Energy maximisation strategies of different African herbivores in a fire dominated and nutrient poor grassland ecosystem

by

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I, CHRISTOPHER BROOKE (212215043), hereby indicate that the dissertation for Magister Scientae in the Faculty of Science is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

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Abstract

Fire and herbivory are both major drivers in grassland ecosystems throughout the world. Although these two driving forces act independently from one another the relationship between fire and herbivory may be more significant than either acting on their own. Heterogeneity within the landscape as a result of fire results in herbivores having to adapt their behaviour in space and time. My research focussed on 1) characterising the fire regime on Mkambati Nature Reserve (hereafter Mkambati) and 2) determining the foraging choices and energy maximisation principles displayed by herbivores in relation to the biomass of vegetation and post fire vegetation age. Fire regimes were characterised between 2007-2016 in the low nutrient coastal grasslands of Mkambati in terms of fire season, seasonality of fire-prone weather conditions, fire return interval (FRI) and influence of poaching-related ignitions. Based on these results I then assessed foraging choices in terms of energy maximisation of four large herbivore species. I explored what energy maximisation strategy was employed, i.e. maximisation of daily digestible energy (DDE) (recently burnt low biomass vegetation) or instantaneous digestible energy (IDE) (older high biomass vegetation), by herbivore species with different morpho-physiological traits. Common reedbuck (*Redunca arundinum*), red hartebeest (*Alcelaphus buselaphus* subsp. *caama*), zebra (*Equus quagga*) and eland (*Tragelaphus oryx* subsp. *oryx*) were fitted with GPS satellite tracking collars, and hourly GPS locations (observed) were taken between 2008 and 2016. Using mixed effects models, I compared observed and an associated set of random locations to determine the energy maximisation strategy employed by each species.

Our results indicated that fires were concentrated in winter when monthly fire danger weather (FDI) was highest. The mean FRI at Mkambati was <3 years, but varied according to vegetation type, and whether censoring (for open ended FRIs) was applied to estimate mean FRIs. Poachers, with the intention of attracting ungulates, are an important source of ignition at Mkambati. Accordingly FRIs were shorter (approximately 2 years) in areas within 3 km of likely poacher entry points. Although all fires recorded at Mkambati during the study period were of anthropogenic origin, mean FRI still fell within the natural range reported for interior grasslands in South Africa. Based on these findings, underpinned by the fire regime information, I showed that red hartebeest and zebra maximised DDE inside and outside of fire seasons and frequently foraged in low biomass recently burnt grasslands. Eland generally favoured areas where they could maximise IDE outside of the fire season, however during the fire season they switched strategy to maximise DDE. Reedbuck did not maximise IDE or DDE at the same scale (patch scale) as the other species, but at a landscape (broader) scale they maximised both IDE and DDE.

Through this research I have shown how regular fire affects the foraging and energy maximisation behaviour of large African herbivores and how morpho-physiological traits affect these decisions. In response to these results I recommend that the management of Mkambati implement a focused monitoring program comparing the frequently and less frequently burnt areas of the reserve in order to understand the complex effects of anthropogenic fire and its subsequent effects on the biota of Mkambati.

Key words: anthropogenic ignitions, fire frequency, fire season, Mkambati Nature Reserve, small protected area, foraging preferences, sourveld grassland, herbivores, post-fire vegetation age, morpho-physiological traits.

Thesis layout

Through this study we sought to improve understanding of anthropogenic fire regimes on Mkambati Nature Reserve, Eastern Cape, South Africa. In understanding these fire regimes we then applied energy maximisation principles to explain foraging preferences between four large herbivore species.

Chapters have been written as independent papers for publication in different journals necessitating some repetition and non-uniform formatting. However despite the independence of each chapter they contribute toward the general theme of the thesis. The publication status of each chapter can be found below (Publications and presentations related to this research).

The layout of this thesis is as follows:

Chapter 1 provides a brief rationale and literature review expressing what is currently known about fire and herbivory in the low lying sourveld grasslands, and in particular Mkambati Nature Reserve. In essence chapter 1 provides the background and context for the studies that follow.

Chapter 2 provides an introduction and background to the study site (Mkambati Nature Reserve) and information on the focal study species.

Chapter 3 characterises the fire regime on Mkambati Nature reserve over the past ten years in terms of fire season, fire size, fire return interval and fire danger weather. As this chapter is written in the form of a descriptive study additional information is provided regarding rare and threatened species and how incorrect fire regimes may negatively affect these biota.

Chapter 4 explores the foraging preferences between four herbivore study species of different morpho-physiological characteristics on Mkambati Nature Reserve. Foraging preferences in this context is based on energy maximisation strategies that animals apply to feeding in a heterogeneous environment affected by fire.

Chapter 5 provides a synthesis and emphasises the relevance of these findings in an ecological sense. It furthermore prompts new research questions and opportunities to further our ecological understanding of these anthropogenically affected systems and provides recommendations for future management.

Publications and presentations related to this research

Details of publications that form part of the research presented in this thesis.

Scientific articles

Chapter 3: Brooke, C.F., Venter, J.A., Kraaij, T. 2018. Characterising a poacher-driven fire regime in low nutrient coastal grasslands of Pondoland, South Africa. Fire Ecology. 14(1), in press.

Chapter 4: Brooke, C.F., Fortin, F., Kraaij, T., Kalule-Sabiti, M.J., Venter, J.A. Energy maximisation strategies of different African herbivores in a fire dominated and nutrient poor grassland system. Paper is still being prepared and a target journal has not been decided on.

Conference presentations

Posters

Brooke, C.F., T. Kraaij, and J.A. Venter. 2016. Fire and ungulate dynamics in the low nutrient coastal grasslands of Mkambati Nature Reserve, Eastern Cape, South Africa. *in* Grassland Society of Southern Africa: 51st Annual Congress, Wilderness, Western Cape, South Africa.

Presentations

Brooke, C. F., D. Fortin, T. Kraaij, M. J. Kalule-Sabiti, and J. A. Venter. 2017. Foraging ecology of large ungulates in a vegetation mosaic affected by anthropogenic fire on Mkambati Nature Reserve, Eastern Cape, South Africa. Page 51 *in* South African Wildlife Management Association: Wildlife Management in the Face of Global Change, Worcester, Western Cape, South Africa.

Author contributions

C. Brooke collected, processed and analysed the data as well as designed and wrote the manuscripts. J.A. Venter and T. Kraaij conceptualized the research. J.A. Venter, T. Kraaij and D. Fortin assisted with data analysis. J.A. Venter, T. Kraaij, D. Fortin and M. Kalule-Sabiti provided valuable comments on the contents.

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CHAPTER 1: Introduction

Introduction

Understanding how regular fire affects foraging choices and energy maximisation among large herbivores is important for protected area managers, as it influences how species interact with the ecosystem (Allred et al. 2011). In Africa many large herbivores are in decline (Craigie et al. 2010) and understanding these species' interactions with their environment and anthropogenic influences is important for the long term conservation of species (Bailey et al. 1996, Owen-Smith et al. 2010).

This chapter reviews the different concepts relating to fire and its effects on energy maximisation of large herbivores, with emphasis on the coastal sour grasslands of the Eastern Cape, South Africa, and the influence of small fenced nature reserves. I describe the complex relationship between fire and herbivory and explain the importance of fire in sour grasslands and the anthropogenic influences that affect this. I introduce the concepts of foraging theory, energy maximisation and morpho-physiological adaptations of herbivores, and fire regimes. Finally I provide a rationale for the study and state my aims and objectives.

Mammalian feeding types and morpho-physiological characteristics

African ecosystems are well known for the extremely diverse large herbivore populations made up predominantly of ruminants with a small number of non-ruminants (Grange et al. 2004). This diversity has resulted over evolutionary time from facilitation and competition for resources between herbivores (Prins and Olff 1998). The terms 'grazer' and 'browser' have long been used to characterise herbivore feeding types (Clauss et al. 2008), however broad feeding types of large herbivores include grazers, mixed feeders preferring grass, mixed feeders preferring browse, and browsers (Gordon 2003). Grazers are those species that feed on monocotyledonous graminaceous (mostly C_4) plants whereas browsers are those that feed on woody and non-woody dicotyledonous (mostly C_3) plants (Codron et al. 2008). Both grazers and browsers have specialised adaptations to dealing with their chosen food sources (Clauss et al. 2008). Attributed to these feeding types herbivores have various morpho-physiological adaptations such as different digestive tracts (ruminant and non-ruminant) and mouth morphology (Gordon and Illius 1988, Gordon 2003). For example grazers, and in particular bulk grazers, have wider muzzles than browsers (Codron et al. 2008). Browsers have a narrower incisor arcade to selectively feed between branches (Clauss et al. 2008). The digestive tracts of grazers are structured to increase the retention time of forage and the salivary glands are larger than those of browsers as grasses are generally lower in nutrients than browse and thus harder to digest (Gordon 2003). Feeding in ruminants relies on the effective extraction of energy and nutrients from vegetation while maintaining a limited intake rate (Duncan et al. 1990). Alternatively non-ruminants are adapted to feeding on low quality vegetation, but need to maintain a higher intake rate as they have a faster throughput of forage (Menard et al. 2002). The selectivity among ruminants is considered to be much higher than that of non-ruminants (Bell 1971).

Body weight is another important factor affecting herbivore foraging choices. The allometric relationship between body size, metabolic rate, and gut capacity predicts that larger bodied herbivores should be able to consume lower quality vegetation (Demment and Van Soest 1985) and be better adapted to low nutrient environments (Olff and Ritchie 1998). This theory suggests that herbivores with a similar body weight are more likely to share the same niche space and experience competition (Prins and Olff 1998). Facilitation, on the other hand may occur when foraging by larger herbivores helps to remove vegetation biomass, creating a suitable habitat for smaller species that require better quality vegetation (Prins and Olff 1998).

Foraging theory and habitat selection

Optimal foraging theory (Stephens and Krebs 1986) predicts that the distribution of herbivores within an environment can be explained by the heterogeneity of resources within the landscape, and optimal digestive theory predicts that herbivores are adapted to forage in areas that yield energy and nutrients more rapidly (i.e. forage that requires a shorter retention time, Clauss et al. 2008). By foraging optimally, herbivores aim to optimize metabolic function (Owen-Smith and Novellie 1982), a foraging strategy that is most likely used in nutrient poor environments (Babin et al. 2011). The foraging behaviour of large herbivores, particularly in nutrient poor grassland, is driven by the nutrient content and biomass of vegetation (Shipley et al. 1994). The rate of nutrient consumption determines how much time needs to be invested in feeding to meet metabolic and energy requirements (Shipley et al. 1994). Smaller herbivores may be limited by the quality while larger herbivores are limited by the quantity of vegetation (Hopcraft et al. 2010). This type of habitat selection to meet metabolic and energy requirements is a fundamental process that structures the distribution and abundance of herbivores within a landscape. Smaller plants are generally more nutritious and thus should be favoured by all herbivores, whereas smaller herbivores may be limited in their ability to consume larger plants as these are unlikely to meet their energy and nutrient demands (Arsenault and Owen- Smith 2008). At a finer scale (minutes) the consumption rate and intake of energy by herbivores are limited by the spatial distribution and characteristics of vegetation, and the cropping and digestive mechanisms of herbivores (Shipley et al. 1994, Farnsworth and Illius 1998). Furthermore spatial distribution, morphological properties and nutrient concentrations of vegetation can vary seasonally within vegetation (Hopcraft et al. 2010, van den Berg et al. 2016). Resource selection functions (RSFs) may be used to study the way in which herbivores are influenced by the scale and heterogeneity of resources within habitats (Boyce et al. 2003). The RSF's that herbivores select for can be related to forage quality or quantity and can be defined as the maximisation of a foraging currency (Fortin 2003). Knowledge of the energy maximisation by herbivores can provide stronger grounds for understanding why herbivores distribute themselves within an environment (Adler et al. 2001, Hopcraft et al. 2012, Chirima et al. 2013). Thus understanding habitat section and energy maximisation in herbivores should underpin conservation management strategies, especially in anthropogenically affected systems (Venter et al. 2014a).

Functional response and energy budgets

Functional response in herbivores is the change in foraging rate that results from changes in the abundance of food (Gordon 2003). Functional response links foraging behaviour in herbivores to the abundance and quality of vegetation within a heterogeneous environment (Spalinger and Hobbs 1992). The rate at which herbivores can crop and process vegetation determines their nutrient and energy intake (Spalinger and Hobbs 1992).

Foraging goals are what drive the choices that herbivores have within a heterogonous environment (Babin et al. 2011). In this study the choices available to herbivores are expressed as two divergent foraging currencies that relate to energy budgets, i.e.: 1) herbivores can forage to maximise their instantaneous intake of digestible energy (IDE) by consuming large amounts of vegetation that allow for fast satiation, but which is often limited in its digestibility; or 2) herbivores can maximise their daily intake rate of digestible energy (DDE) by foraging on relatively smaller/immature plants that provide greater digestible energy than larger/older plants, although these smaller plants often require longer cropping times (Wilmshurst et al. 1999, Shipley 2007, Babin et al. 2011). In other words, rather than foraging on plant species that provide the fastest short-term intake rate of energy (IDE) (Owen-Smith and Novellie 1982, Belovsky 1986, Bergman et al. 2001) herbivores may extend their foraging time and select resources that are more digestible (DDE) (Fortin et al. 2002). The adoption of either of these currencies may be driven by, or require, the consumption of different plant species. Energy maximisation strategies may also change seasonally depending on the availability and quality of resources (Meissner and Paulsmeier 1995, Fortin et al. 2002). Thus the temporal and spatial complexity and heterogeneity within a habitat may result in foraging strategies that are not necessarily similar among species or constant in space and time, and may shift between energy maximisation strategies (Bergman et al. 2001).

Heterogeneity and scale

Large herbivores react to spatial patterns in the landscape, especially topography and distribution of forage (Bailey et al. 1996). Thus considering the scale at which to measure foraging in a heterogeneous environment is important as herbivores vary their use of resources within the landscape (Bailey et al. 1996). Scales that herbivores forage at are defined by the boundaries between vegetation units, foraging and ecosystem processes and herbivore behaviour (Senft et al. 1987). The spatial scales that herbivores can choose range between a bite (physical movement of the tongue and jaw), feeding station (placement of the front feet), patch (reorientation to a new location defined by a break in foraging), feeding site (short period of time spent feeding), camp (central area where animals drink and rest over a period of hours or days), and home range/landscape (the entire area where an animal can be found) scale (Senft et al. 1987, Bailey et al. 1996). At bite and patch scale herbivores are given the choices of what to forage for within their direct vicinity (i.e what plant species to select within a patch of vegetation, Senft et al. 1987) whereas at greater spatial scales such as a landscape scale herbivores can show their relative preference for plant communities within a much larger area (Senft et al. 1987, Owen-Smith et al. 2010). Resource selection at these different spatial scales is thus a major driver in the foraging activities of herbivores (Venter 2014).

Predation

In addition to finding suitable quality forage, herbivores need to avoid becoming prey to predators (Creel et al. 2005, Fortin et al. 2005, Creel et al. 2008, Ferrari et al. 2009). The potential risks of foraging in areas that cannot offer suitable protection results in herbivores avoiding these areas, especially smaller species (Hopcraft et al. 2010, Burkepile et al. 2016). To avoid becoming prey to predators herbivores display a variety of anti-predation behaviours that relate to the direct or indirect threat of predation (Creel et al. 2008). Anti-predation effects include altering ones habitat (Fortin et al. 2004), foraging behaviour and gregariousness (Valeix et al. 2009). Predator avoidance behaviour may have an influence on environmental heterogeneity, the spatial distribution and behaviour of herbivores (Fischhoff et al. 2007, Thaker et al. 2011). Herbivores may choose to ignore the risks of predation and rather focus on the quality of resources in the landscape (Prins 1996, Ferrari et al. 2009). Alternatively they may respond to predation by avoiding high risk areas (Creel et al. 2005, Fischhoff et al. 2007). Predation on mammals in the eastern part of the Eastern Cape occurs mainly in the form of bush meat poaching by humans (De Villiers 2002). Unfortunately bush meat is becoming more accessible to local communities due to the increase in firearms, transport and technology in these areas (Hayward et al. 2005).

Fire regimes

Within Africa, ‘the fire continent’ (Archibald et al. 2010), fire is an essential ecosystem process (Bond et al. 2005). Fire regimes can be defined as the average fire conditions occurring over a defined period of time (Gill 1975, Brooks and Zouhar 2008, Chuvieco et al. 2008) in terms of frequency, seasonality, size and type (Gill 1975), whereby individual fire events contribute to the overall fire regime (Van Wilgen et al. 2010). However, in many of these ecosystems fire regimes have been altered by anthropogenic interference (de Klerk et al. 2012). Dynamics that influence fire regimes and thus the probability in time of a given area burning include fuels, topography, weather conditions, ignition rates, anthropogenic influences such as fire management effort (Archibald et al. 2009, Fernandes et al. 2012), and grazing regimes which interact with fuels (Govender et al. 2006, Fuhlendorf et al. 2009, Ladbrook 2015). On the other hand, fire is a significant agent of disturbance with profound effects on ecosystem functioning, structure and composition (Bond and Keeley 2005). Understanding fire regimes is thus important as it may assist to mitigate negative effects often associated with anthropogenic fire

(Chuvieco et al. 2008), and to inform the management of fire and herbivory as these processes are interrelated (Morgan et al. 2001).

Fire in sourveld grasslands

Grass dominated systems (grasslands and savannas) cover approximately 40% of the earth's land surface area (Breman et al. 2012) and account for roughly two-thirds of the vegetation in South Africa (Mucina and Rutherford 2006). High seasonal rainfall in grasslands typically allows rapid accumulation of fine fuels resulting in some of the shortest fire return intervals (often <2 years) on earth, which may be shortened further by anthropogenic ignitions (Archibald et al. 2010, Bond and Parr 2010). In sour grasslands, in particular, fires tend to be more frequent in the dry season (winter) when fire danger conditions are at their highest and grass curing result in accumulation of dead fuels (Van Wilgen et al. 2000). Large quantities of fine, flammable fuels make these sour grasslands highly adaptable to changing weather conditions, thus strongly influencing grassland fire regimes (Cheney and Sullivan 2008, Bond and Parr 2010).

Historically within Highveld grassland systems in South Africa, high fuel loads as a result of high rainfall and rapid vegetative growth, and an abundance of lightning strikes have allowed for frequent fires, roughly every two to four years (Cowling et al. 2003), especially during the dry winter months (Koerner and Collins 2014). Many grassland species are adapted to fire, surviving fire via resprouting and/or displaying fire-stimulated flowering (Van Wilgen and Forsyth 2010), and are thus reliant on fire for persistence (Van Wilgen et al. 2010). Although fire is ecologically important in sourveld grasslands, there has been little research into fire ecology in the coastal grasslands of the Eastern Cape despite this area being an internationally important hotspot for biodiversity, i.e. the Maputaland-Pondoland-Albany biodiversity hotspot (Conservation International Southern African Hotspots program 2010). Current information suggests that fire regimes in these grasslands (Van Wilgen and Forsyth 2010) are comparable to those in other grassland types on the high lying interior of South Africa (Mucina et al. 2006), with fires occurring at one to four year intervals and mostly in late winter when humidity is low, vegetation is dry and wind speeds are high (Mucina et al. 2006, Van Wilgen and Forsyth 2010).

At Mkambati Nature Reserve (hereafter referred to as Mkambati) fires are not limited by the availability of fuel and fire-prone weather conditions (Shackleton 1989), as may be the case in some other vegetation types in the interior of South Africa (Bond and Archibald 2003, O'Regan 2007). Rather fires are limited by the availability of ignitions. This suggests that human-caused ignitions, such as those associated with poaching, may play an important role at Mkambati (Van Wilgen et al. 2010), a potential problem directly related to the proximity and density of human settlements (Syphard et al. 2007). Frequent fires in grassland vegetation types in Mpumalanga do not appear to have profound effects on grassland community composition, with the exception of areas that have been previously disturbed (Bachinger et al. 2016), indicating that the vegetation composition in South African grasslands may be relatively independent of fire frequency (Uys et al. 2004, Bachinger et al. 2016). Within Mkambati, grassland fires temporarily stimulate new grass growth with higher nutrient contents (Shackleton 1989, Venter et al. 2014a). This increase in the nutritional value of vegetation may cause a temporary shift in regional herbivore abundance as certain species favour new vegetative growth (Shackleton 1989, Venter 2014, Venter et al. 2014b, Green et al. 2015).

Fire and herbivory

Fire and herbivory are both major drivers in ecosystems throughout the world and their interactions play a crucial role in establishing and maintaining grassland and savanna environments (Allred et al. 2011) as well as the abundance and composition of vegetative species (Archibald and Bond 2004, Burkepile et al. 2016). Burning affects grazing by influencing the amount and quality of forage available to herbivores (Archibald and Bond 2004, Parrini and Owen- Smith 2010), and herbivory affects the quantities and patchiness of vegetation that fuel fires (Archibald et al. 2005). Although fire and herbivory act independently of one another the relations between these drivers may be more ecologically significant than each acting alone. Thus grazing by fire (the interactions between fire and herbivory) can be defined as 'pyric herbivory' (Fuhlendorf et al. 2009, Allred et al. 2011). Pyric herbivory occurs most often in areas where frequent fires produce palatable fire adapted species, for example couch grass (*Cynodon dactylon*) in Bontebok National Park (Novellie and Kraaij 2010). When fire occurs in patches in the landscape, herbivores will preferentially select these younger, nutrient rich patches of vegetation (Biondini et al. 1999, Tomor and Owen-Smith 2002, Watson et al. 2005, Sensenig et al. 2010, Allred et al. 2011) provided there is enough green regrowth (Parrini and Owen- Smith 2010), competing for highly palatable (Shackleton and Mentis 1992, Biondini et al. 1999, Parrini and Owen- Smith 2010) and limited food resources (Tomor and Owen-Smith 2002). Even with competition for these food resources in the savannas of West Africa, different weight herbivores did not differentiate between how they used post fire regrowth (Klop et al. 2007). These fire grazing interactions are dynamic in space and time and are continually shifting and creating heterogeneity within the landscape (Allred et al. 2011). Nutrient rich post fire patches may also be prolonged by the presence of herbivory (Biondini et al. 1999, Kraaij and Novellie 2010). Heterogeneity in the landscape and the constant shifting of herbivores to follow the occurrence of fire is known as the 'magnet effect' (Archibald et al. 2005). Herbivores need to be able to adapt their behaviour to the heterogeneity caused by fire both spatially and temporally (Archibald and Bond 2004). Heterogeneity between burnt and unburnt grass could provide the greatest benefit to herbivores by partitioning grazing between recently burnt and older more moribund vegetation (Parrini and Owen- Smith 2010).

In grassland ecosystems these relationships between fire and herbivory play a key role in the distribution of nutrients within the landscape, and the cycling of these nutrients (Archibald and Bond 2004). The frequency of fire may also have an effect on herbivore population growth, especially in nutrient poor vegetation (Watson et al. 2005). For instance in Gamka Mountain Nature Reserve in the Western Cape 80% of Cape mountain zebra (*Equus zebra zebra*) population growth occurred within the first three years after fire (Watson et al. 2005). Once grasses are dominant, resulting from frequent fire, biotic (grazing) and abiotic (fire) factors are responsible for maintaining biomass and recycling of nutrients and energy (Govender et al. 2006, Ladbrook 2015). In Kgaswane Mountain Reserve in the North-West Province sable (*Hippotragus niger*) herds preferred recently burnt vegetation throughout the dry season, provided there was enough green vegetation (Parrini and Owen- Smith 2010). Changes in vegetation structure resulting from fire thus influence the distribution and availability of habitats available to herbivores and more generally the functioning of ecosystems (Baker 1992).

In high rainfall systems grazing pressure is often too low to prevent the rapid build-up of moribund vegetation and thus fire is essential for recycling nutrients (Sensenig et al. 2010, Venter et al. 2014a). Rapid growth allows plants to invest in structural support and protection against herbivory (Hopcraft et al. 2010). Thus the incidence of fire results in a vegetation mosaic of highly nutritious newly burnt patches of vegetation interspersed with older more moribund material (Shackleton and Mentis 1992, Venter et al. 2014a). In addition to fire, vegetation mosaics are driven by a number of other abiotic (rainfall, Archibald and Bond 2004) and anthropogenic (poaching and management practices, Oneka 1990, Archibald and Bond 2004) disturbances. When fire occurs is also important, if fires occur too early in the dry season, limited biomass might not be able to sustain herbivores throughout winter (Parrini and Owen-Smith 2010). Environmental heterogeneity and the spatial distribution of large herbivores within an environment thus result from disturbances from fire, predation, and the competition amongst herbivores.

Management of fire and herbivory

Landscape scale conservation efforts that relate to herbivory in grazing ecosystems often revolve around the management and reintroduction of herbivorous species (Fuhlendorf et al. 2009). This species-centric approach often works well for the conservation of herbivores within simple systems, but fails to adequately incorporate natural disturbance regimes such as fire (Donlan 2005, Fuhlendorf et al. 2009). A good example of managing the fire regime to ensure the longevity of both herbivores and vegetation is that of Bontebok National Park where certain areas of the park were burnt using frequent fire return intervals to promote grazing, while others were burnt less often to promote fynbos vegetation (Kraaij and Novellie 2010, Novellie and Kraaij 2010). An understanding of the combined dynamics and effects of fire and herbivory is essential for natural resource managers in small fenced reserves (Venter et al. 2015). In turn, these dynamics can influence the capacity of an environment to sustain herbivore populations (Watson et al. 2005, Novellie and Kraaij 2010).

Protected areas and their management

Humans have long set aside areas of land with the intention of conserving nature in its various forms (Hansen and DeFries 2007, Vačkář et al. 2016), an area that now covers approximately 11.5% of the earths land surface (Rodrigues et al. 2004). Within South Africa, conservation and the creation of protected areas have resulted in a large number of small fenced nature reserves, with the intention of safeguarding important species and biodiversity, but which also prevents the uninhibited movement of species within their natural home ranges (Newmark

2008). In addition to protected areas there are also a large number of private game ranches that serve a similar purpose (Lindsey et al. 2009).

Protected areas are an effective tool for protecting wildlife (Balmford et al. 1995), however managers of these areas face a great deal of challenges in understanding and conserving biodiversity features (Venter et al. 2008). The challenges facing protected areas include alien plant and animal invasions, uncontrolled fires, bush encroachment, artificial water sources, dam building, disease, erosion, land invasion by humans, land use change, solid waste management, mining, isolation, poaching, purposeful species eradication, resource utilization, siltation and tourism (Venter 2014). Thus the adaptive management of protected areas is becoming ever more important to achieve desired management outcomes (Venter et al. 2008), especially as this varies between objectives and protected areas. Adaptive management allows managers to manage protected areas within predetermined thresholds of potential concern (TPC), i.e. the ability to measure if a management action needs to be adapted or not (Venter et al. 2008, Biggs et al. 2011). Social and biophysical sciences are critical in the formulation of TPCs as an in-depth socio-ecological understanding forms the cornerstone of its implementation. Furthermore protected area managers cannot be expected to understand the meaning of such thresholds without a link between a social and ecological understanding of the functioning of the environment (Biggs et al. 2011, Venter 2014). Adaptive management has been applied and TPCs developed relating to the management of fire and herbivory in certain protected areas in South Africa (for example in Bontebok National Park, Van Wilgen et al. 2011). Within small fenced nature reserves understanding how species vary their behaviour to meet a number of biological needs while coping with anthropogenic influence should form a key concept in the management of herbivores (Venter et al. 2014a, Venter et al. 2015).

Rationale

Herbivores foraging in a heterogeneous environment are faced with a number of choices related to finding enough high quality food (Owen-Smith et al. 2010) especially in low nutrient grasslands. Conflicting demands when herbivores are foraging may lead to changes in resource use across seasons (Fortin et al. 2003) and between post fire patches (Archibald and Bond 2004). Information regarding how fire drives habitat selection and energy maximisation in low nutrient coastal grasslands is inadequate. Understanding the importance of fire ecology in the low nutrient coastal grasslands of the Pondoland centre of plant endemism and how it relates to foraging in herbivores is important for conservation. However little is known about the fire ecology of this area (Van Wyk and Smith 2001).

This study was undertaken on a small fenced nature reserve in the coastal grasslands of southern Africa where herbivores are faced with the challenge of securing enough energy and nutrients from nutrient poor grasslands within a heterogeneous environment. Mkambati provided the ideal opportunity to study anthropogenic fire and energy maximisation principles in large herbivores (and the interactions therein) and how this influences their foraging behaviour when faced with a variety of foraging choices. Ideally Mkambati provided one of few areas of untransformed habitat in the Eastern Cape available for study. Most fires at Mkambati are caused by anthropogenic ignitions associated with poaching (Shackleton 1989, Van Wilgen and Forsyth 2010) which furthermore enabled an investigation into the effects of anthropogenic influences on the fire regime. Large free ranging herbivores are found throughout the reserve, and Venter et al. (2014a) have examined how red hartebeest and zebra vary their utilization of patches and post fire vegetation. However the energy maximisation strategies applied by different herbivores with different morphology within this heterogeneous environment are not known.

Aims and objectives

The overall aim of this study was to understand habitat selection and energy maximisation of large herbivores and how regular anthropogenic fire drives these choices in low nutrient coastal grasslands. Therefore chapters 3 and 4 had the following objectives:

Chapter 3

To characterise the fire regime in the coastal sourveld grasslands of Mkambati over the past ten years in terms of frequency, seasonality, size and potential importance of anthropogenic sources of ignition.

a. To characterise the fire regime on Mkambati we intend to provide a basic understanding of fire which would be used to study the role of fire in large herbivore feeding.
b. To consider whether the fire regime in this coastal sourveld system differs from that in the more extensive interior Highveld grassland systems of South Africa and consider potential biodiversity implications.

Chapter 4

To understand foraging choices between four large herbivore species with differing traits (i.e. body mass, digestive strategy and mouth morphology) by considering their energy maximisation strategies at Mkambati.

a. To assess whether choices in foraging currencies are driven by fire, biomass of vegetation and vegetation type and compare these choices inside and outside of the fire season.
b. To explore how morpho-physiological traits enable herbivores to forage successfully in the low nutrient coastal grasslands.

Summary

Chapter one outlined the important relationships between fire and herbivory in a broad context as well as its significance in grassland ecosystems. Furthermore I looked at each of the concepts (fire in sourveld grassland, functional response and energy maximisation), independently. I gave insight into different herbivores' foraging within a heterogeneous environment by explaining the basic principles of mammalian feeding types, morpho-physiological adaptations and how these enable efficient feeding. Finally I gave a rationale as to why this study was needed and indicated my aims and objectives for this study.

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CHAPTER 2: Study site and species

Introduction

This chapter provides a detailed description of Mkambati Nature Reserve, specifically in terms of climate, vegetation, geology and soils and herbivory. In this chapter we also provide descriptions of the focal herbivore species in this study, namely; common reedbuck, red hartebeest, plains zebra and common eland.

Study site

The study site is Mkambati Nature Reserve (hereafter Mkambati), situated in the eastern part of the Eastern Cape (former Transkei). The former Transkei stretches approximately 250km along the southeast coast of South Africa from the Great Kei River in the south to the Mtamvuna River along the border of KwaZulu-Natal in the north (De Villiers and White 1999), and is dominated by communal farm land (Pfeiffer 2016). Prior to the 1994 democratic election in South Africa the Transkei was governed by self-rule (Pfeiffer 2016). Mkambati provided the ideal opportunity to study how regular anthropogenic fire influenced forage selection and energy maximisation in large herbivores in a small fenced nature reserve. Herbivores in this environment are faced with a variety of foraging choices in a constantly changing environment as a result of regular anthropogenic fire. Mkambati is a small (7 700ha) fenced provincial nature reserve (31.26°S and 29.99°E) situated within the northern Pondoland region of the Eastern Cape, and located within the Indian Ocean Coastal Belt Biome (Mucina et al. 2006, Venter et al. 2014a, Venter and Kalule-Sabiti 2016). Mkambati is managed by Eastern Cape Parks and Tourism Agency under a land claim settlement agreement with the local Mkambati community as the land owners (Kepe 2004). Mkambati falls within two important biodiversity areas 1) Maputaland-Pondoland-Albany biodiversity hotspot (Conservation International Southern African Hotspots program 2010, Perera et al. 2011) and 2) the Pondoland centre for plant endemism (Van Wyk 1996) which is one of 235 internationally important sites identified for their unique combination of rare and endemic plant species (De Villiers and Castello 2013). There is an abundance of water in the form of streams and wetlands (Venter et al. 2014a). The reserve is bordered on three sides by natural boundaries, i.e. the coastline to the southeast, the Mtentu River to the northeast and the Msikaba River to the southwest (Shackleton 1989, Venter et al. 2014a) with the only unnatural boundary being a fence line inland to the northwest (Shackleton 1989).

Climate is mild subtropical with high annual rainfall (1200mm annually, Figure 1A) and relatively high humidity (Figure 2A) (Shackleton 1989). Rainfall can be expected throughout the year with the highest mean rainfall occurring in March and the driest months being June to August (Shackleton et al. 1991). Average daily temperatures ranged from 18°C in winter and 22°C in summer (Figure 2B) (Venter et al. 2014a). The small differences in temperature between winter and summer on the reserve can be attributed to the warm Agulhas oceanic current that runs along the east coast of southern Africa (De Villiers and Castello 2013).

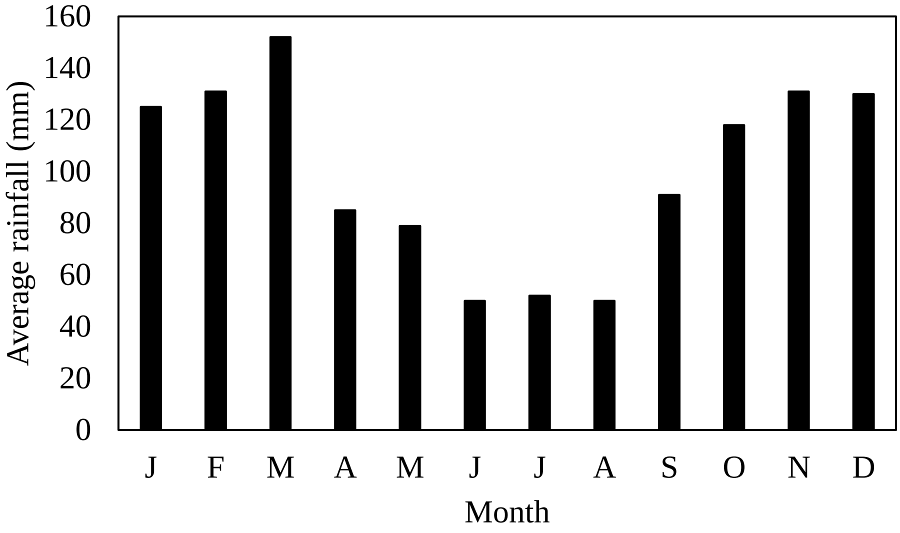

Figure 1: The average monthly rainfall for Mkambati Nature Reserve over the course of a 65 year period (Shackleton 1989).

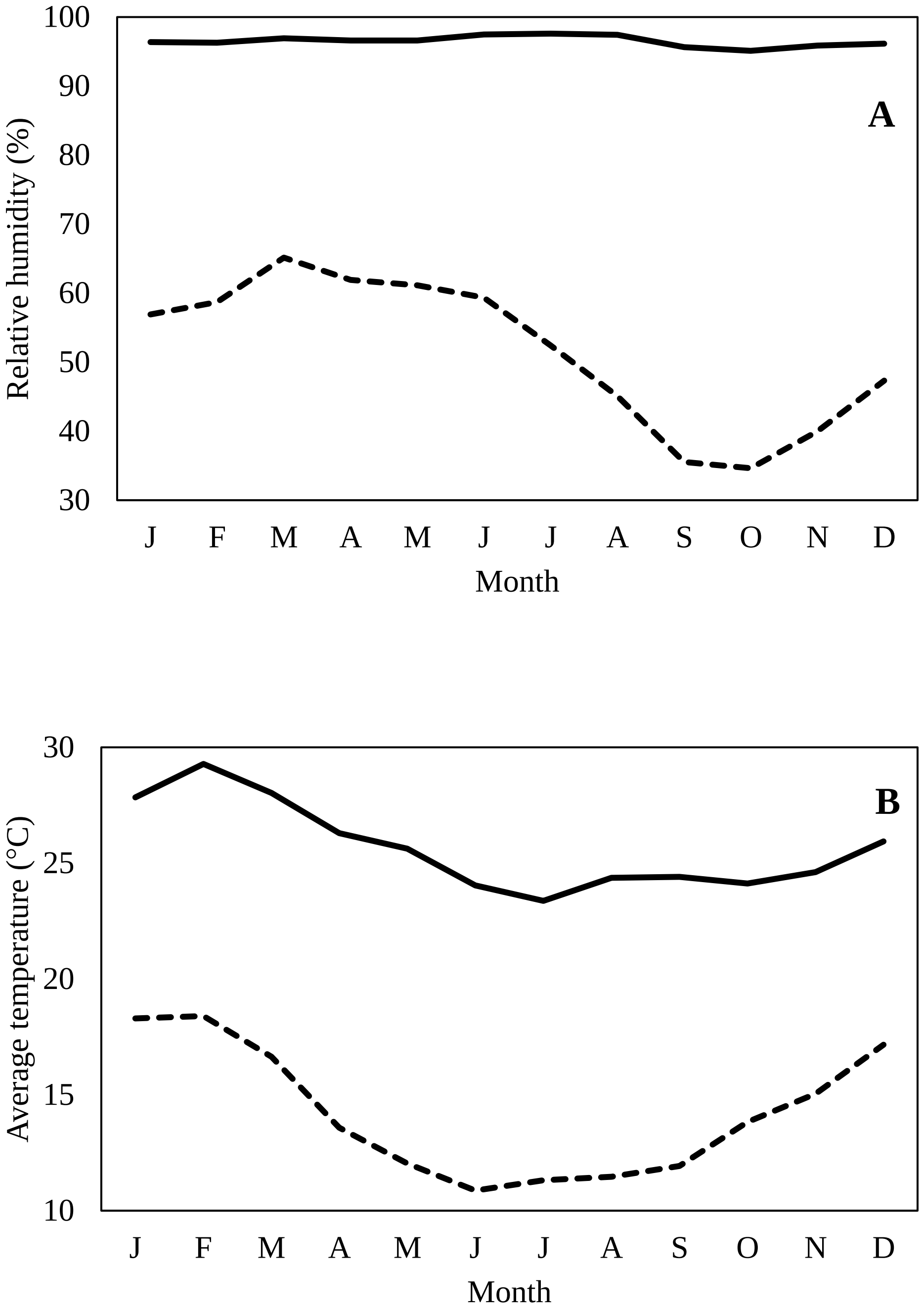

Figure 2: Records of, A) the average maximum and minimum relative humidity and B) the average maximum and minimum daily temperature (recorded as a percentage) from 2007 to 2016. The solid lines are maximum relative humidity and temperature, whereas the dotted lines are minimum relative humidity and temperature. The average temperatures and humidity are from Port Edward (30 km to the north east of Mkambati, South African Weather Service).

Vegetation

Vegetation of Mkambati is dominated by Pondoland-Ugu Sandstone Coastal Sourveld (<80%) interspersed with patches of forests, wetlands and rocky outcrops (Mucina et al. 2006). However the more detailed classification of the vegetation at Mkambati identified six distinct grassland communities and 11 vegetation communities in total on the reserve (Figure 3A, Shackleton 1989). Of these grassland communities *Tristachya leucothrix - Loudetia simplex, Themeda triandra – Centella asiatica* and *Aristida junciformis - Helichrysum mixtum* communities make up the short grasslands; *Festuca costata - Albuca setosa* and *Cymbopogon validus - Digitaria natalensis* communities make up the medium grasslands and *Stoebe vulgaris - Athanasia calva* make up the short shrub-grassland communities (Shackleton 1989).

Prolific vegetative growth results in the production of large quantities of moribund material, even with heavy grazing (Shackleton 1990, Venter et al. 2014a) and as a result of this prolific growth vegetation is low in nutrients. High levels of rainfall and soil leaching also contribute to the low nutrient levels of the vegetation (Mucina et al. 2006, Hopcraft et al. 2010). Fire and herbivory are both important for limiting biomass accumulation and stimulating the rejuvenation of vegetation (Archibald et al. 2005, Van Wilgen and Forsyth 2010). In these grasslands fire stimulates a short term spike (for the first six months after fire) in nutrients when crude protein increases from 4.6% - 8.6%, phosphorous from 0.01 - 0.05% and dry matter digestibility from 27.1 - 38.6% (Shackleton and Mentis 1992). Frequent fire causes a dynamic landscape matrix of low nutrient moribund material interspersed with recently burnt nutritious patches of young vegetation (Venter et al. 2014a). The majority of fires on the reserve are ignited by poachers with the intention of attracting herbivores into areas close to the reserve boundaries and in the more remote sections of the reserve where herbivores are easier to poach (Venter 2014).

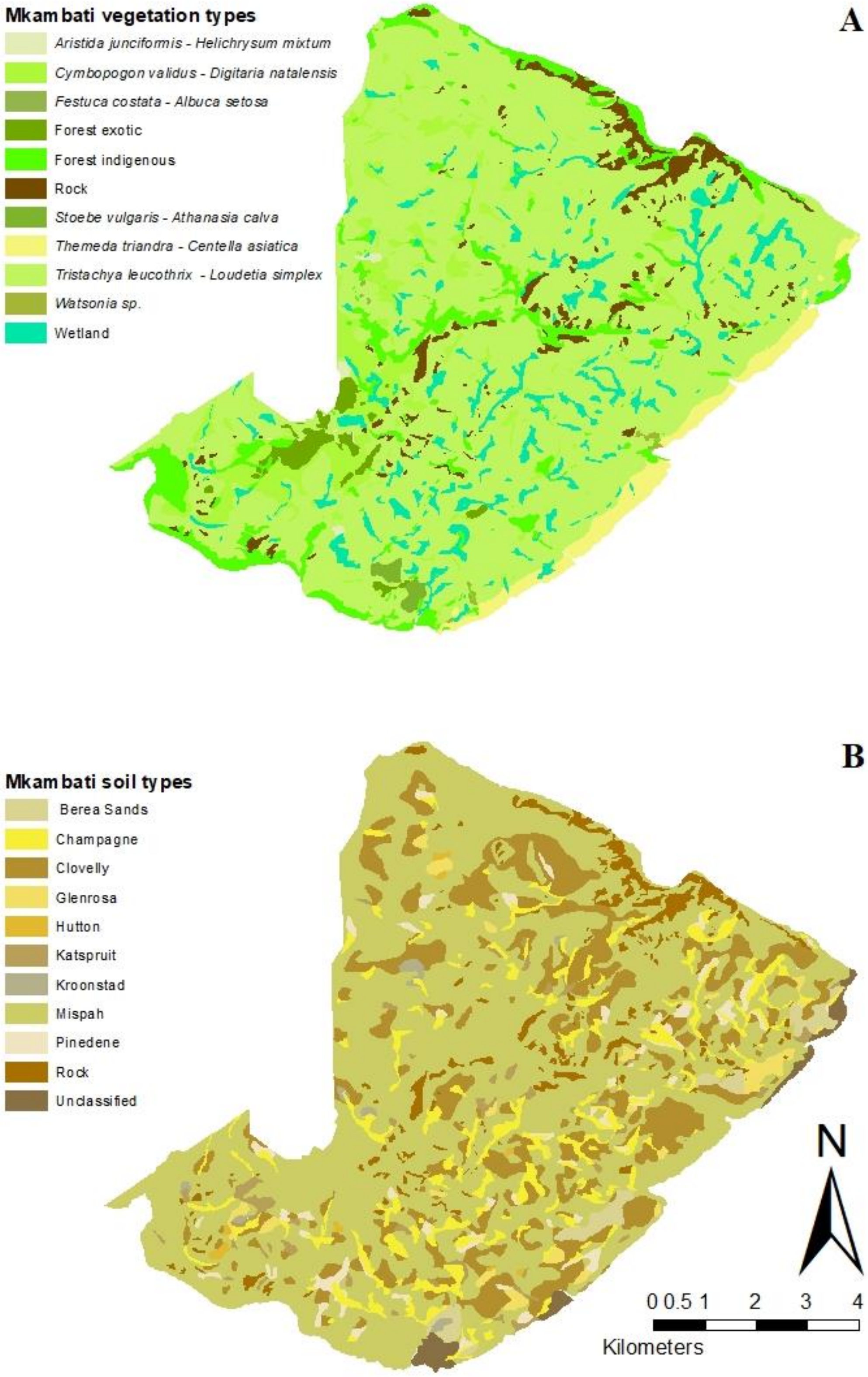

Figure 3: The, A) vegetation and, B) soils of Mkambati Nature Reserve (Shackleton 1989).

Geology and soils

The Pondoland-Ugu Sandstone Coastal Sourveld is strictly characterised by the underlying geology (Mucina et al. 2006). Geology of Mkambati is dominated by Msikaba Formation sandstones (a narrow sandstone belt approximately 20km wide stretching from Port St Johns in the south to Margate in the north along the coast, Fisher et al. 2013) that formed during the Devonian Period (385 - 359 million years ago, Mucina et al. 2006, Fisher et al. 2013). Msikaba Formation sandstones are part of the broader Cape Supergroup (Fisher et al. 2013). The historic geological shifting of the Msikaba Formation has given rise to the stepped landscape along the coastline (Fisher et al. 2013). Dolerite intrusions characteristic of the Msikaba Formation can be found throughout the reserve (De Villiers and Castello 2013). The resulting soils that dominate the reserve are Mispah (65%), Clovelly (16%), Champagne (7%) and Pinedene (2%, Figure 3B, Shackleton 1989).

Herbivory

Mkambati was established in 1977 prior to which the area was used by local communities for grazing by livestock (Venter et al. 2014b). In 1979, Mkambati was converted into a hunting ranch where a total of approximately 1344 large herbivores were introduced with the aim of being hunted by international clientele, however this economic venture failed (Skead 2007, Venter et al. 2014b). Approximately 30% of the animals died shortly after introduction, these deaths were attributed to “stress and starvation” (Venter et al. 2014b). The majority of species that went extinct shortly after introduction were browsers and included impala (*Aepyceros melampus*), gemsbok (*Oryx gazelle*), and giraffe (*Giraffa Camelopardalis*) (Venter et al. 2014b). Springbok (*Antidorcas marsupialis*) survived longer but eventually died out and a small population of greater kudu *(Tragelaphus strepsiceros)* still remains on the reserve (Peinke and Gerber 2016). Mkambati was subsequently declared a nature reserve. In 2002, a culling program began on the reserve to regulate the population sizes of species, and ultimately to remove those species from the reserve that were not considered to be indigenous (Venter et al. 2014b). At Mkambati there are currently several large herbivore species (Table 1, Peinke and Gibisela 2013), but no large predators.

Poaching is the main form of predation on large herbivores on Mkambati. However there are also a small population of black-backed jackal (*Canis mesomelas*) (Peinke and Gerber 2016).

Poachers enter the reserve by crossing the Mtentu or Msikaba rivers, and use various means of hunting, including rifles, dogs and snares (Venter 2014). As a result of this anti-poaching field patrols are undertaken throughout the reserve (Venter 2014).

Table 1: Study species and population sizes of herbivores present on Mkambati Nature Reserve during the 2016 (most recent) game census. The game census comprised three counts over the course of two days (Peinke and Gerber 2016).

Species	Mean ± standard deviation
Blesbok (*Damaliscus pygargus phillipsi*)	65 ± 7
Bushbuck (*Tragelaphus scriptus*)	7 ± 4
Common duiker (*Sylvicapra grimmia*)	0 ± 1
Eland (*Tragelaphus oryx*)	100 ± 7
Kudu (*Tragelaphus strepsiceros*)	7 ±4
Red hartebeest (*Alcelaphus buselaphus camaa*)	386 ± 7
Common reedbuck (*Redunca arundinum*)	29 ± 6
Plains zebra (*Equus quagga*)	222 ± 4

Study species

Four large herbivore species were selected for this study based on different traits, i.e. feeding type, digestive strategy and muzzle width. Red hartebeest, zebra and common eland were introduced but are considered native to the reserve, whereas common reedbuck have always occurred on Mkambati.

Common reedbuck *(Redunca arundinum)*

Common reedbuck (*Redunca arundinum,* Boddaert, 1785) is a relatively small (51kg) ungulate and is one of two species in the genus *Redunca* and the only one found in southern Africa (Skinner and Chimimba 2005). Common reedbuck (hereafter reedbuck) are listed as least concern according to the IUCN (International Union for the Conservation of Nature) Red list of threatened species. Reedbuck are predominantly grazers feeding almost entirely on C_4 grasses (Gagnon and Chew 2000, Sponheimer et al. 2003). However reedbuck on Mkambati have shown significantly different foraging preferences from other areas indicating only a 55% intake of C_4 grasses with the rest of their diet being made up of C_3 grasses, sedges and forbs (Venter and Kalule-Sabiti 2016). Reedbuck largely occur in open floodplain or drainage line grassland where vegetation is tall enough to hide them from potential predators (Skinner and Chimimba 2005, Estes 2012, du Plessis et al. 2016), and their home ranges vary from 0.8 km^2 in adult males to 1.23 km^2 in adult females (Howard 1983). After disturbance events such as fire, reedbuck may be drawn out into open areas to feed on new growth (Estes 2012), however severe fires will lead to reedbuck fleeing the area until suitable vegetation and cover have recovered (du Plessis et al. 2016). Reedbuck show a distinct lack of endurance when evading predation in comparison to other ungulate species and as a result are commonly predated upon (Estes 2012). Reedbuck exhibit a number of antipredator strategies, the most significant of which is whistling, alternatively they will crouch and slowly move to dense vegetation undetected (Skinner and Chimimba 2005, Estes 2012). Reedbuck are hunted commercially as well as poached for bush meat, and although not known, the impact of hunting is not thought to be severe, whereas poaching may have more severe effects on reedbuck populations (du Plessis et al. 2016).

Red hartebeest *(Alcelaphus buselaphus* subspecies *caama)*

Red hartebeest (*Alcelaphus buselaphus* subspecies *caama*, Pallas, 1776) is one of two species in the *Alcelaphus* genus and have several recognised sub-species (Skinner and Chimimba 2005). Red hartebeest are prolific throughout much of Africa (approximately 130 000 animals) and the population is still experiencing growth, and as a result they are listed as Least Concern according to the IUCN Red list of threatened species (Venter and Child 2016). In southern Africa red hartebeest are predominantly found in the grasslands and savannas of Namibia, Botswana, Zimbabwe and South Africa (Skinner and Chimimba 2005). Red hartebeest is a medium sized (150kg) ungulate (Skinner and Chimimba 2005) and a selective grazer that feed on medium height grasslands (Venter and Child 2016) and are known to make use of browse under conditions when resources are limited (Murray and Brown 1993, Venter 2014). At Mkambati red hartebeest frequently foraged on new high quality vegetation soon after fire and tended to spend more time in these grasslands compared to older vegetation (Venter et al. 2014a). Within Mkambati, C_4 grasses make up 87% of red hartebeest diet (Venter and Kalule-Sabiti 2016). As a result of the shape of their muzzle, red hartebeest are able to feed selectively on new plant growth between moribund vegetation, thus creating "feeding holes" in dense stands of vegetation (Schuette et al. 1998). Red hartebeest are utilized by a number of predator species including humans and as a result show a variety of anti-predatory behaviours, including snorting, stamping, style trotting and stotting (Estes 2012). This species is used widely in live game sales throughout southern Africa and is widely used for hunting, both for bushmeat and recreationally as the meat is high quality (Gosling and Camellini 2013).

Plains zebra (*Equus quagga*)

Plains zebra (*Equus quagga,* Boddaert, 1785) is a large (320kg) bulk grazer (Skinner and Chimimba 2005) and is one of four species in the genus that form part of the family *Equidae* (Bronner et al. 2003). Plains zebra (hereafter zebra) occur throughout most parts of southern Africa and have frequently been introduced onto private farms (Skinner and Chimimba 2005). As a result of these introductions and an increasing population (approximately 660 000 individuals in 2002) zebra are listed as Least Concern by the IUCN Red list of threatened species (Stears et al. 2016). Zebra are gregarious and highly social with herds containing a stallion and a number of mares and their foals. It is not uncommon for these herds to exceed 50 animals. Zebra are highly adaptable and utilise a wide variety of both savanna and grassland habitats, in which they feed on both long and short grass types (Hack et al. 2002). They are water dependent and thus the distribution of water within the landscape influences their habitat selection (Skinner and Chimimba 2005, Stears et al. 2016). Zebra are non-ruminants (Stears et al. 2016) and predominantly consume C_4 grasses, making up 89% of zebra diet within Mkambati (Venter and Kalule-Sabiti 2016). Zebra are far more tolerant of large quantities of low quality vegetation because of their digestive system, but compensate for this lack of quality by consuming large quantities of vegetation (Okello et al. 2002). Zebra are largely affected by the sward height of vegetation and tend to avoid grass shorter than 10 cm (Arsenault and Owen- Smith 2008). Zebra are threatened by a number of predatory species including humans. Habitat encroachment by cattle, habitat loss and illegal hunting all contribute to localised population declines (Stears et al. 2016). When a potential predator approaches males will attempt to chase a predator away from a harem, whereas females will attempt to defend young by encircling them within the group. (Estes 2012).

Common eland (*Tragelaphus oryx* subspecies *oryx*)

Common eland (*Tragelaphus oryx* subspecies *oryx*, Pallas, 1766) is a large (700kg) ungulate (Skinner and Chimimba 2005) that belongs to the tribe *Tragelaphini* (spiral-horned antelope). *Tragelaphus* are made up of three sub-species of which the common eland occurs furthest south (i.e. in southern Africa, Skinner and Chimimba 2005). Eland are listed as Least Concern by the IUCN Red list of threatened species as a result of an increasing population comprising between 35 000 and 45 000 individuals (Buijs et al. 2016). Eland have been described as variable feeders, but favour browse (Watson and Owen- Smith 2000, Buijs et al. 2016). Within Mkambati, eland feed predominantly on C_3 plants, with only a small percentage (21%) of their diet comprising C_4 plants (Venter and Kalule-Sabiti 2016). Due to their varied foraging behaviours and water independence eland are able to make use of a wide variety of habitats (Watson and Owen- Smith 2000). In search of high quality browse eland move long distances in search of adequate forage (Buijs et al. 2016). Eland show very little anti-predation behaviour, except for cows with young, and will readily flee from predators. Eland cows will vigorously defend their young alone or in groups (Estes 2012). Eland face imminent threat from poaching as their meat is considered to be of very good quality, and this has led to their exploitation in many areas (Skinner and Chimimba 2005). Poaching and habitat loss have resulted in large population declines in the past, however wildlife ranching and reintroductions ensure the current population remains stable (Driver et al. 2012, Buijs et al. 2016).

Summary

This chapter provided a detailed review of Mkambati Nature Reserve in terms of the climate, vegetation, geology ad soils and herbivory. Furthermore a description was provided for the four study species, namely reedbuck, red hartebeest, zebra and eland which include their taxonomy, IUCN red listing, feeding behaviour, threats and predator avoidance strategies. The description of the study species is pertinent for chapter 4 of this study.

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CHAPTER 3: Characterising a poacher-driven fire regime in low nutrient coastal grasslands of Pondoland, South Africa

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Abstract

Understanding fire regimes in the coastal region of the Pondoland centre of plant endemism, (Eastern Cape, South Africa) is of critical importance, especially in areas where anthropogenic ignitions influence the fire regime. We characterised the fire regime (2007-2016) of Mkambati Nature Reserve (9200 ha) in terms of fire season, seasonality of fire-prone weather conditions, fire return interval (FRI) and influence of poaching-related ignitions. Fires were concentrated in winter when monthly fire danger weather (FDI) was highest. The mean FRI at Mkambati was <3 years, but varied according to vegetation type, and whether censoring (for open ended FRIs) was applied. Mean estimated FRIs were 2.6-3.1 years in the majority of grassland types ('Merged grasslands'), 5.6-8.0 years in 'Forest' and 9.0-44.4 years in *Themeda triandra* grasslands respectively. Poachers, with the intention of attracting ungulates, are an important source of ignitions at Mkambati. Accordingly FRIs were shorter (1.99-2.08 years) in areas within 3 km of likely poacher entry points than in areas further away (2.56-2.88 years). Although all fires recorded at Mkambati during the study period were of anthropogenic origin, mean FRI still fell within the natural range reported for interior grasslands in South Africa.

Keywords: anthropogenic ignitions, fire danger weather, fire frequency, fire season, Mkambati Nature Reserve, small protected area

Introduction

Fire is an essential ecosystem process throughout many of the world's terrestrial ecosystems (Bond *et al.* 2005) and particularly in Africa, 'the fire continent' (Archibald *et al.* 2010b). However, in many of these ecosystems fire regimes have been altered by anthropogenic interference (de Klerk *et al.* 2012). Fire regimes can be defined as the average fire conditions occurring over a defined period of time (Brooks and Zouhar 2008, Chuvieco *et al.* 2008, Gill 1975) in terms of frequency, seasonality, size and type (Gill 1975), whereby individual fire events contribute to the overall fire regime (Van Wilgen *et al.* 2010). Dynamics that influence fire regimes and thus the probability in time of a given area burning, include fuel, topography, weather conditions, ignition rates, anthropogenic influences such as fire management effort (Archibald *et al.* 2009, Fernandes *et al.* 2012) and grazing regimes (Fuhlendorf *et al.* 2009, Govender *et al.* 2006, Ladbrook 2015).

In fire prone ecosystems managers need to understand historical fire regimes and the changes therein, as this gives insight into how the vegetation was shaped by fire, fuel accumulation rates (Bond *et al.* 2005, Kraaij *et al.* 2013a) and biodiversity responses to fire (Driscoll *et al.* 2010). Understanding fire regimes may furthermore assist to mitigate negative effects often associated with anthropogenic fire (Chuvieco *et al.* 2008), and aid with strategic planning for future fire management (Morgan *et al.* 2001). Human interference with fire (in the form of ignitions and suppression) (Archibald *et al.* 2009, Fernandes *et al.* 2012) is often especially evident close to human habitation (Archibald *et al.* 2009, Archibald *et al.* 2010b, Syphard *et al.* 2007). The effects of anthropogenic ignitions on fire regimes are poorly understood (Bond and Parr 2010) but often occur at higher frequencies than natural ignitions (Brooks and Zouhar 2008) and pre-empt natural ignitions (Bond and Parr 2010). Anthropogenic ignitions may thus result in more frequent fires, potentially with additional impacts on the season, intensity and size of fires (Chuvieco *et al.* 2008). On the contrary human-induced suppression of fire and fragmentation of habitat may result in a lack of fires (Archibald *et al.* 2010b).

Grasslands account for a large portion of the earth's fire-prone ecosystems and represent two so-called pyromes (i.e. global syndromes of fire regimes, Archibald *et al.* 2013). In South Africa, grasslands comprise almost one third of the land surface area (Bachinger *et al.* 2016, Mucina and Rutherford 2006). High seasonal rainfall in grasslands typically allows rapid fuel accumulation resulting in some of the shortest fire return intervals (often <2 years) on Earth, which may be shortened further by anthropogenic ignitions (Archibald *et al.* 2010b, Bond and Parr 2010). In sourveld grasslands, in particular, fires tend to be more frequent later in the dry season (winter) when fire danger conditions are at their highest and grass curing result in accumulation of dead fuels (Van Wilgen *et al.* 2000). Large quantities of fine, flammable fuel make these sour grasslands highly adaptable to changing weather conditions, thus strongly influencing grassland fire regimes (Bond and Parr 2010, Cheney and Sullivan 2008).

Little is known about the fire ecology of the low nutrient coastal sour grasslands of the Pondoland centre of plant endemism along the east coast of South Africa (Van Wyk and Smith 2001). Current information suggests that fire regimes in these grasslands (Van Wilgen and Forsyth 2010) are comparable to those in other grassland types on the high lying interior of South Africa (Mucina and Rutherford 2006), with fires occurring at one to four year intervals and mostly in late winter when humidity is low, vegetation is dry and wind speeds are high (Mucina and Rutherford 2006, Van Wilgen and Forsyth 2010). In order to characterise the fire regime of the low nutrient coastal grasslands of Pondoland, we focussed on Mkambati Nature Reserve (hereafter Mkambati) due to it being one of few areas of untransformed habitat in the region. Most fires at Mkambati are caused by anthropogenic ignitions associated with poaching (approximately 90%, personal communication, V. Mapiya, Mkambati Nature Reserve Manager, Eastern Cape, South Africa, Shackleton 1989, Van Wilgen and Forsyth 2010) which furthermore enabled an investigation of the effects of anthropogenic influences on the fire regime.

This research aims to characterise the fire regime in the coastal sourveld grasslands of Mkambati over the past ten years in terms of frequency, seasonality, size and potential importance of anthropogenic sources of ignition. In interpreting our findings, we consider whether fire frequency and season in this coastal sourveld system differs from that in the more extensive interior Highveld grassland systems of South Africa, and whether some of Pondoland's unique biodiversity may be negatively affected by poachers' influence on the fire regime.

Methods

Study site

Mkambati (31.26°S and 29.99°E) is a small (9200 ha) fenced nature reserve situated on the south-east coast of South Africa between Port Edward (30 km to the north-east) and Port St Johns (59 km to the south-east) (Venter *et al.* 2014a). The reserve is managed by Eastern Cape Parks and Tourism Agency under a land claim settlement agreement with local communities (Kepe 2004). High annual rainfall (1200 mm) and mild temperatures (average of 18°C in winter and 22°C in summer) give rise to a mild subtropical climate with relatively high humidity (Shackleton *et al.* 1991). The vegetation is dominated by Pondoland-Ugu Sandstone Coastal Sourveld (Mucina *et al.* 2006) interspersed with patches of indigenous forest (scarp and southern coastal forest; Fig. 1A, Mucina and Rutherford 2006, Shackleton 1989). The vegetation is nutrient poor resulting from the underlying geology and high levels of leaching (Mucina *et al.* 2006, Venter and Kalule-Sabiti 2016). Soils are comprised of Mkambati sandstones of the broader Cape Supergroup (Fisher *et al.* 2013). Frequent fires result in a dynamic mosaic of recently burnt and older grasses (Venter *et al.* 2014a). The vast majority of fires are ignited by poachers with the intention of attracting ungulates to areas where they are easier to hunt (Shackleton 1989, Van Wilgen and Forsyth 2010). Apart from large herbivores at Mkambati there are a number of rare, threatened or endemic species of fauna and flora that are potentially affected by fire (Appendix 1). Mkambati management undertakes limited prescribed burning due to the high incidence of fires associated with poaching (Venter *et al.* 2014b). The spread of fire at Mkambati is limited by surrounding landscape features, in the form of natural boundaries (rivers) to the north-east and south-west, a well maintained firebreak inland to the west, and roads and indigenous forest within the reserve (Shackleton 1989).

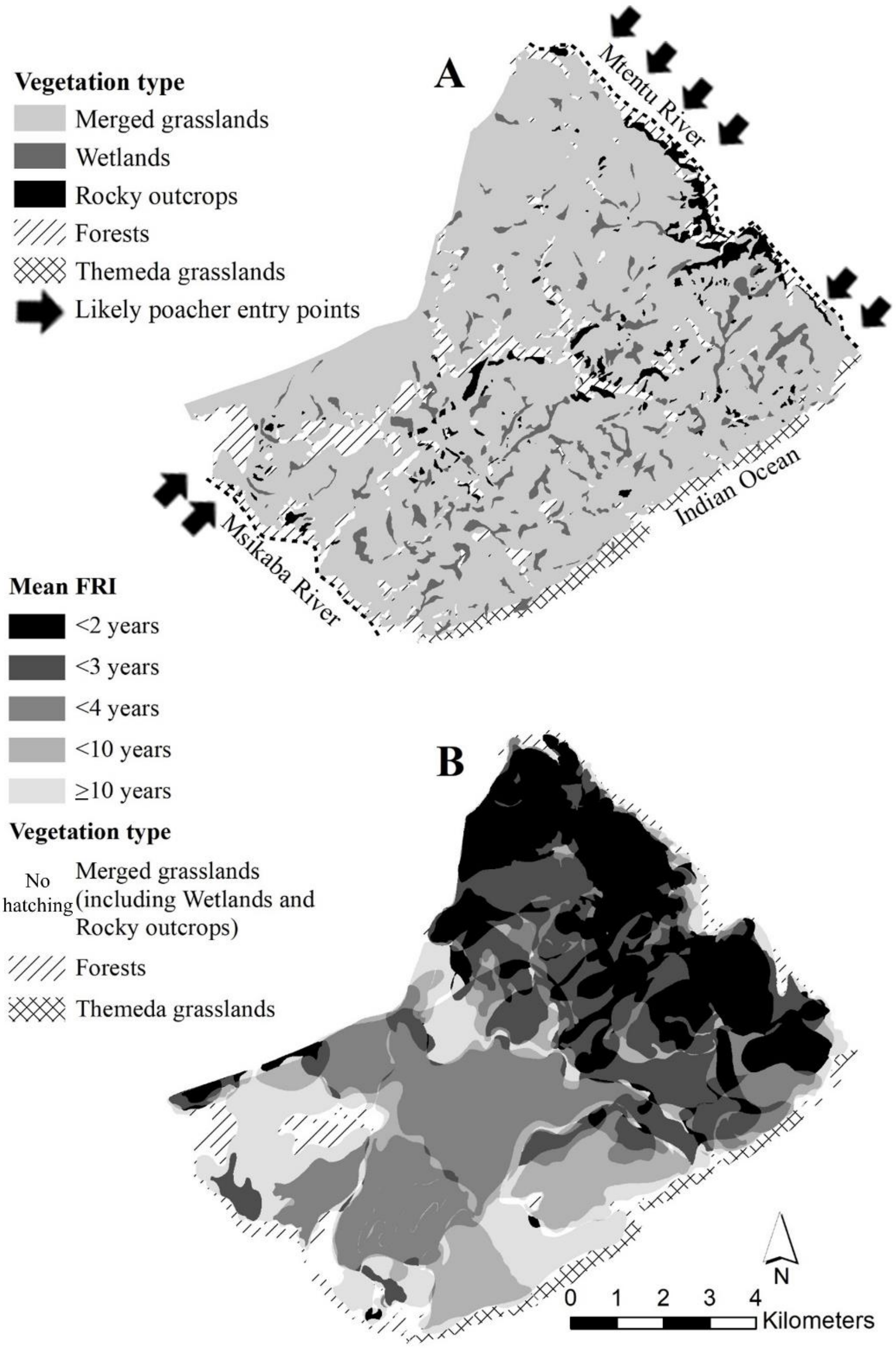

Figure 1. The A) vegetation types at Mkambati Nature Reserve (Shackleton 1989) and potential entry points used by poachers to access the reserve, and B) the mean fire return intervals (FRIs; calculated using the simplistic formula) per unique fire history polygon for the period 2007-2016 as denoted by shading (no shading represents areas that have not burnt during the study period).

Fire records

We compiled a spatial database of fires that occurred at Mkambati during the period January 2007 to August 2016. We used fire records (hand-drawn maps or Global Positioning System (GPS)-tracked fire boundaries) kept by reserve staff and fire boundaries that we digitised in GIS from Landsat TM imagery following methodology similar to that of Bowman *et al.* (2003) who used visual delimitation of fire scars to map fires from satellite imagery. Where both reserve- and Landsat-derived records were available for a fire, the Landsat-derived record was preferred as these were deemed to be more accurate. For some fires Landsat images were not available due to interference of cloud cover (Bowman *et al.* 2003) for which we then used the reserve-derived records. Fire records (each comprising a spatially referenced polygon and date of fire) were assimilated in a GIS database using ArcGIS version 10.1. For fire scars for which we had both reserve- and Landsat-derived records, we compared the areas burnt according to the respective record types, using a paired t-test (Ashcroft and Pereira 2003). Using the same dataset, we also calculated for reserve-derived records the percentage error of omission (false negatives, i.e. burnt areas missed by the reserve-derived records), and error of commission (false positives, i.e. where reserve-derived records over-mapped fires) (de Klerk *et al.* 2012).

Fire size, fire season and fire danger weather

We determined the relationship between number of fires and area burnt, on a monthly basis, using linear regression, as data conformed to a normal distribution. We used Statistica, version 13 (Dell Inc., 2015) for all statistical analyses. To explore fire size distribution, we categorised fires into size classes, i.e. small (<10 ha), medium (≥10 ha), large (≥100 ha) and very large (≥1000 ha). We explored the seasonality of fires by assessing the frequency distribution of fires (in terms of number of fires and area burnt, respectively) across months. We furthermore assessed the seasonality of fire prone weather conditions by calculating daily fire danger index (FDI) scores according to the South African Lowveld Model (Strydom and Savage 2013) for the study period. We used daily weather records for the town of Port Edward (situated 30 km north-east of Mkambati) in terms of maximum temperature, minimum relative humidity, rainfall and average wind speed. FDI scores were categorised as safe (FDI 0-20), moderate (21-45), dangerous (46-60), very dangerous (61-75) or extremely dangerous (75-100) (Meikle and Heine 1987). We explored the relationship between the seasonality of fires and the seasonality of fire prone weather conditions by relating the monthly incidence of fires (in terms of number of fires and area burnt, respectively) to average monthly FDI using regression. We also explored the relationship between fire size and FDI on the day of the fire using regression.

To assess the likely effect of poaching as ignition source on the incidence of fires, we determined (in GIS) for each fire on record the distance between the fire scar centroid and the nearest potential entry point where poachers are known to access the reserve (personal communication, V. Mapiya, Mkambati Nature Reserve Manager, Eastern Cape, South Africa) (Fig. 1A). We subsequently explored the relationship between the number of fires and the distance to likely poacher entry points.

Fire return interval

In order to assess fire return intervals (FRIs), we derived polygons of unique fire history (hereafter 'polygons') by intersecting fire scars in GIS (Forsyth and Van Wilgen 2008, Kraaij *et al.* 2013a). To reduce noise in the dataset, polygons <1 ha in size were merged with neighbouring polygons that had the longest shared boundary. Each polygon was characterised by zero or more fires, and polygons that had two or more fires thus experienced one or more complete FRI. The intervals before the first and after the last fires on record resulted in FRIs that were unknown. These open-ended FRIs were accounted for by means of censoring (Moritz *et al.* 2004) and are hereafter referred to as 'censored', as opposed to 'complete' (i.e. did not require censoring) FRIs. We estimated mean FRIs using two methods. The first method calculates mean FRI using a simplistic formula $FRI = y/(b/a)$ where y is the study period in years, b is the summed area of all the fires recorded over the study period, and a is the area over which fires were recorded (i.e. reserve size) (Forsyth and Van Wilgen 2008, Kraaij 2010, Oliveira *et al.* 2012). Thus, this simplistic formula yields an area-based estimate of the length of time necessary for an area equal in size to the analysis area to burn ('fire rotation'; Romme 1980). In addition to its simplicity, this method does not require a fire frequency model (Oliveira *et al.* 2012), and is inclusive of area but not of censoring. The second method uses maximum likelihood survival analysis by fitting a three parameter Weibull function to the FRI distributions (Grissino-Mayer 2000). We accounted for area by weighing FRI records by polygon size (Fernandes *et al.* 2012). To account for polygons that never burnt during the study period, we specified a constant of 10 (~study period of 10 years) to be used for such double censored FRIs. We calculated mean FRIs according to the above mentioned two methods for

Mkambati as a whole, and for the respective vegetation types to assess whether fire frequency differed among vegetation types. For this purpose we simplified the vegetation categorisation of Shackleton (1989) to be relevant to the accuracy and scale of fire scars, differentiating between (i) 'Merged grasslands (including all Shackleton's grassland types except *Themeda* grasslands, and including rocky outcrops and wetlands within these grasslands), (ii) 'Forest', and (iii) '*Themeda* grasslands (a dwarf grassland in which fire is unlikely due to strong maritime influence; Fig. 1A). To assess the effect of poacher influence on fire frequency, we calculated the mean FRI for Merged grasslands (the predominant vegetation type) close to (within a 3 km buffer of) and away from (outside of a 3 km buffer of) likely poacher entry points, respectively. The 3 km buffer was based on the relationship established between the number of fire scar centroids and distance to likely poacher entry points.

Results

Fire records

Between January 2007 and August 2016, a total of 91 fires were recorded at Mkambati that burnt an area of 27 510 ha. Of these records, ten were Landsat- and not reserve-derived, 20 were reserve- and not Landsat-derived, and the remainder (61 fires) were both Landsat- and reserve-derived. For the latter set of records, the area burnt according to reserve-derived records was significantly larger than the area burnt according to Landsat-derived records ($t = 2.28$, $P=0.03$, $n=61$). Reserve-derived fire records showed a 20% error in commission and a 9% error in omission when compared to the Landsat-derived images.

Fire size, fire season and fire danger weather

Individual fires at Mkambati during the study period varied in size from 6 ha to 2686 ha. Small (3% of fires) and very large (5% of fires) fires were uncommon, although these few very large fires accounted for 34% of the total area burnt (Fig. 2). The number of fires and area burnt per month were significantly correlated ($R^2=0.88$, $P<0.01$ $n=12$) (Fig. 2). Fire activity (when measured as number of fires or area burnt) was concentrated in the winter months, i.e. May to August but with a dip in July (Fig. 2). Very large fires (n=5) almost exclusively occurred during these months. Fire danger weather conditions also peaked during winter (May to August) (Fig. 2), with area burnt per month being significantly and positively related to monthly mean FDI ($R^2=0.47$, $P<0.05$, $n=12$). Accordingly, 57% of fires occurred when FDI conditions were dangerous or higher. Average fire danger weather conditions were moderate (mean FDI of 39) in the study area (Fig. 2). Safe or moderate conditions occurred 66% of the time, while very dangerous or extremely dangerous conditions occurred only 5% of the time. The size of individual fires was not significantly related to FDI on the day of fire (R^2=0.12, P=0.27, n=89).

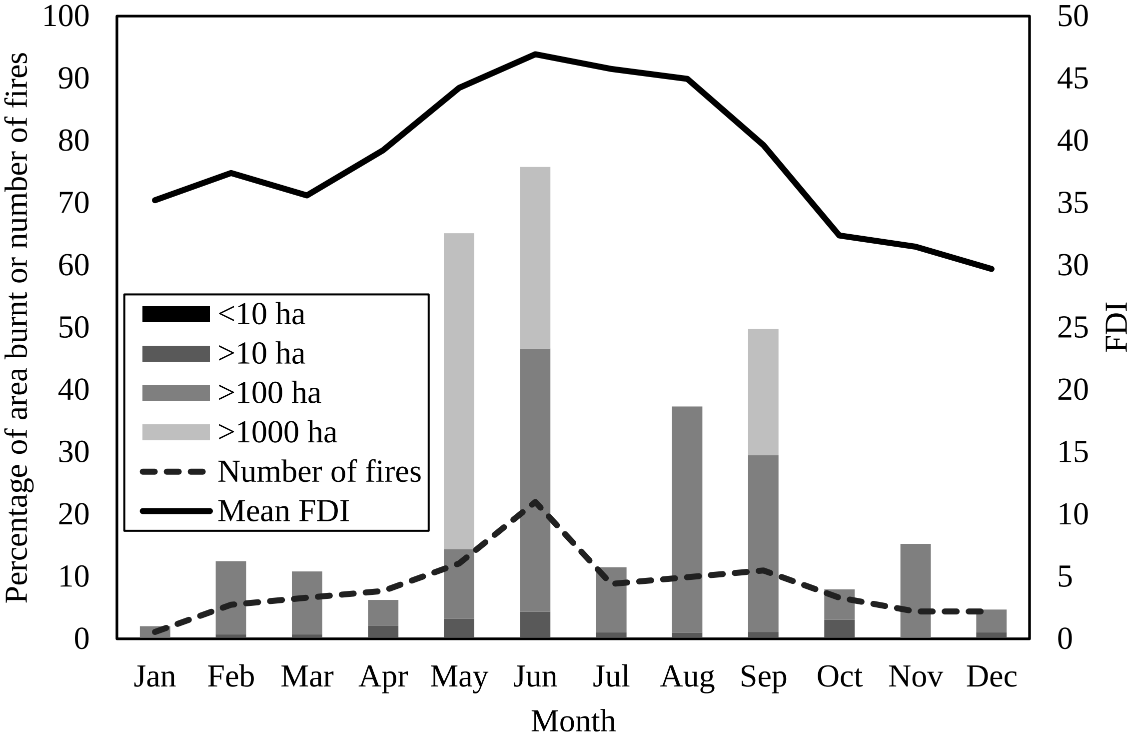

Figure 2. Monthly distribution of fires of different size classes expressed as percentages of the total area burnt and of the total number of fires recorded at Mkambati Nature Reserve during 2007-2016. Mean monthly fire danger index (FDI) score during the same period at the town of Port Edward is additionally shown.

Fire return interval

Intersection of fire scars produced 984 polygons of unique fire history (Fig. 1B), with complete FRIs (areas that experienced at least two fires during the study season) recorded on 78% of Mkambati. Of the FRIs recorded, 1911 (61%) were complete and 1246 (39%) censored. Estimates of mean FRI were influenced by the calculation method employed, with the Weibull function (applying censoring) consistently underestimating mean FRI when compared to the simplistic formula (Table 1). Mean FRI at Mkambati during the study period was estimated at *ca.* 3 years, and differed between vegetation types. Mean FRIs were 2.6 and 3.1 years (Weibull and simplistic formula estimates, respectively) in the Merged grasslands, 5.6 and 8.0 years in Forest, and 9.1 and 44.4 years in the *Themeda* grasslands. Variance in estimates of mean FRI was higher for vegetation types where a large percentage of the FRIs were censored (i.e Forest and *Themeda* grasslands).

Of the fires on the reserve, 69% of the fire scar centroids occurred close to (within 3 km of) likely poacher entry points (Fig. 3). Mean FRIs in areas close to likely poacher entry points were shorter (2.0 and 2.8 years) than those away from likely poacher entry points (2.6 and 2.9 years, Fig 1B). Weibull-derived FRIs differed significantly between these two areas (no overlap in 95% confidence intervals, Table 1).

Table 1. Mean fire return intervals (FRIs) estimated for Mkambati Nature Reserve and its respective vegetation types (see Fig. 1A) for the period 2007-2016, using a simplistic formula (see text) and maximum likelihood survival analysis (the three parameter Weibull distribution). As well as the Mean FRIs for the Merged grasslands (including wetland and rock) within a 3 km buffer of likely poacher entry points (close to likely poacher entry points) and the Merged grasslands (including wetland and rock) out of a 3 km buffer of likely poacher entry points (away from likely poacher entry points).

		Formula	Weibull analysis			
	Proportion of Mkambati	Simplistic FRI	Weibull FRI ± cf95%	Shape parameter	Scale parameter	% of FRI's censored
Entire Reserve	1	3.36	2.59 ± 0.02	1.31	4.83	45%
Merged grassland (inc. wetland and rock)	0.88	3.09	2.56± 0.02	1.29	4.65	42%
Themeda grassland	0.03	44.38	9.06 ± 0.22	1.30	194.46	87%
Forest	0.09	8.00	5.61 ± 0.14	1.05	23.73	66%
Merged grassland close to likely poacher entry points	0.35	2.08	1.99 + 0.02	1.39	3.19	36%
Merged grassland away from likely poacher entry points	0.53	2.88	2.56 + 0.02	1.29	4.65	55%

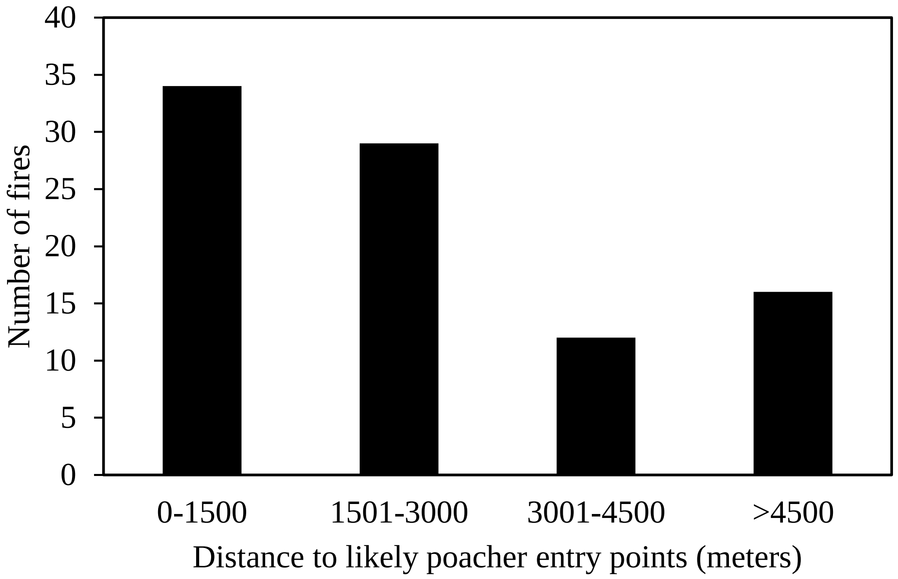

Figure 3. Distances from likely poacher entry points to fire scar centroids (Fig.1) at Mkambati Nature Reserve between January 2007 and August 2016.

Discussion

Fire size and fire records

Fires at Mkambati ranged in size from 6-2686 ha which is small in relation to some grassland fires elsewhere in the world where fires ranged up to 400 000 ha (Bird *et al.* 2012, Ladbrook 2015). The finding that a smaller number of large fires (i.e. fires >1000 ha at Mkambati) contributed substantially to the total area burnt on record has been observed in various ecosystems globally, including Mediterranean-climate shrublands and grasslands (Archibald *et al.* 2010a, Forsyth and Van Wilgen 2008, Kraaij *et al.* 2013a, Moreira *et al.* 2011). The difference in area burnt between Landsat- and reserve-derived records show the importance of using both record sources in conjunction with one another to facilitate the upkeep of comprehensive and accurate fire records. The level of accuracy attained in our study in deriving fire scars from Landsat imagery, especially in Merged grasslands, is comparable to that attained by other studies in the savannas of northern Australia (Russell-Smith *et al.* 2003) and across vegetation types in Nevada, North America (Kolden and Weisberg 2007).

Seasonality of fires and fire danger weather

The fire season at Mkambati was from May to August (the dry season), during which time FDI was highest (average FDI >40). Fire season in these coastal grasslands thus mirror that of other grasslands in South Africa (Archibald *et al.* 2010a). Within the winter season, the number of fires and area burnt at Mkambati peaked in June after which the number of fires declined, suggesting that poachers set fires early in winter when grasses first die off. These fires stimulate new grass growth with elevated crude protein content (8.6% compared to 4.6% in more moribund vegetation; Shackleton 1989), thereby attracting ungulates to feed in these areas. The second peak in area burnt during August-September (which is not reflected in number of fires) is likely explained by fewer but larger fires that are able to spread under high fire danger weather conditions still prevailing during these months, and possibly some prescribed burns undertaken by management towards the end of the dry season.

Fire return intervals

Fire return intervals at Mkambati of approx. 3 years (<3 years in the Merged grasslands which are representative of approx. 80% of the reserve) are within the range (1-4 years) reported for other grasslands in South Africa (Mucina *et al.* 2006). Variance in estimates of mean FRI were greater where high levels of censoring were applied, as found in other studies (Fernandes *et al.* 2012, Kraaij *et al.* 2013a). The level of censoring in our study that applied to the reserve as a whole, and the predominant vegetation type (Merged grasslands) was <45% and variance associated with estimates of mean FRI was low, suggesting that the time series (study period) was sufficient to yield reasonable estimates of mean fire frequency. Accordingly, the two methods used for FRI estimation yielded comparable results for the Merged grasslands. However, greater uncertainty was associated with the estimates of mean FRI derived for forests and *Themeda* grasslands. Here, greater levels of censoring were applied (including double-censoring) and FRIs were longer relative to the length of the time series studied. For these vegetation types, the estimates of mean FRI produced by the simplistic formula are considered to be more reliable. Estimates of mean FRI in vegetation types that do not experience regular fire could be refined if time series data were extended, emphasising the need for comprehensive long-term fire records.

The other vegetation types at Mkambati (i.e. Forest and *Themeda* grasslands) tend to burn much less frequently (>5 years), most likely as a result of localised climatic conditions and different fuel characteristics. Grass fuels are characterised by loosely packed, fine fuels, whereas forests have coarser fuels with higher fuel moisture contents (Hoffmann *et al.* 2012). Being situated along the coast, the *Themeda* grasslands are influenced by salt spray and wind from the ocean, causing cooler, moister conditions and stunted plant growth form, which likely account for the extended FRIs (Shackleton 1989).

It has been proposed that specific, rigid fire regimes will not cater for the needs of a wide variety of fauna and flora, but instead that varied FRIs in space and time (‘pyrodiversity’) would maintain higher levels of biodiversity (Parr and Andersen 2006). Within Mkambati, FRIs were not evenly distributed, with mean FRIs being significantly shorter close to likely poacher entry points than further away. Differences in fire frequency between areas experiencing more and fewer poacher ignitions may provide pyrodiversity within Mkambati allowing for a greater suite of biodiversity to persist in a small area. In the grasslands of Mpumalanga, South Africa, more frequent fires in fire breaks than in the adjacent matrix were found to have no negative effects on plant diversity unless areas had been previously disturbed (Bachinger *et al.* 2016). We did not investigate the effects of pyrodversity on biodiversity at

Mkambati but our findings in terms of differential FRIs across the reserve provide a basis for future research into this aspect.

Effects of poaching and implications for management

It is clear from this study and others (Archibald *et al.* 2012, Bowman *et al.* 2011, Oneka 1990, Shackleton 1989, Veblen *et al.* 2000) that fire regimes may be significantly affected by anthropogenic influences. At Murchison Falls National Park, Uganda, poachers set fires outside the reserve with the intention of drawing animals outside of the protected area where they could be easily poached (Oneka 1990), whereas at Mkambati fires were set inside of the reserve boundary for a similar purpose. Fires were most commonly set in areas that posed a low risk to poachers such as close to entry points and far away from the reserve's law enforcement and infrastructure. The larger number of fire scar centroids situated near the likely poacher entry points is indicative of a larger number of smaller fires in these areas. Similarly, in Australian savanna, a finer scale mosaic of burnt and unburnt areas was evident closer to human settlement (Bowman *et al.* 2004).

In order to formulate appropriate fire management guidelines (i.e. when fires should be suppressed or allowed to burn) an understanding is required of anthropogenic influences on the fire regime and of the potential ecological effects of untimely fires. To facilitate adaptive management of fire for biodiversity conservation, thresholds may be formulated outlining ecologically acceptable limits of variation ('pyrodiversity') (Van Wilgen *et al.* 2011). Such thresholds typically relate to ecological responses of biota to fire (e.g. post-fire recruitment or breeding success) (Kraaij *et al.* 2013b, Van Wilgen *et al.* 2011). Mkambati represents the Pondoland centre of plant endemism (Van Wyk and Smith 2001) and contains various threatened or endemic species of fauna and flora potentially affected by fire (Appendix 1). We considered how knowledge of these species' ecology should be used to inform thresholds for the study area related to fire frequency, fire season, fire size, and interactions between fire and herbivory (Appendix 1; *cf.* Kraaij *et al.* 2013b, Van Wilgen *et al.* 2011). This exercise also highlighted priorities for future research on biological responses to fire. In addition to consideration of threatened and endemic species, fire management at Mkambati also has to take account of species important for resource utilisation (such as *Cymbopogon validus* used for thatching by local communities; Kepe 2005), and interactions between fire and herbivory.

The latter has implications for the availability and quality of forage and thus the performance of ungulates, the availability of fuels and thus fire frequency and intensity, as well as habitat condition (Venter *et al.* 2014a).

Conclusion

It is clear that a number of ecological factors need to be considered when evaluating past management and recommending appropriate future management of fire in protected areas. We have made a start by (i) establishing that past fire regimes at Mkambati broadly fell within ranges deemed natural for other grassland systems in South Africa, and (ii) providing a fire history to underpin evaluations of the effects of different past fire frequencies on biota of the Pondoland centre of plant endemism. Similar approaches may be used to develop and refine thresholds for fire management more generally in the context of protected area management (*cf.* Van Wilgen *et al.* 2011). Establishing links between fire interventions and biodiversity outcomes is particularly important in small, fenced reserves experiencing substantial anthropogenic influence.

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Appendix 1: Species (fauna and flora) of conservation importance at Mkambati Nature Reserve, their conservation status according to the IUCN Red list of threatened species, their ecological characteristics relevant to fire management, and potential impacts of fire regimes.

Species	Status	Ecological characteristics	Potential impacts of fire regimes
Brunia trigyna	Critically Endangered[5]	Slow-growing large woody shrub; Subpopulations are extremely fragmented[5]	Sensitive to frequent fires (grows in sites protected from fire)[5]
Watsonia pondoensis	Endangered[5]	Geophyte	Sensitive to frequent fire and overgrazing[5]
Leucospermum innovans	Endangered[5]	Resprouting shrub; myrmecochorous thus requires high fire intensities to stimulate seed germination[1]	Too frequent fire may result in inadequate seed production and poor recruitment[5]
Kniphofia drepanophylla	Vulnerable[5]	Geophyte	Sensitive to frequent fires associated with heavy grazing and trampling[5]
Leucadendron spissifolium subsp. *oribinum*	Vulnerable[5]	Slow-growing woody shrub; dioecious; serotinous; resprouter[1]	Too frequent fire may result in inadequate seed production and poor recruitment[5]
Leucadendron spissifolium subsp. *natalense*	Near Threatened[5]	Slow-growing woody shrub; dioecious; serotinous; resprouter[1]	Too frequent fire may result in inadequate seed production and poor recruitment[5]
Hyperolius poweri	Not assessed (due to recent taxonomic change)[8]	Frog associated with emergent vegetation on the margins of swamps[8]	Sensitive to habitat loss as a result of regular fire (loss of cover)[3]
Breviceps bagginsi	Endangered[6]	Frog favouring habitat associated with grassland[8,4]	Sensitive to habitat loss as a result of regular fire (loss of cover)[3]
Bradypodion caffer	Endangered[8]	Chameleon represents a grassland ecomorph of *B caffer;* Only occurs in natural grassland[8]	Require long fire free intervals to facilitate dispersal[8]
Insecta (73 species found are endemic to South Africa, and at least 18 species endemic to Mkambati)	21 species not yet assessed by IUCN and thus listed as Endangered[2]	Burning is known to influence invertebrate communities, but further research is required in this diverse group[2]	Burning positively influences species richness; Highest numbers of endemic species were found in unburnt vegetation[2,7]

[1]Rebelo (1995), [2]Hamer and Slotow (2017), [3]Masterson *et al.* (2008), [4]du Preez and Carruthers (2009), [5]Raimondo *et al.* (2015), [6]South African Frog Re-Assessment Group (SA-Frog) (2010), [7]Dippenaar-Schoeman *et al.* (2011), [8]Venter and Conradie (2015).

CHAPTER 4: Energy maximisation strategies of different African herbivores in a fire dominated and nutrient poor grassland ecosystem

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Abstract

In African grazing ecosystems herbivores are offered a variety of choices when foraging in a relatively small heterogeneous area. Understanding what drives these choices and distribution of species is important to interpret how herbivores use their resources. We assessed forage selection in terms of energy maximisation of four large herbivores in a nutrient poor coastal grassland ecosystem subjected to regular anthropogenic fire in Pondoland, Eastern Cape, South Africa. We explored herbivore diets in terms of the energy maximisation strategy employed, i.e. maximisation of daily digestible energy (DDE) or instantaneous digestible energy (IDE), using species from different weight range classes. Common reedbuck (*Redunca arundinum*), red hartebeest (*Alcelaphus buselaphus* subsp. *caama*), zebra (*Equus quagga*) and eland (*Tragelaphus oryx* subsp. *oryx*) were fitted with GPS satellite tracking collars, and hourly GPS locations (observed) were taken between 2008 and 2016. Using mixed effects models, we compared observed and an associated set of random locations to determine the energy maximisation strategy employed by each species. Red hartebeest and zebra maximised DDE both inside and outside of fire seasons and frequently foraged in low biomass, recently burnt grasslands. Eland generally favoured areas where they could maximise IDE throughout the study period, however during the fire season they switched strategy to maximise DDE and only made use of the burnt grasslands after approximately 130 days (220 g/m^2). At a patch scale reedbuck did not maximise IDE or DDE inside or outside of fire seasons, maximised both IDE and DDE both inside and outside of the fire seasons at a landscape scale. These results provide evidence of different foraging strategies applied by herbivores with different traits, emphasising how herbivore body weight, digestive strategy and mouth morphology influence food selection. Furthermore these traits are good indicators of how species distribute themselves within a heterogeneous landscape.

Key words: foraging preferences, sourveld grassland, herbivores, resource selection function, post-fire vegetation age, feeding guild.

Introduction

Optimal foraging theory (Stephens and Krebs 1986) predicts that the distribution of herbivores within an environment can be explained by the heterogeneity of resources within the landscape. Optimal digestive theory predicts that herbivores are adapted to forage in areas that yield energy and nutrients more quickly (i.e. forage that requires a shorter retention time, Clauss et al. 2008). The foraging behaviour of large herbivores is driven by the nutrient content and biomass of vegetation. The rate of nutrient consumption determines how much time needs to be invested in feeding to meet metabolic and energy requirements (Shipley et al. 1994). Smaller herbivores are potentially limited by the quality of vegetation while larger herbivores likely limited by the quantity of vegetation (Hopcraft et al. 2010). Habitat selection is a fundamental process that structures the distribution and abundance of herbivores within a landscape. At a finer scale (minutes) the consumption rate and intake of energy by herbivores is limited by the spatial distribution and traits of vegetation and the cropping and digestive mechanisms of herbivores (Shipley et al. 1994, Farnsworth and Illius 1998). Vegetation may furthermore vary seasonally in terms of spatial distribution, morphological properties and nutrient concentrations (Hopcraft et al. 2010, van den Berg et al. 2016). Thus the way in which herbivores select for forage quality or quantity of vegetation can be defined as the maximisation of a foraging currency (Fortin 2003). Resource selection functions (RSFs) may be used to study the way in which herbivores are influenced by the scale and heterogeneity of resources within a habitat (Boyce et al. 2003). Knowledge of the way in which herbivores maximise their energy intake within their habitat can provide stronger grounds for how and why herbivores distribute themselves within an environment (Adler et al. 2001, Hopcraft et al. 2012, Chirima et al. 2013). Understanding how herbivores use forage resources and habitats should thus underpin conservation management strategies, especially in anthropogenically affected systems (Venter et al. 2014a).

Foraging goals are what drive herbivore choices within a heterogonous environment (Babin et al. 2011). In this study the choices available to herbivores are expressed as two divergent foraging currencies that relate to energy budgets, i.e.: 1) herbivores can forage to maximise their instantaneous intake of digestible energy (IDE) by consuming large amounts of vegetation that allow for fast satiation, but which is often limited in its digestibility, or 2) herbivores can maximise their daily intake rate of digestible energy (DDE) by foraging on relatively smaller/immature plants that provide greater digestible energy than larger/older plants, but these smaller plants often require longer cropping times (Wilmshurst et al. 1999, Shipley 2007, Babin et al. 2011). In other words rather than foraging on plant species that provide the fastest short-term intake rate of digestible energy (IDE) (energy maximisation principles, Owen-Smith and Novellie 1982, Belovsky 1986, Bergman et al. 2001) herbivores may rather extend their foraging time and select resources that are more digestible (DDE) (Fortin et al. 2002). The adoption of either of these currencies may be driven by, or require the consumption of different plant species. Energy maximisation strategies may change seasonally depending on the availability and quality of resources (Meissner and Paulsmeier 1995, Fortin et al. 2002). Thus the temporal and spatial complexity and heterogeneity within a habitat may result in foraging strategies that are not necessarily constant in space and time and that shift between energy maximisation strategies (Bergman et al. 2001).

In grassland ecosystems the relationship between grasses, fire and herbivory are key factors in the distribution of herbivores and nutrient cycling (Archibald and Bond 2004). Once grasses become the dominant vegetation in an area, biotic and abiotic influences are responsible for maintaining biomass concentrations and the cycling of nutrients and energy (Govender et al. 2006, Ladbrook 2015). Persistent heavy grazing may reduce the quantity and continuity of fuels, thereby also limiting nutrient cycling through fire (Archibald and Bond 2004). Fire may also be responsible for heavy grazing by attracting herbivores to nutrient rich post fire areas (Shackleton 1989, Archibald et al. 2005, Brooke et al. 2018). Thus herbivores need to be able to adapt their behaviour within the landscape to fire patterns in space and time (Archibald and Bond 2004).

Choices between foraging currencies may be particularly important where the incidence of anthropogenic fire is high and vegetation nutrients are low, such as in the mesic coastal grasslands of southern Africa. High rainfall allows plants to grow rapidly and to invest in structural support and protection against herbivory (Hopcraft et al. 2010). In these high rainfall systems grazing pressure is often too low to prevent the rapid build-up of moribund vegetation and thus fire is essential for recycling nutrients (Sensenig et al. 2010, Venter et al. 2014a). This often results in a vegetation mosaic of highly nutritious newly burnt patches of vegetation interspersed with older more moribund material (Shackleton and Mentis 1992, Venter et al. 2014a). Soon after fire (within the first six months) a short term spike in nutrients appears, including increases in crude protein (8.6% compared to 4.6% in older grasslands), phosphorous concentrations (0.1% compared to 0.05% in older grasslands) and digestibility (38.6% compared to 27.1% in older grasslands) (Shackleton 1989). In addition to fire, vegetation mosaics are driven by a number of other abiotic (rainfall, Archibald and Bond 2004) and anthropogenic (poaching and management practices, Oneka 1990, Archibald and Bond 2004) factors.

Considering the scale at which to measure foraging in a heterogeneous environment is important as herbivores may vary how they use resources within the landscape (Bailey et al. 1996). In this study we will look at two scales of resource use; 1) landscape scale (i.e. across the entire reserve) and 2) patch scale (the area that an animal uses over a short time scale, Bailey et al. 1996). The different scales that herbivores forage at are well documented in the literature (Bailey et al. 1996, Boyce et al. 2003, Vanak et al. 2013). Changes in observed and random locations across landscape and patch scales will indicate how herbivores adapt their behaviour at these scales (Owen-Smith et al. 2010).

Our study was undertaken on a small fenced nature reserve in the coastal grasslands of southern Africa where herbivores are constantly faced with a variety of challenges when foraging in a relatively small area. Mkambati Nature Reserve (hereafter referred to as Mkambati) provided the ideal opportunity to study energy maximisation principles in large herbivores as species have a variety of foraging choices in a constantly changing environment. Herbivore species were chosen based on varying body sizes, digestive strategy and mouth morphology. In this study we aimed to understand foraging choices between four large herbivore species with differing traits (i.e. body mass and mouth morphology) by considering their energy maximisation strategy. We explored whether choices in foraging currencies are driven by fire and biomass of vegetation by comparing these choices inside and outside of the fire season. Furthermore if a species showed little evidence of energy maximisation strategy at a patch scale we scaled up and explored whether a landscape scale approach would better describe its use of habitat on Mkambati.

Methods

Study site

Mkambati Nature Reserve (31.26°S and 29.99°E) is a small (9200 ha) fenced nature reserve situated on the south-east coast of South Africa within the Pondoland Centre for Plant Endemism (De Villiers and Castello 2013). Mkambati is managed by Eastern Cape Parks and Tourism Agency under a land claim settlement agreement with the local Mkambati community being the land owners (Kepe 2004). Mkambati is bounded on three sides by natural boundaries (river gorges to the north and south and the Indian Ocean to the east) with the only manmade boundary being a fence inland to the west (Shackleton 1989). High annual rainfall (1200 mm) and mild temperatures (average of 18°C in winter and 22°C in summer) give rise to a mild subtropical climate with relatively high humidity (Shackleton et al. 1991). The vegetation is dominated by Pondoland-Ugu Sandstone Coastal Sourveld interspersed with patches of indigenous forest (scarp and southern coastal forest), wetlands and rocky outcrops (Mucina et al. 2006). The vegetation is nutrient poor resulting from the underlying geology and high levels of leaching (Mucina et al. 2006, Venter and Kalule-Sabiti 2016). Soils at Mkambati are comprised of Mkambati sandstones of the broader Cape Supergroup (Fisher et al. 2013). Frequent fires result in a dynamic mosaic of recently burnt, nutrient rich and older, more moribund grasses (Venter et al. 2014b). The vast majority of fires are ignited by poachers with the intention of attracting herbivores to areas where they are easier to hunt (Shackleton 1989, Van Wilgen and Forsyth 2010, Brooke et al. 2018). Mkambati management undertakes limited prescribed burning due to the high incidence of fires associated with poaching (Venter et al. 2014b, Brooke et al 2018). There are a number of indigenous large herbivore species (*n*=8) on the reserve (see Venter et al. 2014b)

Study species

GPS/VHF satellite collars (African Wildlife Tracking) were fitted to four large herbivore species on Mkambati. These species were southern reedbuck (*Redunca arundinum,* small bodied ruminant with a narrow muzzle), red hartebeest (*Alcelaphus buselaphus* subsp. *caama,* medium bodied ruminant with a narrow muzzle enabling them to selectively crop short grasses), plains zebra (*Equus quagga,* medium bodied non-ruminant with a broad muzzle preventing them from cropping very short grass) and eland (*Tragelaphus oryx* subsp. *oryx,* large bodied ruminant with a narrow muzzle adapted for browsing, Codron et al. 2008) (Appendix 1). Collars were fitted at varying times throughout the study period (2008 – 2016) and recorded GPS positions at fixed time intervals of either 30 or 60 minutes over varying periods (Appendix 1). All animals were darted by an experienced veterinarian from a Robinson 44 helicopter. Work on red hartebeest, zebra and eland began in 2008 and was approved by and carried out in accordance with the recommendations in the approved standards protocols of the animal ethics sub-committee of the University of KwaZulu-Natal (Approval number 012/09/Animal). Field work was conducted by or under the direct supervision of the fifth author while he was a staff member of Eastern Cape Parks and Tourism Agency as part of the operational activities of the appointed management authority of Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of 2010, Eastern Cape Province, South Africa). Work on reedbuck began in October 2015 and was approved by and carried out in accordance with the protocols set out by the animal ethics research committee at the Nelson Mandela University (Approval number A15-SCI-ZOO-016) and with a government issued permit (Threatened or protected species permit number O 02263).

Land cover types

More than 80% of Mkambati is sourveld grassland (Venter 2014), with Mkambati's original vegetation classification recognising six distinct grassland vegetation types (Shackleton 1989). For the purposes of this study we consolidated these into two main grassland types (after Brooke et al. 2018), namely those affected by fire (merged grasslands; combining *Aristida junciformis-Helichrysum mixtum*, *Cymbopogon validus-Digitaria natalensis*, *Festuca costata-Albuca setosa*, *Stoebe vulgaris-Athanasia calva* and *Tristachya leucothrix-Loudetia simplex* communities) and those not affected by fire (coastal *Themeda* grasslands, *Themeda triandra-Centella asiatica* community). Indigenous forests, rocky outcrops and wetlands also occur interspersed throughout the grasslands (Appendix 2, adapted from Shackleton 1989).

Characterisation of movement paths

We used step selection functions (SSFs) to determine how foragers selectively adjust their movement paths to habitat features. SSFs are based on a comparison between observed and random steps. Observed steps are the straight lines linking two successive locations travelled by the animals (Turchin 1998, Fortin et al. 2005). For all individuals, each step was associated with 10 random locations to form a stratum. Random and observed locations shared the same starting location, but they differed in length and direction (Figure 1). We used the 'create random points' tool of ArcGIS version 10.1 (Esri, 2012) to draw the endpoint locations of random steps within a predetermined buffer corresponding to the mean daily movement for that species (i.e. the mean daily distance recorded between successive locations of an individual of a species over a 24 hour period). Buffers ranged from 2.5 km in reedbuck, 5.4 km in red hartebeest, 6.2 km in zebra to 7.4 km in eland, which encompassed the 99 percentile of step length for each species. The lengths of random steps were thus drawn uniformly within these buffers, while turning angles were drawn uniformly over 360^o (Figure 1).

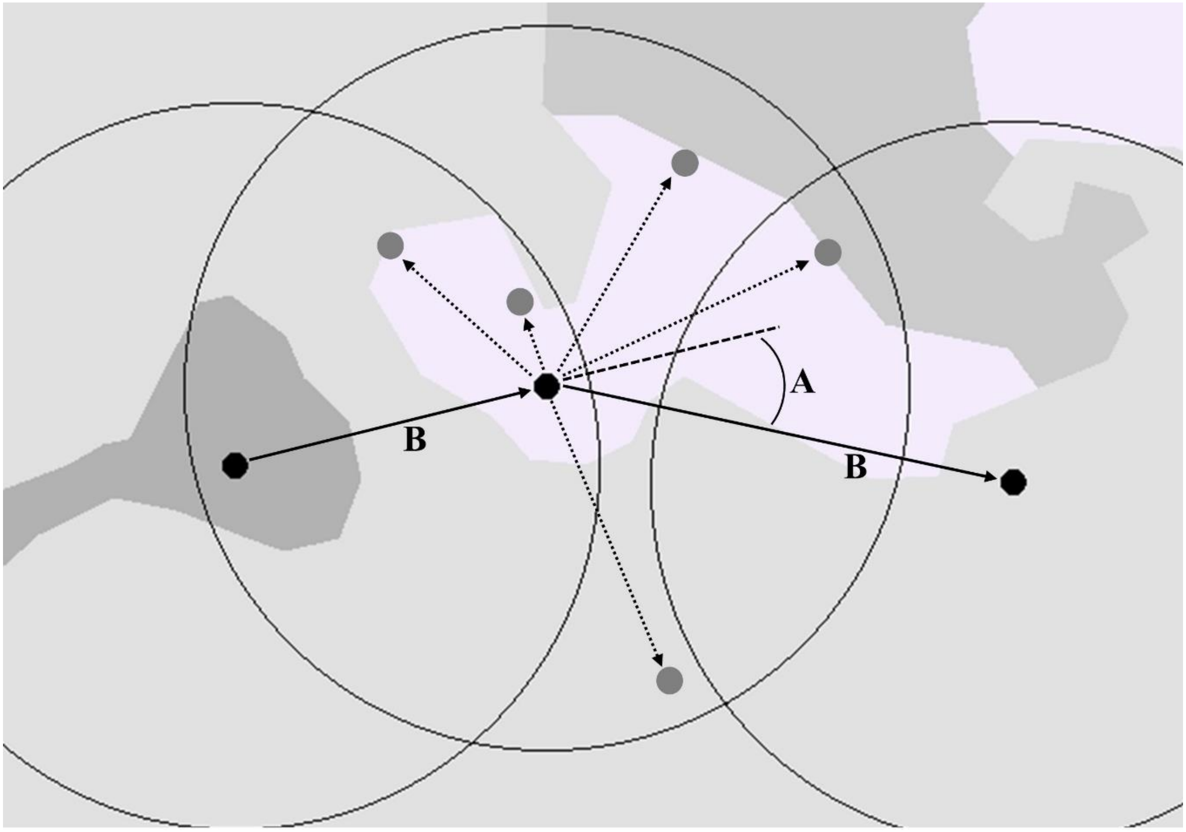

Figure 1: A hypothetical example of a step length (B) and turning angle (A) extracted from the study. Turning angle can be defined as the angle that a herbivore turned between the preceding and future location, and step length as the straight line distance between two successive steps. Grey points with dashed lines represent the random choices a herbivore has within the environment, and the background is representative of different vegetation types on Mkambati Nature Reserve.

Observed and random locations were intersected in GIS with layers of vegetation type and post fire vegetation age (Brooke et al. 2018); i.e the total number of days since the last fire occurred in a specific polygon. From this we were then able to estimate biomass (g/m^2) of grass for the merged and *Themeda* grasslands. If no fires were recorded at particular locations, post fire vegetation age was calculated based on the start date (1 January 2007, one year before the first tracking devices were fitted to the study animals) of the period for which fire records for Mkambati exists. In the SSF models we considered the instantaneous intake of digestible energy (I_{IDE}) and daily intake of digestible energy (I_{DDE}) that was available at the end of observed and random steps.

Intake rate of digestible energy (I_{IDE} and I_{DDE})

To calculate the biomass and energy content for the merged grasslands we used the results of (Shackleton and Mentis 1992). Digestibility of vegetation was given as a percentage for the two predominant grassland vegetation communities, these two vegetation communities were *T. leucothrix – L. simplex* and *C. validus – D. natalensis* communities. This amalgamation of the *T. leucothrix – L. simplex* and *C. validus – D. natalensis* communities formed the basis of the biomass and digestible energy content for the merged grasslands. To determine the digestible energy content (kJ/g) of the merged grasslands we used a percentage digestibility of vegetation (Shackleton and Mentis 1992). Thereafter digestible energy was calculated based on the energy content of the vegetation in relation to the number of days since fire.

Intake rate (I, g/min) of vegetation for ruminants was based on a type II functional response (Wilmshurst et al. 2000):

$$I = \frac{R_{max} \times V}{b + V}$$

where R_{max} (g/min) is the maximum instantaneous cropping rate and b (g/m^2) is the vegetation biomass at which intake is half of the maximum for a given herbivore species, and V is the biomass of vegetation (g/m^2). To determine R_{max} and b for our three ruminant species, we developed a relationship based on Table 1 of Wilmshurst (2000). We found that R_{max} and b covaried with body mass (M) following $R_{max} = 0.1617 \times M + 1.9771$ and $b = 0.5768 \times M$ Equations were then applied for our three ruminant species assuming a body mass of 38 kg for reedbuck, 120 kg for hartebeest, and 460 kg for eland.

Intake rate (I) of vegetation for zebra was based on the curve of best fit $I = 91.283 \times (1 - \exp(-0.009 \times M))$ from the process 3 of Spalinger and Hobbs (1992):

$$I = \frac{R_{max} \times S}{R_{max}h + S}$$

where S is the bite size (g/bite) and h is the mean handling time (constant of competition between cropping and chewing). This allows for larger bites to enable more rapid intake of vegetation as successive smaller bites require longer cropping times. h was estimated by a non-linear model as 0.02 minutes (Okello et al. 2002). Intake rates of vegetation thus respond to cropping time and the variation in bite size resulting from available biomass (Spalinger and Hobbs 1992).

For each animal, we estimated I_{IDE} (kJ / min) and I_{DDE} (MJ / day) at the location of each step (observed and random). In doing so we calculated biomass and digestibility of vegetation and functional response for ruminants and non-ruminants:

$$I_{IDE} = (D \times 18.41)I$$

where D is the proportion of the vegetation that can be digested, 18.41 kJ/g is the gross energy content of vegetation (National Research Council 1996) and I is the instantaneous rate of vegetation intake (g/min) by a given herbivore species. To estimate the I_{DDE}, we consider two potential constraints, a time constraint:

$$I_1 = \frac{I_{IDE} \times T_{max}}{1000}$$

where the maximum daily intake is constrained by T_{max}, the maximum time that can be spent foraging in a day (780 min / day, Wilmshurst et al. 2000); and a digestive constraint:

$$I_2 = \frac{V_I \times D \times 18.41}{1000}$$

where the constraint is V_I, the daily voluntary intake (kg/day) of vegetation given *ad libitum* food availability. We estimated V_I from the literature. Meissner and Paulsmeier (1995) investigated V_I for ruminants varying broadly in body mass (M; range: 22 - 619 kg) varied linearly with the radio between D and neutral detergent fibre (*NDF*) of vegetation. They showed that V_I (range: 16 and 62 g / $M^{0.9}$ / day) varied linearly with ratio between D and NDF ($D:NDF$). Given that NDF varies linearly with both D and V_I (Wilmshurst et al. 2000) and that Meissner and Paulsmeier (1995) analysis is based on D with a similar range (0.24 – 0.83) than the one we studied (0.16 - 0.61), we assumed that the ratio $D:NDF$ took its lowest of 0.3 when $D = 0.16$, and its highest value of 2.4 for $D = 61\%$, and increased linearly within that range ($D:NDF = 0.0478D - 0.465$). On this basis, we converted our estimates of D into $D:NDF$ ratios, and then used the relationship between V_I and $D:NDF$ for grass provided in Table 3 of Meissner and Paulsmeier (1995) to estimate the voluntary intake of vegetation by our three ruminant species. For zebra, we estimated V_I for our estimates of D based on the relationship between NDF and D and between V_I and NDF (Edouard et al. 2008). Our estimation of V_I were estimated assuming of body mass of 38 kg for reedbuck, 120 kg for hartebeest, 460 kg for eland, and 300 kg for zebra.

The daily energy intake (MJ/day) was then estimated from:

$$I_{DDE} = \min(I_1, I_2)$$

Statistical analysis of herbivore movement and foraging choices

We estimated SSFs using mixed-effects conditional regressions, in using R version 3.4 (R Core Team, 2013) with the R package TwoStepCLogit (Craiu et al. 2011) to analyse the data over the entire study and within (May to October) and outside (November to April) of fire seasons. Observed locations were scored 1 whereas random locations were scored 0, such that our analysis accounted for our paired design (case-control approach) (*cf.* Fortin et al. 2005). Mixed effects models compared observed and random steps within strata based on the different land cover types and potential intake of digestible energy (i.e., I_{IDE} or I_{DDE}, as continuous variables). For these models rocky outcrops and merged grasslands were considered dummy variables while the combination of wetlands, forests and *Themeda* grasslands were not included as some animals recorded no observations in these habitat types. Furthermore for eland and zebra Transformed variables of digestible energy ($IDE^{0.5}$, $DDE^{0.5}$) were used as these transformations better described the data. SSFs included cosine of turning angle, step length and log(step length), as recommended when random steps are drawn from uniform distributions (Nicosia et al. 2017), as in the case of this study. Since conditional regressions have no intercept (Craiu et al. 2011), random effects were integrated through random regression coefficients for I_{IDE} or

I_{DDE}. Prior to running the models, variables were screened for collinearity and problematic variables (mentioned above) were removed.

Habitat selection in reedbuck

In reedbuck the results from mixed effects models yielded no significant result regarding the energy maximisation principles. To further explore how reedbuck used their habitat and explain their energy maximisation principles we looked at a landscape scale (comparison between the observed and a random set of locations throughout the reserve). For these analysis we used generalized linear mixed models (GLMM) (Bolker et al. 2009). The GLMM allowed us to test for reedbuck energy maximisation principles at a landscape scale (entire reserve) rather than at the patch scale (Bailey et al. 1996) used in the other three species. Thus for every observed reedbuck location ten locations were created randomly throughout the reserve. The GLMMs compared the observed and random locations as the dependent variable. The covariates (independent variables) were kept the same as those use in the mixed effects models (see above) in order for results to remain comparable; however variables of step length and turning angle were not included. Within the models individual reedbuck were included as random factors.

Results

Locations and steps

Mean daily movement of species and standard errors were 2.4±0.2 km in reedbuck, 3.4±0.2 km in red hartebeest, 6.1±0.2 km in zebra and 7.4±0.6 km in eland. There was a significant positive linear relationship between daily distance travelled and herbivore body mass (Figure 2). In terms of selection by herbivores of post-fire vegetation ages, 11% of reedbuck observations occurred within the first 300 days after fire and 9% of observations within the first 180 days after fire. (Figure 3). Forty percent of red hartebeest observations occurred within the first 300 days after fire and 30% of observations within the first 180 days after fire. Fifty-three percent of zebra observations were recorded within the first 300 days after fire and 42% of observations within the first 180 days after fire. Five percent of eland observations were recorded within the first 300 days after fire and 3% of observations within the first 180 days after fire. In terms of biomass selection 9% of reedbuck, 24% of red hartebeest, 33% of zebra and 5% of eland (Figure 4) observations occurred in areas with biomass of >250 g/m^2 (available approximately six months after fire in merged grasslands).

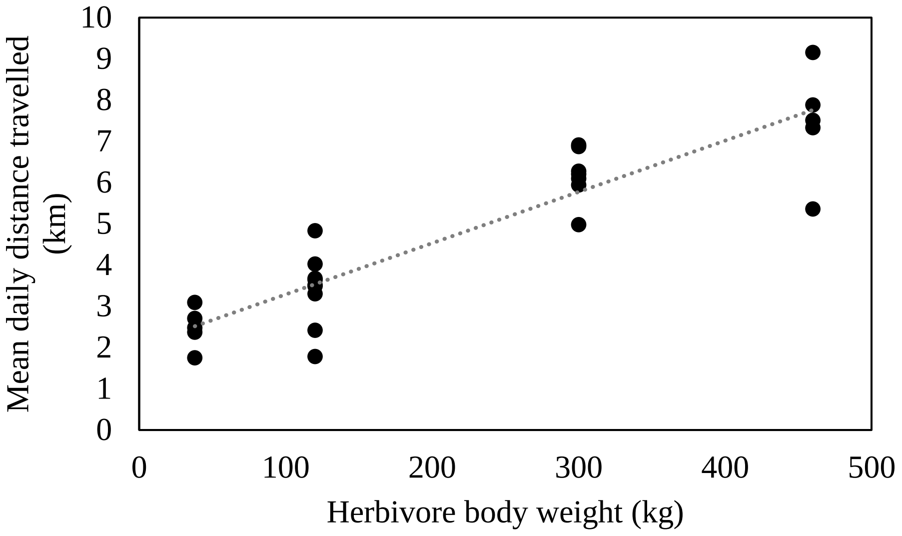

Figure 2: The positive relationship ($R^2 = 0.83$; $y = 0.0124x + 2.0445$) between mean daily distance travelled and body weight (BW) of reedbuck (BW 38 kg, *n*=5), red hartebeest (BW 120 kg, *n*=9), zebra (BW 300 kg, *n*=7) and eland (BW 460 kg, *n*=5).

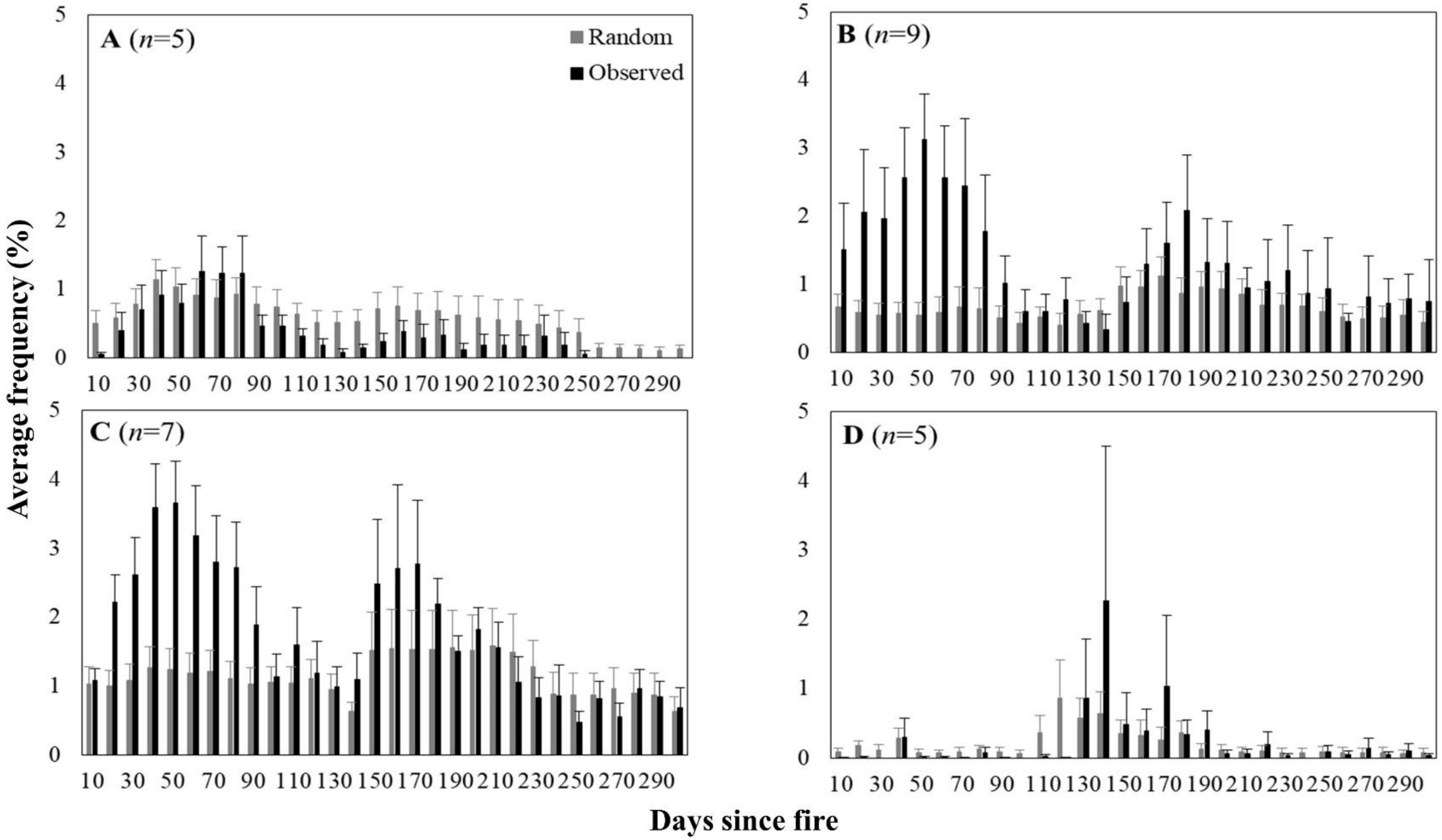

Figure 3: Frequency of incidence (%) of herbivores, A) reedbuck, B) red hartebeest, C) zebra and D) eland of the random (grey bars) and observed (black bars) locations on Mkambati Nature Reserve in relation to the number of days since the last fire (only the first 300 days are shown). Foraging preference can be determined based on the average frequency of observations in relation the average frequency of random locations.

Energy maximisation

Mixed effects models showed that energy maximisation strategies employed differed between species with different morphological traits (Table 1). Red hartebeest, zebra and eland foraged in ways that significantly maximised their DDE ($P<0.05$) whereas reedbuck foraged in a way that did not maximise either of the energy maximisation strategies over the entire study period. Furthermore red hartebeest and zebra showed preference to the low biomass (Figure 4) and young vegetation (soon after fire, Figure 3) favouring areas with biomass of <140 g/m^2 and vegetation younger than 90 days, compared to the other two species. Results for red hartebeest and reedbuck were best described through the use of the untransformed variables, whereas eland and zebra were best described by $DDE^{0.5}$ and $IDE^{0.5}$ (Table 1) as these showed clearer preferences. Seasonally however, a number of discrepancies could be observed. Zebra continued to forage for DDE throughout the year but inside the fire season they also maximised IDE (i.e. they foraged in a manner that could maximise both IDE and DDE) as they needed to forage in areas with high enough biomass. Eland continued to forage in a manner that maximised DDE outside of the fire season but foraged to maximise IDE inside the fire season, congruent with foraging in areas of high biomass (Figure 4) and older vegetation (Figure 3). The energy maximisation strategy of reedbuck and red hartebeest did not differ inside and outside of the fire season.

Our conclusions are robust to the V_I estimates because, in the end, most foraging opportunities led to I_{DDE} intake being largely limited by V_I, a digestive constraint that varies linearly with D (Wilmshurst et al. 2000, Bergman et al. 2001) which were directly measured by Shackleton and Mentis (1992). V_I estimates were restricted by time constraint (how much vegetation could be cropped in one minute) for only 0.25 ± 0.01% (mean ± SE, n = 5) of the available steps for eland, 0.28 ± 0.01% (n = 5) for reedbuck, 0.28 ± 0.01% (n = 9) for hartebeest, and 0.30 ± 0.01% (n=7) for zebra). Accordingly, the main driver of the I_{DDE} is digestibility (> 99% of the time) of vegetation.

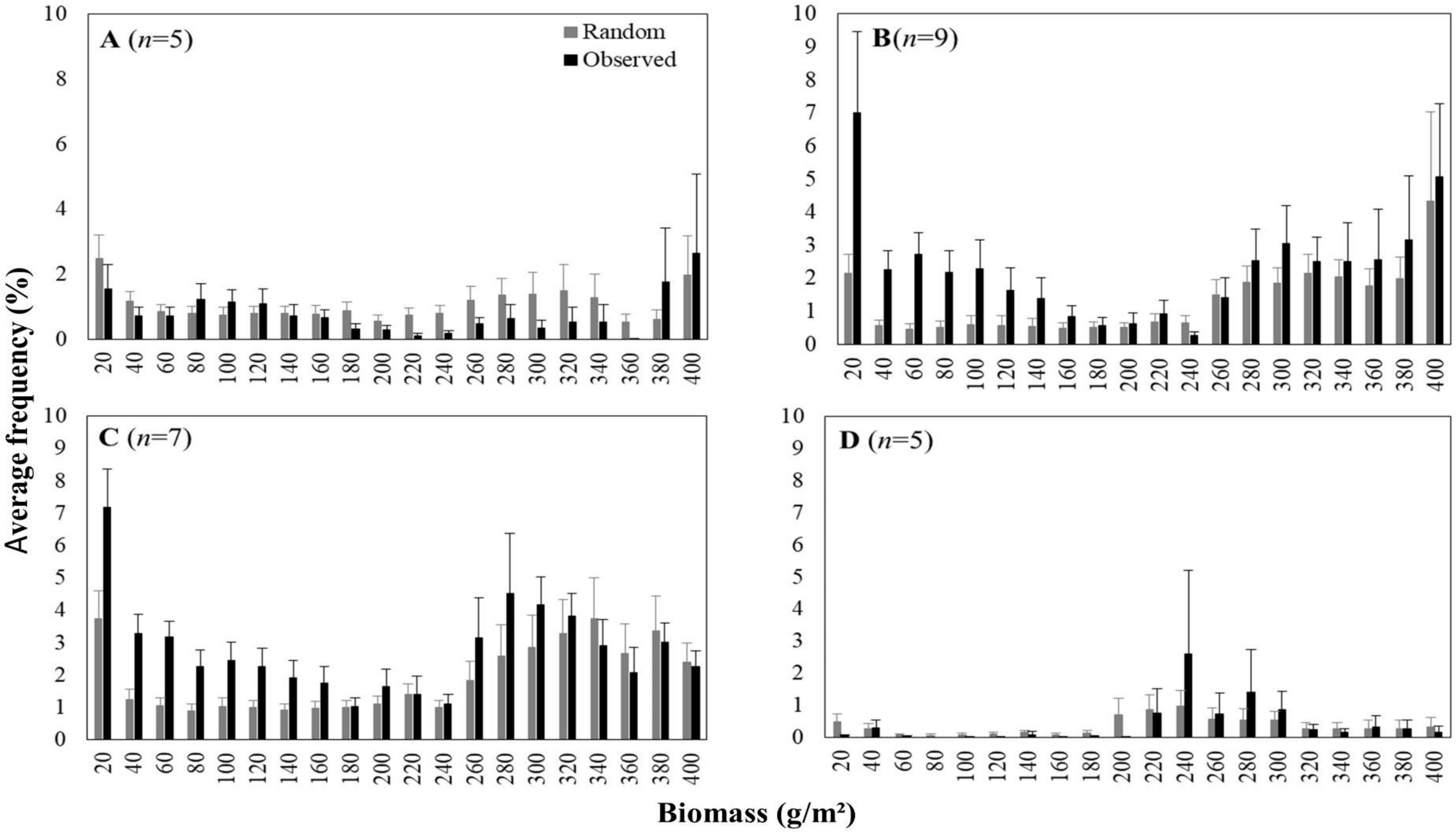

Figure 4: Frequency of incidence (%) of herbivores, A) reedbuck, B) red hartebeest, C) zebra and D) eland of the random (grey bars) and observed (black bars) locations on Mkambati Nature Reserve in relation to the available biomass of vegetation (biomass is only plotted up until 400 g/m^2). Foraging preference can be determined based on the average frequency of observations in relation to the average frequency of random location.

Table 1: Model estimates indicating the strength of preference toward a foraging currency (instantaneous digestible energy (IDE) or daily digestible energy (DDE)) and standard errors (SE) from the mixed effects models for the four study species over a) the complete study period and b) inside (May to October) and outside (November to April) of the fire season (Brooke et al. 2018) on Mkambati Nature Reserve. Separate models were run for both IDE and DDE for each species (column 1), and results have been multiplied by 1000 in order remove excessive preceding zeros. IDE and DDE for reedbuck and red hartebeest have been calculated using untransformed variables and zebra and eland were calculated to the power of 0.5 (indicated by an *), and significant preferences within the models are in bold (significant preferences are determined by calculating the 95% confidence intervals and if these confidence intervals are not negative a significant relationship is apparent).

		Reedbuck		Red hartebeest		Zebra		Eland	
		Model estimate	SE	Model estimate	SE	Model estimate	SE	Model estimate	SE
Throughout the year									
DDE	DDE	0.40	0.42	**0.72**	0.22	**12.62***	2.60	**68.16***	31.71
	Step length (log)	-1158.77	30.58	-952.92	15.40	-4185.68	69.13	-1673.90	39.23
	Step length	-3993.59	96.43	-419.86	13.01	-174.62	73.43	600.17	13.46
	Turning angle (cosine)	453.68	28.89	-618.81	11.64	1154.11	28.21	35083.35	348.69
	Merged grasslands	-475.74	75.69	-568.22	27.19	-35.24	101.63	-2604.42	49.10
	Rocky outcrops	-723.78	156.04	171.52	72.63	294.54	138.33	-645.39	76.04
IDE	IDE	0.12	0.21	0.12	0.08	-0.75*	0.64	49.07*	22.35
	Step length (log)	-1161.95	30.65	-974.43	15.40	-4181.67	69.04	-1548.19	39.34
	Step length	-3982.85	96.30	-393.02	12.86	-185.38	73.46	546.19	13.51
	Turning angle (cosine)	454.72	28.90	-644.30	11.61	1153.21	28.15	34252.44	349.28

Table 1 continued

		Reedbuck		Red hartebeest		Zebra		Eland	
		Model estimate	SE	Model estimate	SE	Model estimate	SE	Model estimate	SE
	Merged grasslands	-438.62	146.18	-249.77	29.70	605.66	94.31	-4673.71	132.93
	Rocky outcrops	-718.78	156.18	-7.40	72.95	148.74	137.50	-531.73	75.83
Inside fire season									
DDE	DDE	0.46	1.12	**0.84**	0.43	**15.35***	4.14	111.08*	76.13
	Step length (log)	-1330.84	83.86	-1202.02	25.10	-4146.17	92.49	-1748.78	65.43
	Step length	-3254.49	232.25	-284.27	18.88	-141.49	95.89	587.50	22.05
	Turning angle (cosine)	647.60	79.13	-565.18	17.98	1102.58	37.64	26780.08	470.67
	Merged grasslands	198.34	219.05	-240.93	44.39	-263.10	152.20	-2076.85	69.37
	Rocky outcrops	284.95	339.27	138.08	101.31	201.15	170.70	-779.67	117.70
IDE	IDE	0.21	0.49	0.08	0.17	**-1.83***	0.86	**114.68***	44.29
	Step length (log)	-1332.30	83.96	-1249.89	25.26	-4137.45	92.19	-1582.97	65.43
	Step length	-3242.85	232.72	-269.02	18.91	-150.81	95.73	517.91	22.15
	Turning angle (cosine)	647.86	79.10	-602.97	17.86	1099.25	37.51	26157.34	470.08
	Merged grasslands	376.08	402.31	-199.03	101.54	787.29	129.70	-3978.93	143.83
	Rocky outcrops	275.09	339.25	734.30	51.11	75.68	170.23	-596.95	117.67
Outside fire season									
DDE	DDE	0.34	0.45	**0.71**	0.21	**11.65***	3.63	**82.80***	12.37
	Step length (log)	-1130.19	33.16	-814.32	19.61	-4202.61	104.87	-1660.98	53.92

Table 1 continued

		Reedbuck		Red hartebeest		Zebra		Eland	
		Model estimate	SE	Model estimate	SE	Model estimate	SE	Model estimate	
	Step length	-4076.38	106.18	-466.20	18.06	-204.62	114.30	592.41	18.52
	Turning angle (cosine)	422.94	31.28	-663.13	15.72	1226.09	43.02	32484.11	448.80
	Merged grasslands	-550.57	81.60	-647.08	37.26	111.18	138.36	-3053.00	75.08
	Rocky outcrops	-996.63	179.90	543.94	106.26	409.61	238.52	-459.97	102.76
IDE	IDE	0.11	0.21	0.14	0.08	0.67*	0.97	37.95*	21.35
	Step length (log)	-1133.06	33.22	-827.38	19.61	-4200.34	104.85	-1563.46	54.11
	Step length	-4068.48	106.01	-429.89	17.82	-211.76	114.37	549.24	18.59
	Turning angle (cosine)	424.12	31.28	-672.96	15.69	1223.62	42.95	32051.73	450.40
	Merged grasslands	-540.18	158.26	-748.04	40.26	385.16	141.74	-5059.45	245.40
	Rocky outcrops	-985.10	180.10	570.22	107.17	326.35	238.35	-403.94	102.28

The mixed effect logistic regression GLMM for reedbuck indicated that reedbuck applied energy maximisation principles at the landscape scale rather than at the patch scale. At the landscape (~reserve) scale reedbuck maximised both DDE and IDE throughout the study period, inside and outside of fire seasons (Table 2). Reedbuck foraging to maximise both IDE and DDE at a landscape scale indicates that they are foraging at a broader (landscape) scale and selecting for vegetation type, rather than more fine scale parches within a vegetation type to fulfil their energy requirements.

Table 2: The results of the generalized linear mixed model (GLMM) testing energy maximisation principles shown by reedbuck at the landscape (~reserve) scale over the entire study period, and inside (May to October) and outside (November to April) of the fire season, respectively, on Mkambati Nature Reserve.

		Model estimate	Standard error	z value	*P*
Throughout the year					
DDE	DDE	0.071	0.00	23.34	<0.01
	Merged grasslands	-0.06	0.02	-3.47	<0.01
	Rock	-0.76	0.05	-14.65	<0.01
IDE	IDE	0.82	0.06	31.81	<0.01
	Merged grasslands	-0.12	0.02	-6.42	<0.01
	Rock	-0.80	0.05	-15.47	<0.01
Inside fire season					
DDE	DDE	1.23	0.07	16.67	<0.01
	Merged grasslands	0.35	0.06	6.15	<0.01
	Rock	0.18	0.11	1.6	>0.05
IDE	IDE	0.14	0.01	15.62	<0.01
	Merged grasslands	0.40	0.06	7.03	<0.01
	Rock	0.26	0.11	2.3	<0.05
Outside of fire season					
IDE	IDE	0.76	0.03	27.64	<0.01
	Merged grasslands	-0.18	0.02	-9.26	<0.01
	Rock	-1.01	0.06	-16.81	<0.01
DDE	DDE	0.06	0.00	19.2	<0.01
	Merged grasslands	-0.12	0.02	-6.53	<0.01
	Rock	-0.97	0.06	-16.19	<0.01

Discussion

Steps and use of post fire vegetation

We found a linear (positive) relationship between herbivore body weight and the mean daily movement travelled by herbivores as documented by others (Milton and May 1976, Cumming and Cumming 2003, Venter et al. 2017). In addition, the extent of daily movement by herbivores may be related to a herbivore's response to environmental heterogeneity and travelling between forage patches (Johnson et al. 2002). The short mean daily distances travelled by red hartebeest are consistent with foraging in patches of uniform vegetation (i.e. recently burnt areas) (Owen-Smith et al. 2010, Venter et al. 2014a), whereas the long distances travelled by eland result from having to move further to find adequate food; i.e. browse (Owen-Smith et al. 2010) in a landscape dominated by C_4 grasses.

Red hartebeest and zebra were observed foraging in the recently burnt low biomass grasslands (10-80 days after fire, Figure 3, and biomass of 180 g/m^2, Figure 4) which could be expected resulting from the peak in nutrient content of vegetation shortly (within the first six months) after fire (Shackleton and Mentis 1992), as grazers are well known t maintaining patches of short grasses (Fleurance et al. 2009). Similar nutrient peaks have been observed in the coastal grasslands of Ghana where crude protein was highest after four weeks since fire (Sen and Mabey 1965). However a second peak in utilisation of habitat longer after fire (150-210 days after fire, Figure 3, and biomass of 260-320 g/m^2, Figure 4) is more complex to understand. It is conceivable that increased herbivore pressure on the vegetation soon after fire (between 10 and 90 days) may lead to a depletion in plant biomass and increased competition among herbivores, which then forces herbivores to forage elsewhere. The second peak after fire observed in zebra and red hartebeest may be related to these herbivores returning to the post fire patches when biomass has again increased to a utilisable level, at a time when resources are more limited in other older vegetation in the reserve. Red hartebeest begun using the post fire patches sooner than zebra, but also spent more time in both the burnt and older grassland patches than zebra (i.e. zebra arrived in the post fire patches after red hartebeest, but continued used the post fire vegetation for longer). Zebra were less likely to enter older vegetation than red hartebeest (Venter et al. 2014a). These findings were consistent with those of Burkepile et al. (2016) in Kruger National Park, but not with those of (Hack et al. 2002) whom indicated that zebra made use of older grasslands given their ability to consume large quantities of nutrient poor vegetation. In older grasslands it must be noted that zebra may facilitate grazing for more selective grazers (e.g. red hartebeest) by removing vegetation biomass (Hack et al. 2002).

According to calculated requirements of eland, sufficient biomass should have been available for this species from 68 days after fire onwards, however eland observations only peaked much later (>130 days after fire). Eland are primarily browsers (Venter and Kalule-Sabiti 2016) and it is conceivable that C_3 vegetation (in a C_4 grass-dominated vegetation) was not yet available in sufficient quantity shortly after fire. Accordingly, during the fire season eland foraged (in older vegetation) to maximise IDE. Eland favouring IDE during the fire season and DDE outside of the fire season is in accordance with the finding that 79% of their diet at Mkambati was made up of C_3 plants with little/no seasonal variation (Venter and Kalule-Sabiti 2016).

Reedbuck's preference to high biomass vegetation and areas that can offer adequate protection is well documented (Skinner and Chimimba 2005, du Plessis et al. 2016, Venter and Kalule-Sabiti 2016). Reedbuck had very few observations in vegetation less than 380 g/m^2 (Figure 4) is congruent with these studies. However the high number of observations of reedbuck in relatively young vegetation (40-90 days after fire) indicate that reedbuck are indeed using the post fire vegetation on Mkambati in some way. These results suggest that although reedbuck are sheltering in high biomass vegetation, they may be feeding in young vegetation surrounding sheltered areas (i.e. feeding on the fringes of the fire scars). For all four herbivore species fire appears to play a substantial role in how they distribute themselves within the environment (*cf.* Allred et al. 2011).

Energy maximisation

Higher intake rates of digestible energy occur in areas of elevated vegetation nutrient content and can account for increased use by herbivores of these more productive sites (Bailey et al. 1996). Red hartebeest and zebra in this study were observed favouring the younger grasslands and the higher intake rate of digestible energy (DDE), with red hartebeest slightly more than zebra (*cf.* Venter et al. 2014a). Under most short term grazing situations (where herbivores forage to maximise IDE as is the case in eland) intake rate of energy is primarily controlled by bite size rather than the availability of biomass (Bailey et al. 1996). However it must be noted that calculations of R_{max} (functional response calculations for ruminants) do not consider mouth morphology necessary to crop vegetation, but only the intake rate in relation to body mass (Shipley et al. 1994).

Eland, although they preferred DDE overall, were the only species to show a seasonal preference to IDE inside the fire season. As highly adaptable ruminants favouring browse (Buijs et al. 2016), this shift from DDE outside the fire season to IDE inside the fire season is not surprising. On Mkambati there is limited browse, as more than 80% of the reserve is made up of low nutrient sour grasslands (Venter 2014). Eland are known to extensively use grasslands that are rich in forbs (Rowe-Rowe 1982), and in Mountain Zebra National Park Watson and Owen- Smith (2000) found that eland selected for vegetation types containing higher densities of browse species. We thus suggest that eland's switch between energy maximisation strategies is dependent on the availability and palatability of C_3 plant species. Our study was limited for a browsing species such as eland because we did not measure browse (forbs and woody plants), nutrient content, availability or biomass, and the calculations are based on the grass layer and not inclusive of other larger woody species. Until the role of these vegetation variables are considered we will thus not be able to present a comprehensive view on this species' foraging strategy for browsing species on Mkambati.

Energy maximisation in reedbuck is somewhat more complex than that of the other three species, as mixed effects models revealed that at the patch scale reedbuck did not maximise IDE or DDE over the entire study period, inside or outside of fire seasons. At a landscape scale (GLM models) reedbuck favoured both IDE and DDE over the entire study period, inside and outside of the fire seasons. A lack of clear preference for either energy maximisation strategy across seasons is rarely observed in herbivores (Bergman et al. 2001). This lack of a choice between foraging strategies by reedbuck at different scales and inside and outside of fire seasons indicates that there are probably factors (cover, distance to water and predator avoidance) other than forage that drive the movements of reedbuck within Mkambati. Reedbuck diet on Mkambati comprises approximately 45% C_3 plants (Venter and Kalule-Sabiti 2016) as opposed to other studies where reedbuck fed predominantly on C_4 grasses in savanna ecosystems (Gagnon and Chew 2000, Skinner and Chimimba 2005). This discrepancy in the diet of reedbuck on Mkambati compared to that of Skinner and Chimimba (2005) and Gagnon and Chew (2000) further suggests that reedbuck are driven by something other than energy at Mkambati (see below).

Body size, digestive strategy, mouth morphology and resource selection

Species coexistence is facilitated by the influences of body mass allowing larger herbivores to tolerate a wider range of forage qualities than smaller herbivores (Pretorius et al. 2016). Furthermore in poor quality vegetation such as at Mkambati one would expect to find larger herbivores that can tolerate such vegetation (Olff and Ritchie 1998), with smaller herbivores aggregating in patches of higher quality vegetation (Burkepile et al. 2016). We have shown how species foraged differently to maximise their energy budgets even though traditional foraging theory predicts that large herbivores will forage to maximise DDE (Owen-Smith and Novellie 1982, Stephens and Krebs 1986, Bergman et al. 2001, Edouard et al. 2010). In this study red hartebeest and zebra (medium bodied herbivores) foraged to maximise DDE in areas of relatively low biomass shortly after fires which is consistent with the findings of Hopcraft et al. (2010) and Kraaij and Novellie (2010) suggesting competition between species. At a patch scale the observed foraging of these species often differed from what is expected of species (e.g. larger bodied herbivores foraging in areas with higher vegetation biomass) through evolutionary behavioural and physiological adaptations (Olff et al. 2002, Hopcraft et al. 2010).

Red hartebeest and zebra fall within a similar weight range class but their digestive strategies differed (Appendix 1) (Wilmshurst et al. 2000, Kuntz et al. 2006). Zebra are non-ruminants and require greater quantities of vegetation as forage passes through their gastrointestinal tract faster, due to their less effective digestive system (Duncan et al. 1990). Mouth morphology of zebra (large premolars and upright mandibles, Codron et al. 2008) also limit the intake of vegetation in a short grass sward as they cannot crop very short vegetation (Janis and Ehrhardt 1988). Red hartebeest have a narrower muzzle than zebra and are thus able to selectively crop shorter grass (Gordon and Illius 1988, Janis and Ehrhardt 1988). Theoretically this narrow muzzle will improve their cropping ability on a short grass sward, and will also allow them to selectively feed on green shoots within moribund vegetation (Schuette et al. 1998). Zebra are however better equipped to forage on uniform vegetation as their wider mouth enables bigger bites. The differences in foraging between zebra and red hartebeest as a result of muzzle width were evident as red hartebeest used the low biomass (approximately 20 g/m^2) post fire patches sooner after fire than zebra (approximately 10 days). Similar foraging strategies observed in red hartebeest and zebra in our study support the notion that herbivores of similar body size are more likely to compete for the same resources (*cf*. Prins and Olff 1998, Venter et al. 2014a). In recently burnt areas low vegetation biomass means that intake rate is constrained by cropping (Allred et al. 2011). Under low biomass conditions zebra also need to consume greater amounts of forage due to their digestive system not being as effective as ruminant species (Menard et al. 2002). Red hartebeest should thus outcompete zebra as they are able to make better use of the low biomass vegetation (Arsenault and Owen- Smith 2008). Competition for forage between red hartebeest and zebra has also been observed in a small reserve (Bontebok National Park, South Africa) comprising nutrient poor fynbos shrublands, where 54% of Cape mountain zebra sightings and 46% of red hartebeest sightings were in post-fire vegetation ages of two years or less (Kraaij and Novellie 2010).

The absence of energy maximisation in reedbuck (the smallest of our study species) suggests that their foraging choices are driven by factors that have not been investigated in this study. In smaller herbivores body size may well be a constraint for two reasons; 1) they are forced to forage in areas where they have less chance of falling prey to predators due to the nested nature of predator impact on smaller species (Owen- Smith and Mills 2008, Hopcraft et al. 2012), and 2) the size of their gastrointestinal tract limits the retention time of forage (i.e. they require higher quality forage, Hopcraft et al. 2012). Thus small herbivores cannot effectively consume coarse vegetation, and the high rate of energy expenditure relative to body size forces small herbivores to forage on more nutritious vegetation (Gagnon and Chew 2000, Wilmshurst et al. 2000, Hopcraft et al. 2010). Fire season also coincides with poaching (predation) on Mkambati as poachers enter the reserve and set fires with the intention of attracting herbivores into areas where they are easy to poach (Venter et al. 2014a, Brooke et al. 2018). Furthermore in mesic grasslands, such as at Mkambati, grasses tend to be tall providing good protection (avoiding predation). Reedbuck have a shoulder height of 0.8 m, whereas the predominant tall grass on Mkambati *Cymopogon validus* (Shackleton and Shackleton 1994) attains a height of 2.5 m (Van Oudtshoorn 2012).

Eland, the largest of the study species (Table 1), are relatively unconstrained by the size of their digestive tract and thus less limited by the quality but rather by the quantity of vegetation (Hopcraft et al. 2010). Furthermore they are the only browsing species (Venter and Kalule-Sabiti 2016) considered in this study. Eland foraged for DDE throughout the study period and not showing any preference for recently burnt vegetation is characteristic of large browsers as C_3 biomass is limited shortly after fire (Bond 2008). Eland's adaptation to browse allows them to avoid competition for scarce resources on Mkambati. Eland is the only browsing species with a stable population on Mkambati, whereas springbok (*Antidorcas marsupialis*), impala (*Aepyceros melampus*), giraffe (*Giraffa Camelopardalis*) and kudu *(Tragelaphus strepsiceros)* have been introduced in the past but all experienced a steep population decline (with some going extinct) soon after introduction (Venter et al. 2014b). Eland's large body size may be key to its ability to maintain a stable population at Mkambati, whereby the ability to consume large quantities of lower quality forage make up for the poor quality of browse available.

Conclusion

Our study showed how energy maximisation principles between species with different morphology can explain herbivore foraging preferences within a low nutrient coastal grassland. However there are additional factors not included in this study that may affect herbivores' choice of habitat. Additional factors (some of which have been discussed above) include the influence of poaching (Oneka 1990, Brooke et al. 2018), variations in rainfall throughout the study period (Fryxell 1991) and how parasites affect herbivores' foraging preferences (Hutchings et al. 2003, Edouard et al. 2010). This study has made a start in unravelling the influences of energy budgets, body size and mouth morphology on herbivore movement dynamics within small, fenced protected areas. Habitat selection and energy maximisation by herbivores should form an integral part of managing protected areas as these results have indicate how fire could impact habitat selection of large herbivores. Furthermore investigating herbivores response to energy maximisation can help managers to predict herbivore responses to environmental change,

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Appendix 1: Composition of study species, recording interval, number of observations and length of data collection.

Species	Collar	Digestive strategy	Feeding strategy	Muzzle width	Mean Body Weight	Frequency of recordings	Number of observations	Recorded from	Recorded to
Reedbuck	NAN106	Ruminant[2]	Grazer[5]	31 mm[3]	38 kg[2]	60 min	3097	Oct-15	Mar-16
	NAN107						5327	Oct-15	Jun-16
	NAN108						4966	Oct-15	Jun-16
	NAN109						5278	Oct-15	Jun-16
	NAN110						4953	Oct-15	Jun-16
Red hartebeest	AU063	Ruminant[2]	Grazer[5]	52 mm[3]	120 kg[1]	30 min	9304	Oct-08	May-09
	AU064						18066	Oct-08	Oct-09
	AU065						7060	Oct-08	May-09
	AU066						4360	Oct-08	Jan-09
	AU371						24450	Nov-09	Dec-09
	AU372						19293	Nov-09	Dec-09
	AU373						3398	Nov-09	Dec-09

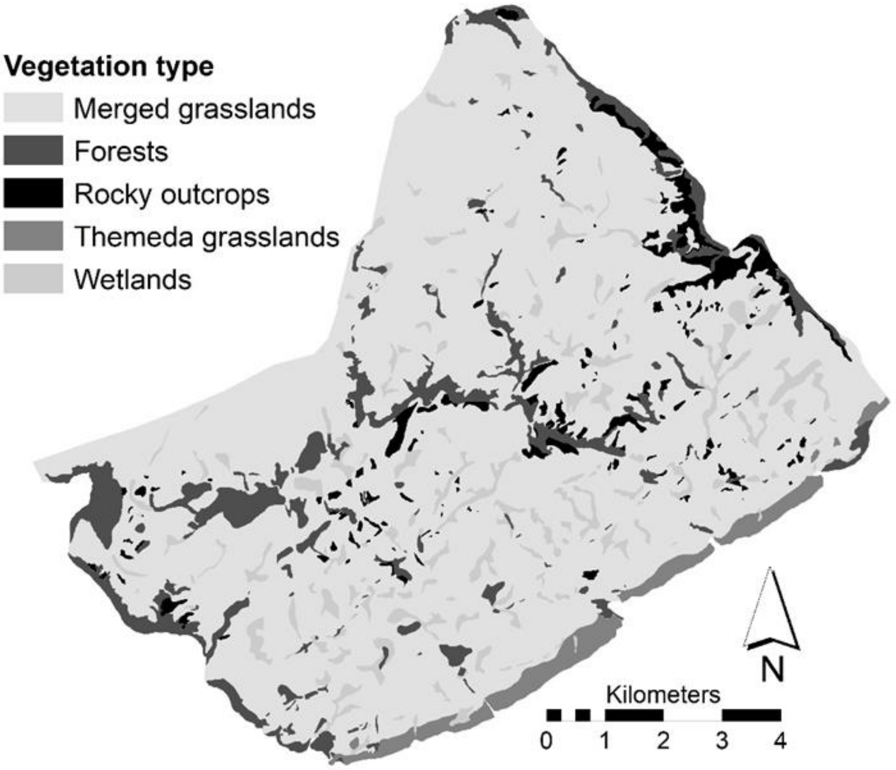
Appendix 1 continued

Species	Collar	Digestive strategy	Feeding strategy	Muzzle width	Mean Body Weight	Frequency of recordings	Number of observations	Recorded from	Recorded to
	AU451						2472	Jun-10	Sep-10
	AU452						7244	Jun-10	Sep-10
Zebra	AU067	Non-ruminant[2]	Grazer[5]	65 mm[4]	300 kg[2]	30 min	17430	Oct-08	Oct-09
	AU069						17726	Oct-08	Oct-09
	AU070						17836	Oct-08	Oct-09
	AU074						15411	Oct-08	Oct-09
	AU374						16545	Nov-09	Sep-10
	AU375						7438	Nov-09	Sep-10
	AU376						4223	Nov-09	Feb-10
Eland	AU071	Ruminant[2]	Browser[5]	61 mm	460 kg[2]	30 min	514	Oct-08	Nov-08
	AU072						3356	Oct-08	Dec-08

Appendix 1 continued

Species	Collar	Digestive strategy	Feeding strategy	Muzzle width	Mean Body Weight	Frequency of recordings	Number of observations	Recorded from	Recorded to
	AU073						18104	Oct-08	Oct-09
	SAT64						10086	Aug-11	Mar-12
	SAT65						11666	Aug-11	May-12

[1](Sponheimer et al. 2003), [2](Skinner and Chimimba 2005), [3](Gordon and Illius 1988), [4](Janis and Ehrhardt 1988), [5](Venter and Kalule-Sabiti 2016)



Appendix 2: Vegetation map of Mkambati Nature Reserve. Merged grasslands include *Aristida junciformis-Helichrysum mixtum, Cymbopobon validus-Digitatia natalensis, Festuca costata-Albuca setosa Stoebe vulgaris-Athanasia calva and Tristachya leucothrix simplex* grassland communities (adapted from Shackleton 1989).

CHAPTER 5: Synthesis

Introduction

In this chapter I highlight the main findings and how these addressed the aims and objectives of my research. I also provide recommendations relating to the management of herbivores and fire and the interactions therein in a small fenced nature reserve. In concluding I suggest possible focal avenues for future research.

Within Africa fire is an essential ecosystem process, fire regimes vary in terms of frequency, seasonality, size and type (Gill 1975), however many of these fire regimes have been influenced by anthropogenic disturbance (de Klerk et al. 2012). This has led to managers in fire prone areas needing to know not only the historical fire regimes in an area and how they have shaped the current vegetation (Bond et al. 2005, Kraaij et al. 2013b), but also how to mitigate the negative effects associated with potentially inappropriate fire regimes (Chuvieco et al. 2008). Fire and herbivory are furthermore interrelated, the dynamics of which create heterogeneity within the landscape; herbivores break up the continuity in biomass, often limiting the spread of fire, while fire recycles nutrients and energy creating new vegetative growth and thus attracting large herbivores (Archibald and Bond 2004, Archibald et al. 2005, Fuhlendorf et al. 2009, Allred et al. 2011). In this context my study has addressed these topics, by 1) considering the role of fire on Mkambati and 2), by understanding how fire influences the foraging choices that herbivores make regarding their energy maximisation strategy in a heterogeneous environment.

Humans have played a role in provisioning both fire and herbivory through management interventions (Burkepile et al. 2016). These management interventions are particularly prevalent in small fenced nature reserves (Newmark 2008). Utilisation resulting from management and manipulation of the environment is important to consider when investigating the scale of herbivore selection. In this study I considered two scales; 1) patch scale for all species (i.e. the area an herbivore used over a short time scale) and 2) landscape scale (across the entire reserve, Bailey et al. 1996) to better explain energy maximisation and how reedbuck distribute themselves within the environment. Patch scales are short term (few minutes) whereas landscape scale is long term (a few years or the animal’s lifetime) (Bailey et al. 1996, Owen-Smith et al. 2010). At these scales herbivore choices may also change in a heterogeneous environment. Smaller herbivores are potentially constrained to feeding in areas where the quality of vegetation is higher, whereas larger herbivores are possibly less limited as they are able to process larger quantities of lower quality material (Shipley et al. 1994, Hopcraft et al. 2010). By foraging in areas with either low or high vegetation biomass herbivores may change their functional response patterns (Gordon 2003) and thus are able to maximise different foraging currencies. These foraging currencies are what drives a herbivore's choice within a heterogeneous environment (Babin et al. 2011). In this study I focussed on two divergent foraging currencies both relating to herbivores' energy budgets: 1) herbivores could forage to maximise their daily intake rate of digestible energy (DDE), and 2) herbivores could forage to maximise their instantaneous intake rate of digestible energy (IDE). Furthermore I explored whether these energy maximisation strategies changed inside or outside of fire seasons.

Many studies have looked into the effects of fire and herbivory (Archibald and Bond 2004, Fuhlendorf et al. 2009, Allred et al. 2011, Burkepile et al. 2016), but few studies have linked fire to energy maximisation in herbivores. Through the characterisation of the fire regime on Mkambati I aimed to better understand how regular anthropogenic fire influenced the energy maximisation strategies applied by four large herbivore species.

Research findings

My first study objective was to characterise the fire regime on the coastal sourveld grasslands of Mkambati over the past ten years in terms of frequency, seasonality, size and the potential importance of anthropogenic sources of ignitions. It was important to have a clear understanding of the fire regimes on Mkambati as this allowed us to investigate the energy maximisation of herbivores in relation to biomass and post fire vegetation age. I concluded that although fire regimes are severely impacted by anthropogenic influence, the fire regimes in Mkambati fell within the realm of what is deemed to be natural for grasslands in South Africa (Mucina et al. 2006). The mean fire return interval (FRI) on Mkambati was estimated at approximately three years for the entire reserve, but differed amongst vegetation types. The simplistic formula used for calculating FRIs was regarded as reliable, especially in those vegetation types where open ended FRIs exceeded 50% of the total. In these cases, levels of censoring were high, yielding high variances in estimates of mean FRI when derived from maximum likelihood survival analysis (as found by others, Fernandes et al. 2012, Kraaij et al. 2013a). Fires were concentrated between May and August during which time fire danger weather conditions also peaked. Approximately 70% of fire scar centroids were located within 3 km of the nearest likely poacher entry point, resulting in slightly shorter FRIs in these areas.

My second study objective was to understand foraging choices between four large herbivore species with differing morpho-physiological traits (i.e. body mass, digestive strategy, and mouth morphology) by considering their energy maximisation strategy resulting from biomass and post fire vegetation age. Using step selection functions (Fortin et al. 2005) I showed how the mean daily distance travelled by large herbivore species increased linearly with body mass. Zebra and red hartebeest showed greater preference for low biomass vegetation, both maximising DDE, suggesting interspecific competition between the two species. Competition for resources between herbivores of similar body weight is not uncommon in African grazing ecosystems (Tomor and Owen-Smith 2002, Kraaij and Novellie 2010). Eland too favoured DDE throughout the study, however a seasonal change to IDE inside the fire season could be observed. At a patch scale, reedbuck showed no preference to either IDE or DDE, but showed a preference to both IDE and DDE at a landscape scale, suggesting that reedbuck are selecting habitats rather than areas that can maximise energy within a habitat. This is indicative that foraging choices in reedbuck were driven by something other than energy constraints.

Discussion

I have shown through this study, and it is clear from others (Shackleton 1989, Oneka 1990, Veblen et al. 2000, Kraaij 2010, Bowman et al. 2011, Archibald et al. 2012), that fire regimes may be significantly affected by anthropogenic influences. Furthermore the dynamics between fire and herbivory are essential for the effective functioning of grassland ecosystems (Archibald and Bond 2004, Allred et al. 2011). Through the manipulation of fire regimes it becomes possible for managers to create favourable vegetation types for certain species (Murray and Brown 1993, Kraaij and Novellie 2010). Seasons with high incidence of fire on Mkambati corresponded with times when the fire danger index (FDI) was highest during the drier months of the year (May to August). Poachers with the intention of attracting herbivores into recently burnt areas are thus aware of the ease of burning during the dry saeson. Parr and Andersen (2006) proposed that rigid fire regimes will not cater adequately for the conservation of a wide suite of biodiversity. In the case of Mkambati higher incidence of anthropogenic fire, and thus shorter FRIs, closer to the likely poacher entry points serve to introduce a level of pyrodiversity in the reserve. This potentially allows a greater suite of biodiversity to persist within a small area creating a grazing mosaic of recently burnt and older moribund patches of vegetation.

Morpho-physiological traits influence the way in which herbivores interact with their environment (Bell 1971, Bailey et al. 1996) and allow species to have different forage preferences relating to energy maximisation. In small protected areas managers are facing increasingly complex challenges in conserving biodiversity features, especially in the face of anthropogenic interference (Biggs et al. 2011, Venter 2014). In this thesis I have demonstrated how morpho-physiological traits and anthropogenic fire have influenced energy maximisation strategies in large herbivores. The lack of clear choice between foraging currencies at both the landscape and patch scales in reedbuck (the smallest herbivore in this study) is indicitive that their habitat preferences are driven by something other than forage. Red hartebeest and zebra both favoured DDE and low biomass (young) vegetation, but red hartebeest's narrow muzzle (Gordon and Illius 1988) allowed them to selectively crop younger shoots (Schuette et al. 1998) (when there was not enough biomass to sustain zebra), and make use of the older moribund grass by selecting for green shoots (Venter et al. 2014). Eland (the largest herbivore in this study) switched between IDE inside of fire seasons and DDE outside of fires seasons indicating their preference for browse.

Management recommendations and future research

Based on the findings and insights obtained during the course of this study, I propose the following recommendations and research questions to aid in the effective management of fire, herbivory and the interrelations therein. I have indicated that I have only laid out the groundwork for fire research on Mkambati through characterising the historic fire regime. I have also indicated a number of factors that were not included in our analysis of energy maximisation in large herbivores. I therefore suggest the following aspects for management and research:

1. Formulate a focused monitoring program for fauna and flora on Mkambati to compare the frequently and less frequently burnt areas of the reserve in order to understand the

effects that regular anthropogenic fire is having on the biota of the reserve. I recommend this be done through the use of monitoring plots inside and outside of the 3 km buffer that was outlined in Chapter 3. For fauna, biodiversity surveys need to be conducted inside and outside of fire scars and in areas that burn frequently and those that burn less frequently (*cf.* Venter and Conradie 2015, Hamer and Slotow 2017).

2. Centred on an understanding of how fire affects biota on Mkambati (obtained in point 1 above) I recommend that the reserve base their management of fire on thresholds outlining acceptable limits of variation within the fire regime (*cf.* Van Wilgen et al. 2011, Kraaij et al. 2013a). These thresholds need to cater for both the conservation of biodiversity (especially those species outlined in Appendix 1 of Chapter 3) on the reserve as well as resources on the reserve that are used by the surrounding local communities (e.g. thatching grass *Cymbopogon validus*).
3. Promote research into additional factors that were not included in this study but may also influence foraging behaviour and energy maximisation in herbivores. These factors include: cover, predator avoidance, rainfall, parasite load, interspecific and intraspecific competition between species with different morpho-physiological traits.
4. Compare the scales at which herbivores forage and how this affects their functional response. I have shown how reedbuck alter their energy maximisation preferences at different scales (landscape versus patch scale), however it is important for scale to be considered for the other three study species as well.
5. Investigate how vegetation type (browse or graze) and digestibility differs between ruminants and non-ruminants in low nutrient grasslands. In this study digestibility of vegetation was calculated (Shackleton 1989) as a single value based on vegetation age of each vegetation type and there was no definitive of a browse component of vegetation.
6. Management on Mkambati needs to consider how different herbivore species interact with fire. This will influence introductions and removals of species and how they can expect species to respond to fire. A monitoring plan relating to the interrelations between fire and herbivory is essential for this. Management will need to monitor the total area burnt in a given year and how soon after fire herbivores make use of these areas.

Within this study there were also a number of additional factors that were not included, but may still have influences on herbivore foraging and their energy maximisation principles. These included: 1) cover available to herbivores, as smaller herbivores may preferentially select for areas where there is greater protection from predation rather than forage quality or quantity (Hopcraft et al. 2012, Burkepile et al. 2016); 2) plant species composition of each vegetation type as I was unable to conclude whether vegetative composition influenced the selection of habitat by herbivores. Individual plant selection may influence the occurrence of a herbivore in a vegetation type (Fortin et al. 2003) or vegetation age.

Concluding remarks

In this study I characterised the fire regime of Mkambati in the recent past and indicated how fires affected the foraging choices of large herbivores in nutrient-poor coastal grasslands. Through characterising the fire regime on Mkambati over the past ten years I have made a start by establishing that fire regimes, although anthropogenically influenced, fell within ranges deemed natural for grasslands in South Africa and provided a fire history to underpin the evaluations of the effects of fire frequencies on the biota of Mkambati. The outputs from my third chapter allowed us to determine habitat selection and energy maximisation in large herbivores based on the post fire age of the fire prone grasslands on Mkambati. I have shown how morpho-physiological adaptations of herbivores have influenced their energy maximisation strategies and how they distribute themselves within the environment through foraging by selecting for different foraging currencies in a vegetation mosaic of recently burnt and older grassland. Finally I have discussed implications of these findings for the management of fire and herbivory in small fenced nature reserves in the interest of biodiversity.

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