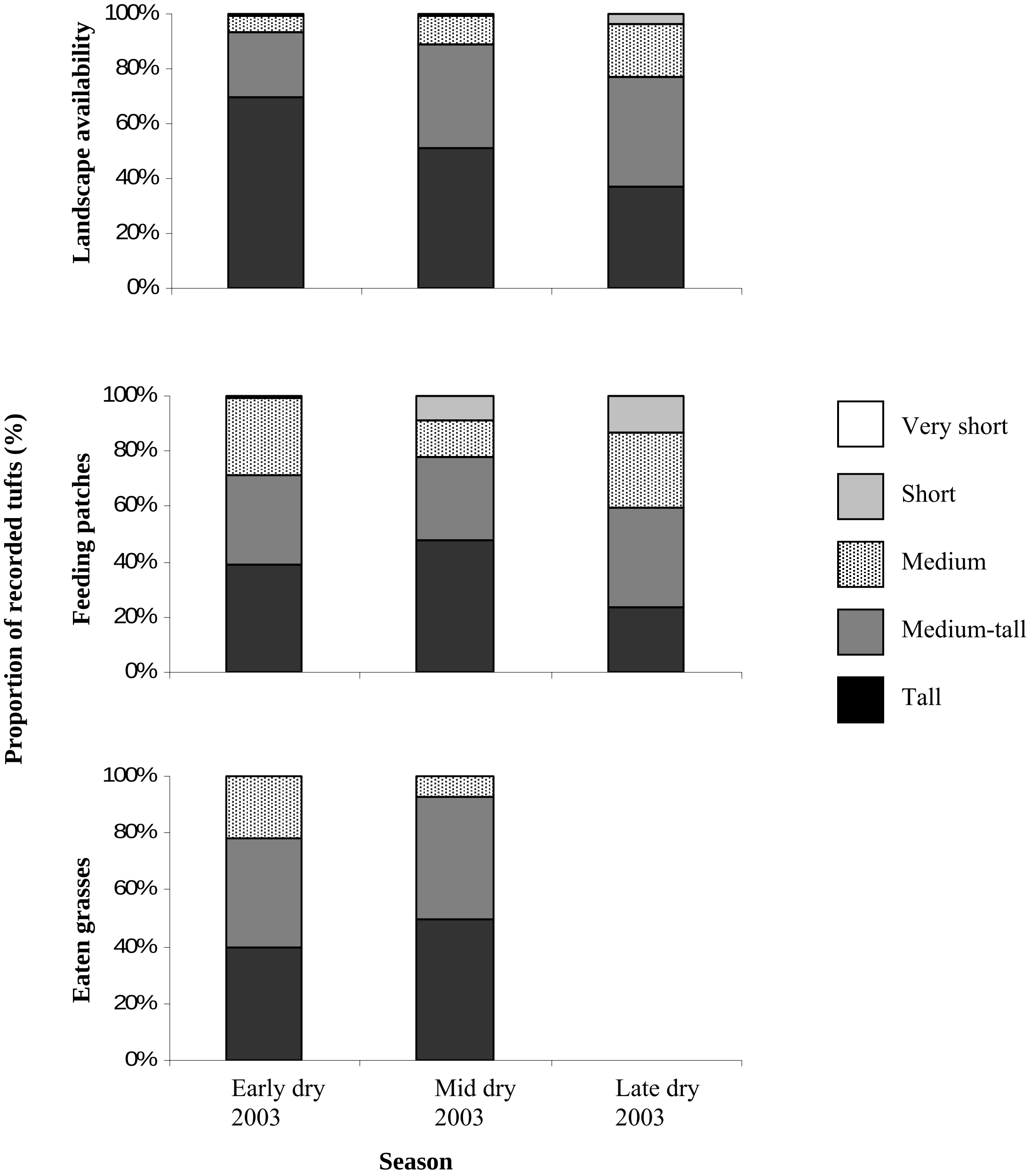

Proportion of recorded tufts (%)
Landscape availability
Feeding patches
Eaten grasses
100%
80%
60%
40%
20%
0%
Very short
Short
Medium
Medium-tall
Tall
Early dry 2003
Mid dry 2003
Late dry 2003
Season

Fig. 3.4B **other grassland and woodland**

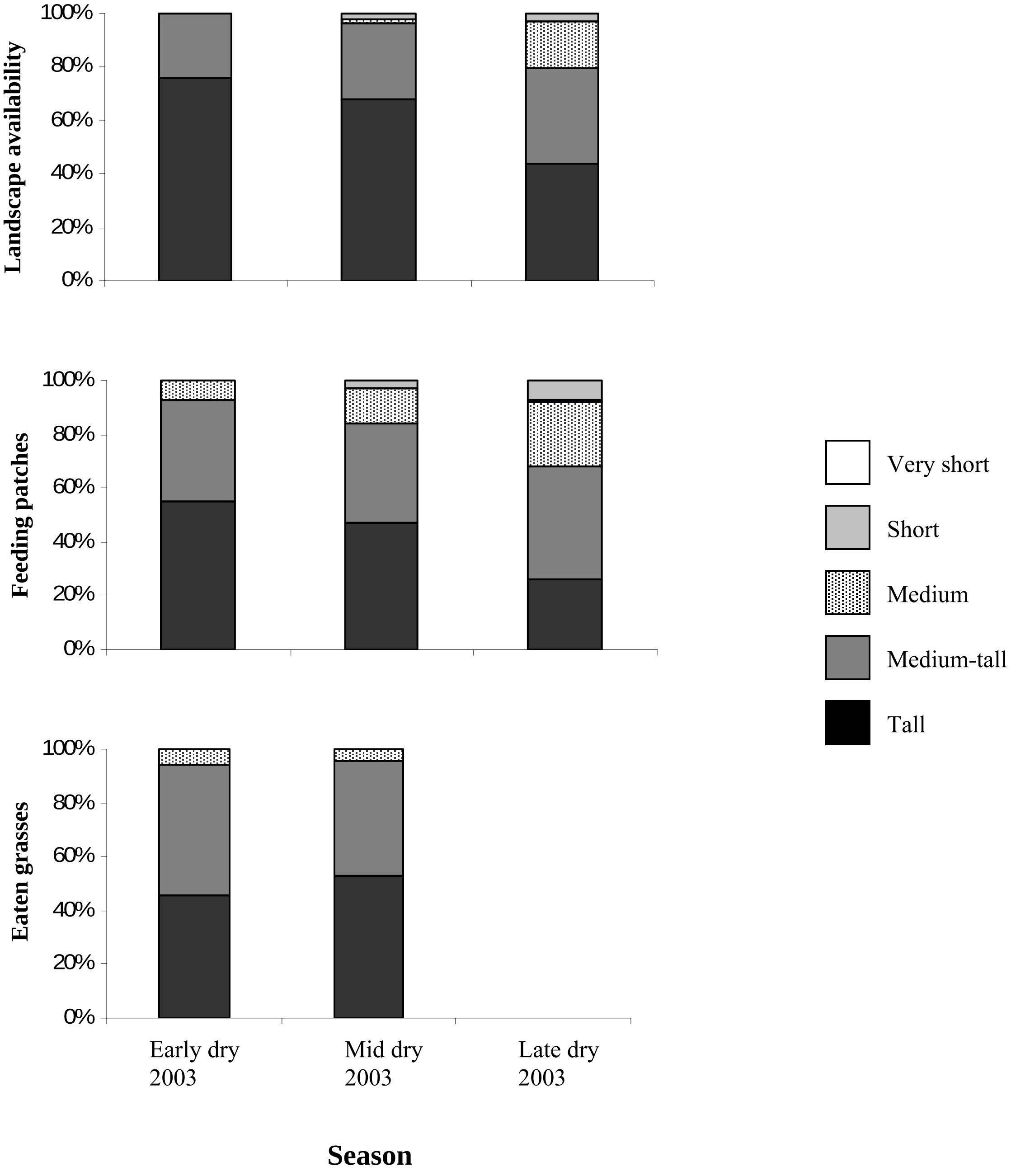
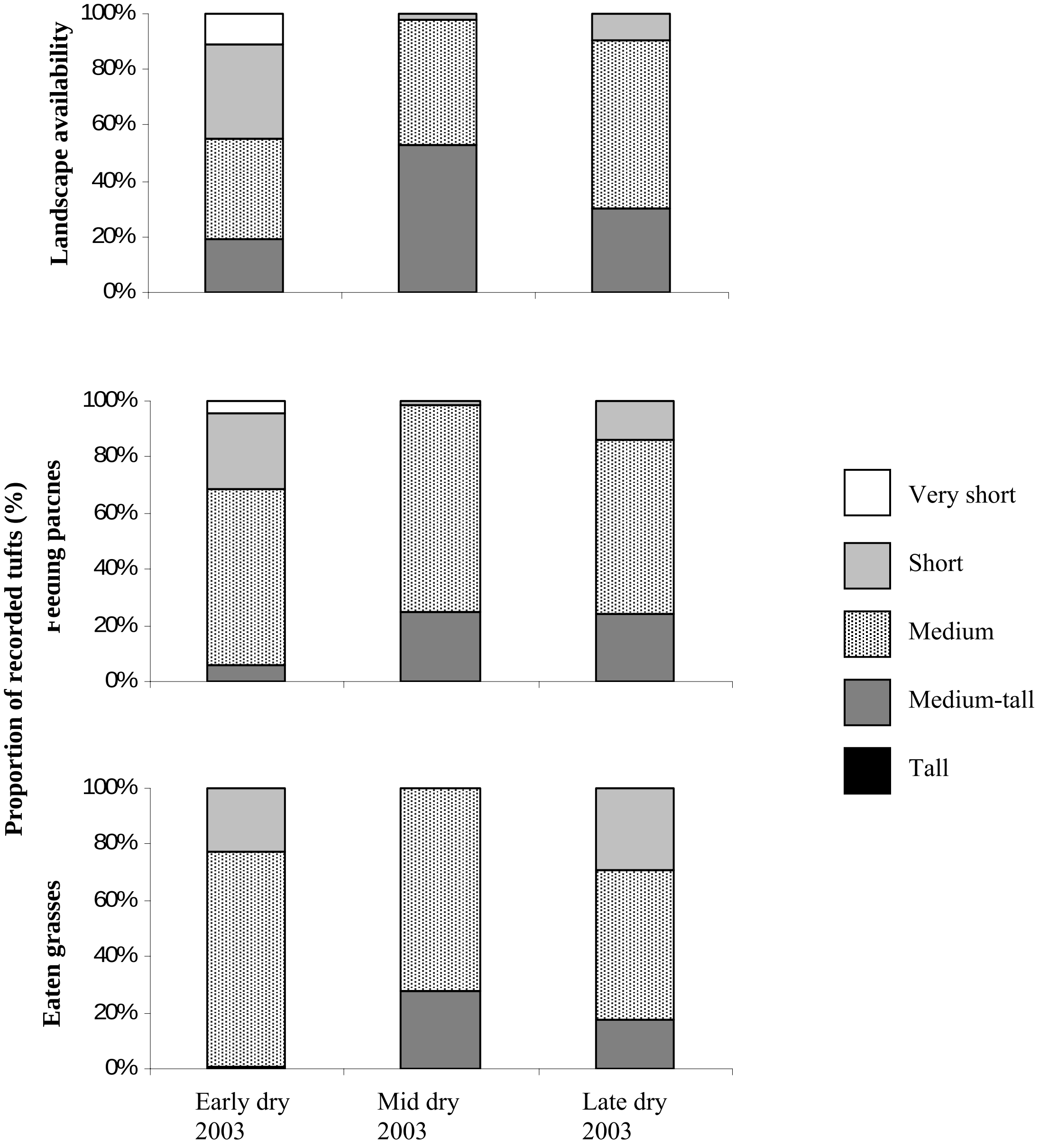


Fig. 3.5 **all vegetation types**



CHAPTER 4.

How does season and use of burnt areas affect which grass species sable choose to eat?

Abstract

I investigated the use of grass species by sable antelope in the Kgaswane Mountain Reserve, South Africa. I recorded changes in the grazing of different grass species during the dry season and the transition period to the wet season both when burnt areas were available and when not. I derived the acceptability of the different grass species from field observations in the sable feeding sites. I studied the dietary contribution by means of faecal analysis of plant epidermal fragments. Sable antelope favoured *Themeda triandra* and *Panicum maximum*, which were the prevalent species in the reserve and amongst the species that retained greenness for longer during the dry season. Other tall species that retained a high proportion of green leaves, such as *Hyparrhenia hirta* and *Andropogon schirensis*, were also opportunistically selected despite being stemmy. Sable did not widen their diet during the dry season when burns were not available. Instead, a wider range of species was accepted on burnt than on unburnt grassland. Preference for two widely favoured grass species and relying on a narrow range of species could make sable susceptible to competition from other more abundant herbivores. Since on burnt areas sable do not rely as strongly on these two species and use a wider range of species the availability of burnt areas could potentially minimize the grazing pressure on the otherwise preferred species.

INTRODUCTION

Leaf production and crude protein levels decline and fibre levels increase as grasses become senescent over the course of the dry season (Owen-Smith 2002). Plant species vary in morphology and growth form, differing in nutritional value (O'Reagain et al. 1995) and influencing bite size and hence potential intake rate (Cooper & Owen-Smith 1986, O'Reagain 1993). Therefore, variation in the growth phase of grass species can influence the degree to which herbivores discriminate and select between grass species (Owen-Smith 1982). Species selection also depends on the abundance and distributions of the different plants (O'Reagain 1996). During the dry season when there is little regrowth, the grass biomass progressively declines leading, according to foraging theory, to a widening of the diet to incorporate less nutritious species (Emlen 1966, Owen-Smith & Novellie 1982). Widening of the diet composition has been reported for browsing ruminants (Owen-Smith & Cooper 1987, 1989) and grazers (e.g. Mc Naughton 1985, Bodenstein et al. 2000, Macandza et al. 2004). Also, an increase in the number of species accepted as the grass biomass declines, has been documented for domestic grazers confined in fenced paddocks for short periods (O' Reagain & Mentis 1989, O' Reagain & Grau 1995).

To understand the food resources that support herbivores is important to determine habitat suitability (McNaughton 1985, Wilmshurst et al 1999). Food influences social structure, spatial behaviour and habitat choice (Jarman 1974). In addition, grazing is a prominent factor in shaping the structure and composition of the vegetation of African savannas (Cumming 1982, McNaughton & Georgiadis 1986).

As a part of a wider study on the foraging and social behaviour of a population of sable antelope in the Kgaswane Mountain Reserve, South Africa, I investigated 1) the grass species selection through two dry seasons and 2) the relationships between the acceptance of grass species and their physical characteristics. Sable were feeding in burnt areas during the one year, and grass nutritional content on newly burnt areas increases (Dörgeloh 1999). Therefore, I also investigated 3) how the use of burnt areas during the dry season may have influenced sable food choice by comparing grass species acceptance and diet composition during a dry season with burnt areas and one without.

METHODS

This study was conducted in the Kgaswane Mountain Reserve (KMR-25° 41’- 25° 45’ S, 27° 09’- 27° 13’ E), near Rustenburg, in the North-West Province, South Africa. For a detailed description of the study area, see chapter 2.

Sable were divided into two herds, ‘vlei herd’ and ‘woodland herd’. The ‘vlei herd’, lived mainly in areas dominated by open grassland, whereas the ‘woodland herd’ lived in areas dominated by woodland vegetation types (Chapter 2).

I did all field observations during the dry season and transition to the wet season months, from August to December 2002 and again from April to December 2003. Management policy is to implement burns at the beginning of winter, in May-June, to provide herbivores with green grass during the dry season months. At the time of study, green regrowth on burnt areas was available during the dry season in 2002 and after an accidental fire in late October 2003, but not during the dry season in 2003 when the burns did not flush.

Data collection

To collect data on grass species selection, I visually located one of the sable herds during the early morning and late afternoon foraging periods. Once sable had moved away, I approached the foraging area and identified the foraging path through the presence of fresh dung, tracks and fresh saliva on grass and cut leaves marks. Along the path, I placed twelve 0.5 x 0.5 m quadrats, representing roughly the area that an adult sable reaches by swinging its head without moving its forefeet. If there were no signs of recent bites inside the selected quadrats, but there were signs within 0.5 m on either side, I flipped the quadrat one time in order to contain the eaten grasses.

Within each quadrat, I identified grazed and ungrazed grass species. I identified grazed species from signs of fresh bites. For each grazed tuft, I also recorded height of the tallest basal leaf above ground, the ratio green leaves/ total number of leaves, and the number of stems, from an adjacent ungrazed plant of the same species. I classified the green leaf proportion following Walker's 8-point scale (Walker 1976). On burnt areas, I used grass height as a measure of the grass regrowth following the fire.

I collected field data on grass species eaten by sable from August until December 2002 for both herds and again from April until September 2003 for the 'vlei herd' and from May 2003 until September 2003 for the 'woodland herd'. At the end of the dry season of 2003, fresh bites were difficult to identify on the extensively brown grasses and during December and November of 2003, following the accidental fire, grasses were difficult to identify reliably by species.

Therefore, I also used the microhistological technique described by Stewart (1967) as an indicator of sable diet throughout the year. I collected samples as soon as the animals left the area, then air-dried the samples and stored them in paper bags. To prevent confusing the faecal pellets of sable with those of other ungulates, I only collected fresh pellets. Later, I combined all daily samples for one herd and milled these composite samples through a 1 mm sieve, to avoid identification bias due to different size of the fragments. I treated the milled samples with nitric acid to separate the epidermal cells and used a light microscope (x100 magnification) to examine slides of the samples. I identified the fragment by the shape and size of silica bodies and stomata, and by the presence/absence of hairs, comparing them against a reference collection prepared from the most common grass species occurring in the areas where the sable herds grazed. From each composite sample, I identified 50 fragments. I considered only fragments above approximately 2 mm, to avoid bias in favour of grass species that break up into smaller and more numerous fragments during the digestion process.

In order to assess the availability of the grass species in the study area, I placed nine transects, (each 1-1.5 km long), in different vegetation types. I walked them once during the wet season in 2003 and recorded the grass species present inside a 0.5 x 0.5 m quadrat placed every 10 m.

Data analysis

Based on rainfall pattern, I distinguished six periods when analysing the data: late dry season of 2002 (September-October); transition period of 2002 (November-December); early dry season of 2003 (April-May); mid dry season of 2003 (June-July-August); late dry season of 2003 (September-October); transition period of 2003 (November-December). During the late dry season of 2002, transition period of 2002 and transition period of 2003 sable made extensive use of green regrowth following the fire, while during the dry season of 2003 sable were grazing on unburnt areas.

I calculated the grass species available in the study area by dividing the number of times a species was recorded present inside the quadrats placed along the fixed transects by the total number of quadrats laid along the transects. I calculated the grass species available along the sable foraging path by dividing the number of quadrats where the species was present by the number of quadrats sampled. I determined the frequency of acceptance for each grass species by dividing the number of quadrats where the species was eaten by the number of quadrats where the species was present (Owen-Smith & Cooper 1987). I estimated the proportion contributed by each species to the diet by dividing the number of identified fragments of one species in the faecal samples by the total number of identified fragments for all grass species.

I compared the dietary contribution of each grass species between periods and herds using a 2-way ANOVA. Prior to analysis, I normalized the proportions by arcsin transformation (Quinn & Keough 2002). Acceptance values follow a binomial distribution and therefore I calculated 95% binomial confidence limits. I performed linear regression to measure the relationship between species acceptance and greenness, height and stemminess on unburnt areas during the dry season of 2003 and between species acceptance and height in the dry season of 2002, transition periods of 2002 and 2003. I performed all analyses using STATISTICA 6.0 (Stat Soft Inc., Tulsa, Oklohama, USA) at 95% confidence level.

RESULTS

Grass species availability along the transects

The prevalent grass in the reserve was *Themeda triandra* in grassland and open woodland habitats, while *Panicum maximum* was the prevalent one in woodland habitats (Table 4.1). *Brachiaria serrata*, *Eragrostis* spp, S*chizachyrium sanguineum* and *Tristachya leucothrix* had a prevalence of more than 20% in grassland habitats. *Setaria* spp, *Diheteropogon amplectens* was present in more than 20% of the quadrats in open woodland habitats. *Themeda triandra* and *Setaria* spp were present in more than 20% of the quadrats in woodland habitats. I recorded the other species present in the reserve in less than 20% of the quadrats sampled along the fixed transects (Table 4.1).

Grass species availability along sable foraging paths

Themeda triandra was also the most prevalent species in the foraging sites of both the 'vlei herd' and 'woodland herd' (Table 4.2). Its availability in the feeding sites of the 'woodland herd' remained lower than in the 'vlei herd' sites in all the seasons. The prevalence of most other species in the sable feeding sites was lower than 20%, with a few exceptions including *Setaria* spp during the mid dry season of 2003 for the 'woodland herd', *Heteropogon contortus* for the 'woodland herd', *Hyparrhenia hirta* in the burnt feeding sites of the 'woodland herd' during the transition period of 2003. *Heteropogon contortus* availability was higher for the 'woodland herd' than for the 'vlei herd' and *Hyparrhenia hirta* was present in the 'vlei herd' feeding sites only on unburnt areas. The other notable difference between feeding sites of the two herds was the availability of *Panicum maximum*, recorded only during 2003 in the 'vlei herd' feeding sites, with the highest value at the beginning of the dry season on unburnt areas. *Panicum maximum* was instead always present in the 'woodland herd' feeding sites.

Grass species acceptability

Both sable herds used only burnt areas during 2002 and unburnt areas during 2003 (Chapter 2). Therefore, I will first show the results relative to 2003 and then compare how the use of burnt areas in 2002 influenced grass species acceptability. During the first part of the dry season in 2003, acceptability values by the 'vlei herd' fell into three clusters (Fig. 4.2a): four highly accepted species having acceptability >0.80, a group of five species that appeared intermediate in acceptability (0.1<

acceptability <0.8) and three species that sable neglected (acceptability <0.1). The vlei herd completely neglected five species. Of the highly accepted species, only *Themeda triandra* and *Panicum maximum* remained highly accepted also in the mid dry season. Of the other two, *Hyparrhenia hirta* became neglected and *Andropogon schirensis* was not even recorded in the sable feeding sites in the mid dry season. Only three species remained moderately accepted in the mid dry season: *Heteropogon contortus, Diheteropogon amplectens* and *Digitaria* spp. Sable in the 'vlei herd' neglected all other species. In contrast, the 'woodland herd' highly accepted only *Themeda triandra*, and moderately accepted six species, including *Hyparrhenia hirta* and *Panicum maximum*.

On burnt areas, no species yielded an acceptability higher than 0.8, but a larger number of species than on unburnt areas yielded values between 0.1 and 0.8 (moderately accepted) (Fig. 4.2b). These included *Themeda triandra, Heteropogon contortus, Diheteropogon amplectens, Digitaria* spp, *Trachypogon spicatus, Tristachya leucothrix, Schizachyrium sanguineum* and *Setaria* spp for both herds, *Hyparrhenia hirta* and *Panicum maximum* for the 'woodland herd', and *Eragrostis* spp and *Cymbopogon validus* for the 'vlei herd'. Fewer species than on unburnt areas yielded acceptability values lower than 0.1.

Among the measured features, only grass greenness in the early dry season of 2003 was positively related to acceptance for unburnt grass (F=34.38, p<0.001).

Dietary contribution

Dietary contribution as assessed from faecal samples differed among grass species (F=81.2, d.f. =12, p<.0001), among seasons (F=2.68, d.f. =5, p=0.04) and between herds (F=6.7, d.f. =1, p=0.006). The most common grass fragment identified in the faecal samples of both herds was *Themeda triandra,* always more represented in the diet of the 'vlei herd' than in the 'woodland herd' diet (Table 4.3). The contribution of *Panicum maximum* to the faecal fragments was highest during the early and mid dry season for the 'vlei herd', and lowest when the herd was feeding on burnt areas during the late dry season 2002 and the two transition periods. *Panicum maximum* represented a constant proportion of the 'woodland herd' diet the whole time. A variable number of other species showed seasonally variable intermediate contributions (Table 4.3). This species included *Heteropogon contortus*, *Diheteropogon amplectens*, *Digitaria* spp, *Andropogon schirensis*, *Hyparrhenia hirta* and *Setaria* spp. The contribution of *Digitaria* spp to the diet increased as the dry season progressed. *Setaria* spp become important for both herds in the mid-dry season and *Heteropogon contortus* become important for the 'woodland herd' during the mid-dry season, while its contribution to the diet of the 'vlei herd' stayed constant throughout the dry season. During the dry season, a higher number of less common species (contributing less than 2% each) and a higher proportion of unidentified grasses was evident in the faecal samples from the 'woodland herd' than in the samples from the 'vlei herd' (Table 4.3).

DISCUSSION

Themeda triandra and *Panicum maximum* were the most favoured grass species by sable during the dry season on unburnt areas, while other tall species such as *Hyparrhenia hirta* and *Andropogon schirensis* were also favoured. Although most of the grass species were present in the feeding sites of both herds, the differences in the diet composition between the two herds could be a consequence of their use of different areas (Chapter 2) and can be attributed to the differences in the local availability of grasses.

Themeda triandra and *Panicum maximum* were among the species that retained greenness for longer during the dry season. In addition, *Themeda triandra* was the prevalent grass species in the reserve. *Themeda triandra* is a highly important species for cattle during the dry season (O'Reagain & Mentis 1989, Stoltz & Danckwerts 2005) and for other wild herbivores such as wildebeest and zebra (Ben-Shahar 1991, Bodenstein et al. 2000, Ego et al 2003). It was not as important during the dry season for African buffalo and roan antelope in Kruger National Park (Funston et al 1994, Macandza et al 2004, Knoop & Owen-Smith 2006).

Observations on sable in Zimbabwe (Grobler 1974), in the Percy Fyfe Nature Reserve, Rustenburg Nature Reserve, Hans Merensky Nature Reserve and the Pilanesberg National Park in South Africa (Wilson & Hirst 1977, Magome 1991) likewise indicate that *Themeda triandra* is one of the preferred species by sable. The preference for *Panicum maximum* during the dry season is again similar to cattle (van Oudtshoorn 1998), other wild herbivores (e.g. Ben-Shahar 1991, Macandza et al. 2004, Knoop & Owen-Smith 2006) and sable antelope in Pilanesberg National Park (Magome 1991).

Hyparrhenia hirta becomes stemmy and low in nutritional value as the dry season progresses (Tainton 1981). Nevertheless, the species was important in contributing to the diet of sable at the beginning of the dry season when it offered the highest amount of green forage at that time and in the mid dry season despite its decreased green leaves proportion. Wilson & Hirst (1977) documented how *Hyparrhenia hirta* was well grazed by both semi-tame sable and roan antelope in a feeding enclosure experiment in the Percy Fyfe Nature Reserve. Similarly, *Andropogon schirensis* became seasonally important at the beginning of the dry season when it offered a high amount of green forage but its dietary contribution remained low.

Heteropogon contortus, *Diheteropogon amplectens* and *Digitaria* spp, were stable components of the sable diet, but being less common made a smaller dietary contribution than *Themeda triandra*. *Digitaria* spp were eaten the whole year by cattle and wild ungulates in Kenya (Ego et al 2003). Cattle utilize *Diheteropogon amplectens* and *Heteropogon contortus* early in the season when the leaves are palatable and these species grazing value decreases as the dry season progresses (van Oudtshoorn 1988). The acceptability of *Heteropogon contortus* by sable antelope in the Pilanesberg National Park, increased during the dry season (Magome 1991).

During the dry season, contrary to the prediction of the foraging theory, more species become neglected. The availability of preferred species in the sable feeding areas did not decline during the dry season in the KMR. Ego et al (2003) found that wildebeest, kongoni and cattle did not shift their diet during the dry season because of the high forage abundance in the Kenyan ranch.

Certain grass species remained constantly neglected or eaten very little throughout the dry season by the sable. These included *Cymbopogon validus*, an aromatic grass considered highly unpalatable to cattle, and fibrous grasses regarded as low in nutritional value, such as *Aristida* spp, *Tristachya leucothrix*, *Bewsia biflora*, *Schizachyrium sanguineum*.

Previous studies have documented a preference by sable for burnt areas, which provide green grass during the critical dry season (Magome 1991, see also chapter 2). Grasses that were neglected or totally rejected on unburnt grass swards, such as *Setaria* spp, *Cymbopogon validus, Aristida* spp. *Tristachya leucothrix* and *Eragrostis* spp, increased their dietary contribution when sable were feeding on burnt grass swards. Similarly, Field (1975) found that a number of grass species were more favoured after burning that when compared with unburnt plants. *Themeda triandra* and *Panicum maximum* were less favoured than on unburnt areas, but still contributed much of the diet. On burnt areas, the higher acceptance of species otherwise avoided might have influenced the relative acceptance of *Themeda triandra* and *Panicum maximum*. Field (1975) compared the diet of the African buffalo on burnt and unburnt areas and found a decrease in preference for *Themeda triandra* when comparing burnt and unburnt plants.

Overall, the results show that sable adjusted their grass species selection in relation to seasonally changing grass quality and availability of burnt grasses through the dry season. Because of their indifference to the number of stems, sable included tall stemmy species, such as *Hyparrhenia hirta* and *Andropogon schirensis* to bridge the critical dry season on unburnt areas. However, both on burnt and unburnt grass swards, sable strongly relied on *Themeda triandra* and *Panicum maximum* the same as most grazers. Widening the diet to incorporate less nutritious species is common among herbivores (e.g. Owen-Smith & Cooper 1987, Mc Naughton 1985, Bodenstein et al 2002, Macandza et al 2004). However, sable appear to differ in this regard, since they focussed on a narrow range of species during the whole dry season. If only a few key species are important for sable to bridge the dry season, sable would face a critical situation if these preferred species availability declined during the dry season. However, it is possible that the lack of diet breadth widening observed in this study, was just a consequence of the preferred species availability remaining constant through the dry season in the sable feeding sites.

FIGURE CAPTIONS

Fig. 4.1. Seasonal changes in grass species acceptance on unburnt and burnt areas by the two sable herds in KMR. I ranked the grass species in descending order based on the acceptability estimates of the ‘vlei herd’ on unburnt grass in the early dry season of 2003. No data for the early dry season were available for the woodland herd. Vertical bars indicate 95% binomial confidence limits. a) Unburnt, b) burnt

Table 4.1. Grass species available in the KMR. Grass species names (from Van Oudtshoorn, Guide to Grasses of Southern Africa) are listed in alphabetical order.

Grass spp.	Acronyms	Species presence in quadrats sampled along transects (%)		
		Grassland *(N = 265)*	Open woodland *(N=294)*	Woodland *(N=298)*
Andropogon schirensis	*As*	0.4	1.4	0.0
Aristida spp.	*Ari*	14.0	2.7	2.0
Bewsia biflora	*Bb*	1.9	14.6	2.7
Brachiaria serrata	*Bs*	20.0	8.2	8.4
Cymbopogon validus	*Cv*	1.9	7.5	0.3
Digitaria spp	*Dig*	8.3	8.2	4.4
Diheteropogon amplectens	*Da*	14.0	20.1	0.7
***Eragrostis* spp.**	*Era*	23.8	5.4	8.1
Eustachys paspaloides	*Ep*	0.0	0.0	11.1
Heteropogon contortus	*Hc*	2.3	0.3	17.1
Hyparrhenia hirta	*Hh*	0.0	18.0	0.7
Loudetia simplex	*Ls*	6.8	0.0	0.0
Melinis nerviglumis	*Mn*	15.5	3.4	0.0
Melinis repens	*Mr*	1.9	3.1	0.0
Monocymbium cerensiiforme	*Mc*	1.1	0.0	0.0
Panicum maximum	*Pm*	0.0	4.8	50.3
Perotis patens	*Pp*	2.3	0.0	0.0
Phragmites mauritianus	*Phm*	2.8	0.0	0.0
Pogonarthria squarrosa	*Ps*	1.5	0.0	0.0
Schizachyrium sanguineum	*Ss*	22.6	19.0	0.0
***Setaria* spp**	*Set*	3.8	34.0	30.9
Themeda triandra	*Tt*	88.7	50.3	26.2
Trachypogon spicatus	*Ts*	8.7	11.2	1.0
Tristachya biseriata	*Tb*	2.8	0.0	0.0
Tristachya leucothrix	*Tl*	21.5	17.0	0.3
Urelytrum agropyroides	*Ua*	1.9	0.2	1.3
Urochloa panicoides	*Up*	0.0	0.0	1.0

Table 4.2. Seasonal changes in proportion (%) of grass species recorded as available in the feeding sites of the two sable herds in the KMR. No data was available at the beginning of the dry season 2003 for the 'woodland herd'. Acronyms are the ones listed in Table 4.1.

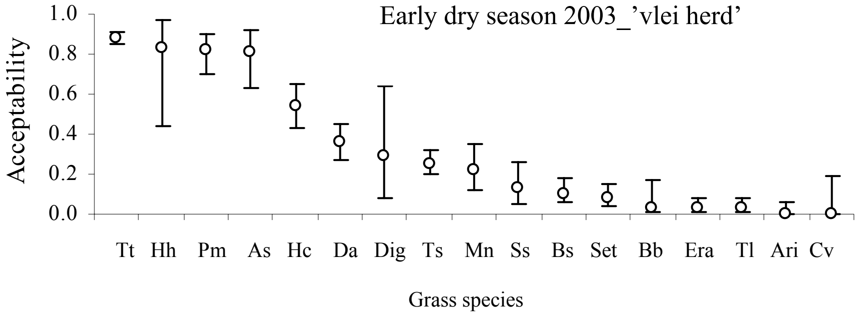
Grass species	Late dry season 2002/burnt		Transition period 2002/burnt		Early dry season 2003/unburnt		Mid dry season 2003/unburnt		Late dry season 2003/unburnt		Transition period 2003/burn	
	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd
Tt	80	44	86	51	80	na	98	47	75	69	78	41
Pm	0	7	0	11	22	na	11	13	0	20	5	7
Era	6	0.2	3	2	18	na	17	29	8	19	6	19
Tl	12	28	22	3	15	na	8	10	18	10	17	13
Da	10	11	6	8	14	na	8	12	7	16	20	13
Bs	10	3	9	5	13	na	9	5	10	5	14	5
Set	27	21	12	14	12	na	11	44	10	8	11	29
Hc	4	11	6	27	11	na	3	50	3	40	80	20
Ss	3	6	4	4	8	na	4	5	6	5	4	6
Mn	3	1	4	0	7	na	3	10	4	1	4	2
Phm	17	0	3	0	7	na	9	0	14	4	0	0
Ts	2	2	19	0	7	na	9	12	13	16	8	1
Hh	0	8	0	1	5	na	3	11	0	0	0	26
As	0	0	0	0	4	na	0	0	0	0	0	0
Bb	0	2	3	0	4	na	4	7	3	1	3	2
Ps	0	0	0	0	3	na	2	0	2	0	0	0
Cv	0	0	5	4	2	na	3	1	2	1	2	3
Ls	0	0	0	0	2	na	1	1	1	0	0	0
Dig	16	9	9	9	1	na	5	7	3	4	9	6
Ari	4	3	2	32	0	na	4	2	3	5	1	7
Mr	0	0	0	0	0	na	0	0	0	0	0	0

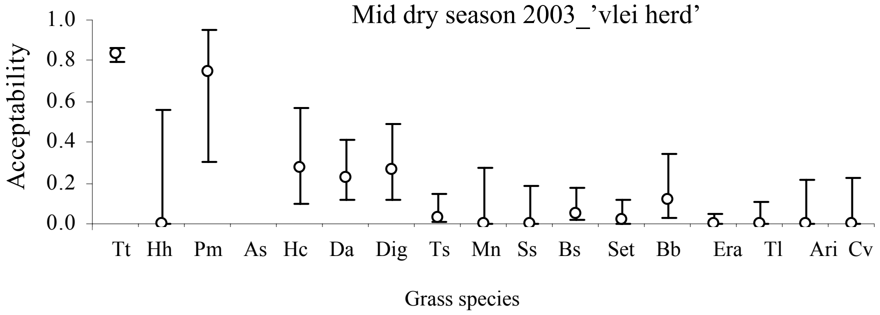
Table 4.3 Seasonal changes in the proportion (%) of grass fragments recorded by microhistological analysis in the faeces of the 'vlei herd' and 'woodland herd'.

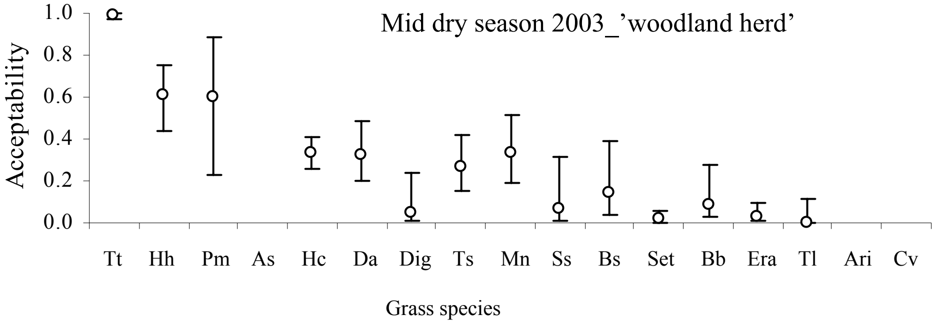
Grass species	Late dry season 2002/burnt		Transition period 2002/burnt		Early dry season 2003/unburnt		Mid dry season 2003/unburnt		Late dry season 2003/unburnt		Transition period 2003/burn	
	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd	Vlei herd	Woodland herd
Tt	44	29	41	29	31	23	33	21	38	13	40	29
Pm	2	17	3	16	16	22	24	15	7	15	2	12
Hc	0	12	0	11	10	7	12	13	11	13	7	9
Hh	0	7	0	7	10	10	2	11	0	1	0	4
Da	8	8	16	11	9	9	9	12	5	1	10	11
As	0	0	0	0	7	4	0	4	1	3	0	1
Dig	10	9	11	13	5	0	12	1	20	11	19	17
Bs	0	2	0	2	3	2	2	1	0	0	0	0
Set	11	10	10	7	3	3	2	4	8	9	10	2
Mn	3	0	0	0	2	11	1	4	3	5	2	1
Ts	4	2	3	2	2	4	0	4	3	0	6	5
Bb	1	1	4	0	1	1	1	1	0	5	1	2
Tl	1	0	0	0	1	1	0	0	0	0	0	0
Others	0	2	1	1	1	5	2	7	2	18	2	3
Era	3	1	2	1	0	0	0	2	2	6	2	3

Fig. 4.1

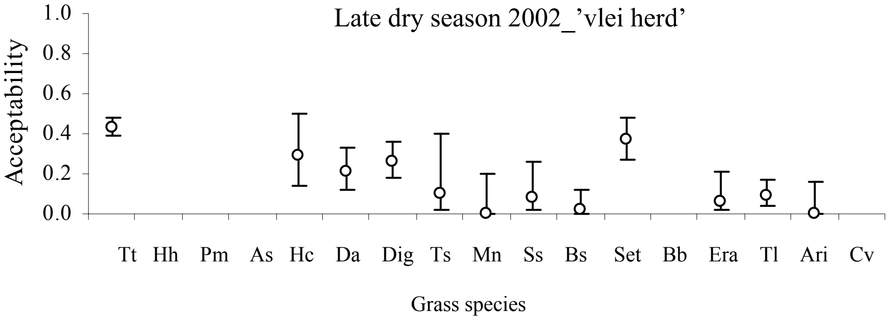
a) Unburnt

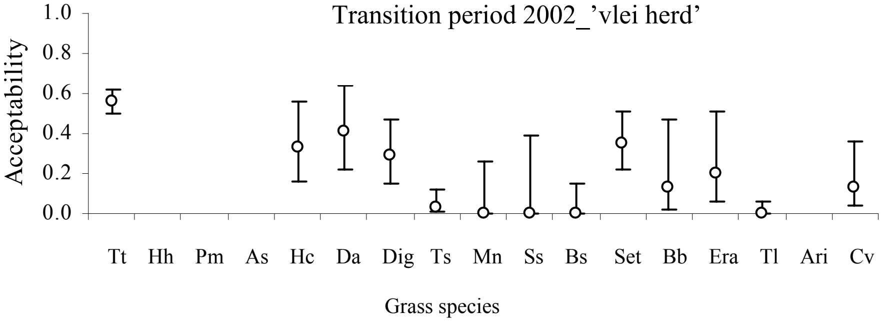






b) Burnt


Late dry season 2002_'vlei herd'
Acceptability
1.0
0.8
0.6
0.4
0.2
0.0
Tt
Hh
Pm
As
Hc
Da
Dig
Ts
Mn
Ss
Bs
Set
Bb
Era
Tl
Ari
Cv
Grass species


Transition period 2002_'vlei herd'
Acceptability
1.0
0.8
0.6
0.4
0.2
0.0
Tt
Hh
Pm
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Hc
Da
Dig
Ts
Mn
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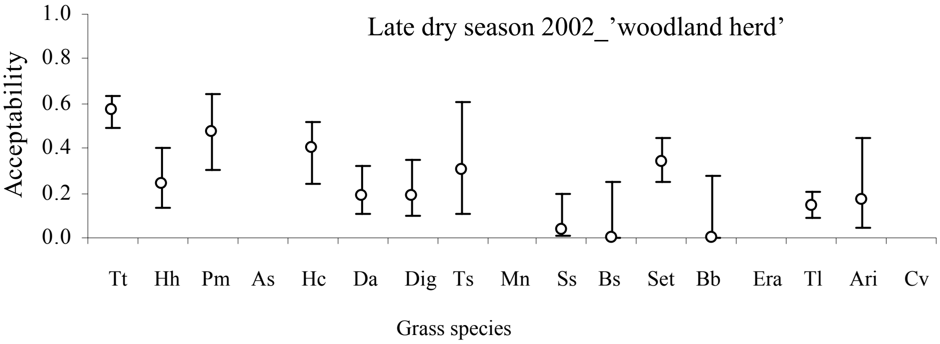
Era
Tl
Ari
Cv
Grass species


Late dry season 2002_'woodland herd'
Acceptability
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0.8
0.6
0.4
0.2
0.0
Tt
Hh
Pm
As
Hc
Da
Dig
Ts
Mn
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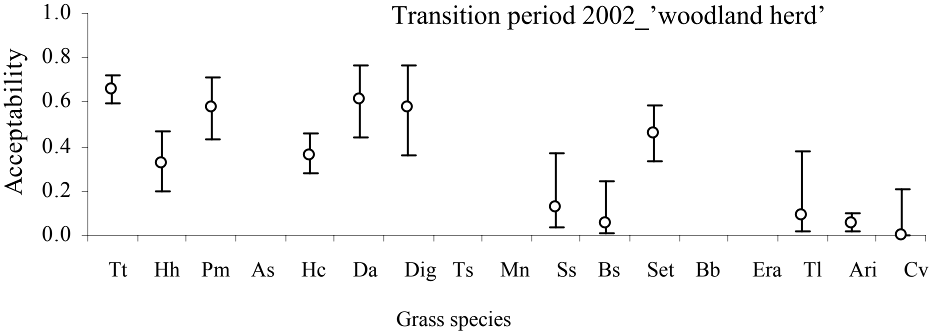
Bb
Era
Tl
Ari
Cv
Grass species


Transition period 2002_'woodland herd'
Acceptability
1.0
0.8
0.6
0.4
0.2
0.0
Tt
Hh
Pm
As
Hc
Da
Dig
Ts
Mn
Ss
Bs
Set
Bb
Era
Tl
Ari
Cv
Grass species

CHAPTER 5.

Foraging performance of sable on burnt vs. unburnt grassland

Abstract

Burning is commonly used in savanna ecosystems to alleviate the nutritional stress of herbivores during the dry season. The influence of burns on habitat use by wild herbivores has been widely studied but little information is available on the effect of burning on foraging behaviour. The primary aim of this study was to investigate how sable responded to changes in food availability during the dry season, by monitoring bite rates, time spent feeding per feeding station, movement rates and length, and daily time spent foraging both when burnt areas were available and when not. I also investigated how sable responded to changes in food quantity on burnt areas by comparing their foraging behaviour on an early winter burn before and after the start of spring rains and on a late winter burn. I used sable faecal quality as a measure of nutritional gains to changing food quality and quantity during the two dry seasons and on burnt areas at different stages of grass regrowth. During the one dry season, burnt grassland was not available, and bite rate and the daily time spent foraging of sable increased, as the grass quality and quantity both declined seasonally. During the other dry season, sable grazed on burnt areas and the length and rate of the movements between the feeding stations was shorter than on non-burnt areas. The bite rate and grazing time remained similar both on burnt and unburnt areas. Faecal nitrogen (N) and phosphorus (P) values were both lowest at the end of the dry season when no burnt areas where available, but while N was already low in the first part of the dry season, P only decreased in the second half. When burnt areas were available, the faecal quality did not decrease during the dry season. I conclude that sable respond more successfully to food quantity limitations they may face on burnt areas than to food quality limitations they face on unburnt areas. However, in both situations sable were able to compensate behaviourally to buffer seasonal variability of their food supply.

INTRODUCTION

Nutrient contents of grasses decrease as stem to leaf and fibre to protein ratios increase as the dry season progresses (Dove & Mayes 1996, Dörgeloh, 1999, Meissner et al. 1999) and herbivores may incur nutrient deficiencies (Owen-Smith 1982). However, the nutritional quality of grass available may be improved as a result of burning (Hobbs & Spowart 1984, Moe et al. 1990, Dörgeloh 1999). Fire is frequently applied at the end of the growing season, after the first summer rains and immediately before spring growth. Under these conditions, the recovery of the vegetation is fast (Bosh et al. 1984). In addition, fire can be applied at the beginning of winter at the start of the dry season, to improve the grazing value of the vegetation, since it is known that burning stimulates sprouting of plants even in the dry season (Vesey-Fitzgerald 1971). The sprouting plants contain high amounts of protein, calcium, phosphorus and other elements (Dörgeloh 1999). Indeed wildlife seems to be attracted to burnt areas (e.g. Rowe-Rowe 1982, Moe et al. 1990, Wilsey 1996, Gureja & Owen-Smith 2002). Burning is commonly used as a management tool in savanna systems during the dry season to alleviate the nutritional stress of herbivores during this time of the year (Moe et al. 1990, Grossman et al. 1999).

Because of the spatial and temporal variability of grasslands, grazers face a trade-off between quality and quantity of the diet (McNaughton & Georgiadis 1986). Food selection by animals is determined by the preference associated with food quality, but also by the costs involved in gathering foods and by food availability (Logue 1986). Mammalian herbivores can adapt their foraging behaviour to compensate for the changing nutritional value of forage available (e.g. Novellie 1978, Underwood 1983, Bradbury et al. 1996, Fortin et al. 2002).

Foraging behaviour is a hierarchical process in space and time (Senft et al. 1987, Stuth 1991, Bailey et al. 1996, Owen-Smith 2002). In the spatial dimension, the following levels range from the very small to the very large: the bite, the feeding station (i.e. the area available to the animals without taking a step *sensu* Novellie 1978), the plant community and the landscape. Grazing can be seen as an alternation of 'bite-sets/grazing time' within feeding stations and of 'step-sets/moving time' between feeding stations (Novellie 1978). Bite dimensions and bite weight are a function of sward height and bulk density (Black & Kenney 1984, Laca et al 1992), therefore bite rate declines with increasing bite size and senescence of the forage (Penning et al. 1991, Spalinger & Hobbs 1992). This leads to a progressive increase in feeding time per feeding station as the dry season progresses (Novellie 1978, Underwood 1983), since the number of bites taken and the time needed to look for and chew those bites explain the time spent eating per feeding station (WallisDeVries et al 1998).

Forage availability also influences the rate at which an animal searches its environment (Owen-Smith & Novellie 1982). Search behaviour (rate and length of movement) determines the rate at which an herbivore encounters potential food items but it is also a measure of the animal's perception of food quality and quantity in the environment. Underwood (1982) and Roguet et al. (1997) have previously used changes in the length of the movements between feeding stations to describe environmental heterogeneity from the animals' point of view, defined as 'cognitive patchiness' by Wien (1976, in Arditi & Dacorogna, 1988). To compensate for the reduced nutritional value of the food during the dry season, mammalian herbivores may also extend daily foraging time (Illius & Gordon 1991).

Limited information is available on the effect of burning on the foraging behaviour of wild ungulates (Novellie 1978, Underwood 1983, Wronski 2003, Tomor & Owen-Smith 2002). On burnt areas, grazers encounter high quality food items, but grasses are short and therefore quantity may be a factor limiting intake rate. To compensate for small bites, grazers usually increase bite rate and/or grazing time (WallisDeVries & Daleboudt 1994).

Faecal nitrogen and phosphorus have been widely used to assess diet quality of wild herbivores (e.g. Hobbs et al. 1981, Leslie et al. 1989, Irwin et al. 1993, Grant et al. 1995, Duncan et al. 1997). For grazing livestock, P deficiency appears to be the most important mineral limitation in tropical countries (McDowell 1985). In previous studies on sable and roan antelope, these nutrients were found to be lowest at the end of the dry season (September-October) (Dörgeloh et al. 1998, Heitkönig 1993, Magome 1991).

Therefore the objectives of this study were 1) to document how sable adjusted bite rates, feeding time per feeding station, rate and length of movement between feeding stations and daily time spent foraging, comparing a dry season with burnt areas and a dry season without burnt areas available, as well as burnt areas at different stages of grass regrowth, 2) to monitor changes in faecal N and P both on burnt and unburnt areas.

MATERIAL AND METHODS

Study area

The Kgaswane Mountain Reserve (KMR, 25º 41'- 25º 45' S, 27º 09'- 27º 13' E) is a 4,257 ha protected area in the Magaliesberg range in South Africa. The Magaliesberg are characterized by sandy soils poor in nutrients, typical of the Sourveld (Carruthers 2000). The vegetation of the reserve, which lies at an altitude of 1250-1600 m a.s.l., consists of deciduous *Acacia caffra* woodlands, evergreen *Protea caffra* woodlands, grasslands communities and a *Phragmites australis* reed marsh.

The area is characterized by a defined wet and dry season (Chapter 2). Since 1994, early winter burns were implemented in the KMR. The burns ignited in June 2002 provided green grass as soon as July. During the following dry season and transition period sable consistently grazed on these burnt areas. The following winter, the prescribed fire occurred in May, but the burnt area did not flush, probably because of being on a north-facing slope subjected to higher water evaporation (Shevenell

1999). During the dry season of 2003, sable foraged in non-burnt areas. Green regrowth was available in the transition period in 2003: an accidental fire occurred at the end of October 2003 just before the first spring rains. Sable were feeding exclusively on these burnt areas during the transition period.

Study design

The study focused on the second part of the dry season of 2002 (August – October), the following transition period to the wet season (November & December 2002), the dry season of 2003 (April – October) and following transition period (November & December 2003). To avoid confounding effects of burnt status (i.e. burnt/ non-burnt, stage of burn regrowth) and season, I compared (Fig. 5.1):

1) early (April-June) and late (July-September) dry season of 2003, to asses how sable responded to decreased quality of grasses when foraging in unburnt areas,

2) late dry seasons in 2002 and 2003, to compare sable foraging behaviour on burnt areas (2002) and unburnt areas (2003),

3) winter burns before the rains (late dry season of 2002) and after the rains (transition period of 2002) and late winter burns (transition period of 2003), to asses how sable changed their behaviour as grass on burns grew taller .

I did the observations on two different herds ('vlei' and 'woodland') which occurred in separate sections of the reserve. I tested all behavioural data for group influence and if no significant difference was found, I combined the observations from the two herds.

Data collection and analyses

Bites and steps while foraging were recorded on focal animals (Altman 1974) using a Psion Organizer II that had been programmed to enable the number of bites taken per minute and the number of steps taken per minute to be recorded (see Appendix I for the program). Observation periods varied from five to 8 minutes. I counted only foraging steps (i.e. sable moving with head down looking for food). I excluded walking steps, (i.e. steps taken with the head up), and subtracted the time spent walking with the head up from the final calculation. I considered one observation session (morning and afternoon) as an independent observation of foraging behaviour. I derived the following indices of foraging behaviour:

- *Feeding time per feeding station* (FTFS): measured as the time spent in a feeding station (i.e. where one or more bites were taken without moving). It is a potential measure of the density of bites on offer at the feeding station level and time needed to look for them.
- *Bite rate* (BR): calculated as the number of bites per minute spent foraging.
- *Step rate* (SR): measured as the number of steps per minute spent foraging
- *Number of consecutive step sets between feeding stations:* a measure of the spatial separation of feeding stations

I pooled together all indices recorded within one observation session. Data were collected during 123 observation sessions ('vlei' herd N = 72 sessions, 'woodland' herd N = 51 sessions). For observations on daily foraging time, I observed a focal group from sunrise to sunset, using 10 min. scan sampling (Altman 1978). For more details on the method, see Chapter 6. I had 61 observation-days ('vlei' herd N = 37 days, 'woodland' herd N = 24 days).

Fresh faecal samples were collected whenever a sable was observed defecating. The pellets were broken apart, air-dried and stored in sealed paper bags for analysis. I combined samples collected from different animals on the same day and considered these samples as the independent unit. The faecal samples were analysed for nitrogen and phosphorus as a proportion of dry matter by the Nelspruit laboratory of the Agricultural Research Council using Kjeldahl digestion ('vlei' herd N = 64, 'woodland' herd N= 53).

I measured grass greenness and height as an indication of food quality and quantity. The measures were taken from the same areas were the animals were observed foraging as part of a broader study on feeding area and plant species selection (Chapter 3 for details).

I log-transformed feeding time per feeding station, bite rate and step rate, and arcsin-transformed proportions (time spent grazing, nitrogen and phosphorus values) to conform with the normal distribution assumption for parametric tests (Quinn & Keough, 2002). I used a t-test to compare early vs. late dry season of 2003 and the late dry seasons of 2002 vs. 2003 for all measures. I performed a 1-way ANOVA with season as a factor to compare burnt areas at three stages of grass regrowth: transition period of 2002 and 2003 and late dry season of 2002. The frequency distribution of number of consecutive steps between patches followed the negative exponential distribution of a survivorship curve. I tested the different slopes for homogeneity using an F-test (Sokal & Rolf 2000). I performed all statistical tests with Statistica 6.0. I reported all results as mean ± standard error unless otherwise specified.

RESULTS

Grass greenness and height

Grass was taller on non-burnt areas than burnt areas and taller on post-rain burns (Fig. 5.2). During the dry season when no burns were available, grass greenness declined from 50 % in the early part of the season to 15% in the last part of the season (Fig.5.2). The availability of burnt areas improved the availability of green leaves during the dry season to 100%.

Foraging behaviour

Feeding time per feeding step, bite rate, step rate and time spent grazing did not differ between herds (ANOVA, FTFS p=0.686, BR p=0.513, SR p=0.347, grazing time p=0.278), therefore I combined the data from the two herds.

Sable spent similar time per feeding station in the early and late dry season in 2003 (11.7±1.0 sec vs. 12.7±1.1 sec, t_{44}=0.87, p=0.384, Fig. 5.3). However, during the late dry season sable spent less time per feeding station when grazing on burnt areas than when grazing on unburnt areas (late dry season 2002/burnt: 7.0±1.0 sec;

late dry season 2003/unburnt: 12.7±1.1 sec, t_{45}=4.14, p=0.0002, Fig. 5.3). On burnt areas, although the grass available was taller after the rains than before the rains, feeding time per feeding station was always similar (late dry season 2002: 7.0±1.0 sec; transition period 2002: 8.1±1.1 sec; transition period 2003: 6.9±1.0 sec ANOVA, $F_{2,66}$=2.67, p=0.087, Fig 5.3).

Sable increased bite rate from early to late dry season in 2003 (35.9±1.0 bites/min and 40.6±1.1 bites/min respectively, t_{44}=2.29, p=0.026; Fig. 5.4) when burns were not available. However, bite rate at the end of the dry season of 2002, when burns were available, was not significantly different from that of the late dry season of 2003 (late dry season 2002: 41.1±2.6 bites/min; late dry season 2003: 40.6±1.1, t_{45}=0.53, p=0.660; Fig. 5.4). Bite rate at the end of the dry season of 2002 was also not significant different from bite rate on post-rain burns (transition period 2002: 40.1±1.5 bites/min; transition period 2003: 43.5±1.9, ANOVA, $F_{2,66}$=1.92, p=0.155, Fig 5.4).

The rate of movement (SR) was similar in the first and second part of the dry season (9.5±0.7 step/min vs. 10.1±1.8 step/min, t_{44}=0.03, p=0.978, Fig. 5.5). It was higher in the second part of the dry season when sable foraged on burnt areas (late dry season 2002/burnt: 13.9±1.0 step/min; late dry season 2003/unburnt: 10.1±1.8 step/min, t_{45}=3.79, p<0.001, Fig. 5.5). On burnt areas at different stages of grass regrowth, there was no significant difference in step rate (late dry season 2002: 13.9±1.0 step/min; transition period 2002: 15.0±1.4 step/min; transition period 2003: 15.3±0.8 step/min ANOVA, $F_{2,66}$=0.46, p=0.636, Fig 5.5).

In all seasons, I observed an inflection in all sets of log survivor plots after 10 steps. Behavioural event intervals that are randomly terminated should produce a straight-line log-survivor plot (Haccou & Meelis 1994). To limit the influence of non-foraging factors on the step sequences, I restricted the analysis to the first consecutive 10 steps in each season. I found no difference in the probability of step sequence ending between early and late dry season 2003 (p/step = 0.10 ± 0.01 vs. p/step = 0.10 ± 0.01, $F_{1,11}$ = 0.48, p = 0.501, Fig. 5.5). Instead, there was a higher probability of taking shorter movement sets on burnt areas than on unburnt ones (late dry season 2002: p/step = 0.13 ±0.01; late dry season 2003: p/step = 0.10 ± 0.01, $F_{1,12}$ = 15.84, p = 0.002, Fig. 5.6). However, the probability of the step sequence to end on burns was even higher after the start of the spring rains in the transition period of 2002, and on the late winter burn in the transition period of 2003 (p/step = 0.14 ± 0.01 and p/step = 0.13 ± 0.01 /step, $F_{2,24}$ = 20.96, p<0.0001, Fig. 5.6).

Sable foraged for longer during the day in the late dry season than in the early dry season in 2003 on unburnt areas (51.5 ± 2.1% vs. 39.1 ± 1.7%, t_{25} = 4.58, p<0.001, Fig. 5.7). The proportion of daily time spent foraging was not influenced by availability of burnt areas, as the difference between late dry seasons of 2002 and 2003 was not significant (55.4 ± 2.8% vs. 51.5 ± 2.1%, t_{22} = 1.072, p = 0.294, Fig. 5.7). However, daily foraging time decreased on burns after the start of the rains (transition 2002: 42.6 ± 2.1%, transition 2003: 42.0 ± 2.8%, ANOVA: $F_{2,34}$ = 8.50, p = 0.001, Fig. 5.7).

Faecal indices of diet quality

Both faecal nitrogen (N) and phosphorus (P) values did not differ significantly between the two herds (ANOVA, N: p=0.20, P: p=0.753). Therefore, data for the two herds were combined. The faecal N content remained similar in the early and late dry season in 2003 (1.20 ± 0.02 and 1.18± 0.02, $t_{52} = 0.73$, $p = 0.471$, Fig.5.8), whereas faecal P levels decreased in the second part of the dry season (early dry season 2003: 0.269 ± 0.006; late dry season 2003: 0.237 ± 0.005, $t_{52} = 4.11$, $p < 0.001$, Fig. 5.9). Faecal N content was much higher during the dry season of 2002 when burnt areas were available than during the dry season of 2003 when burnt areas were not available (1.61 ± 0.05 vs. 1.18 ± 0.02, $t_{38} = 9.0$, $p < 0.001$, Fig. 5.8), as was P (0.290 ± 0.011 vs. 0.237 ± 0.005, $t_{38} = 5.14$ $p < 0.001$, Fig. 5.9). The season in which the burn was implemented had a significant effect on faecal N content (late dry season 2002: 1.61 ± 0.05; transition period 2002: 1.85 ± 0.07; transition period 2003: 1.70 ± 0.05, ANOVA: $F_{2,39} = 4.30$, $p = 0.021$, Fig. 5.8). On the early winter burn of 2002, faecal N was significant higher after the rains (transition period) than before the rains (late dry season), (Tukey post-hoc test: $p = 0.016$). Faecal P values were similar in burnt areas in all periods (late dry season 2002: 0.290 ± 0.011; transition period 2002: 1.289 ± 0.007; transition period 2003: 0.288 ± 0.007, ANOVA: $F_{2,39} = 1.02$, $p = 0.981$, Fig. 5.9).

DISCUSSION

On unburnt grassland, as both the quality and quantity of the available food declined from early to late dry season, sable increased their bite rate and daily foraging time. An increase in biting rate and/or grazing time is one of the responses available to mammalian herbivores to compensate for progressive food depletion (WallisDeVries & Debauldt 1994, O'Reagain & Schwartz 1995, WallisDeVries et al 1999, Bradbury et al. 1999). Bite mass is primarily determined by grass height and density (Laca et al 1992) and is the major determinant of intake (Hodgson 1985). However, food intake is limited by morphological and functional constraints (Shipley et al 1994), therefore bite rate cannot fully compensate for the decline in bite size (Spalinger et al 1988). Herbivores may then increase their foraging time to compensate for the decreased intake rate (Hudson and Nietfeld 1985, Beekman & Prins 1989). The nutrient intake by the herbivore is the product of rate of intake and available nutrient concentration (i.e. grass quality).

Novellie (1978) described two possible ways in which grazers may respond when faced by low green leaf availability during the dry season. They may search for the available green leaves. As grass greenness declines the potential number of bites at any particular feeding station decreases. Alternatively, they may ingest greater quantities of poor quality material (i.e. brown leaves and stems) with a consequent increase in the number of potential bites available at any particular feeding station. It is possible that sable lowered their acceptance levels and became less selective towards green leaves when these decreased under a certain threshold, so as to increase the number of potential bites available and hence intake. Mammalian herbivores that adopt a strategy of lowering the quality of the diet, may to a certain degree increase the daily bulk of food taken (Underwood 1983), which in turn could again explain the increased foraging time. Sable in this study did not appear to change movement rates while foraging, and hence the probability of encountering food items as a tactic to buffer declining food availability, contrary to other ungulates (Novellie 1978, Wickstrom et al. 1984, Spalinger et al. 1988, Fortin 2002).

During a dry season with burnt areas available, sable did spend less time per feeding station, showed higher step rate, and shorter distances between feeding stations, than on non-burnt areas. Bite rate was as high as on unburnt areas, and no difference was found in foraging time. To overcome the potential low intake derived from the small bites available on burns, sable showed a combination of high bite rate, increased foraging time and movement rate. All are common behaviours adopted by grazers feeding on short grasses on burns (Novellie 1978, Underwood 1983, Heitkönig 1993). In addition, on burnt areas, sable took less steps between feeding stations than on unburnt areas, food distribution was less heterogeneous and clumped closer together, probably contributing to decreasing search time and hence decreased time spent per feeding station. As grass grows taller on burnt areas after the rains or on late winter burns, sable would be expected to increase their intake by increasing their bite size without having to adapt their behaviour as much as on short sward grasses (O'Reagain & Schwartz 1995). Sable in this study did not change their bite and movement rate from pre- to post-rains burns, but decreased daily time spent foraging and the distances between feeding stations. This could be explained through high bite and movement rate being enough to assure the necessary intake with the size of bites available and with the more homogeneous distribution of the food resources, leading to a decrease of the search component of foraging. Alternatively, sable may be forced to forage for shorter periods in November-December on the post-rain burns because of the heat (Moncorps 1997), and therefore the high bite rate would be necessary to get enough food intake despite shorter daily feeding time.

In any case, sable were able to respond to seasonal variability of the food supply, by changing their behaviour both on burnt areas and on unburnt areas. However, there may be some important costs involved: both in burnt and unburnt grassland sable increased foraging time at the end of the dry season. This could lead to a possible increase in predator attrition, in areas where predators are present (Fitzgibbon 1989). Without burnt areas available, the costs may be even higher since the diet quality dropped drastically during the dry season when no burnt areas where available. In such a situation, sable may be able to "survive" through winter, becoming more susceptible to predation, diseases or sudden environmental changes at the end of the critical dry season when their nutrient levels are at the lowest. On the contrary, when feeding on burnt areas, the green grassland available enhanced sable diet quality substantially, without there being evident signs of reduction in quantity of intake. Therefore, the implementation of carefully planned early winter burns in the sable areas is recommended when managing this rare species, since they appear to be able to successfully change their behaviour to adapt to low quantities available on burns and take advantage of the high quality food available.

FIGURE CAPTIONS

Fig. 5.1. Schematic outline showing the comparisons done in order to avoid the confounding effect of burnt status and season. 1) early dry season 2003/unburnt vs. late dry season 2003/unburnt 2) late dry season 2002/burnt vs. late dry season 2003/unburnt, 3) early winter burn before the rains (late dry season 2002) vs. early winter burn after the rains (transition period 2002) vs. late winter burn (transition period 2003).

Fig. 5.2. Grass greenness and grass height variation during the study period in sable feeding areas.

Fig. 5.3. Changes in feeding time spent per feeding station (FTFS) during different seasons and burnt regrowth stages. Geometric means and 95% confidence interval are reported.

Fig. 5.4. Bite rate (BR) changes during different seasons and burnt regrowth stages. Geometric means and 95% confidence interval are reported.

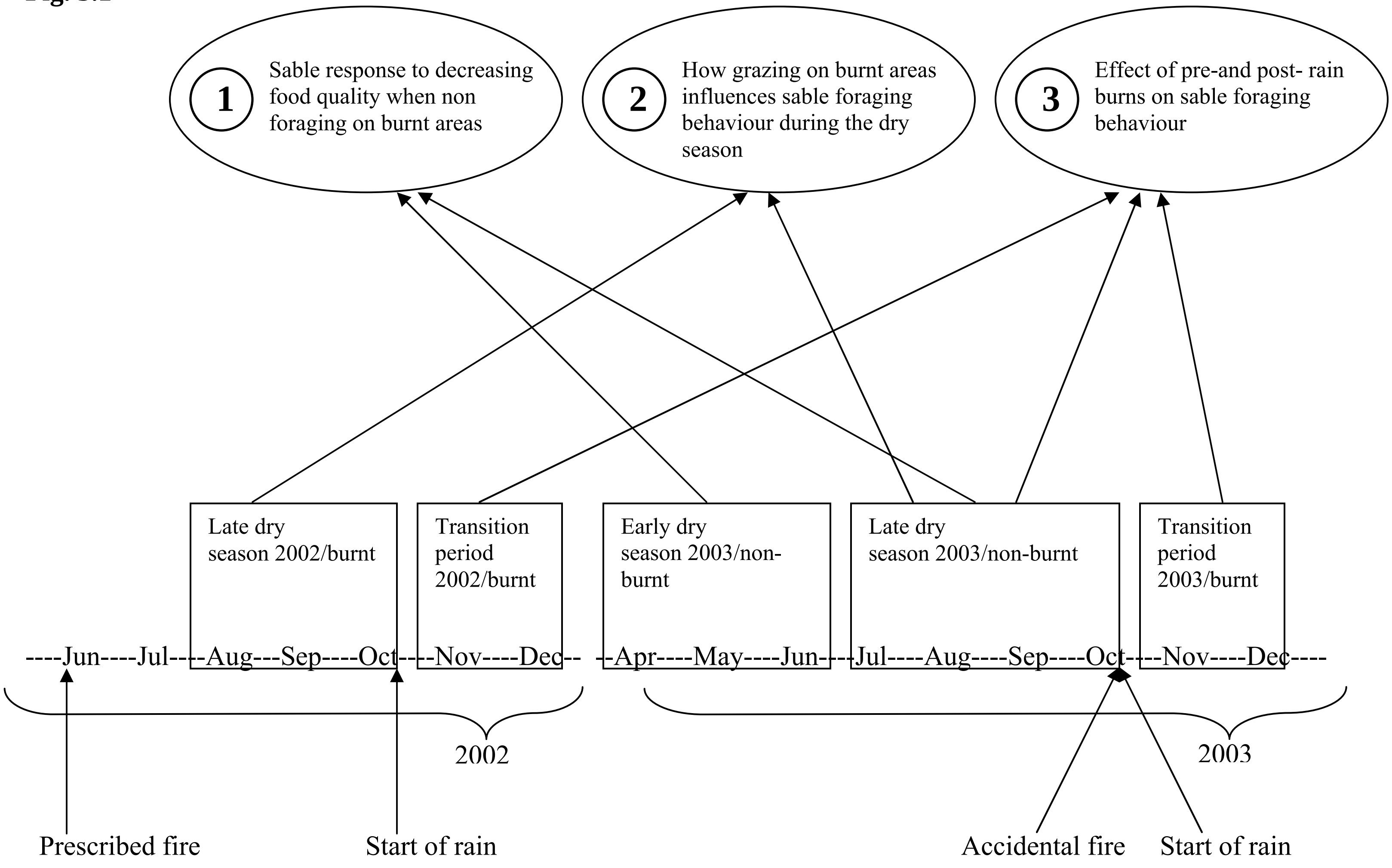
Fig. 5.5. Step rate (SR) variation during different seasons and burnt regrowth stages. Geometric means and 95% confidence intervals are reported.

Fig. 5.6. Changes in proportion of daylight hours spent foraging. Means are reported with 95% confidence limits.

Fig. 5.7. Nitrogen (N) content variation in sable faeces. Means and 95% confidence limits are reported.

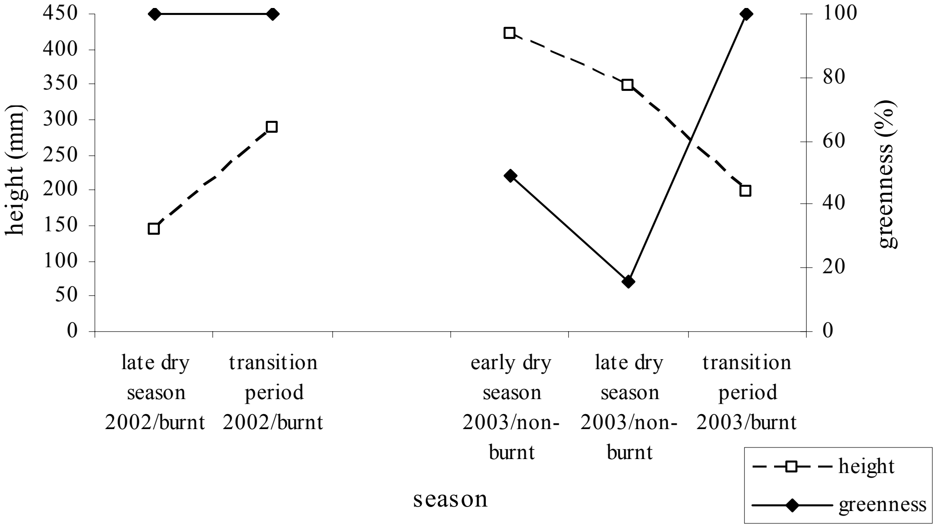
Fig. 5.8. Phosphorus (P) content changes in sable faeces. Means and 95% confidence limits are reported.

Fig. 5.1



1
Sable response to decreasing food quality when non foraging on burnt areas
2
How grazing on burnt areas influences sable foraging behaviour during the dry season
3
Effect of pre-and post- rain burns on sable foraging behaviour
Late dry season 2002/burnt
Transition period 2002/burnt
Early dry season 2003/non-burnt
Late dry season 2003/non-burnt
Transition period 2003/burnt
----Jun----Jul----Aug---Sep----Oct----Nov----Dec-- --Apr----May----Jun----Jul----Aug----Sep----Oct----Nov----Dec----
2002
2003
Prescribed fire
Start of rain
Accidental fire
Start of rain

Fig. 5.2.



height (mm)
450
400
350
300
250
200
150
100
50
0
greenness (%)
100
80
60
40
20
0
late dry season 2002/burnt
transition period 2002/burnt
early dry season 2003/non-burnt
late dry season 2003/non-burnt
transition period 2003/burnt
season
height
greenness

Fig. 5.3

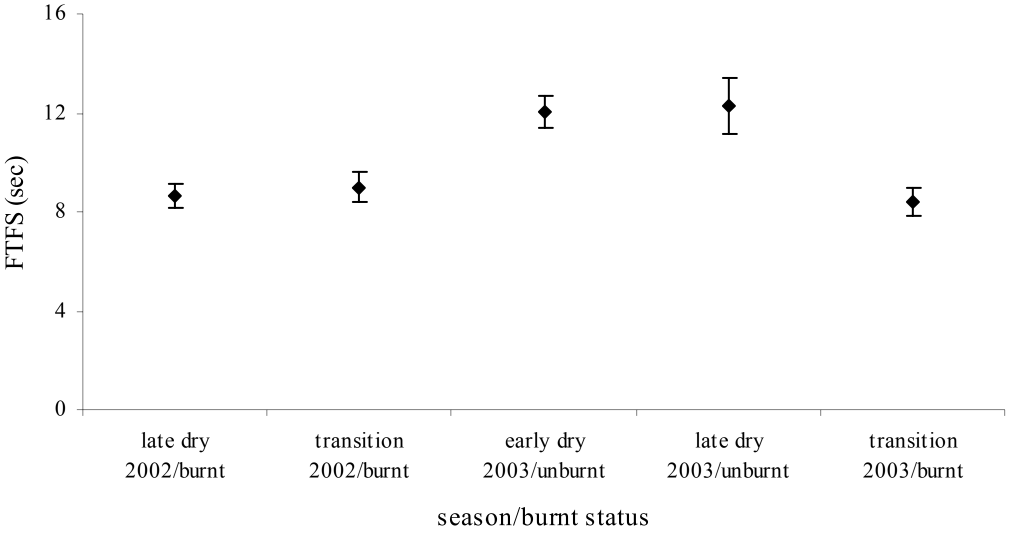

16
12
8
4
0
FTFS (sec)
late dry 2002/burnt
transition 2002/burnt
early dry 2003/unburnt
late dry 2003/unburnt
transition 2003/burnt
season/burnt status

Fig. 5.4

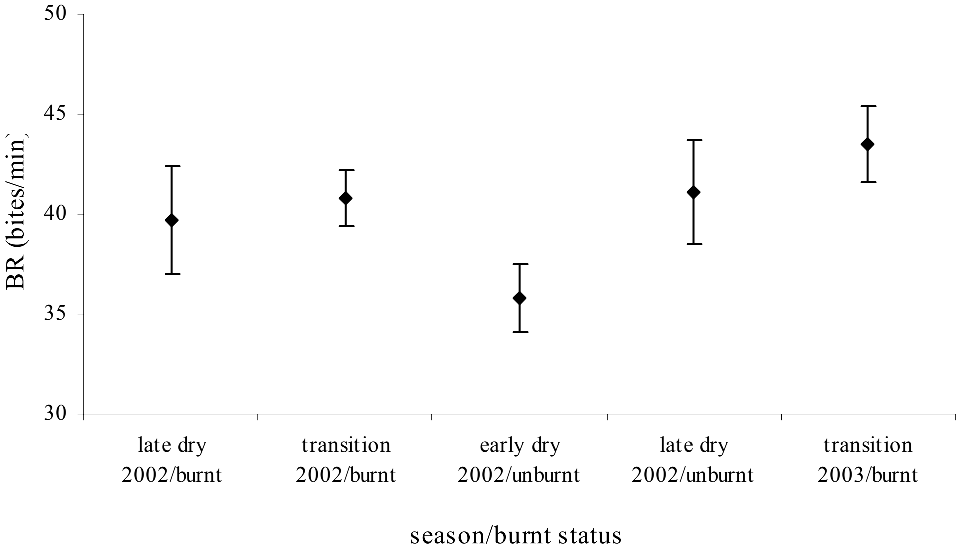

50
45
40
35
30
BR (bites/min)
late dry 2002/burnt
transition 2002/burnt
early dry 2002/unburnt
late dry 2002/unburnt
transition 2003/burnt
season/burnt status

Fig. 5.5

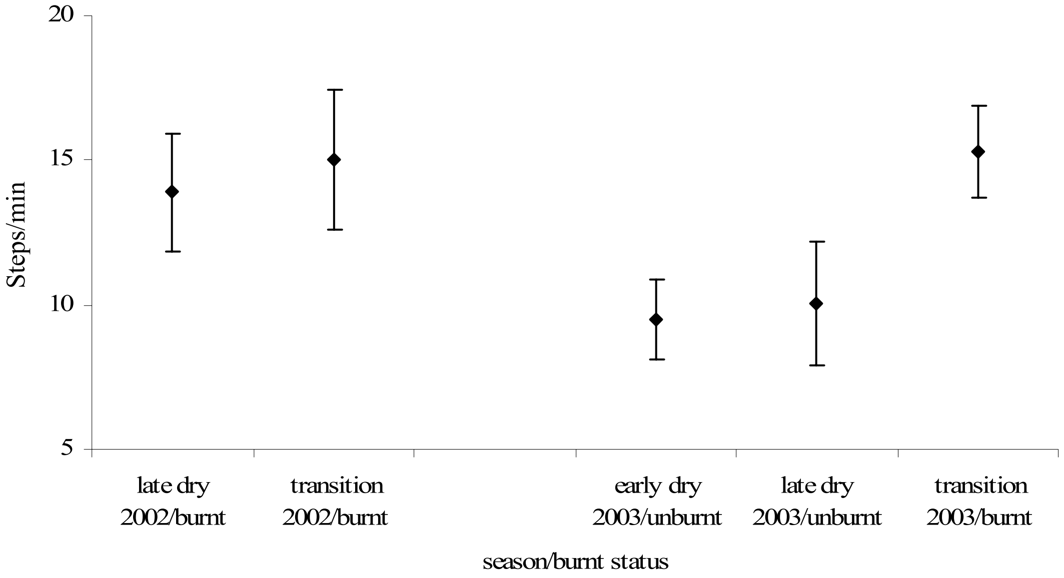

20
15
10
5
Steps/min
late dry 2002/burnt
transition 2002/burnt
early dry 2003/unburnt
late dry 2003/unburnt
transition 2003/burnt
season/burnt status

Fig. 5.6

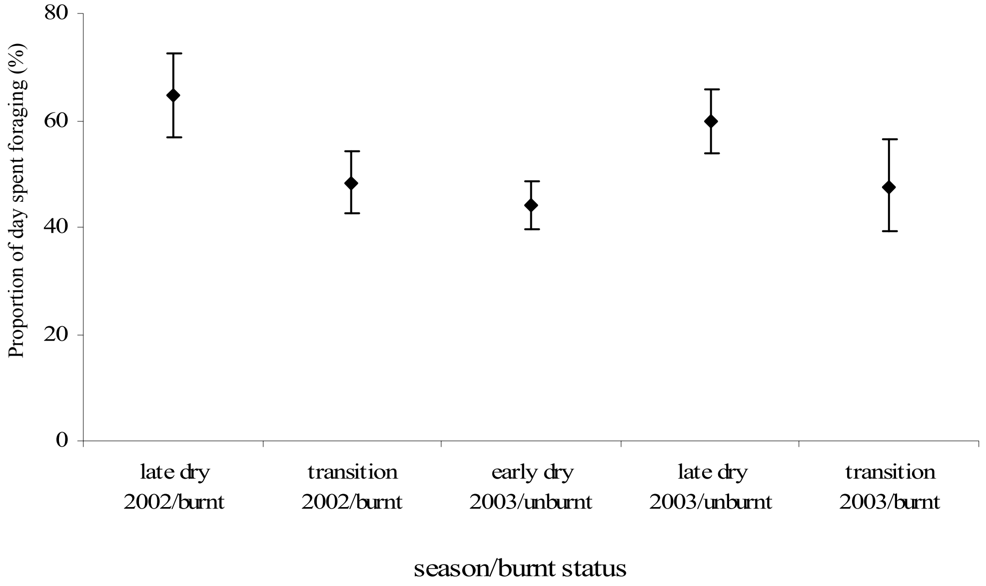

Proportion of day spent foraging (%)
80
60
40
20
0
late dry 2002/burnt
transition 2002/burnt
early dry 2003/unburnt
late dry 2003/unburnt
transition 2003/burnt
season/burnt status

Fig. 5.7

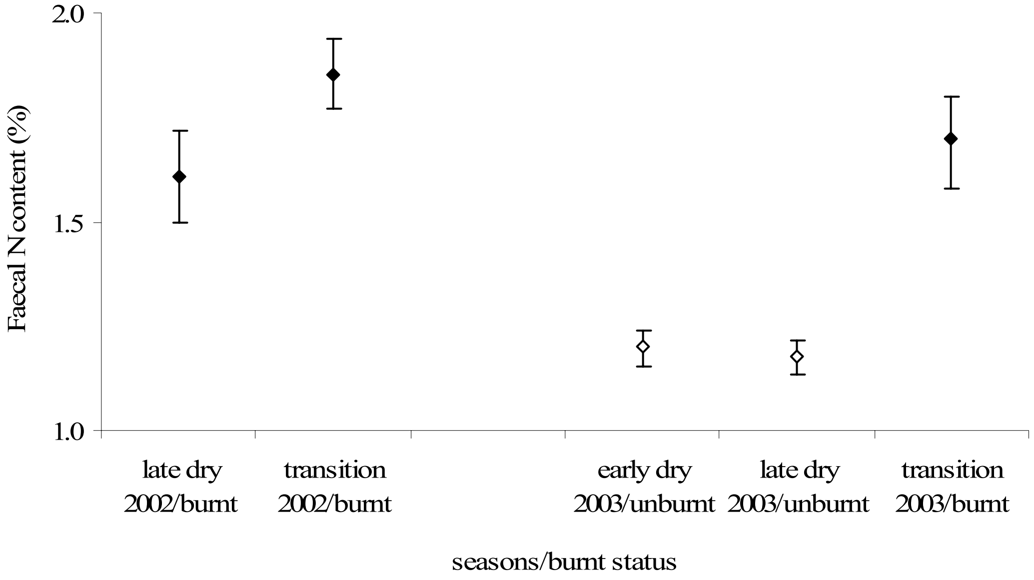
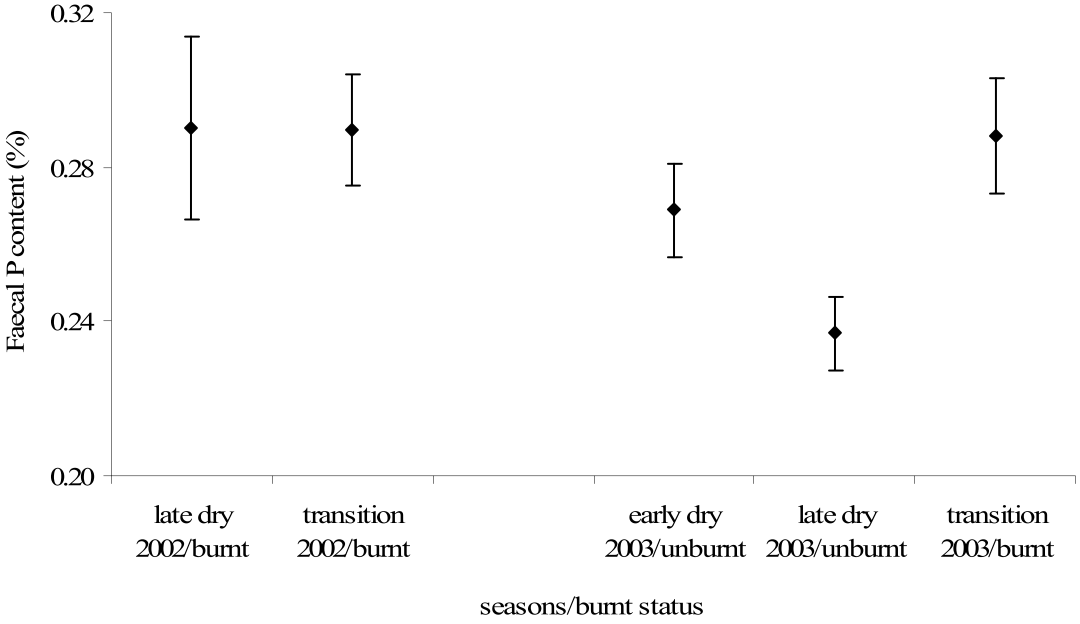

Faecal N content (%)
2.0
1.5
1.0
late dry 2002/burnt
transition 2002/burnt
early dry 2003/unburnt
late dry 2003/unburnt
transition 2003/burnt
seasons/burnt status

Fig.5.8



0.32
0.28
0.24
0.20
Faecal P content (%)
late dry 2002/burnt
transition 2002/burnt
early dry 2003/unburnt
late dry 2003/unburnt
transition 2003/burnt
seasons/burnt status

CHAPTER 6.

Activity budgets, synchronization and social affiliation of a non-dimorphic ungulate.

Abstract

Energy required for maintenance, growth and reproduction depends on the age and sex of the individual. Individuals of different age and sex could benefit from different allocation of time, which could lead to asynchrony of behaviour and finally to segregation. Previous studies on age and sex differences in activity focused mainly on dimorphic ungulates of temperate areas. This study examined activity budgets, social affiliation and synchronization of activity of the non-dimorphic sable antelope (*Hippotragus niger*) in the Kgaswane Mountain Reserve, South Africa. All age and sex classes lived in the same group. For each age/sex class I determined the daily time allocated to various activities and step rate while foraging. I also determined how each class synchronized its activities with that of the other group members. Adult males foraged for less than females, sub adult males and young. They did not synchronize all their activities with that of the other group members. Young and hence smaller animals maintained group cohesion by moving more rapidly than adult males and females. Differences in body size between the sexes are possibly not the only reason explaining sexual segregation. The social function of male groups may provide a more general explanation for sexual segregation, valid also for species with little size dimorphism.

INTRODUCTION

Large herbivores have a greater absolute food requirement than small ones, hence time spent eating should increase with body size (Bell 1970). Indeed, inter-specific comparison of the daily foraging time of African ungulates shows an increase with body mass (Owen Smith 1988, 1992). On the contrary, in temperate ungulates foraging time decreases with increasing body size (Mysterud 1998), since larger animals include lower quality food in their diet (Van Soest 1985). The above relations are based on maintenance requirements, with no allowance made for extra activity costs or growth. Energy and nutrients requirements depend on the age and sex of the individual. Growing animals and pregnant and lactating females have additional needs on top of maintenance (McDowell 1985). Therefore, independently of differences in body size, individuals of different age and sex require differential time allocation of activities (Duncan 1980, Clutton-Brock et al. 1982, Bunnel & Gillingham 1985). In both dimorphic (e.g. kudus, *Tragelaphus strepsiceros,* Owen-Smith 1998, bighorn sheep, *Ovis canadiensis*, Ruckstuhl & Neuhaus 2002) and non-dimorphic species (e.g. topi, *Damaliscus lunatus*, Duncan 1975, feral goat, *Capra hircus*, Shi et al. 2003) females forage for longer than males. However, there was less than 1% difference in daily foraging time of females and males of the non-dimorphic oryx (*Oryx gazella*) and zebra (*Equus burchelli*) (Ruckstuhl & Neuhaus 2002, Neuhaus & Ruckstuhl 2002).). In muskoxen (*Ovibos moschatus*), kudu and feral goat, yearlings spent as much as 6% more time foraging than females (Shi et al. 2003, Owen-Smith 1998, Cote' et al. 1997).

Few studies have examined in detail the causes behind sexual segregation (or lack of it) in non-dimorphic species (zebra, Neuhaus & Ruckstuhl 2002; buffalo, *Syncerus caffer*, Turner et al. 2005). Most studies have dealt with dimorphic ungulate species in temperate regions (see Ruckstuhl & Neuhaus 2002 for an extensive review) proposing different hypotheses (Main et al. 1996, Ruckstuhl & Neuhaus 2002).

(1) The 'predation risk-reproductive strategy hypothesis' states that females use habitats safe from predators (Main & Coblenz 1990, Corti & Shackleton 2002) and males the most nutrient rich ones in order to accumulate reserves to gain advantage for access to mates (Clutton-Brock et al. 1982, Prins 1989).

(2) The 'forage selection hypothesis' proposes that dimorphic males and females differ in their efficiency in digesting food and thus make different habitat choices (Illius & Gordon 1987, Barboza & Bowyer 2000).

(3) The 'social affinity hypothesis' proposes that females and males segregate because they have different motivations to interact (Bon & Campan 1996). Social segregation can also occur between different age groups of the same sex (Cransac et al 1998, Ruckstuhl & Festa-Bianchet 2001).

(4) The 'activity budget hypothesis' (Ruckstuhl 1998, 1999, Ruckstuhl & Neuhaus 2000, 2001, 2002, Neuhaus & Ruckstuhl 2002) proposes that differences in time spent foraging between males and females make it difficult for them to synchronize their activities and stay in the same group (Conradt 1998, Conradt & Rooper 2000, 2003).

A new unexplored hypothesis explores differences in spatial behaviour and movement rates, as a possible cause of segregation (Bon et al. 2006). For groups to be stable individuals must move in the same direction and at similar speed.

Sable antelope show very little dimorphism in body size, since males weigh on average 235 kg (max 263), and females 220 kg (max 232), (Owen-Smith 1988). Females and juveniles live in mixed groups throughout the year, while sub-adult males are associated either with female groups or in small bachelor groups. Mature males are territorial, attached to females groups when the group is in their territory or solitary (Estes 1991).

The overall objective of this study was to determine the effects of age and sex on (*i*) time allocation in sable antelope and (*ii*) the degree of synchrony among group members. More specifically, I investigated whether adult males, sub adult males (2 to 3-years old), yearlings (1-year old) and juveniles (born within the year) differed from females in their daily time allocation, movement rate and degree of synchrony in activity. Because of the expected higher energy requirements of females and sub adult males, I hypothesized sub adult males to have similar time budgets to females, while adult males to spend less time foraging and poorly synchronize their activity with the rest of the herd. I expected both adult and sub adult males to maintain the same movement rate as females while foraging to retain group cohesion. I expected post weaning juveniles and yearlings to spend more time foraging because of growth energy requirements and to take more steps per minute to maintain the same movement rate as adults.

MATERIAL AND METHODS

The study extended from September to December 2002 and from April to December 2003 in the Kgaswane Mountain Reserve (KMR, 25º 41’- 25º 45’ S, 27º 09’- 27º 13’ E), North-West Province, South Africa.

Approximately 75 sable lived in the reserve of which 37 were mature females, divided between two distinct herds. The two herds lived in two separate areas and occasionally split into smaller sub-units. Sub adult males stayed with females and did not form bachelor groups. Outside the breeding season, the same adult male was with the females on 86% of the times I observed a sable group. During the breeding season, one adult male was with the females on 94% of the sable sightings.

I observed sable with 10x40 binoculars or a 20-60x spotting scope from a vehicle or vantage points. I distinguished adult males from females by the tufted penile outgrowth behind the navel and by the more curved and thicker horns. I was able to separate sub adult males (from two to four years of age) from females by the penile tuft and the thicker horns. I defined juveniles as the individuals born within the year (in February-March) and yearlings as the individuals born the previous year. I identified them by the horn length and shoulder’s height in relation to females. I could not distinguish reliably juveniles or yearlings by sex.

For observations on time budgets, I observed a focal group from sunrise to sunset (12-15 hours) using the scan sampling method (Altmann 1974) with 10 minutes intervals. I distinguished between foraging, walking, standing, lying, social behaviours and other miscellaneous activities (scratching, grooming, nursing young, defecating and urinating). When part of the group was not visible, I used two different approaches, depending on the visibility of the area where the group was. When the whole area was visible, I recorded the non-seen animals as lying. However, if at the next scan the missing animals appeared again, I assumed them to have been hidden from sight at the previous scan (i.e. behind a tree or another animal) and engaged in the same activity as at the present scan. When unable to scan the whole area (i.e. part of the group on one side of a hill, part on the other side), I considered the animals in sight as representative of the whole group. I assumed that the missing animals were engaged in the same activities as the observed ones. For each day, I calculated the mean proportion of time devoted to an activity for each age/sex class, averaging per hours. I considered only observations spanning from sunrise to sunset and I discarded days when the whole group disappeared from sight before sunset.

I recorded the number of steps per minute spent foraging on focal individuals (Altmann 1974) during morning and afternoon foraging bouts. I counted foraging steps for 5 to 8 minutes. I did not collect data on the same individual twice in an observation session to avoid pseudo-replication. I considered morning and afternoon sampling sessions to be the separate sampling units. I therefore averaged the step rate across individuals of the same age/sex class collected in the same sampling period.

To analyse synchrony in activity between group members, I adapted the method used by Ruckstuhl and Neuhaus (2002) first described by Ruckstuhl (1999), to scan sampling of unmarked individuals. For each 10-min scan, I assigned a value (S_f) to the behaviour of each animal based on probability that the reference individual had to be engaged in the same/different activity as the other individuals in the herd. If the behaviour of the individual differed from that of more than half of the group members, S_f was 0; if it was engaged in the same activity as more than half the group members, S_f was 1. If half of the group members were engaged in the same activity as the reference animal, while the other half were engaged in a different behaviour, S_f was 0.5. For each 10-min scan, I averaged the S_f calculated for each individual animal over the total number of animals of a particular age/sex class to obtain a mean synchronization factor for each age/sex class (S_c). After we calculated all S_c values for all 10-min scans, we calculated a mean age/sex class synchronization index ($S_{age/sex}$) for each observation-day:

$S_{age/sex} = \sum (S_c) / n$ n = number of 10-min scans.

Multiplied by 100 the synchronization indices represent the percentage of time an individual of one age/sex class was in synchrony with most of the other group members.

To analyse more in detail synchrony of behaviour between adult males and females, I investigated what the adult male was doing during females foraging and resting bouts. I calculated the proportion of time spent foraging, standing and lying by adult males during females foraging bouts. I also calculated the proportion of time spent lying, standing, walking, grazing and in other activities by males during females lying bouts. I considered a foraging bout when more than 50% of females were foraging and a resting bout when more than 50% of females were lying.

Prior to statistical analyses, I tested activity budgets, synchronization indices and step rates for normal distribution (Kolmogorov-Smirnov test, Quinn & Keough 2002). I performed an arcsin transformation of time budgets and synchronization indices and a log transformation of step rates to approach the normal distribution required for parametric tests (Quinn & Keough 2002). If transformation did not result in a normal distribution, as in the case of time spent in social activities, I applied the non-parametric Mann-Whitney-U test (Siegel and Castellan 1988). To control for the influence of exogenous factors such as temperature, rain or feeding area characteristics, I carried out paired comparisons between age/sex classes for the days when both classes were present in a same herd. I compared adult males and females on 48 days, sub adult males and females on 57 days, yearlings and females on 48 days, juveniles and females on 52 days. I tested for differences in activity budgets, synchronization indices and step rates between age/sex classes with ANOVA. I included different stages of the reproductive cycle (pre-weaning, post weaning, and rut) and herd (since I did the observations on different herds) as factors in the ANOVA. If a factor had a significant effect on activity budgets, synchronization indices or step rates differences, then I performed separate t tests within each category of the significant factor.

I tested for correlation between group size and synchronization index with Spearman rank order correlation (Siegel & Castellan 1988). Group size and synchrony were not significantly correlated (females: $r_s = -0.21$, $p = 0.10$, sub adult males: $r_s = -0.14$, $p = 0.31$, yearlings: $r_s = -0.16$, $p = 0.23$, adult males: $r_s = 0.84$, $p = 0.55$). Therefore I did not find it necessary to correct the synchronization indices by group size (Engel & Lamprecht 1997).

I used 95% confidence limit to evaluate the significance of all analyses. I report the means with standard error (SE) and, in the case of non-parametric statistics, the median, with minimum and maximum values and interquartile range (IQR).

RESULTS

Adult males spent less time grazing and more time lying than females throughout the study period (Table 6.1). Males spent significant more time standing and engaged in social behaviours than females only during the mating season (Table 6.1 & 6.2). The proportion of time spent grazing decreased during the breeding season while time spent lying remained the same (Table 6.1). The daily allocation of activities of sub adult males and yearlings did not differ significantly from that of females in any season (Table 6.3). Juveniles that were still nursing grazed for less and were standing and lying for longer than females (weaning status effect: $F = 5.25$, $p = 0.02$, Table 6.3). Once juveniles were weaned, their activity budgets were similar to that of females (Table 6.3).

There was no difference in number of steps taken per minute either between adult males and females or between sub adult males and females (Table 6.4). I recorded higher step rates for yearlings and juveniles than for females (Table 6.4).

Indices of synchrony were similar between females, sub adult males, yearlings and weaned juveniles, while adult males were poorly synchronized with the rest of the group (Table 6.5). In particular, during female active bouts, adult males were also active on 91% of time in the morning and afternoons but only on 79% of times over midday (Fig. 6.1). The proportion of observations when the male was lying during female active bouts was as high as 17% during midday (Fig. 6.1). During female resting bouts, I recorded the adult bull feeding on 15 % of the observations in the morning and 11 % of the observations in the afternoons (Fig. 6.2).

DISCUSSION

I found that sub adult males, yearlings and post-weaning calves foraged for a similar amount of time to females and synchronized their activities with the rest of the group. Instead, adult males only loosely synchronized their activities with the rest of the herd and spent less time foraging and more time lying than females. The sex difference in daily foraging time for sable was less than 10% outside the mating season. During the mating period the difference increased, since males increased the time spend standing and engaged in social activities at the expenses of foraging time.

The difference in time spent foraging between adult males and females of sable was smaller than in dimorphic species (e.g. bighorn sheep, Ruckstuhl 1998; Soay sheep, *Ovis aries*, Pérez-Barbería & Gordon 1999; Alpine ibex, *Capra ibex*, Ruckstuhl & Neuhaus 2001). However, other dimorphic species did have an even smaller difference in time spent foraging than sable (e.g. muskoxen, Côté et al. 1997; desert bighorn sheep, *Ovis canadiensis Mexicana*, Mooring et al. 2003; Merino sheep, Michelana et al. 2004). Among non-dimorphic species, the difference in time budgets between adult males and females of sable was larger than that reported for topi, horses, oryx and zebra (Duncan 1975, 1980, Ruckstuhl and Neuhaus 2002, Neuhaus

& Ruckstuhl 2002). The lack of any difference in time budgets between sub adult males and females was instead in line with previous studies (e.g. Duncan 1975, 1980, Turner et al. 2005). The extra time spent grazing by females and sub adult males has been explained with the higher energy demands of both females (lactation, pregnancy) and sub adult males (body growth) compared to adult males. Adult males instead spend more time engaged in social activities when with the herd at the expenses of their foraging time (e.g. Turner et al 2005). Because, a part from the mating period, adult males of sable did not spend more time than females in social activities, we suggest that the difference in time budgets between the two sexes outside the mating period was only a consequence of the different energy requirements of adult males and females.

I did not find any difference in time spent foraging and lying between post weaning juveniles, one-year-old individuals and females. Previous studies show how yearling forage for as much as 6% of daytime longer than females (Boertje 1985, Cote' et al 1997, Oakes et al. 1992, Shi et al. 2003). Both yearlings and females require additional feeding time, the first to obtain enough energy and nutrition to meet their growth requirements, the latter require additional energy and nutrition for lactation and pregnancy.

Males and females had similar step rates, which in theory should help maintaining group cohesion (Bon et al 2006). However, a similar step rate is not a prerequisite to live in the same group, since Merino sheep had a steps frequency twice as high in males as in females and still maintained group cohesion (Michelana et al. 2004). Group cohesion can still be maintained by having trajectories that are more sinuous than the ones of the slower individuals or by speeding up. Young sable had indeed a higher movement rate: since smaller animals take shorter steps, they had to increase the step frequency to keep up with the group.

In this study, sable adult males were the least synchronized with the rest of the group members (0.69 vs. 0.80 for sub adult males and 0.82 for females). In contrast, the degree of activity synchrony of males and females was similar in mixed-sex groups of merino sheep (0.93 and 0.92) and bighorn sheep (0.78 and 0.79)(Ruckstuhl 1998, Michelana et al. 2004).

Despite the similarity in body size, adult males and females had different activity budgets and were loosely synchronized but adult males still joined the females herd when in their territory. Ruckstuhl and Neuhaus (2002) proposed that activity asynchrony arising from differences in activity budgets could explain sexual segregation, accentuated by size dimorphism between adult males and females. Sable groups in the KMR often moved little around midday, allowing some animals to rest while others continued foraging without become separate.

Adult males were able to stay with the group despite the different activity budgets. Therefore, it should not be necessary for sub adult males to have similar time allocation to females to be in the same group as them. Sub adult males have additional energy requirements for growth (Bunnel & Gillingham 1985), females for lactation and pregnancy (McDowell 1985), and therefore a similar activity budget should be expected independently from being in the same group or not. Therefore, activity budget and synchrony cannot be the explanation for sexual segregation.

Gregariousness is a trade-off between optimal time budgets, social preferences and increased protection from predators (Krause & Ruxton 2002). A male in a group can afford to spend less time watching and more time grazing because of group related benefits such as increased vigilance and dilution of predation risk (Krause & Ruxton 2002) but at the same time there is greater food competition and risk of losing condition (Turner et al. 2005). Single-sex groups are much smaller than mixed groups and the risk of food competition lower than in larger groups, therefore males should benefit more in staying in such groups instead than with the larger females groups. Moreover, bachelor groups provide a context in which dominance relationships can be established (Owen-Smith 1993, Villaret & Bon 1998). This function of male groups may provide a more general explanation for sexual segregation (Bon & Campan 1996, Bon et al. 2001), valid also for species with little size dimorphism (e.g. wildebeest, topi, hartebeest, Estes 1991). The rationale is that males and females differ in their behavioural repertoire and motivation to interact (Legault & Strayer 1991).

However, sable do not often form bachelor groups (Estes 1991). Possibly, there were not enough sub adult males to form groups of sufficient size to provide adequate anti-predator protection. In small or low-density populations, the need to reduce predation risk by forming large groups may override the need to optimize social encounters by forming peer groups. Thirgood (1991), in a study on fallow deer (*Dama dama*) sexual segregation, found that when male deer numbers were low, males joined females groups. Reisenhoover & Bailey (1985) observed that in mountain goats (*Oreamnus americanus*) and bighorn sheep, a minimum group size of five was required to significantly decrease vigilance and increase individual feeding rate. However, kudu are known to form bachelor groups of just two-three individuals (Owen-Smith 1998). In addition, the study population of sable was in a predator free area. Alternatively, it could be that at high densities sable territorial males are more aggressive, evicting sub adult males from their territory and therefore forcing them to form bachelor groups.

The fact that adult territorial males join the mixed groups shows how potentially the advantages of being in a large group are more than the costs of non-synchronization. Joubert (1974) described a similar situation, with one single male was usually attached to a group of females even outside its territory boundaries, for roan antelope in the Kruger National Park (described as a form of territoriality at low population density by Owen-Smith 1977).

One single hypothesis cannot explain the lack of sexual segregation in sable antelope. Interplay of different costs and benefits is more likely to govern sociality, rather than one single cause. Further studies need to compare populations at different densities and focus on the potential role of different environments, to understand the driving force behind ungulate social systems and to gain a more complete understanding on the causes of sexual segregation in both non-dimorphic and dimorphic species.

FIGURE CAPTIONS

Fig. 6.1 Activity of adult males during active bouts of females, distinguishing morning, midday and afternoon periods.

Fig. 6.2 Activity of adult males during inactive bouts of females, distinguishing morning, midday and afternoon periods

Table 6.1. Comparison of time allocated to grazing, walking, standing, lying between adult males and females observed on the same day outside and during the mating period. I report the whole study period, when the time period was not a significant factor in the ANOVA.

		Time allocation (%)		t test	
Activity	Time period	Adult male	Adult female	t statistic (n)	P value
Grazing	whole period	41.4±1.7	46.0±1.5	6.23 (48)	0.014*
Walking	whole period	8.2±1.0	9.4±1.0	1.43 (48)	0.227
Standing	non mating period	5.8±0.8	6.9±0.7	1.71(40)	0.091
	mating period	10.2±1.0	6.6±1.1	7.30 (8)	<0.001*
Lying	whole period	44.0±1.0	36.6±1.4	7.41 (48)	0.023*

* significant difference

Table 6.2. Comparison of time allocated to social activities by adult males and females.

Time Period	Age/sex class	Time allocation (%) median	Min	max	IQR	Mann-Withney U test z (*n*)	P value
non mating period	Adult male	0.1	0.0	8.3	2.4	1.45 (*40*)	0.152
	Adult female	0.1	0.0	3.5	0.4		
mating period	Adult male	12.3	5.4	18.5	10.7	2.88 (*8*)	0.004*
	Adult female	0.2	0.0	0.9	0.6		

* significant difference

Table 6.3. Comparison of time allocated to grazing, lying, standing and walking by females versus sub adult males, yearlings and juveniles observed on the same day. Means are reported ± s.e.

		Time allocation (%)		T test	
Activity	Age/sex class	Age/sex class	Adult female	t statistic(*n*)	P value
Grazing	Sub adult male	46.7±1.6	45.9±1.2	0.48 (*57*)	0.49
	Yearling	47.4±1.5	46.2±1.3	0.31 (*48*)	0.73
	Pre weaning juvenile	36.4±3.1	49.0±2.6	4.97 (*13*)	0.003*
	Post weaning juvenile	46.9±1.7	46.2±1.5	0.11 (*39*)	0.74
Walking	Sub adult male	9.1±0.9	9.6±0.8	0.14 (*57*)	0.71
	Yearling	10.0±0.9	9.8±0.9	0.30 (*48*)	0.74
	Juvenile	9.7±0.8	9.5±0.8	0.20 (*52*)	0.65
Standing	Sub adult male	4.1±0.7	6.8±0.5	6.89 (*57*)	0.012*
	Yearling	3.2±0.4	6.8±0.6	9.07 (*48*)	0.003*
	Pre weaning juvenile	9.1±2.7	7.2±1.0	0.57 (*13*)	0.57
	Post weaning juvenile	3.9±0.6	6.6±0.6	3.76 (*39*)	<0.001*
Lying	Sub adult male	39.7±1.7	36.9±1.3	1.40 (*57*)	0.243
	Yearling	38.8±1.4	36.4±1.3	0.58 (*48*)	0.438
	Pre weaning juvenile	46.4±3.7	38.4±2.4	4.43 (*13*)	0.029*
	Post weaning juvenile	37.4±1.7	35.2±1.4	0.42 (*39*)	0.42

* significant difference

Table 6.4. Comparison of step rates for sable of different age/sex classes. Pairwise comparisons were done on days when both classes were recorded.

	Step/min.			ANOVA	
	Mean	SE	*N*	*F*	*p*
Adult male	12.6	0.01	64	1.04	0.31
Adult female	11.5	0.01			
Sub adult male	12.9	0.01	54	0.06	0.91
Female	12.2	0.02			
Yearling	14.4	0.01	72	4.91	0.03*
Female	11.8	0.01			
Juvenile	13.4	0.01	79	8.51	0.004*
Female	10.7	0.01			

Note: *N* is the number of observation sessions for each pairwise comparison;

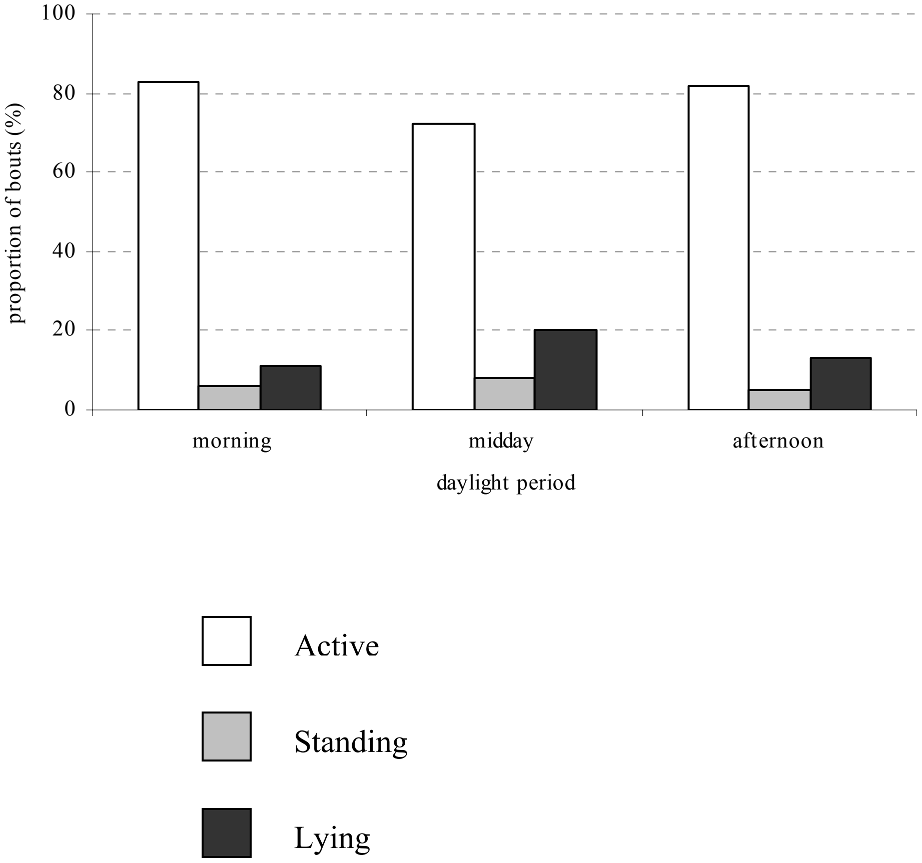
* significant difference

Table 6.5. Percentage of time during which the activity of different age and sex classes was synchronized with that of the majority of the group members.

	Synchronization index (%)			ANOVA	
	Mean	SD	*N*	*F*	*p*
Adult males	69	7	48	72.9	<0.001*
Adult females	82	9			
Sub adult males	80	7	57	1.67	0.20
Females	82	7			
Yearlings	79	6	48	0.85	0.36
Females	81	6			
Juveniles*	78	6	52	0.94	0.32
Females	82	7			

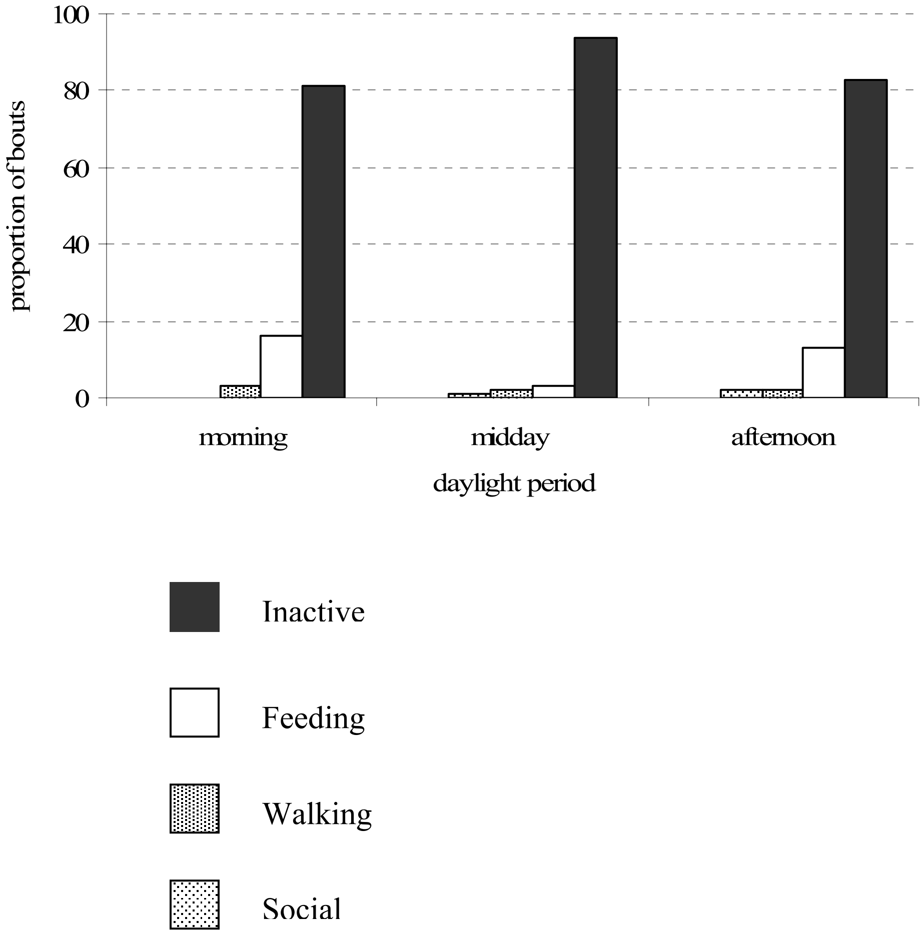
Note: *N*, number of days when the two age/sex classes being compared were both present in the observed herd; *only post-weaning juveniles were considered.

Fig. 6.1



100
80
60
40
20
0
proportion of bouts (%)
morning
midday
afternoon
daylight period
Active
Standing
Lying

Fig. 6.2


100
80
60
40
20
0
proportion of bouts
morning
midday
afternoon
daylight period
Inactive
Feeding
Walking
Social

CHAPTER 7

Conclusion and recommendations

The broad aim of this study was to identify the factors influencing the habitat use and ecological requirements of the thriving sable population in KMR. These finding would then be contrasted with the declining population in Kruger National Park. One of the hypotheses for the decline of the Kruger population suggests that they may suffer from a decrease in green grass availability during the dry period and consequently become more susceptible to predators (Ogutu & Owen-Smith 2005, Owen-Smith et al. 2005). However, all grazers face similar conditions during the dry season, so why are sable declining while other ungulate species are still abundant? Are there differences in the ecology of sable that could explain this decline? At KMR I was able to undertake a detailed study on the factors influencing the foraging and social ecology of a population of sable not subjected to predation pressure. During the study, a winter burning programme was implemented in the reserve. The study had been designed as a comparison with a similar study in the Kruger National Park. However, the study in Kruger is still underway. As a result, I will compare my findings with those available in the literature. In addition, I will highlight differences to other more common grazers that may help explain the greater susceptibility of sable to adverse conditions. To do this, I will address the following questions:

1) What habitat conditions do sable favour?

2) Do sable use key resource areas to overcome the limitations of the dry season?

3) If so, are these areas the same as the ones used by other herbivores?

4) Do sable depend on the availability of green flushes in burnt areas to overcome nutritional limitations at the end of the dry season?

5) Do sable differ from other grazers in their selection of grass height, greenness and avoidance of stems?

6) Do sable select similar grass species to other grazers?

The different survival rates of adult and juvenile age classes affect population trends in African ungulates (Owen-Smith & Mason 2005). Therefore, certain age-sex classes may be more vulnerable than others may. To explore this, I ask:

7) Do different age and sex classes differ in their foraging behaviour?

8) Have certain segments of the population lower chances of survival than others?

Most previous studies on sable antelope agree that they prefer woodland areas to open grasslands (Pienaar 1974, Wilson 1975, Grobler 1981, Ben-Shahar & Skinner 1988, Scogings et al. 1990, Magome 1991). The only exception was in Kenya where sable preferred open grasslands. This, however, was likely due to the absence of open woodlands (Estes & Estes 1974). My results indicate that sable use woodland areas. In addition they utilise open areas, provided these areas remain green during the dry season and contain preferred grass species. Other grazers, such as wildebeest, zebra, hartebeest and waterbuck, primarily prefer open grasslands. Therefore, there is not an ecological separation between sable and these other grazers at the habitat level.

Are there differences in other aspects of habitat use? My results indicate that vlei areas are key resource to sable during the dry season. Other grazers also use these bottomlands during the dry season. However, sable do not rely exclusively on them. During the dry season, they also used wooded hill slopes where *Panicum maximum* retains its greenness.

The pressure on these key resources is further reduced by implementing winter burns that allow sable to exploit areas and grass species otherwise not used during the dry season. As a result, are these burnt areas important in improving nutritional deficiencies in sable? As food availability in the burnt areas is greatly reduced, are nutritional gains in these areas are adequate to compensate for lower food intake? Magome (1991) found that sable nutritional deficiencies improved by using burnt areas in the Pilanesberg National Park, while Henley (pers. comm.) found they did not use burnt areas in Kruger National Park. Impala, wildebeest, tsessebe, hartebeest and roan all feed on burnt areas. Thus, it is possible that they could keep grass regrowth below the height at which sable could graze efficiently (Grobler 1981, Gureja & Owen-Smith 2002). Despite these pressures, I found that sable adapted to feeding on short grass and thus benefited from the high nutritional quality of the new grasses. I showed that grass flushes on the burnt areas are important in alleviating the nutritional shortfalls sable may incur in at the end of the dry season.

Magome (1991) described a negative correlation between grass height and feeding preferences by sable in the Pilanesberg National Park. Grobler (1974) recorded sable feeding on short-medium grasses (50-300 mm) in Zimbabwe. I show instead that sable are able to adapt to a wider range of grass heights, since there was great variation in grass height in preferred sable habitats and selected grass species. To maximise nutritional intake, herbivores should select for green leaves that are low in fibre. Surprisingly, sable did not avoid the brown leaves. As the dry season progressed and the proportion of green leaves available decreased, sable increased the proportion of brown leaf they ingested. This is similar to what has been reported for topi (Duncan 1975). At the same time, sable did not avoid stemmy grass tufts. Unfortunately, I am unable to determine whether these stems were eaten, or whether the sable selected the leaves from these tufts. Thus, I cannot determine whether sable were as tolerant of low quality food as suggested for roan (Heitkönig 1993) or if they selected for leaves at the plant part level, as observed in cattle, sheep, bison and topi (Fortin et al 2002, O'Reagain & Mentis 1988, Duncan 1975).

Magome (1991) described sable as grazing on a limited number of grass species throughout the year. This has also been observed elsewhere (Estes & Estes 1974, Wilson & Hirst 1977). During my study, sable constantly fed on species such as *Heteropogon contortus, Panicum maximum* and *Themeda triandra*. These species are highly favoured by a wide range of domestic and wild grazers (Ben-Shahar 1991). Sable primarily fed on these species, except on burnt areas where they expanded their diet to include a wider range of species. In addition, sable included tall stemmy species avoided by short grass grazers. By exploiting these grass species sable may have been able to reduce grazing competition.

Adult males had a different time allocation of daily activities compared to females and young. Despite the potential costs of not being synchronized with the rest of the herd, one adult male was seen with the breeding herd even outside the breeding season. Grobler (1974) observed a similar situation for sable in the Matopos National Park. A similar social structure, described as 'loosely territorial' has been described in the roan antelope. The breeding herd included subadult males that were synchronized in their activities with the rest of the herd. If there were costs to being synchronized, I would have expected bachelor males to form same sex groups like other African ungulates (e.g. wildebeest, topi, hartebeest and kudu; Estes 1991). Without detailed information on the nutritional status of the different age and sex classes, I am unable to conclude if a certain age-sex class was more vulnerable than others. Future research will need to focus on the nutritional status of the different age-sex classes. This will then allow the potential costs involved in the sable social structure to be quantified and thus identify if certain age-sex classes are more vulnerable than others.

The findings of my study suggest that a combination of factors contribute to the success of sable in KMR. These included the large vlei area that remains green well into the dry season, the abundance of *Themeda triandra*, flushes of green regrowth in the burnt areas and a lack of predators. I was not able to identify many of the differences from other grazers as a reason to why sable should be doing poorly compared to grazers that are more common. The only difference that I identify as potentially making sable more vulnerable is the limited number of grass species they feed on. If the availability of these grass species is low and/or the grazing pressure on them by other grazers is high, then sable might not be able to widen their diet to make up for the decline in preferred species. The tall and stemmy species that sable sporadically include in their diet can partly separate them from other grasses, but their availability is usually limited and therefore they cannot constitute the bulk of the diet.

To further our understanding of the differences between sable and other common grazers, future research will have to focus on comparing the ecology of sable and other grazers in the same area. This will control for habitat and environmental variables, and highlight the different behavioural responses under similar conditions. However, if sable are able to adapt their feeding ecology to varying conditions as I suggest, the causes of their decline may include a higher vulnerability to predation or disease compared to common species.

Management implications

The findings of the study provide a wide range of insight into what can be done to improve conditions for sable. Sable appeared to do well in woodland - open grassland mosaic. Woodland habitats provide *Panicum maximum*, a key resource during the dry season. Grasslands need to include grass species preferred by sable (*Themeda triandra, Heteropogon contortus, Diheteropogon amplectens, Setaria* spp.) and occupy a position in the landscape as to retain water so that grasses retain green leaves into the dry season. Thus, reserves that include a combination of these areas should be favoured when considering where to introduce sable.

On burnt areas sable feed on a wider range of grass species than on non-burnt areas, decreasing the grazing pressure on the usually preferred grass species. Moreover, sable are able to adapt well to the short grass on these areas and thus take advantage of the high quality food. The use of these burnt areas during the dry season improves sable nutritional deficiencies during this critical time. Therefore, the implementation of a winter burning regime is recommended. The home range of each sable heard should be treated as a distinct management unit so that each heard may benefit from the burning programme. Areas to be burnt need to be chosen carefully, in landscape positions, that will provide green flushes.

Areas suitable for sable need to be large enough to sustain the breeding herds. For each breeding herd, there needs to be between 10- 20 km^2 of the woodland – grassland matrix.

My study suggests that sable do not compete with other grazers in situations where vlei areas are available and high abundance of preferred grass species. Interspecific competition may be a problem in small reserve with limited suitable habitat, but in general, sable appear to do well despite high numbers of other grazers.

In conclusion, the causes of sable decline need to be explored outside of their feeding ecology , most likely in their susceptibility to predators (Owen-Smith & Mills 2006) and diseases. Thus as a precaution, I suggest choosing reserves and parks lacking predators when deciding on where to introducing sable.

APPENDIX I

Psion program

The computer program “Rhino” was used to record the number of bites and the number of steps that an individual sable took per minute. The program was written for a Psion Organiser II by James Murray at Psion, South Africa for a study on food use by white rhino (Shrader 2003).

Keys and their functions:

Y - Initiated the program and printed the date (day/month/year) and “Start” followed by the time (hour/minute/second).

Z - Terminated the program and printed “Stop” followed by the time (hour/minute/second).

S - Recorded a single bite.

T - Recorded a step, printed the time (hour/minute/second).

M - Paused the program and printed the time (hour/minute/second) when program was paused.

Once started the program required the ID number of the animal that was being observed. In this study, a two-letter code (AF for adult female, AM for adult male, SM for subadult male, YY for yearling and JJ for juvenile) was entered. Once the ID number was entered, the program was ready for imput. To initiate the program the ‘Y’ key was pressed when the sable took what was the first step of the feeding observation. When ‘Y’ was pressed, the date and the start time of the initial step were printed. The ‘T’ key was pressed when the sable took a step. Each time the ‘T’ key was pressed, the time of the step was printed.

The original program written for the rhino study was designed so that the Psion beeped once ten feeding steps had been recorded. In my sable study, a feeding observation was not defined on the base of the number of steps recorded, hence I ignored the signal. A feeding observation was an 8 – 10 min sequence. After at least 8 minutes of recording, the ‘Z’ key was pressed to terminate the program and print the stop line.

When an animal forages, it divides its time between looking for and ingesting food. As the study was focused on feeding time, if a sable stopped feeding and started chewing the grass in its mouth, the ‘M’ button was pushed on the Psion. When ‘M’ was pushed, the time and the word ‘Pause’ was printed. If the sable resumed feeding without taking a step, the ‘S’ button was pushed and the time with the word ‘Resume’ was printed. If however the sable took a step and moved to a new feeding station the ‘T’ button was pushed.

Bites were recorded for one feeding minute by pushing the button ‘S’ each time the observed sable was taking a bite.

The Psion computer code for the ‘Rhino’ program follows.

```
rhino:

local kp%,rhino$(10),b$(250),cnt%,pse%

if exist(“a:bites”)
 open “a:bites,a,a$
else
 create “a:bites”,a,a$
```

```
endif

cls
print “Rhino:”
edit rhino$
if rhino$=””
 return
endif
a.a$=rhino$
append
a.a$=mid$(datim$,5,11)
append

do
 kstat 1
 kp%=get
 if kp%=%Y
  if len(b$)
   a.a$=b$
   append
   b$=””
  endif
  cnt%=0
  pse%=0
  print “Start”+right$(datim$,9)
  a.a$=”Start”+right$(datim$,9)
  append
 elseif kp%=%Z
  if len(b$)
   a.a$=b$
   append
   b$=””
   endif
   cnf%=0
   print “Stop”+right$(datim$,9)
   a.a$=”Stop”+right$(datim$,9)
   append
   break
 elseif kp%=%S
  if pse%=1
   print”Resume”+right$(datimS,9)
   a.a$=”Resume”+right$(datimS,9)
   append
   pse%=0
  endif
  b$=b$+”S”
```

```
 elseif kp%=%T
  pse%+0
  if len(b$)
   cnt%=cnt%+1
   print b$
   a.a$=b$
   append
   b$=””
  endif
  print “Step”+right$(datim$,9)
  a.a$=”Time”+right$(datim$,9)
  append
elseif kp%=%M
  pse%=1
  if len(b$)
   cnt%=cnt%+1
   print b$
   a.a$=b$
   append
   b$=””
  endif
  print “Pause”+right$(datim$,9)
  a.a$=”Pause”+right$(datim$,9)
  append
 else
  beep 200,200
 endif
 if cnt%=10
  beep 250,200
  beep 280,230
  beep 250,200
  print “10 steps with bites”
  cnt%=0
 endif
until 0
return
```

The Psion used in the study was unable to delete the data files generate by the above program. Once I the data were transferred from the Psion to a PC, the following program was run to delete the bites/steps data stored on the ‘A’ drive in the Psion.

```
Delfile:

If exist(“a:bites”)
 kstat 1
if view (2, “Delete Bites File (Y/N)”+ chr$(63))=%Y
 delete “a:bites”
endif
endif
```

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