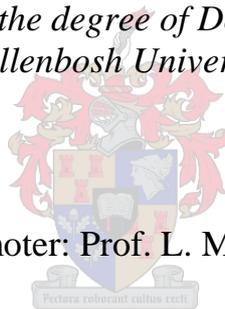


**The ecology of large herbivores native to the coastal lowlands
of the Fynbos Biome in the Western Cape, South Africa**

by

Frans Gustav Theodor Radloff

*Dissertation presented for the degree of Doctor of Science (Botany) at
Stellenbosh University*



Promoter: Prof. L. Mucina

Co-Promoter: Prof. W. J. Bond

December 2008

DECLARATION

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: 24 November 2008

Copyright © 2008 Stellenbosch University

All rights reserved

ABSTRACT

The south-western Cape is a unique region of southern Africa with regards to generally low soil nutrient status, winter rainfall and unusually species-rich temperate vegetation. This region supported a diverse large herbivore (> 20 kg) assemblage at the time of permanent European settlement (1652). The lowlands to the west and east of the Kogelberg supported populations of African elephant, black rhino, hippopotamus, eland, Cape mountain and plain zebra, ostrich, red hartebeest, and grey rhebuck. The eastern lowlands also supported three additional ruminant grazer species - the African buffalo, bontebok, and blue antelope. The fate of these herbivores changed rapidly after European settlement. Today the few remaining species are restricted to a few reserves scattered across the lowlands. This is, however, changing with a rapid growth in the wildlife industry that is accompanied by the reintroduction of wild animals into endangered and fragmented lowland areas. These reintroductions, together with the realisation that we have limited knowledge of the functional role of native large herbivores in the fynbos ecosystem, provided the rationale for this study. Questions on large herbivore ecology were addressed at three different spatial scales.

At the biome level, the reason for the absence of three ruminant grazers from the western lowlands was investigated. It was hypothesised that the absence of adequate high quality fodder in the form of C₄-grass during the hot and dry summers made it impossible for buffalo, blue antelope, and bontebok to survive on the western lowlands. The results from carbon isotope analysis of late prehistoric, historic and contemporary large herbivore remains were consistent to this Summer Nutritional Stress Hypothesis. I found that eland, elephant, grey rhebuck, ostrich, and red hartebeest (all species that historically occurred in both coastal lowlands) can survive with very little (< 15%) C₄ grass in their diet. In contrast, bontebok utilized at least 43% C₄ grass biomass in what was considered their natural habitats.

At a regional level, I tested the hypothesis that the large herbivores avoid nutrient-poor sandstone, sand, and limestone fynbos shrublands in favour of the more nutrient-rich shale renosterveld habitats. Support for this Renosterveld Preference Hypothesis was found by means of dung count surveys, which showed that both eland and bontebok readily utilize renosterveld, but avoid sandstone and limestone fynbos. In the latter they only utilize grassy microhabitats such as karstic sinkhole depressions. The same hypothesis was addressed in a novel way by using strontium isotope analysis and concluded that the technique needs more refinement for it to produce reliable results.

At a landscape level, interactions between fire and grazing by native large herbivores in relation to renosterveld vegetation dynamics were addressed. I conclude that the disappearance of the native herbivores probably had little bearing on the putative structural changes in renosterveld (grassland-shrubland dynamics). Support was found for the notion that a high fire frequency followed by intense grazing by livestock could have converted original renosterveld grasslands to unpalatable shrublands. Herbivory by native grazers/browsers, or the release from it, cannot by itself bring about the vegetation-state (structural) changes in renosterveld patches which had already been altered to herbivore-tolerant plant communities. However, in combination with fire, the presence or absence of large herbivores can change the trajectory of the system among the alternative structural states.

Die Suidwes-Kaap is 'n unieke gebied in suidelike Afrika weens sy algemene lae grondnutriëntstatus, winterreënval en buitengewone spesierike gematigde plantegroei. 'n Verskeidenheid van groot herbivoorspesies (> 20 kg) het ten tyde van permanente Europese vestiging (1652) hier voorgekom. Die laaglande wes en oos van die Kogelberg het populasies van die Afrika olifant, swartrenoster, seekoei, eland, berg- en vlaktesebra, volstruis, rooihartebes en vaalribbok bevat. Die oostelike laaglande is ook deur drie herkouende grasvreterspesies, naamlik die Afrika buffel, bontebok en bloubok, bewoon. Die diere se lot het drasties verander na Europese vestiging. Slegs enkele spesies kom vandag nog voor, en is beperk tot 'n paar verspreide reservate oor die laaglande heen. Hierdie situasie is egter aan die verander danksy die snelle groei van die wildindustrie, wat gepaard gaan met die hervestiging van wilde diere in bedreigde en gefragmenteerde laaglandgebiede. Hierdie hervestigingsaktiwiteite, tesame met beperkte beskikbare kennis oor die funksionele rol van groot herbivore in die fynbos-ekosisteem, het die rasionaal vir die studie verskaf. Vrae oor die ekologie van groot herbivore is aangespreek op drie verskillende ruimtelike skale.

Die rede vir die afwesigheid van die drie herkouende grasvreters spesies in die westelike laaglande is op bioomvlak ondersoek. Daar is gepostuleer dat die afwesigheid van genoegsame hoë kwaliteit voer in die vorm van C₄-grasse tydens die warm en droë somers dit onmoontlik gemaak het vir buffels, bloubokke en bontebokke om daar te oorleef. Koolstof isotoop-analises van die oorskot van laat prehistoriese, historiese en huidige groot herbivore het hierdie Somer Voedings Druk Hipotese ondersteun. Ek het gevind dat elande, olifante, vaalribbokke, volstruise en rooihartebes (almal spesies wat histories in beide kuslaaglandgebiede voorgekom het) baie min (< 15%) C₄ gras in hul dieet nodig het. Daarenteen bevat bontebokke se dieet minstens 43% C₄ gras in gebiede wat as hul natuurlike habitat beskou word.

Op 'n streeksvlak is die hipotese getoets dat die groot herbivore die nutriënt-arme sandsteen-, sand- en kalksteenfyfynbosstruikland vermy het en die meer nutriëntryke renosterveld op skalieland verkies het. Ondersteuning vir hierdie Renosterveld Voorkeurhipotese is gevind deur middel van mistellings. Dit het aangedui dat elande en bontebokke almal renosterveld geredelik benut, maar sandsteen- en kalksteenfyfynbos vermy. In laasgenoemde geval benut hul slegs grasryke mikrohabitate soos karstiese sinkgatholtes. Hierdie hipotese is ook op 'n unieke wyse aangespreek deur strontium isotoop-analises te gebruik. Die slotsom is egter dat die tegniek verder verfyn moet word voordat dit betroubare resultate kan verskaf.

Die interaksie tussen vuur en beweiding deur inheemse groot herbivore op renosterveld plantegroeidinamiek is op 'n landskapsvlak aangespreek. Ek het tot die slotsom gekom dat die verdwyning van die inheemse herbivore heel waarskynlik min te doen gehad het met die veronderstelde strukturele verandering van renosterveld (grasland-struikland dinamiek). Ondersteuning is gevind vir die idee dat 'n hoë brandfrekwensie, gevolg deur intensiewe beweiding deur vee, eerder verantwoordelik kon wees vir die verandering van renosterveld vanaf 'n graslandgebied tot 'n struiklandgebied. Beweiding deur inheemse gras-/blaarvreters, of die afwesigheid daarvan, kan nie op sigself die struktuur van renosterveld verander wat reeds uit 'n beweidingsbestande plantgemeenskap bestaan nie. In kombinasie met vuur kan die teenwoordigheid of afwesigheid van groot herbivore egter die trajeksie van die sisteem tussen alternatiewe strukturele toestande verander.

ACKNOWLEDGEMENTS

The goodwill and help of numerous people from diverse institutions and organisations made this study possible.

I thank CapeNature for permission and collection permits for the various studies conducted in De Hoop Nature Reserve. Within De Hoop Nature Reserve, I am particularly thankful to Peter Chadwick for his help, advice and encouragement. He was prepared to burn the renosterveld plots under difficult circumstances and was instrumental in orchestrating the collection of the large herbivore bones. For the collection of the bones and controlled burn I thank all the field rangers of De Hoop that participated and especially Andre Marè, At Witbooi and Keith Spencer. Marinus Stoltz of Denel Corporation Overberg Toetsbaan went out of his way to help whenever I needed access to the area or needed information. I am also indebted to Sanparks for allowing me to collect bones at Table Mountain and Bontebok National Parks. In Bontebok National Park, Roland January was particularly helpful and in Table Mountain National Park I am thankful for Amos Lombo's and Christopher's co-operation. At Elandsberg Nature Reserve I received great support from Bernard Wooding that made bone collection there a breeze. In Koeberg Nature Reserve, Hilton Westman provided valuable support.

I thank Heritage Western Cape for their permission and permit to sample the historic and late pre-historic large herbivore bones. At the Iziko museum Petro Keene, Sarah Wurz and Graham Avery provided valuable support and I really appreciate their help. I am in great debt to Richard Klein that helped a tremendous amount by re-identifying a large number of the pre-historic bone samples. I also appreciate his thoughtful discussions on large herbivore ecology in pre-historic times. Andrew Kandel is also thanked for his contribution on the elephant at Geelbek.

At the Archaeology Department of UCT I am indebted to Prof. Sealy for her patient help in explaining aspects of stable isotope research to me. John Lanham and Ian Newton are thanked for their help in the isotope lab and for always finding a gap to fit my samples in for analysis. I am very thankful to Daryl and Jacqui Codron for their discussions on stable isotopes and their application in ecology. Daryl gave me advice and direction on isotope matters at crucial times, which I appreciate very much. At the AEON EarthLab of Geological Sciences I am indebted to Shireen Govender and Petrus le Roux for their patient help in teaching me the intricacies of strontium isotope analysis both by means of laser ablation and by conventional solution analysis. I am thankful to Petrus who always patiently answered all my questions on Sr analysis – even in the maternity ward awaiting his second child! I am also grateful to Prof. Anton le Roux for allowing me to use the EarthLab facilities.

The Agricultural Research Council and in particular Ritha Wentzel is thanked for the weather data provided. I am also thankful to Sanet Briel from the Department of Agriculture that kept me up to date on her study regarding wildlife production units in the Western Cape.

To all my field assistants over the four years I express my sincere gratitude. The 17 700 plant height measurements would certainly not have been possible without your help. I want to thank Fynn Corry, Ben Walton, Jaco Stofberg, Marius Kieck, Maud Benato, Ivana Šibičková and Jozef Šibič. Gerhard Jakubowsky, Eugene Pienaar and Dirk Snyman need special mention as they assisted on repeated field trips, which must be a sign of stupidity, bravery, loyalty or simply true friendship and I like to believe it is the latter. Thank you very much. Dirk needs further acknowledgement as he assisted without complaint in dung counts, rodent trapping, plant measurements and bone collection in some really horrible weather at times. I am very grateful to Craig Beech that taught me everything I know about GIS and always managed to find the shape files and satellite images I needed.

My parents-in-law, Jan and Ronica Frick, deserves a huge word of thanks for all the meals and hospitality provided to me and all my assistants during the years. If it wasn't for the good cooking, I would certainly have had field assistant mutiny at times. My father-in-law is further thanked for his assistance in the construction of the enclosure camps and for designing and building an ingenious devise to pull the 100 metal droppers out of the ground after the dung counts were completed. My own parents also deserve a special word of thanks for their continued support and encouragement. The air tickets to attend the isotope workshop in Utah are certainly not taken for granted, thank you very much! I am in grate debt to Louw Hoffman for his friendship, support and interest during the years. Making it possible for me to attend the SAWMA conference in 2006 gave me a huge motivational boost that put everything back into perspective. Thanks is also due for his assistance with the strontium isotope and ostrich experiment.

I will never be able to repay my gratitude to Prof. Mucina, my supervisor, for all the time, money and wisdom invested in me. He took me in as his student on face value and that can only be described as blind faith in my abilities. Thank you very much for the opportunity to design and steer this study in the directions I took it. I will certainly miss our arguments about everything from science to politics. I also want to thank Prof. Bond for introducing me to stable isotopes as a research tool and for his guidance during this study. He certainly gave the study a new twist after each meeting.

I am very grateful for the financial support provided by the National Research Foundation, Grintek, Harry Crossley Foundation, Stellenbosch University and the Biogeosphere-Atmosphere Stable Isotope Network.

Finally but most importantly I want to thank my wife for standing by me during this time. Few wives would have stayed – never mind supported – their husbands when they announced their return to university at thirty. Your love, patience and support meant the world to me.

Oh, and then there is the cat, Katryn, who was always next, on and under the computer during the final months of write-up.

Die buffel ken geen metafisika:
hy soek die soetgras
en die kuil,
hy sal die kalf karnuffel,
horings in sy vyand gra,
die koei besnuffel,
teen hael gaan skuil,
maar geen vrae oor môre vra -
die buffel ken geen metafisika.

Alleen die mens
tref in sy swerwe
tussen hede, toekoms en verlede
die spleet tot grotte
van die rede:
hy maak 'n mes,
'n vuur,
skep gode,
dink aan sterf,
prewel gebede
em moet beswerend teen 'n muur
van sy spelonk die buffel verf:

die buffel van die metafisika:
die vuurbees in homself volg, buig of bars,
enduit sy drif en drome na,
en prikkels van die brein word piramides, Laaste Avondmaal,
wiel, chroom,
projektiele, produkte van atoom,
et cetera.

En voor sy besete blik
besef die enkeling
ontsteld
hy sal ook nie terugskrik
vir die alles-uitwissende slagveld -
stukkend lê alreeds
die Parthenon en Hirosjima
in die bese skoonheid van geweld.
Die buffel ken geen metafisika.

DJ Opperman (*Dolosse*, 1963)

TABLE OF CONTENTS

Declaration.....	ii
Abstract	iii
Opsomming.....	iv
Acknowledgements.....	v
Vuurbees.....	vii
CHAPTER 1: General introduction.....	1
Background.....	1
Objectives of this study.....	8
Structure of this dissertation.....	9
References.....	10
CHAPTER 2: Stable isotope inference of the historic distribution of large herbivores in the Cape lowlands, South Africa.....	16
Introduction.....	16
The Summer Nutritional Stress Hypothesis.....	17
Methods.....	23
Results.....	27
Discussion.....	33
References.....	39
CHAPTER 3: Habitat selection of large herbivores native to the nutrient-poor fynbos and renosterveld shrublands of the Western Cape, South Africa.....	49
Introduction.....	49
Methods.....	50
Results.....	54
Discussion.....	57
References.....	62

CHAPTER 4: Strontium-isotope analytical determination of the habitat preference of large herbivores in the nutrient depleted shrublands of the Western Cape, South Africa.....	69
Introduction.....	69
Background and methods.....	70
Results.....	76
Discussion.....	80
References.....	86
CHAPTER 5: The impact of herbivory and fire on grass-shrub dynamics of multi-structural vegetation states of the Cape renosterveld.....	91
Introduction.....	91
Methods.....	94
Results.....	99
Discussion.....	104
References.....	110
CHAPTER 6: Dealing with structurally diverse vegetation: a quick and robust method for biomass estimation.....	116
Introduction.....	116
Testing of the method.....	118
Results of the field tests.....	121
Discussion.....	123
References.....	124
Appendix 1.....	126
Appendix 2.....	128
CHAPTER 7: Conclusions with implications for wildlife management and suggestions for future research.....	130
References.....	134

Background

The southwestern Cape is a unique region of southern Africa with regards to climate, geomorphology, and vegetation. It receives a significant amount of rainfall during the cool winter months, while summers are hot and dry (Cowling *et al.* 1997; Rebelo *et al.* 2006; Chase & Meadows 2007). This region is an intricate mosaic of geological substrates that gave rise to a multitude of predominantly nutrient-poor soils (Specht & Moll 1983; Deacon *et al.* 1992; Cowling *et al.* 1997; Rebelo *et al.* 2006) and supports an exceptionally high plant diversity – it is the home of the Fynbos Biome characterised by shrublands dominated by small-leaved, evergreen shrubs whose regeneration is intimately linked to fire (Cowling *et al.* 1996; Rebelo *et al.* 2006). This unique environment also supported a diverse large mammal fauna before permanent European settlement in the mid-17th century heavily impacted on the region (Kerley *et al.* 2003).

Historical documents from the 17th and 18th century are an important source of information on the occurrence of large mammal species in the Fynbos, and its coastal lowlands in particular (see Du Plessis 1969; Skead 1980, and Rookmaker 1989 for reviews on historical accounts, and Boshoff & Kerley 2001 for a summary). The coastal lowlands can be divided into two major sub-regions based on the historic large herbivore (>20 kg) distributions and the current climate. The north-south and west-east running Cape Fold Belt mountain ranges converge in the SW Cape to form a natural physical barrier (Kogelberg area) separating the coastal lowlands of the West Coast from those of the Overberg (and those further east along the South Coast). The coastal lowlands west of Kogelberg (further western lowlands) receive predominantly winter rain (> 66%, Rebelo *et al.* 2006; Chase & Meadows 2007) and supported populations of African elephant (*Loxodonta africana*), black rhino (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibius*), eland (*Tragelaphus oryx*), Cape mountain zebra (*Equus zebra zebra*), plains zebra/quagga (*Equus quagga*), ostrich (*Struthio camelus*), red hartebeest (*Alcephalus buselaphus*), and grey rhebuck (*Pelea capreolus*) in the past (Du Plessis 1969; Skead 1980; Rookmaker 1989; Boshoff & Kerley 2001). The lowlands to the east of Kogelberg (further southern lowlands) have a more evenly distributed rainfall pattern (Rebelo *et al.* 2006; Chase & Meadows 2007) and supported the same large herbivore assemblage, but with the notable addition of three ruminant grazers: African buffalo (*Syncerus caffer*), blue antelope (*Hippotragus leucophaeus*; became extinct around 1800), and bontebok (*Damaliscus pygargus pygargus*) (Du Plessis 1969; Skead 1980; Rookmaker 1989; Boshoff & Kerley 2001). The southern lowlands also supported bushbuck (*Tragelaphus scriptus*) in local forest patches occurring at the base of the mountain ranges and in the kloofs. It is not clear how far west the quagga/plains zebra ventured, and what ecological relationship this species had to mountain zebra, but it is presumed that these two equids co-occurred in both lowland areas. On the West Coast gemsbok (*Oryx gazella gazella*) has been reported as far south as Saldanha but is believed to have been only an occasional visitor here and has been more abundant to the

north in Namaqualand. Springbok (*Antidorcas marsupialis*) occurred inland in both the Warm and Cold Bokkeveld, but it was most likely restricted to this area in the Fynbos Biome.

Archaeological evidence suggests that the described distribution pattern of the large herbivores remained unaltered for at least the 5 000 years before the written records mentioning the large mammals were made (Klein 1980; Klein 1983; Cruz-Uribe 1988). Lion (*Panthera leo*), leopard (*Panthera pardus*), wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), and brown hyena (*Hyaena brunnea*) (Skead 1980; Rookmaaker 1989; Boshoff & Kerley 2001) were all found in association with the large herbivores. Cheetah was, however, never recorded in the lowland areas, and most likely had the same distribution range as the springbok in the interior (Boshoff & Kerley 2001).

The abundance and distribution of the large mammals changed rapidly after permanent European settlement in the Cape (1652). It is presumed that by the year 1700 there was no big game within 200 km of Cape Town and that by 1800 most large mammals (above 50 kg) had been driven close to extinction within the Cape Floristic Region (Rebello 1992b). Most of these extinctions were due to hunting for meat and sport, or through the elimination of predators, scavengers and so-called “problem” animals (Rebello 1992b; Krug *et al.* 2004b). The last decade, however, witnessed a profound change in land use in the Western Cape, with a sharp increase in wildlife numbers due to the rapid growth in the wildlife industry (Kerley *et al.* 2003; Briel & Nowers 2007). Sixty-four of the 115 wildlife production units in the Western Cape have been established in the past 10 years (Briel & Nowers 2007). Wildlife is no longer confined to the few isolated provincial reserves and national parks. This development lead to an increased need for guidelines on the reintroduction and management of the appropriate large herbivore species in order to harmonise the need of the wildlife industry with the conservation practices implemented to preserve the mega-biodiversity of the Cape Floristic Region (CFR) – a global biodiversity hotspot (Myers *et al.* 2000).

It is now well appreciated that herbivores change the structure, biomass, production, and species composition of vegetation in heavily browsed or grazed areas of diverse ecosystems around the world (Owen-Smith & Danckwerts 1997; Frank *et al.* 1998; Olofsson *et al.* 2001; Augustine *et al.* 2003; Augustine & McNaughton 2004; Archibald *et al.* 2005; Danell *et al.* 2006; Harrison & Bardgett 2008; Skarpe & Hester 2008; Van Wieren & Baker 2008). The influence of large herbivores on the Fynbos ecosystems has, however, been by large a neglected topic. During the Third International Conference on mediterranean-type ecosystems held in 1980, it was concluded that there was very little understanding of the relationship between soil nutrient status, plant nutrition, and the vertebrate faunas of any of the mediterranean ecosystems (Cody *et al.* 1983; Morrow *et al.* 1983). It appears that, for at least the Fynbos Biome, very little actually changed and our relative ignorance still prevails – all this despite assertions (e.g. Hendey 1983) that the influence of these animals must have been “significant and is under-appreciated”. Hendey (1983) went as far as postulating that the large mammals might have been able to keep the fynbos shrubland more open than today and that fynbos might have been more

grassy in the past. This is in contrast to the opinions of Rebelo (1992a), Cowling *et al.* (1997) and Campbell (1986) who suggested that large herbivores never played a major role in the dynamics of nutrient-poor fynbos communities.

Little is known about the past distribution of native large herbivores on landscape scale in the Fynbos. It appears that the largely accepted opinion is that the sandstone, sand and limestone fynbos vegetation did not support large resident herbivore populations and that these animals rather concentrated in the renosterveld shrubland on more nutrient-rich shale substrates (Bigalke 1979; Cody *et al.* 1983; Morrow *et al.* 1983; Moll 1987; Rebelo 1987; Johnson 1992; Rebelo 1992a, 1996; Owen-Smith & Danckwerts 1997). Both fynbos and renosterveld are evergreen, fire-prone shrublands, but fynbos is characterised by fine-leaved ericoid shrubs, large-leaved proteoid shrubs and evergreen restios, while renosterveld is composed largely of asteraceous shrubs with a sparse understory of grasses and a locally high diversity of geophytes (Rebelo *et al.* 2006). Literature reveals that the large herbivore renosterveld preference hypothesis roots in the fact that fynbos *per se* has an exceptionally low nutritional status (Joubert & Stindt 1979; Specht & Moll 1983; Campbell 1986; Le Roux 1988; Johnson 1992), rather than on studies addressing the habitat preference and grazing behaviour of the herbivores. The reviews of historical accounts (Du Plessis 1969, Skead 1980, Rookmaker 1989) provides a useful general picture, but they are vague with regards to the exact nature of habitats visited and used by the herbivores (Boshoff & Kerley 2001). No published scientific study testing the large herbivore renosterveld preference hypothesis could be found.

Ecological studies on large herbivores in the Fynbos Biome

Large native herbivores in the Fynbos Biome have been especially studied in Bontebok National Park and Elandsberg Private Nature Reserve, with few isolated contributions from the Cape of Good Hope Nature Reserve (now part of Table Mountain National Park) and the De Hoop Nature Reserve.

Van Rensburg (1975) provided a historical account of how bontebok was saved from extinction in the southern lowlands. This paper, as well as that of Barnard and Van der Walt (1961) describe the translocation of bontebok in 1960 from the reserve proclaimed in 1931 to protect them (located near Bredasdorp in sand fynbos, Rebelo *et al.* 2006), to the current Bontebok National Park near Swellendam, which is covered by Swellendam silcrete fynbos (Rebelo *et al.* 2006). This move was necessitated by unfavourable habitat conditions in the former reserve that led to unacceptably high mortalities due to heavy internal parasite infestations and ataxia caused by mineral deficiencies. In the new Bontebok National Park (BNP) early studies focused on bontebok behaviour (David 1973; Van Zyl 1978) and population dynamics (De Graaff *et al.* 1976b). There are also three published accounts on the unsuccessful reintroductions of buffalo (Van der Walt *et al.* 1976b), red hartebeest (Van Der Walt *et al.* 1976a), and eland (De Graaff *et al.* 1976a) into the BNP. The eland and red hartebeest were removed due to their apparent incompatibility with the available habitat that left them in bad health and resulted in low reproductive output. The buffalo on the other hand was removed because of their repeated escapes from the Park that led to costly recapture procedures and their removal

was thus not due to bad health or low reproductive output. It is of interest that there were large numbers of springbok (a non-native species to the area) in the BNP during this period; this might have increased the competition for food between them and the small populations of both red hartebeest and eland (Novellie 1987).

Beukes (1984, 1987) looked at the habitat and diet selection of grey rhebuck and bontebok within the BNP. He found, by analyzing rumen contents, that grey rhebuck predominantly feed on dicotyledonous plants (on average 97% of rumen content) with small amounts of grass taken during the cool and wet winter months of the growing season. He concluded that low shrubs and forbs are the main food plants of grey rhebuck in the BNP. Bontebok, on the other hand, was found to be an obligate grazer (on average 97.5% of the rumen content was grass) which might utilise a small amount of dicotyledonous material during winter months. Both bontebok and grey rhebuck showed strong preference for recently burnt veld with a dramatic drop in the utilization of vegetation older than four years. Novellie (1987) studied the interrelationship between fire, grazing and grass cover and, like Beukes (1987), found that recently burnt areas were preferred by grey rhebuck and bontebok. He also concluded that the intense grazing of recently burnt areas were not deleterious to the preferred grass species. Luyt (2005) studied habitat preference and stocking densities of bontebok within the BNP. Corroborating the findings of Novellie (1987) and Beukes (1987), he found that bontebok preferred recently burnt areas and suggested that the re-establishment of shrubs after a fire might be delayed if too small an area is burnt at a given time. A small burnt patch can attract a very high density of animals that suppress shrub seedling establishment by trampling and indiscriminate grazing of any new plant growth. Of added interest is Luyt's (2005) observation that bontebok seeks out *Cynodon dactylon* grazing lawns and, in his opinion, they might also create and maintain these lawns by means of positive feedback nutrient loops.

Elandsberg Private Nature Reserve recently became a focus point of research on the restoration of West Coast renosterveld (Krug *et al.* 2004a, 2004b). Midoko-Iponga (2005) conducted a field experiment to determine the role of herbivory and competition on the establishment of shrub seedlings (5 cm high) translocated into old agricultural fields. He found that both browsing and competition with grass played a role in the seedling establishment, but that shrub-grass competition was more important. The study did not look into the influence large herbivores might have had on this competition interactions by means of grazing. Shiponeni and Milton (2006) looked at seed dispersal within the West Coast renosterveld of this Reserve. They found that large herbivores played an important role in the dispersal of both indigenous renosterveld and alien plant species (especially *Cynodon dactylon* and some other alien pasture grasses) by means of endozoochory. She postulates that the large herbivores are instrumental in the establishment and maintenance of the grazing lawns dominated by *Cynodon dactylon*. The grazing lawns in her study were located on old agricultural fields. Walton (2005) studied the influence of grazing on renosterveld vegetation dynamics after ploughing. He came to the conclusion that succession on old fields is retarded by grazing and that the establishment of especially palatable shrubs, such as species from the genera *Anthospermum* and *Hermania*, were particularly slow. He also emphasized the

importance of the *Cynodon dactylon* grazing lawns to the existing large herbivores. The results from Elandsberg Nature reserve must, however, be treated with caution, if deductions on natural ecosystem processes are to be made, as nearly two thirds of the large herbivores in the reserve were not indigenous to the area.

In what is now the Cape of Good Hope section of the Table Mountain National Park, Langley and Giliomee (1974) found that the favorite feeding habitats of the introduced population of bontebok were the recently burnt areas, fire breaks, and well established *Stenotaphrum secundatum* lawns. Zumpt and Heine (1977) studied some veterinary aspects of bontebok in the Park and found that ostertagiosis was a problem during winter months and that the animals suffered from severe copper deficiency which led to osteoporosis and a dull appearance of their hair-coat. These authors advised that the number of grazers in this Reserve must be limited to avoid overgrazing of the sparse natural grass components, and that certain grass sections must be judiciously fertilized to eliminate the existing deficiencies.

In the De Hoop Nature Reserve (DHNR) two studies were devoted to the demography of the endangered Cape mountain zebra (Lloyd & Rasa 1989; Smith *et al.* 2008). Smith *et al.* (2008) also commented on the limited habitat utilization of the mountain zebra within the DHNR. They suggested that mountain zebra concentrated on anthropogenically transformed grasslands (only 3.4% of the Reserve) and that they actively avoided 70% of the Reserve. Scott (1993) investigated the possible reasons for the bontebok population decline experienced between 1984 and 1990. She postulated that the main reason for the observed population decline was the lack of suitable bontebok habitat (i.e. recently burnt veld). In support of her hypothesis, a rapid improvement in bontebok body condition did occur after a controlled fire in 1991. However, a sub-population of bontebok without access to this newly burnt area also showed an improvement in body condition and survival. Her study also suggested that bontebok concentrated on *Cynodon dactylon* lawns.

Cape mountain zebra was also studied in the Gamka Mountain Nature Reserve (Watson *et al.* 2005) and Kammanassie Nature Reserve (Watson & Chadwick 2007). Both studies concluded that the mountain (sandstone) fynbos – the dominating vegetation type in both Reserves – was not a suitable habitat for mountain zebra and that it was utilized only for a short period following fire. In both cases the acquisition of adjacent non-mountain fynbos land with a higher grass cover was suggested as the management option that can improve the status of these two important mountain zebra populations.

A number of papers have also addressed the extinct blue antelope and mainly dealt with the taxonomical status and extinction history of the species (Mohr 1967; Klein 1974; Gould 1993; Robinson *et al.* 1996). Both Klein (1974) and Robinson *et al.* (1996) concluded that the blue antelope was a distinct species of the *Hippotragus* genus based on morphological and DNA-analytical evidence. Klein (1974) further suggested that this species was never numerous in historic times and that it only occurred on the southern lowlands in the small triangle of land spanning Swellendam, Caledon and Bredasdorp at the time of European settlement.

Milewski (2002) reported on the diet of introduced elephants roaming the forest-fynbos ecotone near Knysna. Based on opportunistic qualitative data obtained from forest guards, he suggested that elephants do utilize nutrient-poor fynbos shrublands.

As part of a larger systematic conservation planning exercise for the Cape Floristic Region (CFR, Cowling *et al.* 2003) four papers were published on the relationship between large herbivores and their habitat requirements. Boshoff and Kerley (2001) looked at the potential distributions of medium to large-sized mammals based on historical accounts and habitat requirements. Two other papers used the distribution pattern information and together with an adaptation of the agricultural-based Large Stock Unit or Animal Unit approach estimated the distributions and spatial requirements of the native medium and large-sized mammals in the CFR (Boshoff *et al.* 2001, 2002). Kerley *et al.* (2003) used the estimated habitat use and special requirements of the large and medium-sized mammals to assess the options for their protection in the CFR and proposed a reserve network to do so. All four papers, however, emphasise that their results must be treated as testable hypotheses and highlight the lack of natural history data for the large and medium-sized mammals in the CFR.

Domestic livestock in the Fynbos Biome

Around two thousand years ago the Khoekhoen introduced livestock (sheep and later cattle) to what is today known as the Fynbos Biome. The number of domestic livestock roaming the Cape forelands could have run well into the thousands when Dutch colonizers first arrived (Deacon 1992). Entries into Van Riebeeck's diary stated that the Khoekhoen, eager to trade, gathered in such numbers with their livestock around the fort in Table Bay during December 1652 that they (the Dutch) could have easily seized 12 000 cattle if they were so inclined (Thom 1952). A later entry (14 January 1653) gave an estimate of at least 20 000 cattle and sheep present during that time. Whether these animals were permanently kept on the coastal lowlands at such densities is, however, debatable as the same entry mentioned cattle trade by these Khoekhoen with tribes "far inland", indicating migration by these people and their livestock.

The influence of domestic livestock on renosterveld received some attention in Mcdowell (1988). He compared two adjacent sites (one heavily utilized by sheep and the other ungrazed by livestock for 14 years) of the West Coast renosterveld on the farm Eensaamheid (Agterpaarl area) with regards to total vegetation cover and species diversity. He found no significant decline in total cover or species diversity, but he ascertained a definite change in the flora composition. The species richness of Poaceae and Rutaceae declined, while the reverse was recorded for Asteraceae and Iridaceae. The three Protea species present in the ungrazed veld were absent from the grazed area and three members of the Thymelaeaceae showed some dependence on grazing for survival. Mcdowell (1988) concluded that stock grazing can have either negative or positive influences on renosterveld, depending on how it is managed. Le Roux (1988) studied the influence of livestock grazing on mountain (sandstone) fynbos in the Riviersonderend Mountain catchment area and came to the conclusion that frequent burning and intensive

grazing (coupled with trampling) would cause a reduction in floral diversity and can lead to erosion. He recommended that all domestic grazing in mountain fynbos must be stopped, as it is not only detrimental to the vegetation, but also economically unviable due to the low nutritional status of the veld. Teague (1999), on the other hand, argued that sandstone fynbos can be utilized in a sustainable manner if the veld is rested for a couple of months following a fire, and only moderately grazed thereafter. Regular fires (every four to five years) will, however, be necessary to regenerate the forage producing species and he admits that this will lead to a loss in biodiversity and especially proteoid species.

Renosterveld grass-shrub dynamics

An untested but potentially important hypothesis addresses the influence the large herbivores might have had on the vegetation structure of renosterveld. Whether renosterveld has been historically predominantly grassy or shrubby and what might have caused a switch between these vegetation states has been a topic of much speculation over many years (Sparrman 1786; Levyns 1956; Joubert & Stindt 1979; Skead 1980; Boucher & Moll 1981; Cowling 1984; Scholtz 1986; Moll 1987; Stock *et al.* 1992; Rebelo 1995; Balasse *et al.* 2002; Krug *et al.* 2004b; Newton & Knight 2004). The notion that it has been much grassier in the past is largely based on historical observations (see Skead 1980, Cowling 1984, Newton & Knight 2004, and references therein). An attempt was made to deliver scientific proof using isotope analyses but it yielded no evidence that the West Coast renosterveld was once covered by C₄ grass species such as *Themeda trianda* (Stock *et al.* 1992). There is, however, a possibility that the presumed grassland was dominated by C₃ grasses that do occur in this region. C₃ grasses can not currently be distinguished from C₃ dicots by means of stable isotope analysis. Severe and continuous overgrazing of freshly burnt veld by domestic stock is often held responsible for the presumed switch from grassland to shrubland (Sparrman 1786; Du Toit & Du Toit 1938; Joubert & Stindt 1979; Mcdowell 1995). This detrimental practice was presumably brought about with the advent of settled agriculture that changed the disturbance regime from an intense and localized, pulsed grazing system by indigenous and domestic livestock coupled with a variable fire frequency, to a system of continuous overgrazing and a fixed burning cycle (Cowling *et al.* 1986). More recently, however, Rebelo (1995) and Krug *et al.* (2004b) suggested that native large herbivores, or rather their absence for the last 300 years, might also have had a lot to do with the presumed structural changes in renosterveld. No scientific study directly addressing the influence of large herbivores on renosterveld vegetation structure has been undertaken, hence all the suggestions raised above remain, for the moment, mere speculations.

In summary, we know little about large herbivore ecology in the Fynbos Biome. We know with reasonable confidence the regional distribution patterns of the species that occurred here since late pre-historic times, but is it not sure why buffalo, blue antelope, and bontebok were absent from the western lowlands. The habitat preference of large mammals, population densities, and impact in the regions where they did occur, remains largely unknown. We speculate that the large herbivores focused on the more fertile renosterveld areas and that they avoided the nutrient-poor fynbos shrublands, except for brief periods following fire. There is reason to believe that these preferred renosterveld

areas were grassier in the past, but no clear evidence can be presented yet. The interplay between shrubs and grasses in renosterveld is still not well understood, and it probably was greatly influenced by grazing pressure and fire intervals. Presumably some renosterveld areas (at least on the southern lowlands) were well-utilized natural grazing lawns dominated (as today) by *Cynodon dactylon* and other grasses, whereas other renosterveld patches were dominated by shrubs and relatively less grazed. Switching between these states must have occurred, but for the moment the exact mechanisms are unknown.

Objectives of the study

Kerley *et al.* (2003) highlighted the lack of information available on large mammal ecology in the Cape Floristic Region and pleaded for a better understanding of the determinants of their distributions and abundances within the region. CapeNature (the provincial nature conservation authority) identified “an investigation into the role and impact of mammalian herbivores on lowland habitats of the Western Cape” as a research priority as it often needs to make decisions on whether or not mammalian herbivores should be re-introduced to natural (including lowland) remnant habitats. The unusual environment of the Fynbos Biome also provides a unique opportunity to study the ecology of large herbivores in habitats markedly different to that of any other in southern and East Africa. This unique environment provides the opportunity to evaluate the applicability of currently popular hypotheses regarding large herbivore biomass and plant production developed for African savanna systems (Fritz & Duncan 1994; Fritz *et al.* 2002).

This study aims to address some of the most pressing questions regarding large herbivore ecology in the Fynbos Biome; it is specifically focused on the ecology of native large herbivores that presently and historically occurred in the lowland areas. The objectives of the study can be anchored at three different spatial scales:

- a) At a Fynbos Biome level, I am investigating the reasons behind the difference in large herbivore distribution patterns between the two coastal lowland regions. I am addressing the question of why three ruminant grazers (buffalo, blue antelope and bontebok), native to the Fynbos Biome, were absent from the western lowlands. First I construct a hypothesis attempting to explain this regional distribution conundrum; this hypothesis (here dubbed the Summer Nutritional Stress Hypothesis) is then tested. Knowing the reasons behind the absence of these ruminant grazers from the western lowlands will greatly enhance our ability to understand and predict the impact these large herbivores had on the few remaining natural western lowland areas (Von Hase *et al.* 2003; Rebelo *et al.* 2006), where they were already (or are planned to be) inappropriately introduced.
- b) At a regional level I am investigating the landscape scale distribution patterns of large herbivores as delineated by the underlying geology. I am consequently testing the hypothesis that large herbivores avoid nutrient poor sandstone, sand and limestone fynbos in favour of the more nutrient-rich renosterveld areas on

- shale. Verifying or refuting this hypothesis (here dubbed the Renosterveld Preference Hypothesis) using rigorous scientific methods will enable conservation planners to make informed decisions on whether or not large herbivores should be introduced or re-introduced to particular lowland areas. It also provides the opportunity to evaluate the direct link that is believed to exist in African savanna systems between soil nutrient status and large herbivore biomass under given rainfall conditions (Fritz & Duncan 1994; Fritz *et al.* 2002).
- c) At a landscape level I am investigating the role of large herbivores and fire on renosterveld vegetation dynamics. I am consequently addressing the issue on whether the disappearance of large herbivores from the coastal lowlands could have contributed to the putative shrubland-grassland switches in renosterveld. The aim is also to make recommendations regarding the management of large herbivores in this endangered vegetation type (Von Hase *et al.* 2003).

Structure of this dissertation

The Chapters 2 through 6 of this dissertation have been written as separate papers to be submitted to various accredited journals. Chapter 6 has already been published in the *Journal of Vegetation Science*, but is presented here following the uniform format of this dissertation.

Chapter 2 deals with the regional distribution dichotomy that existed between the historic large herbivore assemblages of the western and southern lowlands. First my hypothesis for the absence of bontebok, buffalo and blue antelope from the western lowlands is presented. A test of this hypothesis, the Summer Nutritional Stress Hypothesis, then follow, using C-isotope analysis to determine the C₄ grass usage of numerous large herbivores from late-prehistoric, historic and contemporary times.

Chapters 3 and 4 deal with the Renosterveld Preference Hypothesis stating that large herbivores avoided sandstone, sand and limestone fynbos in favour of renosterveld on shale. More specifically, Chapter 3 investigates the habitat preference of eland and bontebok in the De Hoop Nature Reserve, using traditional dung-count techniques. Chapter 4 addresses the same question in a novel way by using strontium isotope analysis. The applicability of this newly developed technique is evaluated by using it to test the Renosterveld Preference Hypothesis.

Chapter 5 deals with the effect of fire and large herbivores on vegetation dynamics in renosterveld. A detailed account of a two year study that closely monitored the reaction of multiple renosterveld states (shrubland, tussock grassland, and lawn grassland) exposed to combinations of fire and herbivory by a number of indigenous herbivores (eland, bontebok and ostrich) is provided.

Chapter 6 is an extension of Chapter 5, as it describes the new method and apparatus that was developed to accurately measure the change in biomass of the five different growth forms that were monitored as part of the renosterveld vegetation-dynamics study.

In Chapter 7 conclusions from this study with direct implications for wildlife management on the coastal lowlands is discussed and some suggestions for future research made.

References

- Archibald S., Bond W.J., Stock W.D. & Fairbanks D.H.K. (2005) Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications*, 15, 96-109
- Augustine D.J. & McNaughton S.J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, 41, 45-58
- Augustine D.J., McNaughton S.J. & Frank D.A. (2003) Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications*, 13, 1325-1337
- Balasse M., Ambrose S.H., Smith A.B. & Price T.D. (2002) The seasonal mobility model for prehistoric herders in the south-western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. *Journal of Archaeological Science*, 29, 917-932
- Barnard P.J. & Van der Walt K. (1961) Translocation of the bontebok (*Damaliscus pygargus*) from Bredasdorp to Swellendam. *Koedoe*, 4, 105-109
- Beukes P.C. (1984) *Sommige aspekte van die ekologie van die Vaalribbok (Pelea Capreolus, Forster 1790) in die Bontebok Nasionale Park*. MSc. Thesis, University of Stellenbosch
- Beukes P.C. (1987) Responses of grey rhebuck and bontebok to controlled fires in coastal renosterveld. *South African Journal of Wildlife Research*, 17, 103-108
- Bigalke R.C. (1979) Aspects of vertebrate life in Fynbos, South Africa. In: *Ecosystems of the world, 9A, Heathlands and Related Shrublands* (ed. Specht. R.L.), pp. 81-95. Elsevier, Amsterdam
- Boshoff A.F. & Kerley G.I.H. (2001) Potential distribution of the medium- to large-size mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *African Zoology*, 36, 245-273
- Boshoff A.F., Kerley G.I.H. & Cowling R.M. (2001) A pragmatic approach to estimating the distribution and spatial requirements of the medium- to large-sized mammals in the Cape Floristic Region, South Africa. *Diversity and Distributions*, 7, 29-43
- Boshoff A.F., Kerley G.I.H. & Cowling R.M. (2002) Estimated spatial requirements of the medium- to large sized mammals, according to broad habitat units, in the Cape Floristic Region, South Africa. *African Journal of Range & Forage Science*, 19, 29-44
- Boucher C. & Moll E.J. (1981) South African mediterranean shrublands. In: *Ecosystems of the world, 1., Mediterranean-type shrublands*. (eds. Di Castri F., Goodall D.W. & Specht. R.L.), pp. 233-248. Elsevier, Amsterdam
- Briel S.C.P. & Nowers R.J. (2007) *Wildlife production in the Western Cape: A report on the quantification and qualification of wildlife production units*. Western Cape Department of Agriculture, Elsenburg

- Campbell B.M. (1986) Plant spinescence and herbivory in a nutrient poor ecosystem. *Oikos*, 47, 168-172
- Chase B.M. & Meadows M.E. (2007) Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews*, 84, 103-138
- Cody M.L., Breytenbach G.J., Fox A.E., Newsome A.E., Quinn R.D. & Siegfried W.R. (1983) Animal communities: diversity, density and dynamics. In: *Mineral nutrients in mediterranean ecosystems* (ed. Day J.A.), pp. 91-110. CSIR, Pretoria
- Cowling R., Rundel P.W., Lamont B.B., Arroyo M.K. & Arianoutsou M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, 11, 362-366
- Cowling R.M. (1984) A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. *Bothalia*, 15, 175-227
- Cowling R.M., Pierce S.M. & Moll E.J. (1986) Conservation and utilisation of South coast Renosterveld, an endangered South African vegetation type. *Biological Conservation*, 37, 363-377
- Cowling R.M., Pressey R.L., Rouget M. & Lombard A.T. (2003) A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biological Conservation*, 112, 191-216
- Cowling R.M., Richardson D. & Mustart P.J. (1997) Fynbos. In: *Vegetation of southern Africa* (eds. Cowling R.M., Richardson D. & Pierce S.), pp. 99-129. Cambridge University Press, Cambridge
- Cruz-Uribe K. (1988) The use and meaning of species diversity and richness in archaeological faunas. *Journal of Archaeological Science*, 15, 179-196
- Danell K., Bergström R., Duncan P. & Pastor J. (2006) *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge University Press, Cambridge
- David J.H.M. (1973) The Behaviour of the Bontebok, *Damaliscus dorcas dorcas*, (Pallas 1766), with special reference to territorial behaviour. *Zeitschrift für Tierpsychologie*, 33, 38-107
- De Graaff G., Van der Walt P.T. & Van Zyl L.J. (1976a) Lewensloop van 'n elandbevolking *Taurotragus oryx* in die Bontebok Nasionale Park. *Koedoe*, 19, 185-188
- De Graaff G., Van der Walt P.T. & Van Zyl L.J. (1976b) Populasiesamestelling van die Bontebok *Damaliscus dorcas dorcas* in die Bontebok Nasionale Park gedurende Januarie 1974. *Koedoe*, 19, 67-74
- Deacon H.J. (1992) Human settlement. In: *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling R.M.), pp. 260-270. Oxford University Press, Cape Town
- Deacon H.J., Jury M.R. & Ellis F. (1992) Selective regime and time. In: *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling R.M.), pp. 6-22. Oxford University Press, Cape Town
- Du Plessis S.E. (1969) *The past and present geographical distribution of the Perissodactyla and Artiodactyla in Southern Africa*. MSc. Thesis, University of Pretoria
- du Toit R. & du Toit E. (1938) Rhenoster bush as a weed. *Farming in South Africa*, 1938, 429-445
- Frank D.A., McNaughton S.J. & Tracy B.F. (1998) The ecology of the Earth's grazing ecosystems. *Bioscience*, 48, 513-521

- Fritz H. & Duncan P. (1994) On carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society London*, 256, 77-82
- Fritz H., Duncan P., Gordon I.J. & Illius A.W. (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620-625
- Gould J.S. (1993) Four antelopes of the apocalypse. *Natural History*, 102, 16-22
- Harrison K.A. & Bardgett R.D. (2008) Impacts of grazing and browsing by large herbivores on soils and soil biological properties. In: *The ecology of browsing and grazing* (eds. Gordon I.J. & Prins H.H.T.), pp. 201-216. Springer, Berlin
- Hendey Q.B. (1983) Palaeontology and palaeoecology of the Fynbos region: an introduction. In: *Fynbos palaeoecology: a preliminary synthesis* (eds. Deacon H.J., Hendey Q.B. & Lambrechts J.J.N.), pp. 87-99. CSIR, Pretoria
- Johnson S.D. (1992) Plant-animal relationships. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 175-205. Oxford University Press, Cape Town
- Joubert J.G. & Stindt H.W. (1979) The nutritive value of natural pastures in the district of Swellendam in the winter rainfall area of the Republic of South Africa. *Technical Communication, Department of Agriculture, Technical Services, Republic of South Africa*, 156, 1-10
- Kerley G.I.H., Pressey R.L., Cowling R.M., Boshoff A.F. & Sims-Castley R. (2003) Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot, South Africa. *Biological Conservation*, 112, 169-190
- Klein R.G. (1974) On the taxonomic status, distribution and ecology of the blue antelope, *Hippotragus leucophaeus* (Pallas, 1766). *Annals of the South African Museum*, 65, 99-143
- Klein R.G. (1980) Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in Southern Africa. *Annals of the South African Museum*, 81, 223-283
- Klein R.G. (1983) Palaeoenvironmental implications of quaternary large mammals in the Fynbos region. In: *Fynbos palaeoecology: a preliminary synthesis* (eds. Deacon H.J., Hendey Q.B. & Lambrechts J.J.N.), pp. 116-138. CSIR, Pretoria
- Krug C.B., Krug R.M., Midoko Iponga D.M., Walton B.A., Milton S.J. & Shiponeni N.N. (2004a) Restoration of West Coast Renosterveld: facilitating the return of a highly threatened vegetation type. In: *Proceedings of the 10th MEDECOS Conference* (eds. Arianoutsou M. & Papanastasis V.P.), pp. 107-119. Millpress, Rotterdam
- Krug R.M., Krug C.B., Midoko Iponga D., Walton B.A., Milton S.J., Newton I.P., Farley N. & Shiponeni N.N. (2004b) Reconstructing West Coast Renosterveld: past and present ecological processes in a Mediterranean shrubland of South Africa. In: *Proceedings of the 10th MEDECOS Conference* (eds. Arianoutsou M. & Papanastasis V.P.), pp. 120-132. Millpress, Rotterdam
- Langley C.H. & Giliomee J.H. (1974) Behaviour of the bontebok (*Damaliscus d. dorcas*) in the Cape of Good Hope Nature Reserve. *Journal of the Southern African Wildlife Management Association*, 4, 117-121
- Le Roux G.H. (1988) Die gebruik van die Kaapse Fynbos vir weiding en die probleme wat dit skep. *Suid Afrikaanse Bosbouydskrif*, 146, 51-54

- Levyns M.R. (1956) Notes on the biology and distribution of the Rhenoster bush. *Suid Afrikaanse Joernaal van Wetenskap*, 52, 141-143
- Lloyd P.H.L. & Rasa O.A.E. (1989) Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behavioral Ecology and Sociobiology*, 25, 411-420
- Luyt E. du C. (2005) *Models of bontebok (Damaliscus pygargus pygargus, Pallas 1766) Habitat preferences in the Bontebok National Park and sustainable stocking rates*. MSc. Thesis, Stellenbosch University
- McDowell C.R. (1988) *Factors affecting the conservation of renosterveld by private landowners*. PhD. Thesis, University of Cape Town
- McDowell C.R. (1995) Grazing and renosterveld management. In: *The sustainable use and management of renosterveld remnants in the Cape Floristic Region: proceedings of a symposium* (eds. Low A.B. & Jones F.E.). Botanical Society of South Africa, Cape Town
- Midoko-Iponga D., Krug C.B. & Milton S.J. (2005) Competition and herbivory influence growth and survival of shrubs on old fields: Implications for restoration of renosterveld shrubland. *Journal of Vegetation Science*, 16, 685-692
- Milewski A.V. (2002) Elephant diet at the edge of the Fynbos Biome, South Africa. *Pachyderm*, 32, 29-38
- Mohr E. (1967) *Der Blaubock, Hippotragus leucophaeus (Pallas, 1766). Eine Dokumentation*. Paul Parey, Hamburg
- Moll E.J. (1987) Review of some new concepts in "Fynbos" ecology. In: *Papers in the prehistory of the Western Cape. British Archaeological Reports International Series 332*, (eds. Parkington J. & Hall M.), pp. 120-131. BAR, Oxford
- Morrow P.A., Day J.A., Fox M.D., Frost P.G.H., Jarvis J.U.M., Milewski A.V. & Norton P.M. (1983) Interaction between plants and animals. In: *Mineral nutrients in mediterranean ecosystems* (ed. Day J.A.), pp. 111-124. CSIR, Pretoria
- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858
- Newton P.I. & Knight R. (2004) The Matrix: The development of coastal renosterveld. *Veld & Flora*, 90, 162-165
- Novellie P. (1987) Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe*, 30, 1-17
- Olofsson J., Kitti H., Rautiainen P., Stark S. & Oksanen L. (2001) Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, 24, 13-24
- Owen-Smith N. & Danckwerts J.E. (1997) Herbivory. In: *Vegetation of southern Africa* (eds. Cowling R.M., Richardson D. & Pierce S.), pp. 397-420. Cambridge University Press, Cambridge
- Rebello A.G. (1987) Management implications. In: *A preliminary synthesis of pollination biology in the Cape flora* (ed. Rebello A.G.), pp. 193-211. CSIR, Pretoria
- Rebello A.G. (1992a) Preservation of biotic diversity. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 309-344. Oxford University Press, Cape Town

- Rebelo A.G. (1992b) Red Data Book Species in the Cape Floristic Region: threats, priorities and target species. *Transactions of the Royal Society of South Africa*, 48, 55-86
- Rebelo A.G. (1995) Renosterveld: Conservation and research. In: *The sustainable use and management of renosterveld remnants in the Cape floristic region: proceedings of a symposium* (eds. Low A.B. & Jones F.E.), pp. 32-42. Botanical Society of South Africa, Cape Town
- Rebelo A.G. (1996) Renosterveld. In: *Vegetation of South Africa, Lesotho and Swaziland* (eds. Low A.B. & Rebelo A.G.). pp. 63-67. Department of Environmental Affairs and Tourism, Pretoria
- Rebelo A.G., Boucher C., Helme N., Mucina L., Rutherford M.C., Smit W.J., Powrie L.W., Ellis F., Lambrechts J.J., Scott L., Radloff F.G.T., Johnson S.D., Richardson D.M., Ward R.A., Proches S.M., Oliver E.G.H., Manning J.C., Jürgens N., McDonald D.J., Janssen J.A.M., Walton B.A., Le Roux A., Skowno A.L., Todd S.W. & Hoare D.B. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 52-219. SANBI, Pretoria
- Robinson T.J., Bastos A.D., Halanych K.M. & Herzig B. (1996) Mitochondrial DNA sequence relationships of the extinct blue antelope *Hippotragus leucophaeus*. *Naturwissenschaften*, 83, 178-182
- Rookmaaker L.C. (1989) *The zoological exploration of Southern Africa 1650-1790*. A. A. Balkema, Rotterdam
- Scholtz A. (1986) *Palynological and palaeobotanical studies in the Southern Cape*. MA. Thesis, Stellenbosch University
- Scott H.A. (1993) *An investigation into possible reasons for a decline in numbers of bontebok Damaliscus dorcas dorcas (Pallas, 1766) in the De Hoop Nature Reserve, Southwestern Cape*. MTech Thesis, Saasveld School of Forestry, Port Elizabeth Technikon
- Shiponeni N.N. & Milton S.J. (2006) Seed dispersal in the dung of large herbivores: implications for restoration of Renosterveld shrubland old fields. *Biodiversity and Conservation*, 15, 3161-3175
- Skarpe C. & Hester A.J. (2008) Plant traits, browsing and grazing herbivores, and vegetation dynamics. In: *The ecology of browsing and grazing* (eds. Gordon I.J. & Prins H.H.T.), pp. 217-261. Springer, Berlin
- Skead C.J. (1980) *Historical mammal incidence in the Cape Province. Volume 1: The Western and Northern Cape*. Department of Nature and Environmental Conservation of the Cape Provincial Administration, Cape Town
- Smith R.K., Marais A., Chadwick P., Lloyd P.H. & Hill R.A. (2008) Monitoring and management of the endangered Cape mountain zebra *Equus zebra zebra* in the Western Cape, South Africa. *African Journal of Ecology*, 46, 207-213
- Sparman A. (1786) *A voyage to the Cape of Good Hope, towards the Antarctic Polar Circle, and round the world: but chiefly into the country of the Hottentots and Caffres, from the year 1772, to 1776. Vol. 2*. Robinson, London.
- Specht R.L. & Moll E.J. (1983) Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In: *Mediterranean-type ecosystems: The*

- role of nutrients* (eds. Kruger F.J., Mitchell D.T. & Jarvis J.U.M.), pp. 41-65. Springer-Verlag, Heidelberg
- Stock W.D., Bond W.J. & Le Roux D. (1992) Isotope evidence from soil carbon to reconstruct vegetation history in the south-western Cape Province. *South African Journal of Science*, 89, 153-154
- Teague W.R. (1999) Fynbos (macchia). In: *Veld Management in South Africa* (ed. Tainton N.M.), pp. 327-333. University of Natal Press, Pietermaritzburg
- Thom H.B. (1952) *Journal of Jan Van Riebeeck, Volume 1, 1651-1652*. AA Balkema, Cape Town
- Van der Walt P.T., De Graaff G. & Van Zyl L.J. (1976a) Lewensloop van 'n rooihartbees-bevolking *Alcelaphus buselaphus caama* in die Bontebok Nasionale Park. *Koedoe*, 19, 181-184
- Van der Walt P.T., Van Zyl L.J. & De Graaff G. (1976b) Lewensloop van 'n Kaapse buffelbevolking *Syncerus caffer* in die Bontebok Nasionale Park. *Koedoe*, 19, 189-191
- Van Rensburg A.P.J. (1975) Die geskiedenis van die Nasionale Bontebokpark, Swellendam. *Koedoe*, 18, 165-190
- Van Wieren S.E. & Baker P.J. (2008) The impact of browsing and grazing herbivores on biodiversity. In: *The ecology of browsing and grazing* (eds. Gordon I.J. & Prins H.H.T.), pp. 263-292. Springer, Berlin
- Van Zyl L.J. (1978) *Die waterbehoefte en drinkgewoontes van die Bontebok Damaliscus dorcas dorcas (Pallas, 1766) in die Bontebok Nasionale Park*. MSc. Thesis, University of Stellenbosh
- Von Hase A., Rouget M., Maze K. & Helme N. (2003) A fine-scale conservation plan for Cape Lowlands Renosterveld. Technical Report, Botanical Society of South Africa, Kirstenbosch
- Walton B.A. (2005) *Vegetation patterns and dynamics of Renosterveld at Agter-Groenberg Conservancy, Western Cape, South Africa*. MSc. Thesis, Stellenbosch University
- Watson L.H. & Chadwick P. (2007) Management of Cape mountain zebra in the Kammanassie Nature Reserve, South Africa. *South African Journal of Wildlife Research*, 37, 31-39
- Watson L.H., Odendaal H.E., Barry T.J. & Pietersen J. (2005) Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire. *Biological Conservation*, 122, 173-180
- Zumpt F. & Heine E.W.P. (1977) Some veterinary aspects of bontebok in the Cape of Good Hope Nature Reserve. *South African Journal of Wildlife Research*, 8, 131-134

STABLE ISOTOPE INFERENCE OF THE HISTORIC DISTRIBUTION OF LARGE HERBIVORES IN THE CAPE LOWLANDS, SOUTH AFRICA

Introduction

Understanding and predicting the distribution of organisms lie at the heart of ecological science (Gaston 2003; Morris 2003) and have become increasingly important with the threats on biodiversity due to climate change (Root *et al.* 2003; Ibáñez *et al.* 2006). Attempts to predict the effect of climate change on the distribution of mammal species (Johnston & Schmitz 1997; Peterson *et al.* 2002; Burns *et al.* 2003; Ogutu & Owen-Smith 2003) have been hampered by a multitude of factors other than the climate and it is now acknowledged that climatic parameters alone can not be used to explain mammal distribution patterns accurately (Morrison 2001; Gaston 2003; Schmitz *et al.* 2003; Berteaux *et al.* 2006). Other abiotic factors such as edaphic conditions and the physical environment also need to be considered together with both positive and negative biotic interactions, habitat connectivity/accessibility, and the evolutionary capacity of mammal populations to adapt to change (Soberón & Peterson 2005). Scale also needs to be considered since different environmental factors are important to animals at different scales (Senft *et al.* 1987; Willis & Whittaker 2002; Pearson & Dawson 2003). The geographical distribution of an animal can be seen as a complex expression of its ecology and evolutionary history that is governed by a multitude of factors operating with different intensities at different scales (Soberón & Peterson 2005).

The coastal lowlands in the Fynbos biome (Rebello *et al.* 2006) at the SW tip of Africa supported a diverse range of native large herbivores (> 20 kg) at the time of permanent European settlement in the mid 17th century (Du Plessis 1969; Skead 1980; Rookmaaker 1989; Boshoff & Kerley 2001). There was, however, an intriguing dichotomy in ruminant grazer species distribution at the time. The Cape Fold Belt mountain ranges following the coastlines from the East and North meet in the SW Cape where they reach the sea at Cape Hangklip. This mountain mass forms a physical barrier between the coastal lowlands that we refer to here as the western and southern lowlands of the SW Cape. Historical accounts leave little doubt that African elephant (*Loxodonta africana*), black rhino (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibius*), eland (*Tragelaphus oryx*), Cape mountain zebra (*Equus zebra zebra*), plains zebra/quagga (*Equus quagga*), red hartebeest (*Alcephalus buselaphus*), grey rhebuck (*Pelea capreolus*), and ostrich (*Struthio camelus*) occurred on both the western and southern lowlands. However, African buffalo (*Syncerus caffer*), bontebok (*Damaliscus pygargus pygargus*) and the extinct blue antelope (*Hippotragus leucophaeus*) were only reported in the southern lowlands (see Du Plessis 1969, Skead 1980 and Rookmaker 1989 for reviews on historical accounts). The absence of buffalo, blue antelope and bontebok from the western lowlands seems to be substantiated by archaeological studies that suggest an unaltered pattern in large herbivore distributions in the lowland areas for at least 5 000

years before the written records regarding the presence on large mammals were made (Klein 1980; Klein 1983; Cruz-Uribe 1988).

The fate of the native large herbivores changed dramatically after permanent European settlement in 1652. It is estimated that after just 40 years there was no big game within 200 km of Cape Town and that by 1800 most large mammals (above 50 kg) had been driven close to extinction within the Cape Floristic Region (Rebelo 1992). Hunting for meat and sport, as well as the elimination of predators, scavengers and “problem” animals are blamed for these extinctions (Rebelo 1992; Krug *et al.* 2004b). The lowlands were also severely altered by agricultural practices and urban developments during the past 350 years and there are only very small and fragmented areas (< 12%) of the most nutrient rich areas called renosterveld left (Kemper *et al.* 1999; Von Hase *et al.* 2003; Krug *et al.* 2004a; Rebelo *et al.* 2006; Rouget *et al.* 2006). The renosterveld areas (evergreen, fire-prone asteraceous shrubland, in places with sparse understory of grasses and high diversity of geophytes, Rebelo *et al.* 2006) are believed to have been the prime habitat of the large herbivores in the lowlands (Bigalke 1979; Campbell 1986; Johnson 1992; Rebelo 1996; see also Chapters 3 and 4 of this dissertation).

The last decade, however, has witnessed a profound change in land use in the Western Cape, with a sharp increase in native large herbivore numbers due to a rapid growth in the wildlife industry (Kerley *et al.* 2003; Briel & Nowers 2007). This development lead to an increased need for guidelines on the reintroduction and management of the appropriate large herbivore species in order to harmonise the need of the wildlife industry with the conservation practices implemented to preserve the mega-biodiversity of the Cape Floristic Region (CFR) – a global biodiversity hotspot (Myers *et al.* 2000). Both national parks and private reserves have already introduced bontebok to the western lowlands. The problem is that bontebok, as well as buffalo and blue antelope were historically absent from this area. We need to identify the reason behind these grazers presence in the southern, but not in the western lowlands, in order to understand and predict their impact on these ecosystems.

In this paper we first table a hypothesis (that we dub the Summer Nutritional Stress Hypothesis) that can possibly explain the absence of bontebok, blue antelope and buffalo from the western lowlands. Thereafter we subject the hypothesis to testing by determining both contemporary, historic and late prehistoric native large herbivores’ C₄ grass utilization by means of carbon isotope analysis of their bone collagen.

The Summer Nutritional Stress Hypothesis

Due to the unique position of southern Africa at the interface of the tropical, subtropical and temperate climate systems, as well as the Indian, Southern and Atlantic Oceans, the season of maximum rainfall varies considerably along its coastline from west to east (Chase & Meadows 2007). The West Coast receives the majority of its rainfall (> 66%) during the winter months (April-September) and this pattern changes gradually with an increase in summer rainfall as one progresses eastwards till it becomes predominantly summer bound (> 66% between Oct and May) to the east of East London (Rebelo *et al.*

2006; Chase & Meadows 2007). The western lowlands (delineated for this study as the area between the sea in the south and west, the Skurweberg, Piketberg and Olifantsrivier Mountains to the north and Groot Winterhoek, Drakenstein and Hottentots Holland Mountains in the east; see Fig. 2.1) thus experience a true mediterranean winter-rainfall climate, while the southern lowlands (delineated here as the area between the sea in the south and east, the Houwhoek Mountains in the west and Riviersonderend Mountains and Langeberg in the north) receives rain more or less evenly throughout the year with a bias towards the winter in the west and summer in the east (Rebello *et al.* 2006; Rutherford *et al.* 2006; Chase & Meadows 2007).

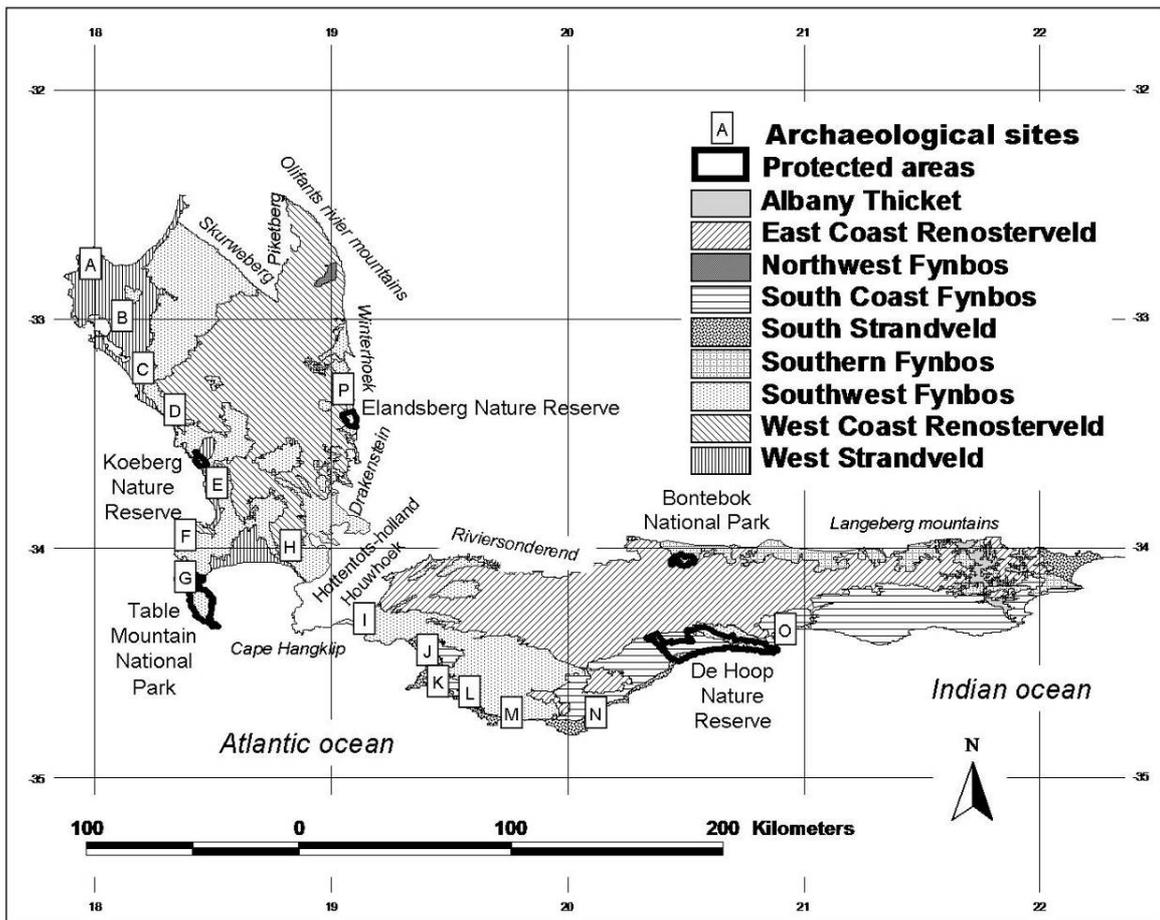


Fig. 2.1 The western and southern coastal lowlands of the SW Cape as delineated by the Cape Fold Belt mountains and the coastline. The different bioregions, as identified by Rutherford *et al.* (2006), are shown together with the protected areas from which contemporary large herbivore bones were obtained. The letters in boxes indicate the locations of the archaeological sites from which late prehistoric and historic bones were retrieved. See Table 2.2 for names of the archaeological sites.

This variation in rainfall seasonality is closely followed by a change in the abundance of C_3 versus C_4 grass species (Vogel *et al.* 1978) along the coast of South Africa. The West

Coast grasses are predominantly C₃ species (> 75%) and these are gradually replaced by C₄ species towards the east until C₄ grass species become the dominating grass component (> 75%) in the regions east of Port Elizabeth (Vogel *et al.* 1978). This grass distribution pattern is explained by the climatic constraints associated with low temperatures in the winter growing season that selects against the C₄ photosynthetic pathway (Vogel *et al.* 1978; Ehleringer 2005). The sparse grass cover of the western lowlands and more specifically the West Coast Renosterveld (Rutherford *et al.* 2006) is thus dominated by C₃ species while the southern lowlands supporting the East Coast Renosterveld has a higher grass biomass that comprises of a mixture of both C₃ and C₄ grass species with a gradual decline in C₃ grass abundance eastwards (Vogel *et al.* 1978; Cowling 1983, 1984; Pierce & Cowling 1984; Cowling *et al.* 1986; Stock *et al.* 1992a; Stock *et al.* 1997; Rebelo *et al.* 2006).

Apart from the difference in the abundance and composition of grass and the timing of rainfall, the two renosterveld areas (the supposed prime large herbivore habitat) are very similar in vegetation structure (Stock *et al.* 1992a; Rebelo *et al.* 2006), topography and climate (Rutherford *et al.* 2006). The mean annual rainfall for the West Coast and East Coast Renosterveld bioregions is 444 mm vs. 389 mm, while the annual precipitation coefficient of variation (32% vs. 33%), mean annual temperature (17.0° C vs. 16.4° C) and mean annual potential evaporation (2230 mm vs. 1948 mm) are also closely matched (Rutherford *et al.* 2006). Prey animals on both the western and southern lowlands were historically also subjected to the same large predator assemblage comprising of lion (*Panthera leo*), leopard (*Panthera pardus*), wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*) (Du Plessis 1969; Skead 1980; Rookmaaker 1989; Boshoff & Kerley 2001).

Bontebok and buffalo are classified as ruminant grazers dependant on a graminoid diet (Skinner & Chimimba 2005). Bontebok is classified as an almost exclusive grazer with a preference for short grass (Skinner & Chimimba 2005). Beukes (1984) found, by analyzing the rumen contents of bontebok across seasons in the Bontebok National Park, that 97.5% of their diet constituted of grass with only a small amount of dicotyledonous plant matter (< 7%) utilized during the winter months. Gagnon and Chew (2000) predicted a diet of 90% grass for the closely related blesbok (*Damaliscus pygargus phillipsii*) and Klein & Fairall (1986) found no traces of dicotyledonous matter in faecal samples of blesbok obtained from three different localities in the interior of South Africa at the end of the dry season. Carbon isotope analysis suggested a 94% grass dependence by *Damaliscus pygargus* in southern Africa (Sponheimer *et al.* 2003a). Gagnon and Chew (2000) predicted a diet of 77.5% grass for buffalo based on field studies and Landman and Kerley (2001) found, by means of faecal analysis, that buffalo can utilize up to 28% dicotyledonous plants in the Addo Elephant National Park. Carbon isotope analysis showed a 100% dependence on grass for buffalo in East Africa (Cerling *et al.* 2003), while studies in southern Africa suggested a diet constituting of 88% grass (Sponheimer *et al.* 2003a; Codron *et al.* 2007). Halley and Minagawa (2005) found, also using carbon isotope analysis, a total dependence on grass for buffalo in Chobe National Park, Botswana. It is believed that the last blue antelope was shot in 1799 (Klein 1974; Gould 1993), hence no records on its ecology exists. This antelope is, however, a close

relative of the ruminating sable (*Hippotragus niger*) and roan antelope (*H. equines*) (Klein 1974; Robinson 1996) which are both grazers (Skinner & Chimimba 2005). Gagnon and Chew (2000) predicted a diet of 85% grass for both sable and roan antelope based on field studies, while carbon isotope analysis suggested a diet that consists of more than 90% grass for both roan and sable antelope in East Africa (Cerling *et al.* 2003) as well as southern Africa (Sponheimer *et al.* 2003a; Codron *et al.* 2007). We consider that the difference in rainfall seasonality and C₃ vs. C₄ grass abundance between the two lowland areas explain the absence of these three ruminant grazers from the western lowlands and their presence on the southern lowlands.

Both the western and southern lowlands experience the driest period of the year during the hottest months of December–March (mean daily max. temp. 28.1° C and 26.3° C West and East Coast Renosterveld respectively for these four months) although the East Coast Renosterveld area receives more rain during this stressful period than the West Coast Renosterveld (29.8 mm vs. 58.4 mm total median rainfall December–March; Rutherford *et al.* 2006). This is in direct contrast to the rest of southern Africa that experience their hottest period of the year during the rainy season. C₃ grasses in the lowlands of the SW Cape grow during the cool, wet winter months and are moribund during the hot and dry summer months (Pierce & Cowling 1984). This is in contrast to the C₄ grass species of the region which can be divided into two groups: (1) those which show a pure summer growth period that restricts them to the eastern less-seasonal rainfall regions receiving critical amounts of summer rain, and (2) those having two growth periods (the second one usually in early mid winter) that enable the later to penetrate further west into the areas receiving more winter rain (Pierce & Cowling 1984). Both C₄ and C₃ grasses experience a decline in digestibility, fibre content and protein content as they mature (Owen-Smith 1982; Demment & Van Soest 1985; Langvatn & Hanley 1993; Fryxell 1995; Wilmshurst *et al.* 1995; Owen-Smith 2008) and it is only the C₄ grass growing during summer that can provide green higher quality forage to grazing mammals during the hot summer months.

We postulate that bontebok, blue antelope and buffalo could not find enough sustenance to survive from the moribund C₃ grasses and very limited C₄ grass available to them on the western lowlands during the summer months, when heat stress in these largely tree-less lowlands (Rebello *et al.* 2006) is highest and water availability lowest. We believe these large herbivores managed to survive on the southern lowlands due to an adequate supply of C₄ grasses that produced some green fodder of higher quality during this critical four month period (December–March).

Early research has shown that the population size of large grazers is restricted by the availability of high-quality food during critical periods in both temperate (Albon & Langvatn 1992; Jefferies *et al.* 1994; Post & Stenseth 1999) and tropical regions (Sinclair 1974, 1975; Fryxell 1987, 1995; Illius & O'Connor 2000). Mduma *et al.* (1999) and Ogutu & Owen-Smith (2003) showed that the persistence of green forage during the dry season can have a more general influence on ungulate population dynamics than the total forage production during the growing season. Fritz *et al.* (2002) found that mesograzers are more sensitive to variation in rainfall and soil nutrient status (i.e. plant quality and

quantity) than mesomix-feeders and mesobrowsers, which can explain why herbivores of the latter two feeding guilds occurred on the western lowlands. Bugalho and Milne (2003) showed how the mix-feeding red deer (*Cervus elaphus*) survive the nutritional constrained summer period in the mediterranean ecosystems of southern Portugal by increasing their browse intake. The lowland areas of the Western Cape are dominated by evergreen sclerophyllous shrubs (Rebello *et al.* 2006) of which a large proportion is believed to be unpalatable (Campbell 1986). During the summer the palatable shrub species should, however, provide more sustenance than the senescent C₃ grass, as crude protein levels in trees and shrubs are higher and more consistent than those of grass (Owen-Smith 2008).

Surface water availability can constrain the distribution of animals during the dry season and can cause nutritional stress when both forage quality and quantity are reduced (Sinclair 1974; Illius & O'Connor 2000; Redfern *et al.* 2003). Bontebok is very dependent on drinking water and stay within 1.5 km from the source of surface water during dry season (Van Zyl 1978). The seasonal range of buffalo is also restricted by the availability of drinking water (Sinclair 1974; Ryan *et al.* 2006) and they drink regularly, generally twice a day (Skinner & Chimimba 2005). Both sable and roan (the closest blue antelope relatives) are water-dependent; sable drinks daily and roan drink at least every second day (Skinner & Chimimba 2005). Feeding time is often influenced by environmental temperature but apparently not to the extent of preventing animals from reaching their daily food requirements (Jeschke & Ralph 2005). Owen-Smith (1998), however, indicated that the feeding activity of browsing kudu (*Tragelaphus strepsiceros*) is constrained when daily maximum temperatures exceeded 30 °C in the dry season (a frequent phenomenon on the western lowlands during summer). Blesbok (the closest relative of bontebok) also showed decreased feeding activity levels when temperature exceeded 31° C (Klein & Fairall 1986). Buffalo is very susceptible to heat stress (Lewis 1977) and as they cease feeding when their subcutaneous temperature approaches 40 °C (Skinner & Chimimba 2005). Buffalo requires shade to rest in during the hottest hours of the day, but is able to feed during the night (Skinner & Chimimba 2005).

Another stress factor affecting at least bontebok would be the additional energetic constrain of lactation (Owen-Smith 1982; Robbins 1983; Rutberg 1987; Jönsson 1997) during the summer months. Bontebok is a short-day seasonal breeder producing offspring between September and November, just before the onset of the critical hot and dry summer period (Rutberg 1987; Skinner & Chimimba 2005). Buffalo appears to be able to vary their calving time in response to resource availability (Sinclair *et al.* 2000; Skinner & Chimimba 2005; Ryan *et al.* 2007). We are not sure whether photoperiod or food supply controlled blue antelope breeding phenology, but the phylogenetically (and possibly also ecologically) related roan and sable appear to be aseasonal breeders (Spinage 1973; Skinner & Chimimba 2005). Skinner & van Jaarsveld (1987) stressed the importance of the timing of the breeding season for the survival of newly born antelope and the need for it to coincide with the time of peak nutrition. Mack (1986) suggested that the lack of large ungulates in the intermountain region of western North America could be explained by the phenology of the C₃ grasses aestivating during the summer calving season when green forage is necessary to sustain lactating females. Thomas *et al.*

(2001) showed how a mismatch of resource supply and demand in seasonally breeding birds can drastically reduce the persistence of adults in a breeding population. Berteaux *et al.* (2006) predicted that a mismatch between resource supply and mammal breeding peaks due to global warming might have significant impacts on mammal distribution ranges.

Red hartebeest is an apparent anomaly to our hypothesis as it can also be classified as a ruminant grazer with a short day seasonal breeding cycle (Skinner & Chimimba 2005). Gagnon and Chew (2000) predicted a diet of 75% grass based on field studies and in the North-West Province of South Africa, a study using faecal analysis, has found that red hartebeest can increase the amount of dicot material in their diet to as high as 30% during the dry seasons as the quality and quantity of grass fodder decrease (Kilian 1993). Carbon isotope analysis revealed a 100% grass dependence in East Africa (Cerling *et al.* 2003), and a 96% grass dependence in southern Africa (Sponheimer *et al.* 2003a). We suggest that the red hartebeest, which used to frequent the western lowlands, could survive the hot and dry summer months of this area due to their ability to utilize some browse during critical times, as well as due to their superior adaptation to hot and arid environments (Stanley Price 1978; Knight 1995; Cain III *et al.* 2006) which they inhabit in other parts of Africa as well (Capellini & Gosling 2007). Red hartebeest is a highly mobile species subject to irregular dispersal related to preferred feeding grounds and rainfall events (Skinner & Chimimba 2005). Hartebeest is a very selective and effective feeder of dry grass swards (Murray & Brown 1993), and able to digest fibre more efficiently and has smaller appetite than other Alcelaphini antelopes of similar size (Murray 1993). Hartebeest is also much less water dependant than buffalo and bontebok (Tailor 1968; Skinner & Chimimba 2005) and can make use of supplementary water supplies in the form of roots and tubers which they obtain by digging (Williamson 1987). It is also physiologically adapted to deal with heat stress as it does not increasing their cutaneous evaporation rate under intense radiation (Finch 1972). The low heat absorptance properties of the hartebeest coat, which is also lower than that of bontebok (Hofmeyr 1981), makes hartebeest independent of shade (Ben-Shahar & Fairall 1987) and capable of enduring extreme heat stress.

Mountain zebra and quagga also occurred in the western lowlands and we believe that these grazing ungulates survived due to their hind-gut fermenting digestive systems (Skinner & Chimimba 2005). It has been shown that hind-gut fermenters can extract more nutrients per day from low quality foods than ruminants of equal size (Owen-Smith 1982; Duncan *et al.* 1990), and when food becomes limiting, they should out compete other ruminant grazers (Menard *et al.* 2002). Zebra is thus less susceptible to drought than grazing bovids (Grange & Duncan 2006) and Redfern (2003) indicated that zebra is less nutritionally constrained by surface water availability than buffalo and wildebeest in the Kruger National Park. Bell (1969, as cited by Owen-Smith 1982) suggest that the wider tolerance range to low quality forage of the non-ruminant digestive system could explain the wider geographic range, and more even dispersion within a region, of zebra compared to wildebeest. Zebra thus most likely survived the hot and dry summers of the western lowlands because of the more efficient use of low-quality fodder available in the form of the senescent C₃ grass. Historical reports also suggest that zebra was never

common on the lowlands and it was certainly much less abundant than red hartebeest and eland in the western lowlands (Skead 1980). The hippopotamus, that used to graze on the banks of the rivers and estuaries of the western lowlands, probably survived due to its amphibious lifestyle that guards them against heat stress (Skinner & Chimimba 2005), as well as their ability to tolerate even lower quality food than zebra. This tolerance of low quality food is due to the fact that hippopotamus is also a non-ruminant (Skinner & Chimimba 2005) and has a low metabolic demand due to their large body size (Du Toit & Owen-Smith 1989; Belovsky 1997; Fritz *et al.* 2002). In addition, it has recently been shown that hippopotamus is not an obligate grazer as commonly believed, but utilize a substantial amount of browse – even as high as 40% of their total diet (Cerling *et al.* 2008).

The reliance of bontebok, buffalo and blue antelope on C₄ grass in summer forms the basis of the Summer Nutritional Stress Hypothesis. The use of C₄ grasses of both contemporary and pre-historic large herbivores can be determined by means of carbon isotope analysis of animal tissue samples. We test the Summer Nutritional Stress Hypothesis by determining whether the obligate ruminant grazing bontebok has a higher C₄ grasses consumption than any of the other native large herbivore species that used to occur on the coastal lowlands at the time of permanent European settlement. More specifically, the diet of bontebok should show a higher utilization of C₄ grasses than both the grazing ruminant red hartebeest and non-ruminant zebra as well as that of the mix-feeding elephant (Cerling *et al.* 1999; Skinner & Chimimba 2005; Codron *et al.* 2006), ostrich (Williams *et al.* 1993; Milton *et al.* 1994), and eland (Gagnon & Chew 2000; Skinner & Chimimba 2005 but see Watson & Owen-Smith 2000, Sponheimer *et al.* 2003, Codron *et al.* 2007 and Wallington *et al.* 2007 featuring eland as browsers) which also obtained their forage from the lowland areas.

Methods

Background

The difference in the ratio of ¹³C to ¹²C isotopes in the tissue of plants using the C₃ (trees, shrub, forbs and most temperate grasses) and C₄ (predominantly tropical grasses) photosynthetic pathways is bimodally distributed (Vogel *et al.* 1978; O'Leary 1988; Farquhar *et al.* 1989; Codron *et al.* 2005c). This bimodal distribution is reliably recorded in the bone collagen of animals feeding on plants (first shown by DeNiro & Epstein 1978) and has consequently been widely used to infer the character of herbivores' diet (Vogel 1978; Ambrose & DeNiro 1986; Van der Merwe *et al.* 1988; Lee-Thorp *et al.* 1989; Sponheimer *et al.* 2003a; Stevens *et al.* 2006; Crawford *et al.* 2008; O'Regan *et al.* 2008). Collagen is continuously resorbed and regenerated during the life of an animal and its isotopic values consequently reflect the average value of the diet of an animal for many years prior to its death (Teitelbaum 2000; Dalerum & Angerbjörn 2005; Bentley 2006). The carbon isotope ratio values obtained from the bone collagen of large herbivores that originated from the coastal lowlands can thus be used as a reliable indicator of their C₄ grass utilisation.

We determined the carbon isotope values of the collagen in the bones of large herbivores that died recently in five lowland protected areas, as well as from large herbivore bones coming from 16 archaeological sites in the lowlands believed to be younger than 4 000 years.

Field sampling

Plant samples

A dual-endpoint mixing model is used to convert the carbon isotope values of the bone collagen to estimates of the percentage C₄ grass in the diet of the large herbivores. Studies using similar approaches have used the global plant mean $\delta^{13}\text{C}$ values of -27.0 ‰ for C₃ and -12.5 ‰ for C₄ plants as source end points (e.g. Sponheimer *et al.* 2003a). These average values, however, vary according to a number of environmental factors (Farquhar *et al.* 1989; Heaton 1999; Codron *et al.* 2005c). In order to gain a more accurate estimation of source end point values specific to the coastal lowlands, we collected plant material from both C₃ and C₄ plants for testing. We collected leaves and stem samples from three different individuals of four C₄ grass species (n = 12) and seven C₃ plant species (n = 21) in the De Hoop Nature Reserve (further DHNR) at the end of the wet season (October 2006) in a patch of shale renosterveld which was heavily utilized by bontebok, eland and ostrich. The targeted four most common C₄ grass species were: *Cynodon dactylon*, *Themeda triandra*, *Cymbopogon pospischilii* and *Sporobolus virginicus*. From the available C₃ species we selected *Ehrharta calycina* (the most common indigenous C₃ grass), *Elytropappus rhinocerotis* (the most dominant indigenous shrub) and a number of European invasive fodder plants (*Avena barbata*, *Trifolium subterraneum*, *Briza maxima*, *Lolium rigidum* and *Medicago sativa*) utilized by the local herbivore fauna. Plant material was sampled into brown paper bags and then oven-dried at 60° C for 24 hours before being mill-ground to a homogenous powder and analysed.

Contemporary bone samples

We collected bones from opportunistically found large herbivore carcasses (died between 2004 and 2007) from near pristine protected areas in the western and southern lowlands. On the West Coast we obtained specimens from the Koeberg Nature Reserve, the Elandsberg Private Nature Reserve and the Cape of Good Hope section of the Table Mountain National Park (Fig. 2.1). Bones were obtained from the Bontebok National Park and the De Hoop Nature Reserve on the South Coast (Fig. 2.1).

The Cape of Good Hope section (c. 14 700 ha) of Table Mountain National Park is predominantly covered by Peninsula Sandstone Fynbos (Rebello *et al.* 2006; Mucina *et al.* 2007) with some *Stenotaphrum secundatum* grazing lawns occurring in disturbed habitats, usually associated with recreational areas (see Taylor 1984 for more detail on the Reserve). Small populations of eland, mountain zebra, red hartebeest, and grey rhebuck occur in the park together with some non-indigenous bontebok. Koeberg Nature Reserve (c. 1 500 ha) is covered by Cape Flats Dune Strandveld (Rebello *et al.* 2006; Mucina *et al.* 2007), with some old agricultural fields now covered by *Cynodon dactylon*

grazing lawns also present. Koeberg Nature Reserve currently supports re-introduced populations of the plains zebra, red hartebeest and eland, but it also has some non-indigenous bontebok, springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella gazella*) and blue wildebeest (*Connochaetes taurinus*). Most of the Elandsberg Reserve (c. 3 900 ha) is covered by Swartland Alluvium Fynbos (Rebelo *et al.* 2006; Mucina *et al.* 2007) with some abandoned agricultural fields (historically supporting Swartland Shale Renosterveld), now covered by *Cynodon dactylon* grazing lawns (see Midoko-Iponga 2004 for more detail on the Reserve). The Elandsberg Reserve hosts populations of eland, red hartebeest, grey rhebuck, plains zebra, and ostrich as well as non-indigenous black wildebeest (*Connochaetes taurinus*), gemsbok, springbok and bontebok. Bontebok National Park (c. 3 350 ha) is covered by Swellendam Silcrete Fynbos (Rebelo *et al.* 2006; Mucina *et al.* 2007) with some disturbed recreational areas supporting *Cynodon dactylon* grazing lawns (see Luyt 2005 for more detail on the reserve). Bontebok National Park supports populations of bontebok, Cape mountain zebra, red hartebeest, and grey rhebuck. De Hoop Nature Reserve (c. 32 300 ha) supports a number of different vegetation types of which Potberg Sandstone Fynbos, Eastern Rûens Shale Renosterveld, De Hoop Limestone Fynbos, Albertinia Sand Fynbos and Overberg Dune Strandveld cover the largest areas (Rebelo *et al.* 2006; Mucina *et al.* 2007). Small sections of DHNR have also been cultivated in the past and parts of these areas (predominantly the shale) are now covered by *Cynodon dactylon* grazing lawns. DHNR supports populations of eland, mountain zebra, bontebok, grey rhebuck, and ostrich (see Chapter 3 of this dissertation for more detail on the Reserve).

Within these protected areas we collected bones (usually femurs or tibias and occasionally skulls) from all the available carcasses of red hartebeest, mountain zebra, grey rhebuck, eland, and ostrich – all believed to be historically native to the respective protected areas. We also collected bones of bontebok from both the western and southern protected areas, although the western lowland populations were obviously of non-native origin. For the Summer Nutritional Stress hypothesis to hold, bontebok on the West Coast must have a high percentage of C₄ grass in their diet and that should be from a C₄ food source formerly unavailable to them. We believe that this food source is the *Stenotaphrum secundatum* and *Cynodon dactylon* grazing lawns growing on anthropogenically disturbed areas such as recreational zones and old agricultural fields which the bontebok seem to be concentrating on (Zumpt & Heine 1977, Langley & Giliomee 1974; Shiponeni 2003).

We only collected and analysed bones from individuals believed to have spent the vast majority of their lives in the reserves. A number of species were recently introduced (since 2000) from other parts of the country to some of the protected areas, but carcasses of these animals were strictly avoided. In total, we collected bone samples from 63 different individuals belonging to six species (Table 2.1).

Late pre-historic bone samples

We obtained historic and late prehistoric bone samples believed to be younger than 4000 years old from the Pre-colonial Archaeology Section of the Iziko Museum in Cape Town.

The majority of bones came from the extensively excavated and well-documented archaeological sites of Kasteelberg (Klein 1986; Klein & Cruz-Urbe 1989; Smith 1992), De Kelders (Schweitzer 1979), Byneskranskop (Schweitzer & Wilson 1982), Voëlvlei (Smith *et al.* 1991), and Smitswinkelbaai (Marean 1985). A number of additional samples were also obtained from coastal drift sand areas where dune movement has exposed large herbivore bone remains mostly in association with coastal middens. These coastal shell midden sites represent the refuse dumps made by humans commonly referred to as “strandlopers” that are believed to have been operating along the coast during the 2000–3000 years before Europeans settled in the Cape permanently (Avery 1974; Van Noten 1974).

The eland and red hartebeest bones from Kasteelberg are younger than 1860 years old, which is the oldest radiocarbon date at this excavation, and most bones are from layers younger than a 1300–1200 years old (Klein & Cruz-Urbe 1989). The two elephant bones from Kasteelberg are believed to be younger than 800 years old (Klein & Cruz-Urbe 1989). The elephant and red hartebeest bones from Byneskranskop were from excavation layers that have been radiocarbon-dated as 3900 ± 60 years old (Schweitzer & Wilson 1982). The Smitswinkelbaai bones of eland and red hartebeest came from layers shallower than the radiocarbon dated layer of 1175 ± 35 years old (Marean 1985). The bontebok and red hartebeest bones from De Kelders originated from layers above the dated layer of age 2019 ± 85 years old. The elephant bones at De Mond have been dated at 1000 ± 40 years old (J. van der Heever, personal communication). The oldest radiocarbon date at Voëlvlei is 1920 ± 50 years old (Smith *et al.* 1991) from which a red hartebeest bone was obtained.

Dung samples

Herbivore faeces can be used to reliably distinguish between C_3 - and C_4 -based diets using carbon isotope analysis (Sponheimer *et al.* 2003b; Botha & Stock 2005; Codron *et al.* 2005a; Codron *et al.* 2007; Codron & Codron 2008). We collected and analysed fresh dung samples of bontebok from DHNR at both the end of the wet season (mid-October) and in the middle of the dry season (mid-February) in order to get an approximation of seasonal variation in obligate ruminant grazers' C_4 vs. C_3 diet. During the two collection periods we collected dung pellets from six different freshly deposited (still soft and wet) bontebok dung pellet groups at two widely distant locations (> 8 km apart) and assume that these samples were from six different individuals. The dung pellets were collected in brown paper bags and oven dried at 60° C for 24 hours before being mill-ground to a homogenous powder and analysed.

Laboratory analyses

Collagen extraction

Flakes of bone (± 1 cm²) were removed with a hacksaw from both the recent and historic bone samples and scrubbed with a brush in lukewarm water to remove any superficial dirt. The collagen was prepared as described previously (Lee-Thorp *et al.* 1989) by

demineralization in 0.1 M hydrochloric acid until the mineral fraction dissolved where after lipids were removed by soaking the rinsed samples for 24 hours in a methanol: chloroform: water solution (4:2:1.6 v/v). Humic acid contaminants were removed using a 0.1 M sodium hydroxide solution where after all samples were freeze-dried.

Carbon isotope analysis

Samples of collagen, plant and dung were weighed into tin capsules and individually isotopically analyzed using an automated Elemental Analyzer (Carlo-Erba), and the resultant CO₂ gas was introduced to a Mass Spectrometer (MAT 252 or DELTA XP) using a continuous flow-through inlet system. ¹³C/¹²C ratios are expressed in the delta (δ) notation in parts per mil (‰) relative to the Vienna PeeDee Belemnite (VPDB) standard. Standard deviations of repeated measurements of laboratory standards were less than 0.25‰.

Data analyses

In order to make the carbon isotope data of the bone collagen and dung samples comparable with each other and other field studies, we converted the δ¹³C to estimates of percentage C₄ grass intake using a dual-endpoint mixing model (e.g. Post 2002; Sponheimer *et al.* 2003a; Codron *et al.* 2007) using the following equation:

$$\% \text{ C}_4 \text{ grass in diet} = (\delta^{13}\text{C}_{\text{C}_3\text{plants}} + \Delta\delta^{13}\text{C} - \delta^{13}\text{C}_{\text{collagen/dung}}) / (\delta^{13}\text{C}_{\text{C}_3\text{plants}} - \delta^{13}\text{C}_{\text{C}_4\text{plants}}) * 100$$

where Δδ¹³C is the magnitude of discrimination between the diet and the consumer's tissue or dung [assumed to be +5.0‰ for bone collagen (Lee-Thorp *et al.* 1989, Koch 1998, Hedges *et al.* 2005), and -0.9‰ for dung (Sponheimer *et al.* 2003b; Codron *et al.* 2005)]. The δ¹³C end point values used for the C₃ and C₄ plants were the average values obtained from our DHNR vegetation samples (C₄ = -12.8‰ and C₃ = -28.4‰). The collagen δ¹³C values of the late pre-historic and historic bone samples were made comparable to the modern day samples by correcting for the atmospheric change in carbon isotope composition (-6.5‰ to -8.0‰) over the last 150 years due to the burning of fossil fuels (Friedli *et al.* 1986; Marino & McElroy 1991; Cerling & Harris 1999) by subtracting 1.5‰.

Results

Plant δ¹³C values

The 12 C₄ samples from the three grass species yielded an average of -12.8‰ ± 1.3‰ (range: from -10.8‰ to -14.4‰). The 21 samples obtained from the seven C₃ species provided an average δ¹³C value of -28.4‰ ± 1.4‰ with a range from -25.0‰ to -31.1‰.

Contemporary bone collagen $\delta^{13}\text{C}$ values

The atomic carbon to nitrogen ratios for the collagen of all the contemporary bones were between 3.17 and 3.27 that is well within the range of 2.84–3.52 that indicates good collagen preservation for recent samples (Ambrose 1990).

The recent bontebok samples from five protected areas showed a large range in collagen $\delta^{13}\text{C}$ values from -10.4‰ to -19.3‰, which are indicative of a diet comprising of between 26%–84% of C_4 grass (Table 2.1 and Fig. 2.2). Both the highest and lowest values of this wide range for bontebok were found within DHNR on the South Coast. The bontebok bones from DHNR were obtained from two distinct and spatially separated populations of bontebok (Potberg population on shale renosterveld and Dronkvlei population on limestone fynbos). The diet of these two populations differed significantly from each other (one-way ANOVA, $F = 9.68$, $p = 0.0099$), with the Potberg population ($n = 7$) having an average C_4 grass consumption of $36.0\% \pm 10.5\%$ vs. $58.8 \pm 15.7\%$ for the Dronkvlei population ($n = 6$, see Table 2.1 for individual values). The range of the bontebok $\delta^{13}\text{C}$ values from the West Coast spanned from -12.6‰ to -18.2‰, which indicates a diet of 33%–70% of C_4 grass.

The eland samples reveal a much narrower range of collagen $\delta^{13}\text{C}$ values ranging between -22.5‰ and -19.5‰, which predicts a C_4 grass diet of between 6% and 25%. There is, however, an eland individual from Table Mountain National Park that produced an outlier value of -18.5‰, corresponding to a C_4 grass diet of 32%, which is nearly 20% higher than that any other $\delta^{13}\text{C}$ value measured for eland on the West Coast ($n = 7$, range 6%–13%). The grey rhebuck individuals consumed predominantly C_3 plants as indicated by the very low collagen $\delta^{13}\text{C}$ values (-22.5‰ and -21.7‰, suggesting a diet of between 6% and 13% of C_4 grass). The Cape mountain zebra samples were all from DHNR and had a range of collagen $\delta^{13}\text{C}$ values of between -15.4‰ and -19.6‰, indicating a diet that ranged between 24% and 51% of C_4 grass. The ostriches from DHNR utilised very little C_4 grass with three individuals actually showing a negative C_4 plant consumption as calculated with our dual mixing model using a C_3 plant end member value of -28.4‰. Two ostriches showed a consumption of 6% and 11% C_4 grass, respectively. The two red hartebeest samples from Elandsberg Nature Reserve on the West Coast had very similar $\delta^{13}\text{C}$ values of -14.4‰ and -14.1‰, indicating a high C_4 grass consumption (58% and 60%, respectively). The single red hartebeest sample from DHNR, however, had a low C_4 grass consumption of only 23%.

Table 2.1 The bone collagen $\delta^{13}\text{C}$ and atomic C:N ratio values for 63 large herbivores of six species that lived in five protected areas on the southern and western coastal lowlands of the SW Cape. The % C_4 grass in the diet of the herbivores was calculated with a dual-endpoint mixing model. Codes for protected areas are TMNP – Table Mountain National Park, ENR – Elandsberg Nature Reserve, KNR – Koeberg Nature Reserve, DHNR – De Hoop Nature Reserve and BNP – Bontebok National Park. * The bontebok individuals from the Dronkvlei population in DHNR, the other bontebok from DHNR are from the Potberg population.

Species	Area	Coast	Collagen $\delta^{13}\text{C}$ (‰)	C/N ratios	% C_4 diet	Species	Area	Coast	Collagen $\delta^{13}\text{C}$ (‰)	C/N ratios	% C_4 diet
Bontebok	TMNP	West	-15.68	3.23	49	Eland	ENR	West	-22.53	3.22	6
Bontebok	ENR	West	-18.24	3.18	33	Eland	ENR	West	-21.97	3.20	9
Bontebok	ENR	West	-16.57	3.22	44	Eland	DHNR	South	-22.60	3.20	5
Bontebok	ENR	West	-15.53	3.22	50	Eland	DHNR	South	-21.87	3.20	10
Bontebok	ENR	West	-13.40	3.17	64	Eland	DHNR	South	-21.47	3.20	12
Bontebok	ENR	West	-12.56	3.19	70	Eland	DHNR	South	-21.24	3.20	14
Bontebok	KNR	West	-14.34	3.17	58	Eland	DHNR	South	-20.95	3.24	16
Bontebok	KNR	West	-15.93	3.20	48	Eland	DHNR	South	-20.07	3.21	21
Bontebok*	DHNR	South	-16.73	3.24	43	Eland	DHNR	South	-20.05	3.17	21
Bontebok*	DHNR	South	-16.12	3.18	47	Eland	DHNR	South	-19.49	3.20	25
Bontebok*	DHNR	South	-15.88	3.24	48	Grey rhebuck	ENR	West	-21.68	3.17	11
Bontebok*	DHNR	South	-13.46	3.24	64	Grey rhebuck	ENR	West	-21.44	3.20	13
Bontebok*	DHNR	South	-12.86	3.26	68	Grey rhebuck	DHNR	South	-22.14	3.25	8
Bontebok*	DHNR	South	-10.36	3.24	84	Grey rhebuck	DHNR	South	-22.51	3.24	6
Bontebok	DHNR	South	-19.40	3.22	26	Grey rhebuck	BNP	South	-21.93	3.22	9
Bontebok	DHNR	South	-19.34	3.24	26	Mountain zebra	DHNR	South	-19.63	3.19	24
Bontebok	DHNR	South	-19.28	3.23	26	Mountain zebra	DHNR	South	-19.25	3.21	27
Bontebok	DHNR	South	-17.62	3.26	37	Mountain zebra	DHNR	South	-19.10	3.21	28
Bontebok	DHNR	South	-17.28	3.26	39	Mountain zebra	DHNR	South	-18.78	3.20	30
Bontebok	DHNR	South	-16.22	3.25	46	Mountain zebra	DHNR	South	-17.59	3.20	37
Bontebok	DHNR	South	-15.31	3.21	52	Mountain zebra	DHNR	South	-17.35	3.20	39
Bontebok	BNP	South	-16.31	3.25	45	Mountain zebra	DHNR	South	-15.38	3.19	51
Bontebok	BNP	South	-13.71	3.21	62	Ostrich	DHNR	South	-23.73	3.22	-2
Bontebok	BNP	South	-13.12	3.22	66	Ostrich	DHNR	South	-23.68	3.26	-2
Bontebok	BNP	South	-12.69	3.25	69	Ostrich	DHNR	South	-23.56	3.27	-1
Bontebok	BNP	South	-11.41	3.25	77	Ostrich	DHNR	South	-23.21	3.27	1
Eland	TMNP	West	-22.38	3.22	7	Ostrich	DHNR	South	-22.42	3.25	6
Eland	TMNP	West	-22.27	3.23	7	Ostrich	DHNR	South	-21.65	3.24	11
Eland	TMNP	West	-21.39	3.21	13	Red hartebeest	ENR	West	-14.43	3.24	58
Eland	TMNP	West	-18.45	3.25	32	Red hartebeest	ENR	West	-14.10	3.20	60
Eland	ENR	West	-22.12	3.21	8	Red hartebeest	DHNR	South	-19.85	3.18	23
Eland	ENR	West	-22.13	3.20	8						

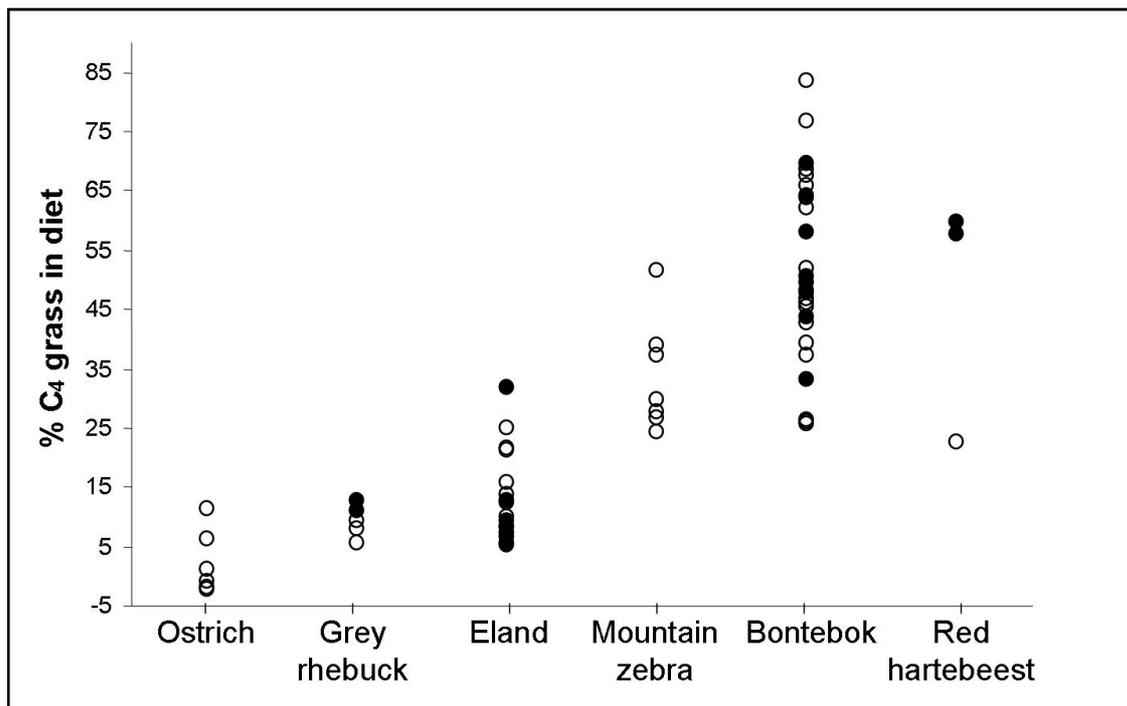


Fig. 2.2 The proportion of C₄ grass in the diet of six large herbivore species from five protected areas on the coastal lowlands in the SW Cape. The C₄ grass consumption was calculated from the bone collagen $\delta^{13}\text{C}$ values of 63 samples with a dual-endpoint mixing model. Filled circles represent values from protected areas in the western lowlands, while open circles represent values from protected areas in the southern lowlands.

Late pre-historic and historic bone collagen $\delta^{13}\text{C}$ values

The atomic carbon to nitrogen ratios for the collagen of all the late prehistoric to historic bones were between 2.96 and 3.45 that is well within the range of 2.90-3.54, which indicate good collagen preservation for prehistoric samples (Ambrose 1990).

The collagen $\delta^{13}\text{C}$ value (-9.8‰) of the bontebok bone from Die Dam indicate that this individual ate less C₄ grass (54%) than the two individuals from De Kelders that had a diet consisting of 68% and 78% C₄ grass respectively (Table 2.2 and Fig. 2.3). These values fall well within the range measured for contemporary individuals on the South Coast (26%–84%). The eland bone $\delta^{13}\text{C}$ collagen values are in a narrow range of -18.9‰ to -19.8‰, which indicate a diet of predominantly C₃ plants with only 13% to 20% C₄ grass consumed. These late pre-historic eland values compare well with the contemporary eland values that range between 5%–25%. The elephant collagen $\delta^{13}\text{C}$ values (n = 6) were all in a narrow range of between -19.2‰ and -22.6‰, indicative of a low C₄ grass utilisation spanning 9%–17%. The red hartebeest bone samples from the South Coast (n = 9) revealed collagen values ranging from -11.7‰ to -17.1‰, indicative of a C₄ grass diet of between 31%–66%. The West Coast red hartebeest samples cover a much wider range of collagen $\delta^{13}\text{C}$ values from as low as -19.7‰ to as high as -10.6‰, which means that these animals consumed anything from 14% to 72% C₄ grass.

Table 2.2 The bone collagen $\delta^{13}\text{C}$ and atomic C:N ratio values for 34 specimens of large herbivores (four different species) that lived in the coastal lowlands in late pre-historic to historic times. Bones were obtained from 16 archaeological sites (see Fig. 2.1 for the locations, map codes A-P). The proportion of C_4 grass in the herbivores' diet was calculated with a dual-endpoint mixing model.

Species	Site	Coast	Map code	Collagen $\delta^{13}\text{C}$ (‰)	C/N ratios	% C_4 in diet
Bontebok	De Kelders	South	J	-11.22	3.00	68
Bontebok	De Kelders	South	J	-9.78	3.00	78
Bontebok	Die Dam	South	M	-13.52	3.13	54
Eland	Smitswinkelbaai	West	G	-19.28	3.15	17
Eland	Smitswinkelbaai	West	G	-19.47	2.97	16
Eland	Kasteelberg	West	A	-19.80	3.03	13
Eland	Kasteelberg	West	A	-18.86	2.96	20
Eland	Kasteelberg	West	A	-19.79	3.03	14
Eland	Pearly Beach	South	L	-19.30	3.03	17
Elephant	Kasteelberg	West	A	-20.12	3.10	11
Elephant	Kasteelberg	West	A	-20.55	3.45	9
Elephant	Yzerfontein	West	C	-19.22	3.06	17
Elephant	Geelbek	West	B	-19.85	3.02	13
Elephant	Byneskranskop	South	K	-20.54	2.97	9
Elephant	De Mond	South	N	-20.13	3.19	11
Red Hartebeest	Smitswinkelbaai	West	G	-19.74	3.00	14
Red Hartebeest	Kasteelberg	West	A	-18.94	3.02	19
Red Hartebeest	Smitswinkelbaai	West	G	-18.66	2.99	21
Red Hartebeest	Kasteelberg	West	A	-18.25	3.01	23
Red Hartebeest	Kasteelberg	West	A	-16.64	3.01	34
Red Hartebeest	Modder rivier	West	D	-16.33	3.06	36
Red Hartebeest	Melkbos	West	E	-14.88	2.98	45
Red Hartebeest	Gordons bay	West	H	-12.70	3.01	59
Red Hartebeest	Voëlmei	West	P	-11.81	3.04	65
Red Hartebeest	Houtbay	West	F	-10.60	3.07	72
Red Hartebeest	De Mond	South	N	-17.12	3.19	31
Red Hartebeest	Hawston	South	I	-16.25	3.01	36
Red Hartebeest	Pearly Beach	South	L	-15.84	3.00	39
Red Hartebeest	Witsand	South	O	-15.60	3.10	40
Red Hartebeest	De Kelders	South	J	-14.10	2.97	50
Red Hartebeest	De Mond	South	N	-13.36	3.26	55
Red Hartebeest	Byneskranskop	South	K	-12.89	2.97	58
Red Hartebeest	Byneskranskop	South	K	-12.88	3.00	58
Red Hartebeest	Byneskranskop	South	K	-11.66	3.00	66

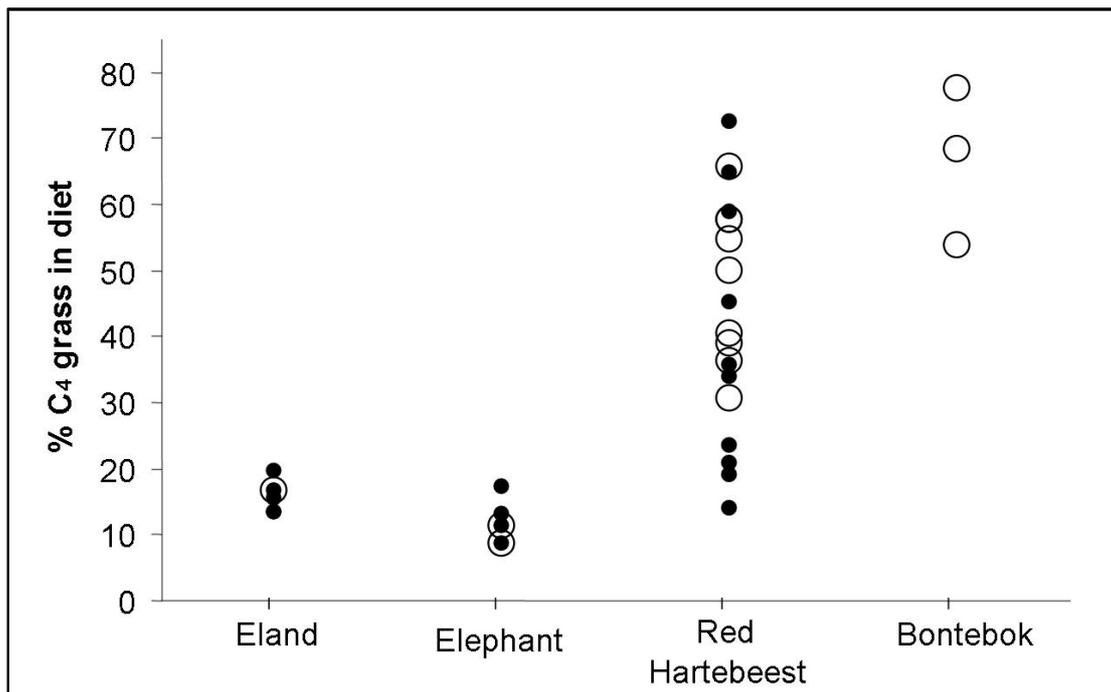


Fig. 2.3 The proportion of C₄ grass in the diet of 34 individuals of four large herbivore species which occurred on the coastal lowlands of the SW Cape in late pre-historic and historic times. The C₄ grass proportion was calculated from the bone collagen $\delta^{13}\text{C}$ values with a dual-endpoint mixing model. Filled circles represent values from the western lowlands, while open circles represents values from the southern lowlands.

Bontebok dung $\delta^{13}\text{C}$ values

The six bontebok dung samples collected in DHNR at the end of the wet winter period in mid-October revealed an average $\delta^{13}\text{C}$ value of $-26.9\text{‰} \pm 0.84\text{‰}$, indicative of a diet consisting of 15% C₄ grass. The six samples obtained during the summer (mid-February) showed a significantly higher C₄ grass utilisation (One-way ANOVA, $F = 242.06$, $p < 0.00001$) with an average $\delta^{13}\text{C}$ value of $-17.9\text{‰} \pm 1.2\text{‰}$ that relates to an average C₄ diet of 73%. During each collection bout we collected three dung samples from the Potberg population and three from the Dronkvlei population of bontebok. During summer there was no significant difference (One-way ANOVA, $F = 1.10$, $p = 0.35$) between the two dung sub-samples $\delta^{13}\text{C}$ values ($-18.3\text{‰} \pm 1.4\text{‰}$ vs. $-17.4\text{‰} \pm 0.8\text{‰}$). The winter samples were slightly, but statistically significantly, different (One-way ANOVA, $F = 38.10$, $p = 0.003$) with the $\delta^{13}\text{C}$ values from the Potberg population being lower than those of the Dronkvlei population (average $\delta^{13}\text{C}$: $-27.6\text{‰} \pm 0.3\text{‰}$ vs. $-26.2\text{‰} \pm 0.2\text{‰}$). This suggests that the bontebok at Potberg utilized less C₄ grass at the end of winter than the Dronkvlei population (average: $20.0\% \pm 0.9\%$ vs. $10.7\% \pm 2.4\%$ of C₄ grass in diet).

Discussion

Plant $\delta^{13}\text{C}$ values and mixing models

The estimated C_4 grass consumption by the large herbivores presented here is sensitive to the $\delta^{13}\text{C}$ end member values used for C_3 and C_4 plants, respectively. C_3 plants in particular can have significant variations in $\delta^{13}\text{C}$ values (Farquhar *et al.* 1982; Heaton 1999) and our results from only a small plant sample ($n = 21$, average = -28.4‰) suggest that the C_3 plants in our study area have a more depleted $\delta^{13}\text{C}$ value than the frequently used average value of -27‰ (Vogel *et al.* 1978; O'Leary 1988; Cerling *et al.* 1999; Sponheimer *et al.* 2003a). The negative C_4 grass consumption values obtained for three ostriches in DHNR indicate that our end member value for C_3 plants (-28.4‰) is most likely still too high. The most depleted collagen $\delta^{13}\text{C}$ value for the ostriches (-23.73‰) suggests a diet of C_3 plants with a $\delta^{13}\text{C}$ value of -28.73‰ and using this value in the mixing model will cause an increase of 2% in the presented C_4 diet values. Ostriches have the habit of uprooting and swallowing whole plants with their roots and associated soil (Williams *et al.* 1993). This is different to the dietary habits of all the other studied large herbivores, which concentrate on above ground vegetation and do not tend to swallow soil. This habit might have exerted an influence on the ostrich $\delta^{13}\text{C}$ values. The 5‰ value used here to correct for the fractionation that occur between the plant and collagen values also varies between animal species (Hedges *et al.* 2005) and we consequently decided to retain the measured $\delta^{13}\text{C}$ plant value of -28.4‰ for C_3 plants in the mixing model. The average $\delta^{13}\text{C}$ value for the C_4 plants in our plant sample ($n = 12$, average = -12.8‰) is very close to the frequently used average value of -12.5‰ (Vogel *et al.* 1978; Sponheimer *et al.* 2003a).

Another source of bias, which needs to be addressed in interpretations of the data from late prehistoric and historic bone samples, is the large temporal scale involved. The oldest samples are probably around 3900 years old (Byeneskranskop), while some of the coastal midden samples can be as young as 300 years (elephant at Geelbek). Some climatic variation might have occurred during this period with an episode of more arid conditions suggested between 2700 and 1300 yrs BP (Scholtz 1986; Chase & Meadows 2007). Climatic variation could thus have altered the $\delta^{13}\text{C}$ values (Heaton 1999) of the C_3 plants during this period with consequent errors in our interpretation of C_4 grass consumption. Apart from correcting for the industrial effect on the atmospheric carbon, we did not take any climatic variation into account when calculating the C_4 grass consumption of the different herbivores. The prehistoric bone sample results can thus have a bias of up to 2‰ (Heaton 1999), which can translate to a difference of up to 13% in our calculation of C_4 plant diet and we consequently refrain from applying rigorous statistical testing to this data set.

C_4 grass consumption by large herbivores

The coastal lowlands of the SW Cape are unique when compared to other regions in Africa where carbon isotope analysis had been used to determine the character of an animal's diet (e.g. Ambrose & DeNiro 1986; Van der Merwe *et al.* 1988; Cerling *et al.*

2003; Botha & Stock 2005; Codron *et al.* 2005a; Codron *et al.* 2005b; Halley & Minagawa 2005; Cerling *et al.* 2007) as it is the only region which supports both C₃ and C₄ grasses in significant quantities. This means that we can not make the distinction between browsing and grazing behaviour of herbivores based on carbon isotope values, unlike in other studies where almost all the grasses were characterised by the C₄ photosynthetic pathway. C₃ plant diet in our study can also contain a significant percentage of C₃ grass which will not be revealed by the $\delta^{13}\text{C}$ collagen values. Plants using the CAM photosynthetic pathway are rare in the study area (Stock *et al.* 1992b), except perhaps in the Strandveld areas where succulent plants of the family Aizoaceae/mesembs are more common. These succulent plants are generally believed to be unpalatable to large herbivores and certainly do not play an important role in the diet of grey rhebuck or bontebok for which a detailed dietary study has been made (Beukes 1984). We consequently do not consider CAM plant consumption in this study to be altering our C₄ grass consumption values significantly.

The very low C₄ grass consumption by grey rhebuck in this study is not surprising as this antelope is considered to be an almost exclusive browser (Beukes 1984, Gagnon & Chew 2000; Skinner & Chimimba 2005). Eland also fed predominantly on C₃ plants on the Cape coastal lowlands, which corroborates the findings of other studies which have shown that eland is predominantly a browser in southern Africa (Watson & Owen-Smith 2000; Sponheimer *et al.* 2003a; Codron *et al.* 2005b; Wallington *et al.* 2007). The use of C₄ grasses by eland in this study is, however, higher than that found in the other studies using carbon isotopes (5%: Wallington *et al.* 2007; 8%: Sponheimer *et al.* 2003a; 3%: Codron *et al.* 2005b), with individual eland diets comprising of as much as 25% of C₄ grass (even 32% if an outlier is also considered). The eland of DHNR is especially fond of C₄ grass with an average usage of $15.6\% \pm 6.7\%$ (n = 8). The $\delta^{13}\text{C}$ collagen values of the prehistoric eland bones suggested that the C₄ grass consumption of these eland were very similar to that of the contemporary eland analyzed. The low consumption and even avoidance of C₄ grass by ostriches is surprising considering that these birds are known to utilize and even seek out green grass (Williams *et al.* 1993; Milton *et al.* 1994), which can only be available in the form of C₄ grass during summer. The diets of the eland, grey rhebuck and ostrich analyzed in this study is consistent with our Summer Nutritional Stress Hypothesis by showing that these three herbivores can survive in the coastal lowlands with as little as 5%, 6% and 0% C₄ grass in their diets, respectively. The distribution ranges of eland, ostrich and grey rhebuck were thus not confined by the historic distribution of C₄ grass on the coastal lowlands, and they also occurred historically in both the western and southern lowlands.

The late prehistoric and historic bone samples of elephants revealed a very low C₄ grass consumption (n = 6, average = $11.7\% \pm 3.2\%$). This low value is consistent over a period of nearly 4000 years as the individual from Byeneskranskop (Percentage of C₄ = 9%) comes from an excavation layer dated 3900 yrs BP (Schweitzer & Wilson 1982), while the elephant from Geelbek (Percentage of C₄ = 13%) was found in association with musket balls – suggesting that it had been hunted sometime shortly after European colonization in 1652 (A. Kandel, personal communication). The elephants in this study utilized much less C₄ grass than the elephants in the Kruger National Park, which use on

average 35% C₄ grass (Codron *et al.* 2006). We cannot, unfortunately, comment on the amount of C₃ grass utilized by the elephants of this study, but the low percentage of C₄ grass in their diet indicates that C₄ grass cannot be considered a limiting factor to their distribution.

The mountain zebra samples we analyzed all came from DHNR; no historic or late prehistoric zebra bones were found in any lowland excavation sites. Archaeologists find the absence of zebra remains in archaeological sites puzzling (R. Klein, personal communication) as these striking animals are well attested for in historical documentation and there is no doubt that they did occur in the lowlands (see Skead 1980; Rookmaker 1989). The available contemporary bones of zebra from reserves other than DHNR were all from individuals introduced from regions very distant to the study area and were consequently omitted. The diet of the mountain zebra at DHNR comprised of at least 24% and even as much as 51% C₄ grass. We can consequently not view the diet of these animals as consistent with the Summer Nutritional Stress Hypothesis. It does, however, also not falsify the hypothesis either, since the utilisation of C₄ grass (when readily available) is not necessarily an indication of dependence on it. It would have been odd if these animals had avoided green C₄ grass during summer when the only C₃ grasses available are moribund and less palatable. Support for our hypothesis might, however, be found in the fact that the mountain zebra of DHNR are on average using significantly (One way ANOVA, $F = 12.62$, $p = 0.005$) less C₄ grass than the Dronkvlei bontebok population ($34\% \pm 9.5\%$, $n = 7$ vs. $59\% \pm 15.7\%$, $n = 6$) with which they share the same habitat.

The contemporary bontebok samples revealed a wide range in C₄ grass consumption (26%–84%). Both the lowest and highest values of C₄ grass consumption by bontebok were recorded in DHNR and this merits further discussion. The $\delta^{13}\text{C}$ collagen values of the samples from the two separate bontebok populations in DHNR were also significantly different from each other. The Potberg bontebok population (average percentage of C₄ grass usage = 36%) of DHNR utilizes shale renosterveld patches bordering on intensively farmed agricultural land. The dominant grasses in this renosterveld are *Cymbopogon pospischilii* and *Cynodon dactylon* (both C₄). However, a significant amount of C₃ annual European pasture grasses (e.g. *Avena*, *Briza*, *Bromus* and *Lolium*) also flourish in this vegetation during the wet and cooler winter months (April-October). The Dronkvlei bontebok population dwells in extensive limestone fynbos vegetation in which distinct karstic sinkhole depressions covered by short creeping grasses (mainly *Cynodon dactylon*) occur. The Dronkvlei area is isolated from agricultural land and does not support large populations of alien European C₃ grasses. We believe that the presence of the alien C₃ grass cover in the Potberg area is responsible for the significant difference in the diets between the two studied bontebok populations. This idea is supported by the results of the bontebok dung analysis. The significant difference in the % C₄ grass between the winter dung samples (10.7% vs. 20.0%) of the two populations suggests that the Potberg population is less dependant on C₄ grass in winter due to the availability of more nutritional alien C₃ grasses. C₃ grass should have higher crude protein levels and be more digestible than C₄ grass (Wilson & Hacker 1987; Owen-Smith 2008) during the cool and wet winter months. During summer, when the C₃ grasses are senescent, both

bontebok populations use similar but significantly higher amounts of C₄ grass fodder (70.1% ± 9% and 76.3% ± 4.9%) than in the winter. Alien annual C₃ grass invasion is a serious problem on the coastal lowlands (Milton 2004), hence it is very difficult to judge what the natural diet of bontebok might have been. The habitats used by the bontebok population at Dronkvlei in DHNR and the population in Bontebok National Park are probably the least affected by alien C₃ plants and therefore can serve as our best approximation to the natural diet of bontebok. Our samples from these two populations indicate an average C₄ grass consumption of 61.0% ± 13.5% (n = 11) with a range from 43%–84%. The average value of 61% compares favourably with the average value of 67% obtained from the three prehistoric bontebok samples – our best indication of bontebok C₄ grass usage before alien C₃ invasive plants became available. The bontebok samples from the West Coast reveal an average C₄ grass use of 52% ± 11.6%, with the lowest C₄ grass use (33%) found in a bontebok of Elandsberg Nature Reserve, an area also seriously affected by alien C₃ plant invaders (Shiponeni & Milton 2006). The West Coast values suggest that C₄ grass is important to the bontebok in the western lowland reserves and probably explains their preference for the disturbed areas that are supporting C₄ lawn grasses (Langley & Giliomee 1974; Zumpt & Heine 1977; Walton 2005).

The two contemporary red hartebeest bone samples from the Elandsberg Nature Reserve revealed a high C₄ grass consumption of 58% and 60%, while the individual from DHNR had only 23% C₄ grass in its diet. These values must be treated with caution as the population of 12 red hartebeest that were introduced from the Eastern Cape into DHNR in 1992 went extinct (P. Chadwick, personal communication), while the Elandsberg population of red hartebeest, where the last introduction was made in 1982, failed to increase beyond their initial number of 16 individuals (B. Wooding, personal communication). This suggests that the sampled individuals were in suboptimum habitat and they most likely did not feed on vegetation of their choice. We do, however, have a large sample of prehistoric material (n = 19), which indicates a wide range in C₄ grass usage (14%–72%) by red hartebeest. We find it surprising that the highest C₄ grass consumption by red hartebeest occurred on the West Coast and not on the South Coast where C₄ grass is believed to have been more abundant. All five West Coast red hartebeest samples with δ¹³C values indicating a C₄ grass diet of above 35% came, however, from areas that were historically either in close proximity, or right next to estuaries or wetlands. Wetlands and saline estuaries support abundant biomass of C₄ grasses on the West Coast with clonal growing grasses such as *Sporobolus virginicus* and *Stenotaphrum secundatum* particularly common (Mucina *et al.* 2006). We believe that these wetland and estuary areas were heavily utilised by those studied five red hartebeest individuals. The West Coast red hartebeest individuals with the low C₄ grass consumption values (i.e. 14%, 19% and 21%) do, however, show that red hartebeest can survive in these lowlands with very little C₄ grass in their diet which is consistent with our hypothesis.

C₃ versus C₄ grass distribution patterns

A key assumption of our hypothesis is that there is clear differentiation between the abundance of C₃ and C₄ grasses on the respective coastal forelands. This notion is well

substantiated (Cowling & Holmes 1992; Cowling *et al.* 1986; Stock *et al.* 1997; Rebelo *et al.* 2006) in the literature featuring isotopic (Stock *et al.* 1992a), phenologic (Pierce & Cowling 1984), and phytogeographic (Acocks 1975; Vogel *et al.* 1978; Cowling 1983, 1984) studies. We did, however, point out that the wetlands and saline estuaries might have supported sizable grass swards dominated by C₄ species, which raises the question on whether that would not have been sufficient to sustain viable obligate ruminant populations during the summer lean period. The short clonal grasses most common in these azonal habitats are, however, not the preferred food of either buffalo, or the close relatives of the blue antelope (the sable and roan), which all prefer medium to tall grass (Skinner & Chimimba 2005). On the other hand, bontebok specialises on grazing short grasses (Skinner & Chimimba 2005), hence it should thus do well on the grazing lawns. Hippopotamus probably found the majority of their food on the wetland fringes supporting the C₄ grass swards. We are, however, of the opinion that the azonal habitats were historically too small and isolated from each other to facilitate the persistence of viable bontebok populations. The azonal habitats with high densities of bontebok would also have attracted the attention of the large predators, which all would have been able to prey on them (Radloff & Du Toit 2004) who, in turn, would have had no alternative but to persist in using these high-nutrition spots during summer. The much less water-dependant red hartebeest on the other hand must have been able to move between these azonal areas and utilize much larger parts of the surrounding habitat as well during the hot and dry summer months.

Cynodon dactylon (C₄) is currently widely distributed in anthropogenically disturbed habitats in the western lowlands. Its presence and success in the winter- rainfall regions can be ascribed to its extreme adaptability to adverse conditions, especially drought (Carrow 1996). It is also considered one of the ten worst weeds of the world (Holm *et al.* 1977). We are of opinion that both the populations of bontebok in Elandsberg and Koeberg Nature Reserves would not survive on the West Coast without the presence of this anthropogenically induced *C. dactylon* grazing lawns.

Connectivity between the coastal lowland areas

The absence of obligate ruminant grazers from the West Coast could have simply been blamed on the physical mountain barrier of the Houwhoek and Hottentots Holland Mountains separating the studied western and southern lowlands. The mountains are not only steep, but are also covered by sandstone fynbos that is of low nutritional quality and has very sparse grass cover that is consequently avoided by bontebok (see Chapters 3 and 4 of this dissertation) and presumably historically also by blue antelope and buffalo. Buffalo and blue antelope were, however, found on the western lowlands between 22,000–12,000 years ago when the lowlands were presumably more grassy (Cruz-Uribe 1988) and cooler than today (Chase & Meadows 2007). The coastline was located much further to the south during the last glacial (24,000–18,000 yr BP) than today and large herbivores could have migrated between both lowland areas without the interference of mountainous terrain during this period (Rebelo *et al.* 2006; Chase & Meadows 2007). There is, however, no evidence of bontebok presence in the western lowlands during the last 20,000 years (Klein 1980; Klein 1983; Cruz-Uribe 1988).

We hypothesise that due to the fixed breeding phenology of bontebok (involving lactation during the dry summer months), their strict grass diet and water dependence could not survive in the western lowlands even during the cooler period of the late Pleistocene. Buffalo and blue antelope could, on the other hand, survive on the West Coast due to their flexible breeding phenology and the cooler as well as grassier environment during this time. Buffalo and blue antelope probably went extinct on the West Coast during the Holocene Altithermal (8000–4000 yrs BP) – the warmest period of the Holocene in southern Africa (Chase & Meadows 2007). The rise of the sea level after the last glacial to the feet of the mountains at Cape Hangklip (Fig. 2.1) probably made re-colonization of the western lowlands by buffalo and blue antelope after the Holocene Altithermal very difficult, if not impossible. Whether conditions on the West Coast during the last 4000 years would have been conducive to the persistence of buffalo and blue antelopes – even if they had managed to reach it – is doubtful given the prevailing dry and hot summers and absence of green nutritional grass during this time. Historical accounts also suggest that buffalo was actually rare in the western half of the southern lowlands, and only became frequently encountered in the past much further to the east, closer to the shade-offering forest fringes around George; this region also supports higher C₄ grass cover than the western regions that receive more winter-rainfall (Skead 1980).

Conclusion

Ideally we would have liked to have sampled both buffalo and blue antelope remains from the late prehistoric period as well. Recent DNA testing has revealed that the bones from De Kelders, originally believed to be those of buffalo (Schweitzer 1979), were actually that of cattle (R. Klein, personal communication). The four mounted blue antelope in European museums were also unavailable for testing and no excavation sites revealed any blue antelope remains younger than 10,000 years. Either contemporary or prehistoric zebra remains from the western lowlands could also have contributed substantially to our understanding of this conundrum. The available evidence to date is, however, consistent with our Summer Nutritional Stress Hypothesis that geographic variation in C₄ grass availability in the summer lean season could account for the discrepancy in at least bontebok distributions on the coastal lowlands in historic times. Eland, grey rhebuck, ostrich, elephant, and red hartebeest occurred on both western and southern coastal forelands and individuals tested indicate that they could have survived with as little as 14% C₄ grass in their diet. The lowest C₄ grass consumption value recorded for bontebok was 26%, and they utilized at least 43% C₄ grass biomass in what we believe is more natural habitat. In addition, dung analysis showed a very high C₄ grass consumption by bontebok during summer (73%). The prehistoric bontebok samples also suggest that they ate at least 54% C₄ grass. The tested mountain zebra ate at least 24% C₄ grass, but we have shown that they used much less C₄ grass than bontebok with which they share the same habitat. This supports the notion that zebra was less dependant on C₄ grass biomass than bontebok. High C₄ grass use by grazers on the coastal lowlands of the SW Cape does not necessarily indicate that they are dependent on it for survival, but a low utilisation indicates an ability to survive without it.

The results of this study are broadly consistent with the idea that an inadequate supply of green summer forage due to severe summer drought accounts for the absence of bontebok, buffalo and blue antelope from the winter rainfall regions of the southwestern Cape lowlands. With increasing summer rainfall to the east, C₄ grasses grow during summer and can then maintain these obligate grazers through the lean and hot summer season. A further test would be to determine whether bontebok or buffalo populations could survive and increase on the coastal lowlands in natural habitat with less than 15% C₄ grass biomass in their diet.

References

- Acocks, J.P.H. (1975) Veld types of South Africa. *Botanical Survey Memoir South Africa*, 40, 1-128
- Albon S.D. & Langvatn R. (1992) Plant phenology and the benefits of migration in a temperate ungulate. *Oikos*, 65, 502-513
- Ambrose S.H. (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. *Journal of Archaeological Science*, 17, 431-451
- Ambrose S.H. & DeNiro M.J. (1986) The isotopic ecology of East African mammals. *Oecologia*, 69, 395-406
- Avery G. (1974) Open station shell midden sites and associated features from the Pearly Beach area, south-western Cape. *South African Archaeological Bulletin*, 29, 104-114
- Belovsky G.E. (1997) Optimal foraging and community structure: the allometry of herbivore food selection and competition. *Evolutionary Ecology*, 11, 641-672
- Bentley R.A. (2006) Strontium isotopes from the earth to the archaeological skeleton: a review. *Journal of Archaeological Method and Theory*, 13, 135-187
- Berteaux D., Humphries M.M., Krebs C.J., Lima M., McAdam A.G., Pettorelli N., Reale D., Saitoh T., Tkadlec E., Weladji R.B. & Stenseth N.C. (2006) Constraints to projecting the effects of climate change on mammals. *Climate Research*, 32, 151-158
- Bigalke R.C. (1979) Aspects of vertebrate life in fynbos, South Africa. In: *Ecosystems of the World, 9A, Heathlands and related shrublands* (ed. Specht R.L.), pp. 81-95. Elsevier, Amsterdam
- Boshoff A.F. & Kerley G.I.H. (2001) Potential distribution of the medium- to large-size mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *African Zoology*, 36, 245-273
- Botha M.S. & Stock W.D. (2005) Stable isotope composition of faeces as an indicator of seasonal diet selection in wild herbivores in southern Africa. *South African Journal of Science*, 101, 371-374
- Beukes P.C. (1984) *Sommige aspekte van die ekologie van die Vaalribbok (Pelea Capreolus, Forster 1790) in die Bontebok Nasionale Park*. MSc. Thesis, University of Stellenbosch
- Briel S.C.P. & Nowers R.J. (2007) *Wildlife production in the Western Cape: A report on the quantification and qualification of wildlife production units*. Western Cape Department of Agriculture, Elsenburg

- Bugalho M.N. & Milne J.A. (2003) The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: a case of summer nutritional constraint. *Forest Ecology and Management*, 181, 23-29
- Burns C.E., Johnston K.M. & Schmitz O.J. (2003) Global climate change and mammalian species diversity in U. S. national parks. *Proceedings of the National Academy of Science of USA*, 100, 11474-11477
- Campbell B.M. (1986) Plant spinescence and herbivory in a nutrient poor ecosystem. *Oikos*, 47, 168-172
- Cain III J.W., Krausman P.R., Rosenstock S.S. & Turner J.C. (2006) Mechanisms of thermoregulation and water balance in desert ungulates. *Wildlife Society Bulletin*, 34, 570-581
- Cappelini I. & Gosling L.M. (2007) Habitat primary production and the evolution of body size within the hartebeest clade. *Biological Journal of the Linnean Society*, 92, 431-440
- Carrow R.N. (1996) Drought resistance aspects of turfgrasses in the southeast: root-shoot responses. *Crop Science*, 36, 687-694
- Cerling T.E. & Harris J.M. (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia*, 120, 347-363
- Cerling T.E., Harris J.M. & Leakey M.G. (1999) Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia*, 120, 364-374
- Cerling T.E., Harris J.M. & Passey B.H. (2003) Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy*, 84, 456-470
- Cerling T.E., Omondi P. & Macharia A.N. (2007) Diets of Kenyan elephants from stable isotopes and the origin of confiscated ivory in Kenya. *African Journal of Ecology*, 45, 614-623
- Cerling T.E., Harris J.M., Hart J.A., Kaleme P., Klingel H., Leakey M.G., Levin N.E., Lewison R.L. & Passey B.H. (2008) Stable isotope ecology of the common hippopotamus. *Journal of Zoology*, doi: 10.1111/j.1469-7998.2008.00450.x
- Chase B.M. & Meadows M.E. (2007) Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews*, 84, 103-138
- Codron D. & Codron J. (2008) Reliability of delta ¹³C and delta ¹⁵N in faeces for reconstructing savanna herbivore diet. *Mammalian Biology*, doi:10.1016/j.mambio.2007.12.005
- Codron D., Codron J., Lee Thorp J.A., Sponheimer M. & de Ruiter D. (2005a) Animal diets in the Waterberg based on stable isotope composition of faeces. *South African Journal of Wildlife Research*, 35, 43-52
- Codron D., Codron J., Lee-Thorp J.A., Sponheimer M., de Ruiter D., Sealy J., Grant R. & Fourie N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, 273, 21-29
- Codron D., Codron J., Sponheimer M., Lee Thorp J.A., Robinson T., Grant C.C. & de Ruiter D. (2005b) Assessing diet in savanna herbivores using stable carbon isotopes ratios of faeces. *Koedoe*, 48, 115-124
- Codron J., Codron D., Lee Thorp J.A., Sponheimer M., Bond W.J., De Ruiter D. & Grant R. (2005c) Taxonomic, anatomical, and spatio-temporal variation in the stable

- carbon and nitrogen isotope composition of plants from an African savanna. *Journal of Archaeological Science*, 32, 1757-1772
- Codron J., Lee Thorp J.A., Sponheimer M., Codron D., Grant R.C. & De Ruiter D.J. (2006) Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: Spatial and landscape differences. *Journal of Mammalogy*, 87, 27-34
- Cowling R.M. (1983) The occurrence of C3 and C4 grasses in fynbos and allied shrubland in the South eastern Cape, South Africa. *Oecologia*, 58, 121-127
- Cowling R.M. (1984) A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. *Bothalia*, 15, 175-227
- Cowling R.M., Pierce S.M. & Moll E.J. (1986) Conservation and utilisation of South coast Renosterveld, an endangered South African vegetation type. *Biological Conservation*, 37, 363-377
- Cowling R.M. & Holmes P.M. (1992) Flora and vegetation. In: *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling R.M.). Oxford University Press, Cape Town
- Crawford K., McDonald R.A. & Bearhop S. (2008) Application of stable isotope techniques to the ecology of mammals. *Mammal Review*, 38, 87-107
- Cruz-Uribe K. (1988) The use and meaning of species diversity and richness in archaeological faunas. *Journal of Archaeological Science*, 15, 179-196
- Dalerum F. & Angerbjörn A. (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia*, 144, 647-658
- Demment M.W. & Van Soest P.J. (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*, 125, 641-672
- DeNiro M.J. & Epstein S. (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42, 495-506
- Du Plessis S.E. (1969) *The past and present geographical distribution of the Perissodactyla and Artiodactyla in Southern Africa*. MSc. Thesis, University of Pretoria
- Du Toit J.T. & Owen-Smith N. (1989) Body size, population metabolism, and habitat specialization among large African herbivores. *American Naturalist*, 133, 736-740
- Duncan P., Foose T.J., Gordon I.J., Gakahu C.G. & Lloyd M. (1990) Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia*, 84, 411-418
- Ehleringer J.R. (2005) The influence of atmospheric CO₂, temperature, and water on the abundance of C₃/C₄ taxa. In: *A history of atmospheric CO₂ and its effects on plants, animals, and ecosystems* (eds. Ehleringer J.R., Cerling T.E. & Dearing D.M.), pp. 214-231. Springer, New York
- Farquhar G.D., Ehleringer J.R. & Hubrick K.T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 503-537
- Farquhar G.D., O'Leary M.H. & Berry J.A. (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, 9, 121-137

- Finch V.A. (1972) Thermoregulation and heat balance of the East African eland and hartebeest. *American Journal of Physiology*, 222, 1374-1379
- Friedli H., Lotscher H., Oeschger H., Siegenthaler U. & Stauffer B. (1986) Ice core record of the $^{13}\text{C}/^{12}\text{C}$ ratio of atmospheric CO_2 in the past two centuries. *Nature*, 324, 237-238
- Fritz H., Duncan P., Gordon I.J. & Illius A.W. (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620-625
- Fryxell J.M. (1987) Food limitation and demography of a migratory antelope, the white-eared kob. *Oecologia*, 72, 83-91
- Fryxell J.M. (1995) Aggregation and migration by grazing ungulates in relation to resources and predators. In: *Serengeti II: dynamics, management and conservation of an ecosystem* (ed. Sinclair A.R.E.), pp. 257-271. University of Chicago Press, Chicago
- Gagnon M. & Chew A.E. (2000) Dietary preferences in extant African bovidae. *Journal of Mammalogy*, 81, 490-511
- Gaston K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford
- Gould J.S. (1993) Four antelopes of the apocalypse. *Natural History*, 102, 16-22
- Grange S. & Duncan P. (2006) Bottom-up and top-down processes in African ungulate communities: resources and predation acting on the relative abundance of zebra and grazing bovids. *Ecography*, 29, 899-907
- Halley D.J. & Minagawa M. (2005) African buffalo diet in a woodland and bush-dominated biome as determined by stable isotope analysis. *African Zoology*, 40, 160-163
- Heaton T.H.E. (1999) Spatial, species and temporal variations in the $^{13}\text{C}/^{12}\text{C}$ ratios of C_3 plants: implications for palaeodiet studies. *Journal of Archaeological Science*, 26, 637-649
- Hedges R.E.M., Stevens R.E. & Koch P.L. (2005) Isotopes in bones and teeth. In: *Isotopes in palaeoenvironmental research* (ed. Leng M.J.), pp. 117-145. Springer, Dordrecht
- Hofmeyr M.D. (1981) *Thermal physiology of selected African ungulates with emphasis on the physical properties of the pelage*. PhD. Thesis, University of Cape Town
- Holm L.G., Plucknett D.L., Pancho J.V. & Herberger J.P. (1977) *The world's worst weeds: distribution and biology*. University Press of Hawaii, Honolulu
- Ibáñez I., Clark J.S., Dietze M.C., Feeley K., Hersh M., LaDeau S., McBride A., Welch N.E. & Wolosin M.S. (2006) Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology*, 87, 1896-1906
- Illius A.W. & O'Connor T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos*, 89, 283-294
- Jefferies R.L., Klein D.R. & Shaver G.R. (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos*, 71, 193-206
- Jeschke J.M. & Ralph T. (2005) Predicting herbivore feeding times. *Ethology*, 111, 187-206
- Johnson S.D. (1992) Plant-animal relationships. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 175-205. Oxford University Press, Cape Town

- Johnston K.M. & Schmitz O.J. (1997) Wildlife and climate change: assessing the sensitivity of selected species to simulated doubling of atmospheric CO₂. *Global Change Biology*, 3, 531-544
- Jönsson K.I. (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78, 57-66
- Kemper J., Cowling R.M. & Richardson D.M. (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation*, 90, 103-111
- Kerley G.I.H., Pressey R.L., Cowling R.M., Boshoff A.F. & Sims-Castley R. (2003) Options for the conservation of large and medium-sized mammals in the Cape floristic region hotspot, South Africa. *Biological Conservation*, 112, 169-190
- Kilian J.W. (1993) *The spatial and temporal utilization of resources by the Red Hartebeest (Alcelaphus buselaphus caama)*. MSc Thesis, University of Pretoria
- Klein D.R. & Fairall N. (1986) Comparative foraging behaviour and associated energetics of impala and blesbok. *Journal of Applied Ecology*, 23, 489-502
- Klein R.G. (1974) On the taxonomic status, distribution and ecology of the blue antelope, *Hippotragus leucophaeus* (Pallas, 1766). *Annals of the South African Museum*, 65, 99-143
- Klein R.G. (1980) Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in Southern Africa. *Annals of the South African Museum*, 81, 223-283
- Klein R.G. (1983) Palaeoenvironmental implications of quaternary large mammals in the Fynbos region. In: *Fynbos palaeoecology: a preliminary synthesis* (eds. Deacon H.J., Hendey Q.B. & Lambrechts J.J.N.), pp. 116-138. CSIR, Pretoria
- Klein R.G. (1986) The prehistory of Stone Age herders in the Cape Province of South Africa. *South African Archaeological Society Goodwin Series*, 5, 5-12
- Klein R.G. & Cruz-Uribe K. (1989) Faunal evidence for prehistoric herder-forager activities at Kasteelberg, Western Cape Province, South Africa. *South African Archaeological Bulletin*, 44, 82-97
- Knight M.H. (1995) Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33, 377-394
- Koch P.L. (1998) Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences*, 26, 573-613
- Krug C.B., Krug R.M., Midoko Iponga D.M., Walton B.A., Milton S.J. & Shiponeni N.N. (2004a) Restoration of West Coast Renosterveld: facilitating the return of a highly threatened vegetation type. In: *Proceedings of the 10th MEDECOS Conference* (eds. Arianoutsou M. & Papanastasis V.P.), pp. 107-119. Millpress, Rotterdam
- Krug R.M., Krug C.B., Midoko Iponga D., Walton B.A., Milton S.J., Newton I.P., Farley N. & Shiponeni N.N. (2004b) Reconstructing West Coast Renosterveld: past and present ecological processes in a Mediterranean shrubland of South Africa. In: *Proceedings of the 10th MEDECOS Conference* (eds. Arianoutsou M. & Papanastasis V.P.), 120-132. Millpress, Rotterdam
- Landman M. & Kerley G.I.H. (2001) Dietary shifts: do grazers become browsers in the Thicket Biome. *Koedoe*, 44, 31-36

- Langley C.H. & Giliomee J.H. (1974) Behaviour of the bontebok (*Damaliscus d. dorcas*) in the Cape of Good Hope Nature Reserve. *Journal of the Southern African Wildlife Management Association*, 4, 117–121
- Langvatn R. & Hanley T.A. (1993) Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia*, 95, 164–170
- Lee-Thorp J.A., Sealy J.C. & van der Merwe N.J. (1989) Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science*, 16, 585–599
- Lewis J.G. (1977) Game domestication for animal production in Kenya: activity patterns of eland, oryx, buffalo and zebu cattle. *Journal of Agricultural Science, Cambridge*, 89, 551–563
- Luyt E. du C. (2005) *Models of bontebok (Damaliscus pygargus pygargus, Pallas 1766) habitat preferences in the Bontebok National Park and sustainable stocking rates*. MSc Thesis, Stellenbosch University
- Mack R.N. (1986) Alien plant invasion into the intermountain West: a case history. In: *Ecology of biological invasions of North America and Hawaii* (eds. Mooney H.A. & Drake J.A.), pp. 191–213. Springer-Verlag, New York
- Marean C.W. (1985) The faunal remains from Smitswinkelbaai Cave, Cape Peninsula. *South African Archaeological Bulletin*, 40, 100–102
- Marino B.D. & McElroy M.B. (1991) Isotopic composition of atmospheric CO₂ inferred from carbon in C₄ plant cellulose. *Nature*, 349, 127–131
- Mduma S.A.R., Sinclair A.R.E. & Hilborn R. (1999) Food regulates the Serengeti wildebeest: a 40-year record. *Journal of Animal Ecology*, 68, 1101–1122
- Menard C., Duncan P., Fleurance G., Georges J. & Lila M. (2002) Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology*, 39, 120–133
- Midoko-Iponga D. (2004) *Renosterveld restoration: the role of competition, herbivory and other disturbances*. MSc Thesis, University of Stellenbosch
- Milton S.J. (2004) Grasses as invasive alien plants in South Africa. *South African Journal of Science*, 100, 69–75
- Milton S.J., Dean W.R.J. & Siegfried W.R. (1994) Food selection by ostrich in Southern Africa. *Journal of Wildlife Management*, 58, 234–248
- Morris D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136, 1–13
- Morrison M.L. (2001) A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management*, 65, 613–623
- Mucina L., Adams J.B., Knevel I.C., Rutherford M.C., Powrie L.W., Bolton J.J., Van der Merwe J.H., Anderson R.J., Bornman T.G., Le Roux A. & Janssen J.A.M. (2006) Coastal vegetation of South Africa. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 658–696. SANBI, Pretoria
- Mucina L., Rutherford M.C. & Powrie L.W. (2007) *Vegetation Map of South Africa, Lesotho and Swaziland, 1:1 000 000, 2nd ed.* SANBI, Pretoria
- Murray M.G. (1993) Comparative nutrition of wildebeest, hartebeest and topi in the Serengeti. *African Journal of Ecology*, 31, 172–177

- Murray M.G. & Brown D. (1993) Niche separation of grazing ungulates in the Serengeti: an experimental test. *Journal of Animal Ecology*, 62, 380-389
- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858
- Ogutu J.O. & Owen-Smith N. (2003) ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters*, 6, 412-419
- O'Leary M.H. (1988) Carbon isotopes in photosynthesis. *Bioscience*, 38, 328-336
- O'Regan H.J., Chenery C., Lamb A.L., Stevens R.E., Rook L. & Elton S. (2008) Modern macaque dietary heterogeneity assessed using stable isotope analysis of hair and bone. *Journal of Human Evolution*, doi:10.1016/j.jhevol.2008.05.001
- Owen-Smith N. (1982) Factors influencing the consumption of plant products by large herbivores. In: *Ecology of tropical savannas* (eds. Huntley B.J. & Walker B.H.), pp. 359-404. Springer-Verlag, Berlin
- Owen-Smith N. (1998) How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *Journal of Zoology*, 246, 183-192
- Owen-Smith N. (2008) The comparative population dynamics of browsing and grazing ungulates. In: *The ecology of browsing and grazing* (eds. Gordon I.J. & Prins H.H.T.), pp. 149-177. Springer, Berlin
- Pearson R.G. & Dawson T.E. (2003) Predicting the impact of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography*, 12, 361-371
- Peterson A.T., Ortega-Huerta M.A., Bartley J., Sanchez-Cordero V., Soberón J., Buddemeier R.H. & Stockwell D.R.B. (2002) Future projections of Mexican faunas under global climate change scenarios. *Nature*, 416, 626-629
- Pierce S.M. & Cowling R.M. (1984) Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. *South African Journal of Botany*, 3, 1-16
- Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83, 703-718
- Post E. & Stenseth N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, 80, 1322-1339
- Radloff F.G.T. & du Toit J.T. (2004) Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology*, 73, 410-423
- Rebelo A.G. (1992) Red Data Book species in the Cape Floristic Region: threats, priorities and target species. *Transactions of the Royal Society of South Africa*, 48, 55-86
- Rebelo A.G. (1996) Renosterveld. In: *Vegetation of South Africa, Lesotho and Swaziland* (eds. Low A.B. & Rebelo A.G.), pp. 63-67. Department of Environmental Affairs and Tourism, Pretoria
- Rebelo A.G., Boucher C., Helme N., Mucina L., Rutherford M.C., Smit W.J., Powrie L.W., Ellis F., Lambrechts J.J., Scott L., Radloff F.G.T., Johnson S.D., Richardson D.M., Ward R.A., Procheş Ş.M., Oliver E.G.H., Manning J.C., Jürgens N., McDonald D.J., Janssen J.A.M., Walton B.A., Le Roux A., Skowno A.L., Todd S.W. & Hoare D.B. (2006) Fynbos Biome. In: *The vegetation of South*

- Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 52-219. SANBI, Pretoria
- Redfern J.V., Grant R., Biggs H. & Getz W.M. (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84, 2092-2107
- Robbins C.T. (1983) *Wildlife feeding and nutrition*. Academic Press, New York
- Robinson T.J. (1996) Mitochondrial DNA sequence relationships of the extinct blue antelope *Hippotragus leucophaeus*. *Naturwissenschaften*, 83, 178-182
- Rookmaaker L.C. (1989) *The zoological exploration of Southern Africa 1650-1790*. A. A. Balkema, Rotterdam
- Root T.L., Price J.T., Hall K.R., Schneider S.H., Rosenzweig C. & Pounds J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57-60
- Rouget M., Jonas Z., Cowling R.M., Desmet P.G., Driver A., Mohamed B., Mucina L., Rutherford M.C. & Powrie L.W. (2006) Ecosystem status and protection levels of vegetation types. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 725-737. SANBI, Pretoria
- Rutberg A.T. (1987) Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *American Naturalist*, 130, 692-710
- Rutherford M.C., Mucina L. & Powrie L.W. (2006) Biomes and bioregions of Southern Africa. In: *The vegetation of South Africa, Lesotho and Swaziland*. (eds. Mucina L. & Rutherford M.C.), pp. 31-51. SANBI, Pretoria
- Ryan S.J., Knechtel C.U. & Getz W.M. (2006) Range and habitat selection of African buffalo in South Africa. *Journal of Wildlife Management*, 70, 764-776
- Ryan S.J., Knechtel C.U. & Getz W.M. (2007) Ecological cues, gestation length, and birth timing in African buffalo (*Syncerus caffer*). *Behavioral Ecology*, 18, 635-644
- Schmitz O.J., Post E., Burns C.E. & Johnston K.M. (2003) Ecosystem responses to global climate change: moving beyond color mapping. *BioScience*, 53, 1199-1205
- Scholtz A. (1986) *Palynological and palaeobotanical studies in the Southern Cape*. MA Thesis, University of Stellenbosch
- Schweitzer F.R. (1979) Excavations at Die Kelders, Cape Province, South Africa. The Holocene deposits. *Annals of the South African Museum*, 78, 101-233
- Schweitzer F.R. & Wilson M.L. (1982) Byneskranskop 1: A Late Quaternary living site in the southern Cape Province, South Africa. *Annals of the South African Museum*, 88, 1-203
- Senft R.L., Coughenour M.B., Bailey D.W., Rittenhouse L.R., Sala O.E. & Swift D.M. (1987) Large herbivore foraging and ecological hierarchies. *BioScience*, 37, 789-799
- Shiponeni N.N. (2003) *Dispersal of seeds as a constraint in revegetation of old fields in Renosterveld vegetation in the Western Cape, South Africa*. MSc Thesis, University of Stellenbosch
- Shiponeni N.N. & Milton S.J. (2006) Seed dispersal in the dung of large herbivores: implications for restoration of Renosterveld shrubland old fields. *Biodiversity and Conservation*, 15, 3161-3175
- Sinclair A.R.E. (1974) The natural regulation of buffalo populations in East Africa. *East African Wildlife Journal*, 12, 291-311

- Sinclair A.R.E. (1975) The resource limitation of trophic levels in tropical grassland ecosystems. *Journal of Animal Ecology*, 44, 497-520
- Sinclair A.R.E., Mduma S. & Arcese P. (2000) What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology*, 81, 2100-2111
- Skead C.J. (1980) *Historical mammal incidence in the Cape Province. Volume 1: The Western and Northern Cape*. Department of Nature and Environmental Conservation of the Cape Provincial Administration, Cape Town
- Skinner J.D. & van Jaarsveld A.S. (1987) Adaptive significance of restricted breeding in Southern African ruminants. *South African Journal of Science*, 83, 657-663
- Skinner J.D. & Chimimba C.T. (2005) *The mammals of the Southern African Subregion*. Cambridge University Press, Cape Town.
- Smith A.B. (1992) Kasteelberg. In: *Guide to archaeological sites in the south-western Cape for the Southern African Association of Archaeologists Conference* (eds. Smith A.B. & Mütti B.), pp. 28-30, Cape Town
- Smith A.B., Sadr K., Gribble J. & Yates R. (1991) Excavations in the South-Western Cape, South Africa, and the archaeological identity of prehistoric hunter-gatherers within the last 2000 years. *South African Archaeological Bulletin*, 46, 71-91
- Soberón J. & Peterson A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, 2, 1-10
- Spinage C.A. (1973) The role of photoperiodism in the seasonal breeding of tropical African ungulates. *Mammal Review*, 3, 71-84
- Sponheimer M., Lee-Thorp J.A., DeRuiter D.J., Smith J.M., Van der Merwe N.J., Reed K., Grant C.C., Ayliffe L.K., Robinson T.F., Heidelberg C. & Marcus W. (2003a) Diets of southern African Bovidae: stable isotope evidence. *Journal of Mammalogy*, 84, 471-479
- Sponheimer M., Robinson T., Ayliffe L., Passey B., Roeder B., Shipley L., Lopez E., Cerling T., Dearing D. & Ehleringer J. (2003b) An experimental study of carbon-isotope fractionation between diet, hair, and faeces of mammalian herbivores. *Canadian Journal of Zoology*, 81, 871-876
- Stanley Price M.R. (1978) The nutritional ecology of Coke's Hartebeest (*Alcelaphus buselaphus cokei*) in Kenya. *Journal of Applied Ecology*, 15, 33-49
- Stevens R.E., Lister A.M. & Hedges R.E.M. (2006) Predicting diet, trophic level and palaeoecology from bone stable isotope analysis: a comparative study of five red deer populations. *Oecologia*, 149, 12-21
- Stock W.D., Allsopp N., van der Heyden F. & Witkowski E.T.F. (1997) Plant form and function. In: *Vegetation of southern Africa* (eds. Cowling R.M, Richardson D. & Pierce S.), pp. 376-396. Cambridge University Press, Cambridge
- Stock W.D., Bond W.J. & Le Roux D. (1992a) Isotope evidence from soil carbon to reconstruct vegetation history in the south-western Cape Province. *South African Journal of Science*, 89, 153-154
- Stock W.D., van der Heyden F. & Lewis O.A.M. (1992b) Plant structure and function. In: *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling R.M.), pp. 226-240. Oxford University Press, Cape Town
- Taylor H.C. (1984) A vegetation survey of the Cape of Good Hope Nature Reserve. II. Descriptive account. *Bothalia*, 15, 259-291
- Teitelbaum S.L. (2000) Bone resorption by osteoclasts. *Science*, 289, 1504-1508

- Thomas D.W., Blondel J., Perret P., Lambrechts M.M. & Speakman J.R. (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, 291, 2598-2600
- Van der Merwe N.J., Lee-Thorp J.A. & Bell R.H.V. (1988) Carbon isotopes as indicators of elephant diets and African environments. *African Journal of Ecology*, 26, 163-172
- Van Noten F.L. (1974) Excavations at the Gordon's Bay shell midden, South-Western Cape. *South African Archaeological Bulletin*, 29, 122-142
- Van Zyl L.J. (1978) *Die waterbehoefte en drinkgewoontes van die Bontebok *Damaliscus dorcas dorcas* (Pallas, 1766) in die Bontebok Nasionale Park*. MSc Thesis, University of Stellenbosch
- Vogel J.C. (1978) Isotopic assessment of the dietary habits of ungulates. *South African Journal of Science*, 74, 298-301
- Vogel J.C., Fuls A. & Ellis R.P. (1978) The geographical distribution of Kranz grasses in South Africa. *South African Journal of Science*, 74, 209-215
- Von Hase A., Rouget M., Maze K. & Helme N. (2003) *A fine-scale conservation plan for Cape lowlands renosterveld*, Botanical Society of South Africa, Kirstenbosch
- Wallington B.P., McKechnie A.E., Owen-Smith N. & Woodborne S. (2007) Stable carbon isotope analysis of eland (*Taurotragus oryx*) diet in the Suikerbosrand Nature Reserve. *Journal of Wildlife Management*, 37, 127-131
- Walton B.A. (2005) *Vegetation patterns and dynamics of renosterveld at Agter-Groenberg Conservancy, Western Cape, South Africa*. MSc Thesis, Stellenbosch University
- Watson L.H. & Owen-Smith N. (2000) Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology*, 38, 130-137
- Williams J.B., Siegfried W.R., Milton S.J., Adams N.J., Dean W.R.J., Du Plessis M.A. & Jackson S. (1993) Field metabolism, water requirements, and foraging behavior of wild ostriches in the Namib. *Ecology*, 74, 390-404
- Williamson D.T. (1985) Plant underground storage organs as a source of moisture for Kalahari wildlife. *African Journal of Ecology*, 25, 63-64
- Willis K.J. & Whittaker R.J. (2002) Species diversity—scale matters. *Science*, 295, 1245–1248
- Wilmshurst J.F., Fryxell J.M. & Hudson R.J. (1995) Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology*, 6, 209-217
- Wilson J.R. & Hacker J.B. (1987) Comparative digestibility and anatomy of some sympatric C₃ and C₄ arid zone grass. *Australian Journal of Agricultural Research*, 187, 287-295
- Zumpt F. & Heine E.W.P. (1977) Some veterinary aspects of bontebok in the Cape of Good Hope Nature Reserve. *South African Journal of Wildlife Research*, 8, 131-134

HABITAT SELECTION OF LARGE HERBIVORES NATIVE TO THE NUTRIENT-POOR FYNBOS AND RENOSTERVELD SHRUBLANDS OF THE WESTERN CAPE, SOUTH AFRICA

Introduction

The large spatial variability in abundance and community structure of African ungulates has been a subject of study for decades. Rainfall in combination with soil nutrient content has been identified as the primary drivers of this variability via their control on plant quality and quantity (Coe *et al.* 1976; Bell 1982; East 1984; Fritz & Duncan 1994; Fritz *et al.* 2002). Predictive statistical models have consequently been developed linking large herbivore biomass and primary productivity in southern and East African savanna ecosystems (Fritz & Duncan 1994). The mediterranean climate region (Cowling *et al.* 1996) at the SW tip of Africa known as the Fynbos Biome (Rebello *et al.* 2006) might not, however, conform to the predictions of these models, even though this region did contain a diverse African large herbivore fauna until about the mid 17th century (Boshoff & Kerley 2001; Kerley *et al.* 2003). This is because the major vegetation of the Fynbos Biome (Rebello *et al.* 2006) called fynbos shrublands (covering about 67% of the area of the biome), is believed to have been avoided by large herbivores due to its exceptionally low nutrient status (Specht & Moll 1983; Campbell 1986). Consequently only the more nutrient-rich shrublands on shale, known as renosterveld (29% of the biome), were suggested to be utilised by the large herbivores (Bigalke 1979; Cody *et al.* 1983; Morrow *et al.* 1983; Campbell 1986; Moll 1987; Rebello 1987; Johnson 1992; Rebello 1992a, 1996; Owen-Smith & Danckwerts 1997; Rebello *et al.* 2006; but see Hendey 1983). Fynbos is an evergreen, fire-prone shrubland characterised by fine-leaved ericoid shrubs, large-leaved Proteaceae shrubs and evergreen graminoids of the Restionaceae (Rebello *et al.* 2006). Renosterveld is an evergreen, fire-prone asteraceous shrubland, in places with sparse understory of grasses and high diversity of geophytes (Rebello *et al.* 2006). The perceived avoidance of the fynbos shrublands by large herbivores implies that this vegetation is below the quality threshold (*sensu* Olff *et al.* 2002) that, for the given rainfall and nutrient availability, can sustain even megaherbivores.

Historical accounts leave little doubt that only 350 years ago the lowlands of the Fynbos Biome hosted a diverse large herbivore (>20 kg) assemblage with African elephant (*Loxodonta africana*), black rhino (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibius*), African buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), Cape mountain zebra (*Equus zebra zebra*), plains zebra/quagga (*Equus quagga*), red hartebeest (*Alcephalus buselaphus*), bontebok (*Damaliscus pygargus pygargus*), bush buck (*Tragelaphus scriptus*), grey rhebuck (*Pelea capreolus*), ostrich (*Struthio camelus*), and the extinct blue antelope (*Hippotragus leucophaeus*) all occurring in the area (Du Plessis 1969; Skead 1980; Rookmaaker 1989; Boshoff & Kerley 2001). Unfortunately the status of large native herbivores changed rapidly after European settlement in 1652. It is estimated that after just 40 years of permanent European presence there was no big game within 200 km of Cape Town, and that by 1800 most large mammals (above 50 kg) had

been driven close to extinction within the Cape Floristic Region (Rebelo 1992b) – of which the Fynbos Biome forms the major part (Goldblatt & Manning 2000). Hunting for meat and sport, as well as the elimination of predators, scavengers and “problem” animals are blamed for these extinctions (Rebelo 1992b; Krug *et al.* 2004). Today it is, therefore, difficult to establish the carrying capacity of the Fynbos Biome. The reviews of historical accounts (Du Plessis 1969; Skead 1980; Rookmaker 1989) are useful for determining the incidence of the native large mammal species, but they are very vague in terms of habitat preference and population densities of these animals (Boshoff & Kerley 2001).

The last decade witnessed a profound change in land use in the Western Cape, with a sharp increase in native large herbivore numbers due to the rapid growth in the wildlife industry (Kerley *et al.* 2003; Briel & Nowers 2007). This development led to an increased need for guidelines on the reintroduction and management of the appropriate large herbivore species in order to harmonise the need of the wildlife industry with the conservation practices implemented to preserve the mega-biodiversity of the Cape Floristic Region (CFR) – a global biodiversity hotspot (Myers *et al.* 2000). Efforts have been made to provide an estimate for the spatial requirements of large herbivores within the CFR (Boshoff 2001; Boshoff *et al.* 2002; Kerley *et al.* 2003). These authors did, however, emphasise that their calculations were based on scant information regarding the habitat preference and ecology of large herbivores within the Fynbos Biome and that their values must, at best, be seen as testable hypotheses. In this paper we provide the first scientific evidence of habitat preference by native large herbivores in the Fynbos biome using the geologic substrate – that is known to play a major role in plant-community structuring within this biome (Rebelo *et al.* 2006) – as selection unit. The abundance of large herbivore dung along transects (standardised for slope and distance from permanent water) was used to determine the habitat use of eland and bontebok across different geological substrates within the De Hoop Nature Reserve (DHNR).

Methods

Study area

De Hoop Nature Reserve (34°26'S, 20°30'E), 323 km² in size, is situated on the South Coast of the Western Cape Province (Fig. 3.1). The southern border of the reserve is formed by the Indian Ocean and the eastern border it is marked by the inselberg of the Potberg Mountain (peak: 611 m). The western border comprises of the De Hoop Vlei (a lagoon cut-off from the sea by windblown sand dunes), while the northern border is separated from intensively cultivated private farms by a game fence. DHNR shares its western border with the Denel Corporation Overberg Toetsbaan Conservancy Area (OTB) of 280 km² and together these two reserves cover an area of 603 km² that can be seen as one management unit (Greater De Hoop). When the De Hoop Vlei is filled with water (which was the case for the duration of this study) the movement of animals between the two areas is funnelled into a narrow corridor (\pm 300 m broad) between the southern end of the lake and the sparsely vegetated coastal dunes bordering the sea.

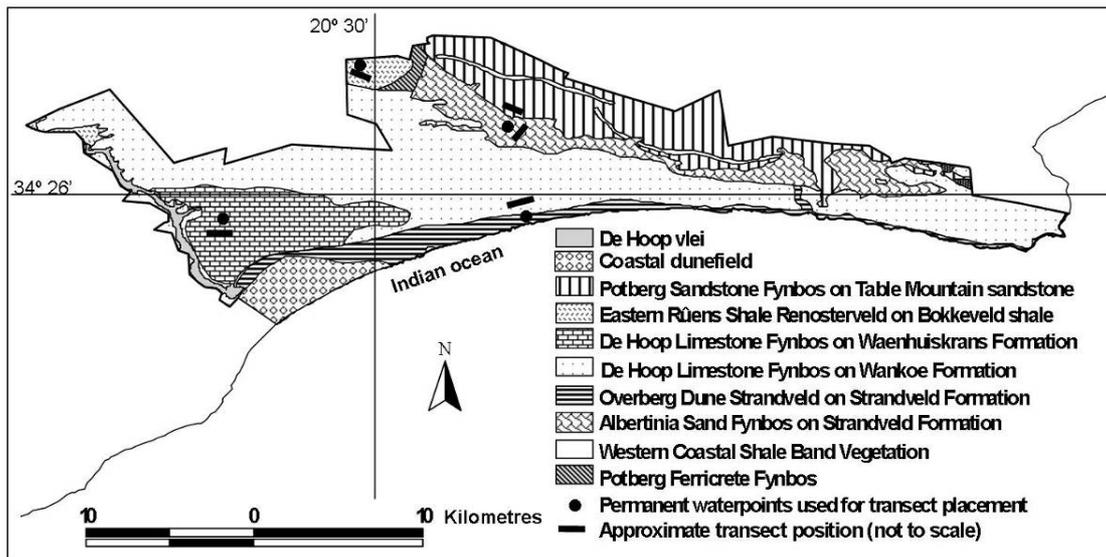


Fig. 3.1 The different vegetation types of De Hoop Nature Reserve as identified by Mucina *et al.* (2007) and its underlying geology as mapped by Coetzee (1993). The Waenhuiskrans and Wankoe limestones and Strandveld sands form part of the Bredasdorp Group. The four permanent waterpoints used as reference for the dung transects and the approximate positions of the five transect lines are also shown.

DHNR is composed geologically by a mosaic of three distinctly different geological substrates (Coetzee 1993): Ordovician sandstones of the Table Mountain Group, Devonian shales of the Bokkeveld Group, and Pleistocene deposited marine and marine-related limestones of the Bredasdorp Group (Malan *et al.* 1994). The Potberg Mountain is predominantly composed of Table Mountain sandstone and supports Potberg Sandstone Fynbos vegetation (Rebello *et al.* 2006). There is also a narrow shale band (< 200 m) running along the length of the Potberg supporting Western Coastal Shale Band Vegetation. The Bokkeveld shales in the north-eastern corner of the reserve support Eastern Rûens Shale Renosterveld (Rebello *et al.* 2006). The limestone of the Bredasdorp Group can be sub-divided into the Wankoe, Waenhuiskrans and Strandveld Formations (Malan *et al.* 1994). The Wankoe Formation consists of calcarenite (limestone) with aeolian cross-bedding and calcrete lenses and forms the dominant substrate of DHNR (Malan *et al.* 1994). The Waenhuiskrans Formation in the west of the Reserve next to the vlei consists of partly calcified dune sand with calcrete lenses (Malan *et al.* 1994) and is dotted with distinct karstic sinkhole depressions filled by light-grey to pale-red sandy soil. Both the Waenhuiskrans and Wankoe Formations support De Hoop Limestone Fynbos vegetation (Rebello *et al.* 2006). However, the karstic sinkhole depressions in the Waenhuiskrans sediments are covered by short creeping grasses dominated by *Cynodon dactylon*. The Holocene Strandveld Formation occurs along the coastline and in the valley between the Potberg Mountain and Wankoe Formation limestone hills. The Strandveld Formation along the coast consists of dune sand with shell fragments (Malan *et al.* 1994) and supports Overberg Dune Strandveld (Rebello *et al.* 2006). The light grey

quartz sand of the Strandveld Formation in the valley is covered by Albertinia Sand Fynbos (Rebello *et al.* 2006) and is a product of the weathering of both the Table Mountain sandstone and the Bredasdorp limestone bordering it. A small section of Potberg Ferricrete Fynbos (Rebello *et al.* 2006) on the NW footslope of the mountain also falls within the boundaries of DHNR. The SW corner of the reserve is filled by windblown sand dunes supporting only sparse vegetation.

The mean annual precipitation (period: 1979–2007) as measured at the Driefontein weather station, situated 4.5 km directly north of the reserve, is 473 mm (CV=19%). Every month of the year contributes at least 30 millimetres of rain to the total, but most (65%) of the rain falls during the winter (April–October) when the evapotranspiration is the lowest. The coldest month is July (Tmax = 18.4°C, Tmin = 6.3°C) and the warmest month is February (Tmax = 27.2°C, Tmin = 16.7°C). The driest months are November, December and January when the evapotranspiration exceeds 200 mm per month. The MAP for the year preceding the study was 459 mm (Nov. 2005–Nov. 2006).

The complete helicopter game count done for the Greater De Hoop Area in October 2006, a month before the start of our survey, gave the following numbers for the most common large herbivores: bontebok – 511, eland – 497, Cape mountain zebra – 76, and ostrich – 460 (Smith 2006).

Sampling design

The indirect method of surveying dung abundance in circular plots along set transects was used to determine the substrate preference of eland and bontebok within DHNR. Eland and bontebok were selected because these were the only large antelope species occurring at densities high enough to provide meaningful dung counts. Bontebok is almost exclusively a grazer with a preference for short grass (Beukes 1984; Skinner & Chimimba 2005). Bontebok males weigh on average 61 kg (Skinner & Chimimba 2005), while females are slightly smaller and weigh 55 kg on average (Owen-Smith 1988). Eland can be classified as a mix feeder with a strong preference for browse (Gagnon & Chew 2000; Skinner & Chimimba 2005) but see Watson and Owen-Smith (2000), Sponheimer *et al.* (2003), Codron *et al.* (2007) and Wallington *et al.* (2007) depicting eland as an almost exclusive browsers. In DHNR, carbon isotope analysis revealed that eland diet consist of around 16% C₄ grass with the rest consisting of either C₃ browse or C₃ grass (see Chapter 2 of this dissertation). Adult male eland can weigh as much as 900 kg, but are mostly between 425 and 840 kg, while females tend to be smaller, weighing around 460 kg (Skinner & Chimimba 2005).

We restricted our study to the five major geological substrates and their associated vegetation in DHNR: a) Bokkeveld shale (supporting renosterveld), b) Table Mountain sandstone (sandstone fynbos), c) Wankoe limestone (limestone fynbos), d) Waenhuiskrans limestone (limestone fynbos with embedded scattered karstic sinkhole depressions supporting grazing lawns), and e) Strandveld highly leached sands in the valley at the base of the Potberg Mountain (sand fynbos). Transect lines of 380 meters each were placed in habitats characterised by the targeted five geological substrates.

Metal stakes were placed along a transect at intervals of 20 meters, and dung counts were done within a circle (radius 2.0 m, area 12.57 m²) around each stake. Plot sampling was used as it has been shown that strip-transect counts are more time consuming and more pellet groups are missed on the border line of strips (Härkönen & Heikkilä 1999).

The exact position of each transect was carefully chosen in order to standardise for the effect of water availability and slope amongst the habitats. These two factors are known to have a significant impact on the herbivore distribution at the landscape scale (Senft *et al.* 1987; Bailey *et al.* 1996; Redfern *et al.* 2003; Archibald *et al.* 2005). A digital elevation model (DEM) of DHNR was developed using 20-meter isohypses. This DEM was used to detect the areas within the Reserve with a slope above and below six degrees. Only the areas having slopes less than six degrees were considered for the transect placement. Both eland and bontebok were regularly observed feeding on slopes up to six degrees and we argued that placing transects on slopes at or below this value would control for slope as a factor having an influence on the animal spatial distribution.

Bontebok stay within 1500 meter from permanent water during the dry summer months (Van Zyl 1978), while eland is much less water dependant (Skinner & Chimimba 2005). In order to eliminate the distance from water as a factor controlling the spatial distribution of the bontebok populations, we therefore placed all transects within 1500 meters from permanent water. Four permanent waterpoints were selected to serve as reference points for the transect placements. Transects were placed in habitats representing the target geological substrates as a tangent line to a circle (radius of 500 meter) with a selected waterpoint as its centre (Figure 3.1). All sampling plots were thus placed between 500 and 640 meters from the permanent water source. We argued that an antelope will only spend a significant amount of time in an area further than 500 meters away from water if the habitat provides suitable forage and not because of vigilant/lingering behaviour associated with the approach of waterpoints for drinking.

The starting point and direction of each transect was also selected to be easily accessible from the current road network, but had to be located at least 50 meters far from it. The starting point of each transect was randomly selected within the identified areas adhering to the slope, accessibility and water availability criteria using GIS maps. The 20 circular plots were then placed exactly in the predetermined positions along the transect lines irrespective of the vegetation structure. By placing the 20 plots in this predetermined fashion within each substrate type we standardised for the vegetation heterogeneity within a substrate by not deliberately selecting preferred or avoided feeding patches which could bias the results.

Eland and bontebok defecate pellet groups, and because these groups often occur in close proximity, certain rules were applied to distinguish between the different pellet groups. A pellet group constituted of at least 5 pellets of similar size, shape, texture, and colour. They were also supposed to be spread out close together or in a line in the cases where animals were moving while defecating. We followed the methodology of Shrestha (2004) who found that the best estimates of the number of pellet groups were made based on age of pellets, colour, sheen, and the level of degradation of the pellets. Pellet groups on the

edge of a plot were included in the survey if at least one pellet fell within the boundaries of the plot, i.e. if the pellet was within two meters of the metal stakes. Eland and bontebok pellets could easily be distinguished due to their size differences.

Previous studies have shown that dung decaying/disappearance rates can differ between seasons and substrates (Massei *et al.* 1998; Telfer *et al.* 2006). We monitored 10 fresh dung piles (5 from eland and 5 from bontebok) placed on each of the respective substrates in both the wet and dry season. We found that the substrate with the quickest dung disappearance rate was Bokkeveld shale; both eland and bontebok dung disappeared within as short a period as 48 hours during the wet season (F.G.T. Radloff, unpublished data). The disappearance rates were much slower during the warm and dry summer months, when the pellets were still countable after two weeks of exposure. We consequently restricted our surveys to the dry season and repeated the counts every 14 days for the duration of the 84 day study period (28 Nov 2006 to 20 Feb 2007). The 'clearance plot' method (*sensu* Marques *et al.* 2001) was used in this survey; all plots were initially cleared of dung before the start of the first survey (14 days later). The plots were surveyed 5 times thereafter, every 14 days (in total 84 days). The number of pellet groups of eland and bontebok present within each of the 100 plots (5 transects x 20 plots) was scored separately. Immediately after each count, all pellets were cleared from the plots so that in the next survey only the dung deposited in the previous 14 days was counted.

Data analyses

The total number of pellet groups per species per plot was calculated by summing the total number of pellet groups found within that plot over the 84 day survey period. The total number of pellet groups (separated for each of the two species) found within each of the 20 plots on each substrate was consequently used in the data analysis. Generalized linear models in Statistica (factorial ANOVA, Poisson distribution, log-link function, type 1 likelihood test; Quinn & Keough 2002) were used to test for significant differences in dung counts among substrate types. To account for overdispersion, standard errors were scaled using Pearson's X^2 as the estimate of the dispersion parameter. A bootstrap analysis (Efron & Tibshirani 1993) was run with 10 000 randomizations to test pair-wise for significant differences between the dung counts on different substrates. In this way the abundance of preferred and avoided feeding patches within a substrate type as unintentionally selected for by the stratified random placement of sampling plots were taken into consideration and accounted for. Alpha level corrections for multiple testing were performed using the step-up false discovery rate (FDR) correction procedure (Benjamini & Hochberg 1995), which has been shown to be the least over-corrective of current alpha-level correction methods (García 2004).

Results

The Type 1 likelihood factorial ANOVA tests indicate that there are highly significant differences in pellet group numbers among the different substrates for both eland ($X^2=30.92$, $p < 0.000003$) and bontebok ($X^2=70.12$, $p < 0.000001$).

The highest number of bontebok pellet groups was found on the Bokkeveld shales (n = 20) followed by the Waenhuiskrans limestone (n = 15) and Strandveld sands (n = 3). No bontebok dung was found in either the Table Mountain sandstone or Wankoe limestone survey plots for the entire 84-day sampling period. After step-up false discovery rate (FDR) corrections were done at the 0.05 level on the bootstrap analysis p-values, the bontebok data (Table 3.1 & Fig. 3.2) indicated that there were on average significantly more pellet groups present on both Bokkeveld shales and Waenhuiskrans limestone as compared to the rest of the substrates. No significant difference was found between the counts on Bokkeveld shales and Waenhuiskrans limestones ($p = 0.419$). The counts in the survey plots for Wankoe limestone, Table Mountain sandstone and Strandveld valley sand did not differ significantly from one another.

Table 3.1: The p-values for the pair-wise bootstrap comparison (10 000 randomizations) of the pellet group counts on the different geological substrates for both eland and bontebok. * Values that were significant after column wide step-up false discovery rate (FDR) corrections ($p < 0.05$).

Substrate pair-wise comparison	Bootstrapped p-values	
	Eland	Bontebok
Wankoe limestone vs. Waenhuiskrans limestone	<0.0001*	0.005*
Table Mountain sandstone vs. Wankoe limestone	0.111	1
Table Mountain sandstone vs. Waenhuiskrans limestone	<0.0001*	0.005*
Bokkeveld shale vs. Wankoe limestone	0.049	<0.0001*
Bokkeveld shale vs. Table Mountain sandstone	0.011*	<0.0001*
Bokkeveld shale vs. Waenhuiskrans limestone	0.338	0.419
Bokkeveld shale vs. Strandveld valley sand	0.108	0.001*
Strandveld valley sand vs. Wankoe limestone	0.617	0.18
Strandveld valley sand vs. Table Mountain sandstone	0.192	0.151
Strandveld valley sand vs. Waenhuiskrans limestone	0.008*	0.021*

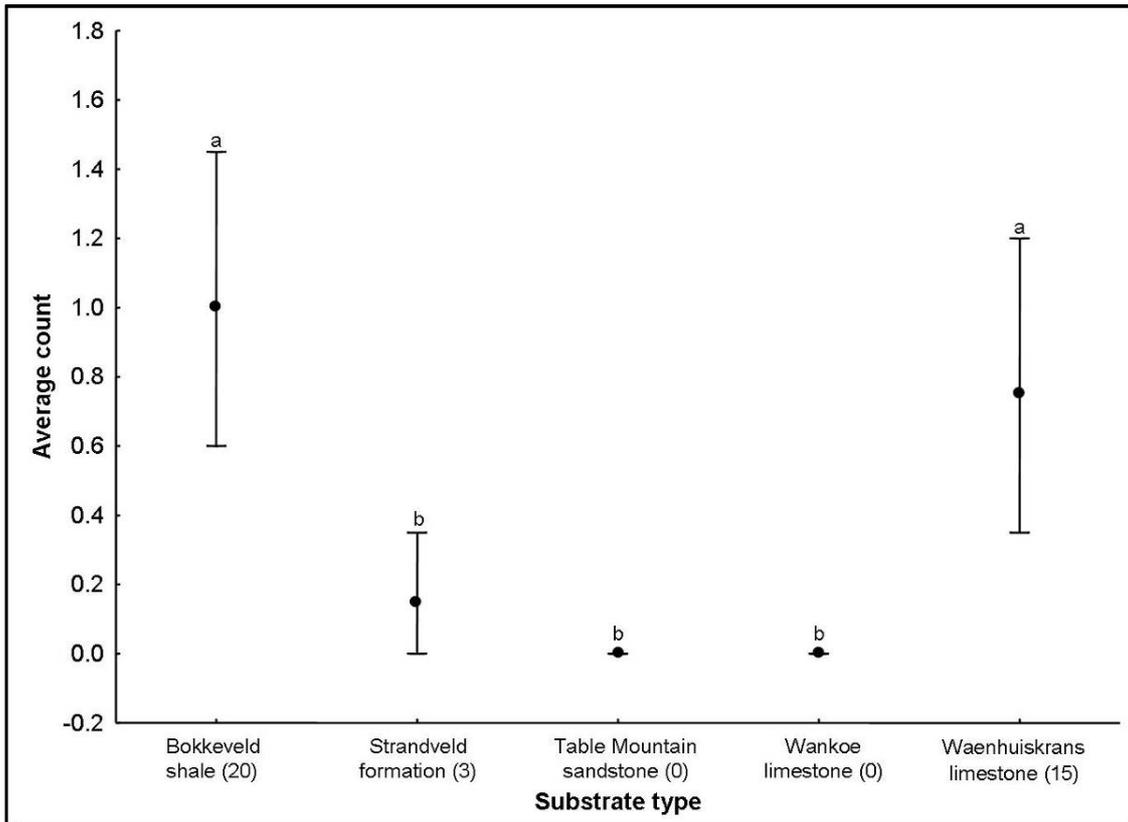


Fig 3.2: Bootstrap confidence intervals of means for bontebok dung counts on the different geological substrates (vertical bars denotes 0.95 bootstrap confidence intervals). Letters indicate significant differences between pair wise comparisons after step-up FDR corrections at the 0.05 level. Count totals for the different substrate types over the 84 day survey period are provided in brackets.

The highest dung count for eland was found on the Waenhuiskrans limestone ($n = 28$) followed by Bokkeveld shale ($n = 20$), Strandveld valley sand ($n = 7$) and Wankoe limestone ($n = 5$). Only one eland pellet group was found in the 20 survey plots of the Table Mountain sandstone during the entire 84 day survey period. The corrected bootstrap analysis p-values (Table 3.1, Fig. 3.3) of the eland data indicate that the dung count on Waenhuiskrans limestone differ significantly from the counts on Table Mountain sandstone ($p < 0.0001$), Wankoe limestone ($p < 0.0001$) and Strandveld valley sand ($p = 0.008$), but does not differ from that on Bokkeveld shale ($p = 0.338$). The dung counts on Bokkeveld shale do not differ significantly from both the counts on Wankoe limestone ($p = 0.049$) and Strandveld valley sand ($p = 0.108$) but do differ from those on Table Mountain sandstone ($p = 0.011$). The counts from the Strandveld valley sand, Table Mountain sandstone and Wankoe limestone do not differ significantly from each other.

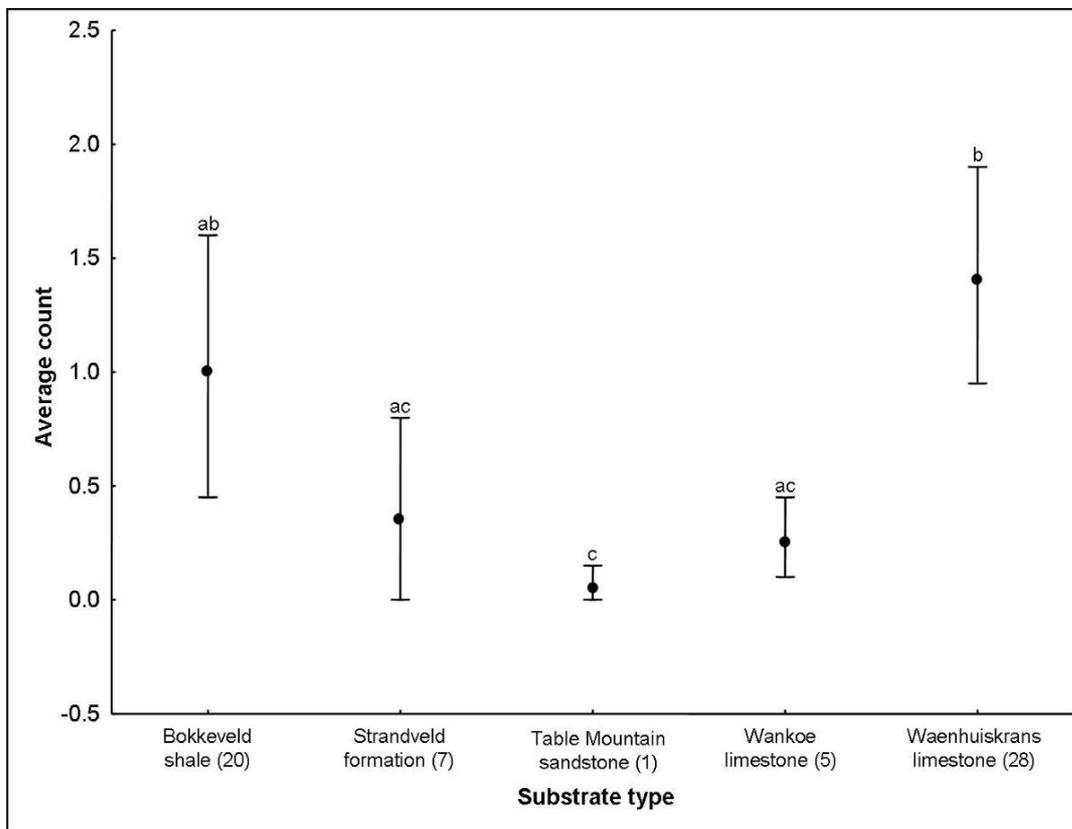


Fig 3.3: Bootstrap confidence intervals of means for eland dung counts on the different substrates (vertical bars denotes 0.95 bootstrap confidence intervals). Letters indicate significant similarities and differences between pair wise comparisons after step-up FDR corrections at the 0.05 level. Count totals for the different substrates over the 84 day survey period are provided in brackets.

Discussion

Dung count validity

Dung counts provide a picture of the average abundance of animals over several months, whereas direct visual counts yield estimates of abundance for the exact time of the survey and may result in misleading information on habitat use (Marques *et al.* 2001). Barnes (2001) found that dung counts give just as accurate an indication of vertebrate population numbers as other count methods, while Jachmann (1991) showed that dung counts are more reliable than line-strip animal counts and line-transect foot surveys. During the early 1980's there was some controversy (centred around mule deer) on whether pellet-group distribution actually indicates the habitat preference of animals (Collins & Urness 1981; Collins 1984; Leopold *et al.* 1984). Later work showed, however, that dung counts for elk and deer compared well with telemetry techniques (Loft & Kie 1988; Edge & Marcum 1989) and with aerial surveys (Forbes & Theberge 1993) for assessing habitat

use. More recently Telfer (2006) also found that dung counts compared favourably to telemetry techniques in determining the habitat preferences of rock-dwelling macropod species. Dung counts have been used to establish large herbivores' habitat use in diverse regions for a wide range of species over many decades (Jachmann & Bell 1979; Cairns & Telfer 1980; Gallina *et al.* 1991; Bozzo *et al.* 1992; Kay 1993; Plumptre & Harris 1995; Young *et al.* 1995; Landsberg & Stol 1996; Härkönen & Heikkilä 1999; Altendorf *et al.* 2001; Barnes 2001; Blake 2002; Jenkins *et al.* 2002; Letnie 2004; Steinheim *et al.* 2005; Watson *et al.* 2005; Young *et al.* 2005).

Corroborating the findings of Massei *et al.* (1998) and Telfer *et al.* (2006), we found that dung decaying/disappearance rates differ between seasons and substrates. Dung disappeared the quickest from the shale substrate, followed by Strandveld valley sand, and Table Mountain sandstone. Disappearance rates were also much quicker during the cooler wet season than during the warm and dry summer months. Interestingly though, was the exceptionally slow decaying rates on both the Wankoe and Waenhuiskrans limestones where, irrespective of the season, all dung piles could still be recognised after more than two months. We attribute this discrepancy in disappearance rates to the variation in dung beetle activity amongst substrates. No dung beetles were observed on the limestone substrates during our study. The variation in disappearance rates were prevented from biasing our results by doing counts only during the warm and dry summer months, at intervals shorter than that recorded for dung disappearance on shales during this period (every 14 days).

By restricting our study to the dry season we are confining our interpretation to the dry season range (*sensu* Illius & O'Connor 2000) of the eland and bontebok. We, however, believe that these animals, in particular the bontebok, are forced to use all available habitat within reach of permanent water during the dry season. Habitat avoidance in close vicinity to water during this period thus enforces rather than refute our findings on habitat use by these animals. By placing all the transects within easy reach of water we are truly identifying the key resource areas as all suitable habitat will be used in contrast to the wet season when more of the prime habitat will be available due to an increase in surface water availability (Illius & O'Connor 2000).

Influence of slope, water, fire, and predators on distribution of herbivores

The landscape scale distribution patterns of herbivores are believed to be determined by the operation of biotic mechanisms within the constraints set by abiotic factors (Bailey *et al.* 1996). In order to determine the effect of geological substrate on eland and bontebok distribution patterns, we had to account for as many as possible of the additional biotic and abiotic distribution factors. Slope and water accessibility are considered to be two important factors influencing large herbivore distribution (Senft *et al.* 1987; Bailey *et al.* 1996; Redfern *et al.* 2003; Archibald *et al.* 2005) and in this study we accounted for their effects by placing transects on similar slopes and at the same distance from permanent water. In addition, the effect of fire on large mammal distribution across African savannas is well appreciated (Wilsey 1996; Archibald & Bond 2004). Burnt areas in fynbos have been shown to attract herbivores for up to four years after the fire event

(Langley & Giliomee 1974; Beukes 1987; Novellie 1987; Teague 1999; Luyt 2005). The transects in this study were all placed in vegetation older than 7 years and the closest recently burnt patch was situated 12 kilometres east of our most eastern transect. Hence we can conclude that the fire history did not influence the distribution patterns found in this study.

Predation risk can alter the distribution patterns of prey animals (Andersen *et al.* 2006) and two predators capable of killing eland and bontebok occur within DHNR. Leopard (*Panthera pardus*) is capable of killing bontebok and eland juveniles (Radloff & du Toit 2004), while caracal (*Caracal caracal*) can prey on animals the size of juvenile bontebok (Skinner & Chimimba 2005). Eland and bontebok might thus avoid vegetation which provides cover for these two stalking predators. A cover assessment was done along transects by estimating the visibility of a 1.80 meter tall person positioned at the centre of each sampling plot and observed from two opposite sides at a distance of 20 meters (the position of the neighbouring sampling plots). This indicated that the two most preferred habitats included both the shortest/most open (Eastern Rûens Shale Renosterveld) and tallest/dense vegetation (De Hoop Limestone Fynbos on the Waenhuiskrans limestones) (F.G.T Radloff unpublished data). We thus conclude that the substrate selection of bontebok and eland was not influenced by visibility restrictions that may increase predation risk. In addition, reported incidences of predation on eland and bontebok by caracal and leopard within DHNR are very rare if not negligible (P. Chadwick, CapeNature, personal communication).

Soil nutrients and geological substrate preference

In the Fynbos Specht and Moll (1983) found a strong link between the nutrient status of the soil and the structure of the vegetation it supports. They divided the soils of this biome and its associated vegetation into three classes: a) the moderately leached soils of the coastal renosterveld which support vegetation with a sclerophyllous overstorey and a seasonal annual and perennial grass/herb understory, b) the strongly leached soils of mountain fynbos (today called 'sandstone fynbos') associated with both a sclerophyllous under- and over-storey, and c) the calcium-rich/high-pH soils of the calcareous coastal fynbos (today called 'limestone fynbos') with a sclerophyllous overstorey and an understory varying from grassy to sclerophyllous depending on the degree of leaching and depth of the surface soils. The moderately leached soils are considered to be reasonably well balanced nutritionally, while the strongly leached soils have a very low nutrient status, especially with regards to nitrogen and phosphorus (Specht & Moll 1983; Campbell 1986). The calcium-rich soils contain a reasonable balance of mineral nutrients, but much of these are not available to the plants due to high pH carrying their precipitation (Specht & Moll 1983). The nutrient stress for plants on the calcium-rich soils is thus often as severe as for the strongly leached soils, though varying more depending on the amount of leaching and depth of the surface soil (Specht & Moll 1983).

Specht and Moll's (1983) classification can be used to describe a soil fertility gradient for DHNR. The Bokkeveld shales supporting renosterveld shrublands are moderately leached and have the highest soil nutrient status in the area. Shale is followed by the nutrient-rich,

deep soils developing over the karstic sinkholes embedded within the Waenhuiskrans limestone pavements. These are filled with deep pale red sand and support a grassy understory in contrast to the rest of the area that has shallow soils with a sclerophyllous understory. Both Wankoe limestones and strongly leached Table Mountain sandstones have a very low nutrient status. The Strandveld sands at the base of Potberg Mountain have a nutrient status between that of the Wankoe limestones and Table Mountain sandstone – these sands are a mixture of weathered material from both the sandstones and limestones (Malan *et al.* 1994).

The results of the dung count survey closely follow the described soil nutrient gradient for DHNR, with the most nutrient-rich substrates (Bokkeveld shales and Waenhuiskrans limestones) having the highest pellet group abundance for both eland and bontebok. The bontebok completely avoided the Wankoe limestone and Table Mountain sandstone and had a very low abundance on the Strandveld sands. Bontebok, being a grazer, needs a grassy ground layer for fodder and it is therefore not surprising that they avoid the sclerophyllous shrublands of the Table Mountain sandstones, Wankoe limestones and Strandveld sands. Occurrence of bontebok on the Waenhuiskrans limestones can be explained by the presence of the grassy sinkhole depressions providing grassy hotspots for the large herbivores.

Eland also seems to avoid Wankoe limestones and sands of the Strandveld Formation in the valley, but less so than the bontebok. This may relate to the fact that eland is a mix-feeder which utilises predominantly browse (Watson & Owen-Smith 2000; Sponheimer *et al.* 2003; Wallington *et al.* 2007) and, as the largest antelope species in Africa (Skinner & Chimimba 2005), is better able to process low quality food than any smaller antelope due to lower metabolic demands (Du Toit & Owen-Smith 1989; Belovsky 1997; Fritz *et al.* 2002; Olf *et al.* 2002). Eland, in contrast to bontebok, thus utilise the edible fodder to be found on the Wankoe and Strandveld substrates – albeit at low population densities. It is surprising though that eland seem to be avoiding the Table Mountain sandstone (only a single pellet group was counted on sandstone during the entire 84-day survey period). This avoidance of sandstone took place despite an apparent overpopulation of eland within DHNR at the time of the survey which should have forced these animals to utilise even sub-optimal habitat. At the onset of this survey the eland numbers were the highest ever recorded in the history of the reserve (around 497 individuals as from the October 2006 helicopter count) and was followed by a population crash with 70% less eland recorded in the aerial survey of February 2008 (147 individuals). Although the accuracy of the February 2008 aerial count is in dispute, there is no question that a dramatic decline in large herbivore numbers occurred during 2007 in the Greater De Hoop area (P. Chadwick, CapeNature and Marinus Stoltz, OTB, personal communications). We must therefore conclude that although limestone fynbos might still be able to support low densities of eland (especially if it possesses grassy hotspots on karstic sinkholes), shrublands on Table Mountain sandstone are so nutritionally depleted that they are consistently avoided by even the biggest antelope on the African continent. This conclusion is further supported by the findings of Watson *et al.* (2005) and Watson and Chadwick (2007) who studied Cape mountain zebra in the Gamka Mountain Nature Reserve and Kammanassie Nature Reserve respectively. Both studies concluded that the mountain (sandstone)

fynbos – the dominating vegetation type in both Reserves – was not a suitable habitat for mountain zebra and that it was utilized only for a short period following fire. Even non-ruminant large herbivores, that should be able to utilize low quality forage better than ruminants of similar size (Owen-Smith 1982; Duncan *et al.* 1990; Menard *et al.* 2002), thus avoid the fynbos vegetation supported by Table Mountain sandstone.

Megaherbivore habitat utilisation – an extrapolation

The results from this study raise the question to which extent megaherbivores – more specifically elephant and black rhino – were able to utilize sandstone and limestone fynbos in the past. Fritz *et al.* (2002) showed in their analysis of large herbivore assemblages across Africa that the biomass density of megaherbivores increased with annual rainfall and that this increase is unrelated to soil nutrient status. The megaherbivores in their analysis also made up a larger portion of the biomass of ungulate communities in ecosystems with high rainfall and low-nutrient soil status. This pattern is supported by Olff *et al.* (2002) in their study on global animal diversity, which found that elephant distribution was independent of plant-available nutrients. Theory thus predicts that megaherbivores should be able to survive on substrates with a very low nutrient status as long as the quantity of fodder is adequate. Carbon isotope analysis on collagen obtained from contemporary elephant bones found at coastal archaeological sites both on the West and South Coasts of the Western Cape revealed that the elephants in this region utilized very little C₄ grass (n = 6, % C₄ in diet = 11.7%, SD = 1.3, see Chapter 2 of this dissertation) . This might suggest that the elephants had to utilize some fynbos to make up the bulk of their diet. However, all the archaeological sites from which samples were obtained are either within, or in very close proximity to, Strandveld vegetation (Rebelo *et al.* 2006) which presumably has a higher nutritional status than sandstone or limestone fynbos. Milewski (2002), on the other hand, did find evidence of fynbos utilization by elephants reintroduced to the Knysna forest area that is surrounded by fynbos shrublands. We currently have no idea of black rhino's historical or potential habitat utilization either in fynbos or renosterveld shrublands.

Implications for carrying capacity

Our study supports the prediction that large herbivores, and in particular large antelopes (> 20 kg), avoid sandstone fynbos vegetation and that they concentrate on the more nutrient rich shale substrates supporting renosterveld and grassy vegetation. Limestone fynbos is also avoided by large antelope, except for grassy hotspots such as the sinkhole depressions on the Waenhuiskrans limestones. This has important management implications for the De Hoop Nature Reserve in particular, but also for the conservation of large herbivores within the Fynbos in general. Carrying capacity estimates for a reserve have to be based on utilisable habitat, not the whole reserve area. Boshoff *et al.* (2002) predicted spatial requirements for bontebok and eland for the broader habitat units in DHNR. They estimated 139 ha needed per bontebok in their habitat unit called De Hoop Limestone fynbos, but our study shows that bontebok avoid this substrate, except in areas with rare grassy hotspots. The spatial requirements of eland in the Potberg Sandstone Fynbos also seem to be an underestimation. Especially since the area per eland

that is estimated to be necessary for their survival in this sandstone habitat (5 184 ha/eland), which they avoid, is less than what they presumably need for survival on the De Hoop Limestone fynbos (6 912 ha/eland) that they at least frequent sometimes. The spatial requirements of eland in renosterveld must be a gross overestimation as it is higher than for any of the other substrates in DHNR (10 800 ha/eland) and is actually one of their most preferred and utilised habitats.

Accurate predictions on the large herbivore biomass that can be sustained in Fynbos will only be possible once we have a better idea of megaherbivores spatial use in this environment and this can only be established by the reintroduction of these animals into fynbos and renosterveld areas. Given the current large ungulate assemblage present in DHNR and our understanding of their spatial use, the predicted large herbivore biomass value of 1 595kg/km² for DHNR, as calculated using the equation of Fritz and Duncan (1994) for nutrient poor savannas and the average rainfall value for DHNR (473mm), appears to be a gross overestimation for this exceptionally nutrient poor African environment. The predicted biomass value imply that the Greater De Hoop area should be able to support a total large herbivore biomass of 961 785 kg. The October 2006 game census that tallied the highest animal numbers in the history of Greater De Hoop (P. Loyd, CapeNature, personal communication) and that occurred just before the mentioned crash in eland as well as bontebok numbers, provides a total large herbivore biomass value of 229 600 kg for the area [calculated using animal unit mass (0.75 adult female body mass, sensu Owen-Smith 1988) for eland, bontebok, ostrich and mountain zebra]. This value of 229 600 kg is only 22% of the predicted value for this area and, given the recent crash in animal numbers, it is doubtful that the Greater De Hoop area can sustain a higher biomass with its current species assemblage. Our results suggest that only 12% of the total area of DHNR is really viable bontebok and eland habitat, and that more than 27 000 hectare of this Reserve is unsuitable for large antelope, except perhaps for short periods following a local fire.

To what extent the conclusions of our study can be extrapolated to the rest of the Fynbos Biome is difficult to tell. However, we are confident that we can apply the extrapolation to at least the bioregion level (Rutherford *et al.* 2006). This implies that the Southern Fynbos and South Coast Fynbos Bioregions were by and large avoided by large antelope which mostly fed in the East Coast Renosterveld Bioregion.

References

- Altendorf K.B., Laundre J.W., Lopez Gonzalez C.A. & Brown J.S. (2001) Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy*, 82, 430-439
- Andersen R., Linnel J.D.C. & Solberg E.J. (2006) The future role of large carnivores in terrestrial trophic interactions: the northern temperate view. In: *Large herbivore ecology, ecosystem dynamics and conservation* (eds. Danell K., Bergström R., Duncan P. & Pastor J.), pp. 413-448. Cambridge University Press, Cambridge

- Archibald S. & Bond W.J. (2004) Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13, 377-385
- Archibald S., Bond W.J., Stock W.D. & Fairbanks D.H.K. (2005) Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications*, 15, 96-109
- Bailey D.W., Gross J.E., Laca E.A., Rittenhouse L.R., Coughenour M.B., Swift D.M. & Sims P.L. (1996) Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49, 386-400
- Barnes R.F.W. (2001) How reliable are dung counts for estimating elephant numbers? *African Journal of Ecology*, 39, 1-9
- Bell R.H.V. (1982) The effect of soil nutrient availability on community structure in African ecosystems. In: *Ecology of tropical savannas* (eds. Huntley B.J. & Walker B.H.), pp. 193-215. Springer-Verlag, New York
- Belovsky G.E. (1997) Optimal foraging and community structure: The allometry of herbivore food selection and competition. *Evolutionary Ecology*, 11, 641-672
- Benjamini Y. & Hochberg Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, 16, 289-300
- Beukes P.C. (1984) *Sommige aspekte van die ekologie van die Vaalribbok (Pelea Capreolus, Forster 1790) in die Bontebok Nasionale Park*. MSc. Thesis, University of Stellenbosch
- Beukes P.C. (1987) Responses of grey rhebuck and bontebok to controlled fires in coastal renosterveld. *South African Journal of Wildlife Research*, 17, 103-108
- Bigalke R.C. (1979) Aspects of vertebrate life in Fynbos, South Africa. In: *Ecosystems of the World, 9A, Heathlands and related shrublands* (ed. Specht. R.L.), pp. 81-95. Elsevier, Amsterdam
- Blake S. (2002) Forest buffalo prefer clearings to closed-canopy forest in the primary forest of northern Congo. *Oryx*, 36, 81-86
- Boshoff A.F. & Kerley G.I.H. (2001) Potential distribution of the medium- to large-size mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *African Zoology*, 36, 245-273
- Boshoff A.F., Kerley G.I.H. & Cowling R.M. (2002) Estimated spatial requirements of the medium- to large sized mammals, according to broad habitat units, in the Cape Floristic Region, South Africa. *African Journal of Range & Forage Science*, 19, 29-44
- Boshoff A.F., Kerley, G. I. H. & Cowling, R. M. (2001) A pragmatic approach to estimating the distribution and spatial requirements of the medium- to large-sized mammals in the Cape Floristic Region, South Africa. *Diversity and Distributions*, 7, 29-43
- Bozzo J.A., Beasom S.L. & Fulbright T.E. (1992) White-tailed deer use of rangeland following browse rejuvenation. *Journal of Range Management*, 45, 496-499
- Briel S.C.P. & Nowers R.J. (2007) *Wildlife production in the Western Cape: A report on the quantification and qualification of wildlife production units*. Western Cape Department of Agriculture, Elsenburg

- Cairns A.L. & Telfer E.S. (1980) Habitat use by 4 sympatric ungulates in Boreal mixed forest. *Journal of Wildlife Management*, 44, 849-857
- Campbell B.M. (1986) Plant spinescence and herbivory in a nutrient poor ecosystem. *Oikos*, 47, 168-172
- Cody M.L., Breytenbach G.J., Fox A.E., Newsome A.E., Quinn R.D. & Siegfried W.R. (1983) Animal communities: diversity, density and dynamics. In: *Mineral nutrients in mediterranean ecosystems* (ed. Day J.A.), pp. 91-110. South African National Scientific Programmes Report, CSIR, Pretoria
- Codron D., Codron J., Lee-Thorp J.A., Sponheimer M., de Ruiter D., Sealy J., Grant R. & Fourie N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, 273, 21-29
- Coe M.J., Cumming D.H.M. & Phillipson J. (1976) Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22, 341-354
- Coetzee F. (1993) *1:250 000 Geological Series Map. 3420 Riversdale*. Government Printer, Pretoria
- Collins W.B. (1984) The pellet-group census technique as an indicator of relative habitat use: Response to Leopold et al. *Wildlife Society Bulletin*, 12, 327
- Collins W.B. & Urness P.J. (1981) Habitat preferences of mule deer as rated by pellet-group distribution. *Journal of Wildlife Management*, 45, 969-972
- Cowling R., Rundel P.W., Lamont B.B., Arroyo M.K. & Arianioutsou M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, 11, 362-366
- Duncan P., Foose T.J., Gordon I.J., Gakahu C.G. & Lloyd M. (1990) Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia*, 84, 411-418
- Du Plessis S.E. (1969) *The past and present geographical distribution of the Perissodactyla and Artiodactyla in southern Africa*. MSc. Thesis, University of Pretoria.
- Du Toit J.T. & Owen-Smith N. (1989) Body size, population metabolism, and habitat specialization among large African herbivores. *American Naturalist*, 133, 736-740
- East R. (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, 22, 245-270
- Edge D.W. & Marcum L.C. (1989) Determining elk distribution with pellet-group and telemetry techniques. *Journal of Wildlife Management*, 53, 621-624
- Efron B. & Tibshirani R. (1993) *An introduction to the bootstrap*. Chapman and Hall, London
- Forbes G.J. & Theberge J.B. (1993) Multiple landscape scales and winter distribution of Moose, *Alces alces*, in a forest ecotone. *Canadian Field-Naturalist*, 107, 201-207
- Fritz H. & Duncan P. (1994) On carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society London*, 256, 77-82
- Fritz H., Duncan P., Gordon I.J. & Illius A.W. (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620-625

- Gallina S., Galina-Tessaro P. & Alvarez-Càrdenas S. (1991) Mule deer density and pattern distribution in the pine-oak forest at the Sierra de La Laguna in Baja California Sur, Mexico. *Ethology, Ecology & Evolution*, 3, 27-33
- García L.V. (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos*, 105, 657-663
- Goldblatt P. & Manning J.C. (2000) *Cape plants. A conspectus of the Cape flora of South Africa*. National Botanical Institute & Missouri Botanical Garden Press, Pretoria & St Louis
- Härkönen S. & Heikkilä R. (1999) Use of pellet group counts in determining density and habitat use of moose *Alces alces* in Finland. *Wildlife Biology*, 5, 233-239
- Hendey Q.B. (1983) Palaeontology and palaeoecology of the Fynbos region: an introduction. In: *Fynbos palaeoecology: a preliminary synthesis* (eds. Deacon H.J., Hendey Q.B. & Lambrechts J.J.N.), pp. 87-99. CSIR, Pretoria
- Illius A.W. & O'Connor T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos*, 89, 283-294
- Jachmann H. (1991) Evaluation of four survey methods for estimating elephant densities. *African Journal of Ecology*, 29, 188-195
- Jachmann H. & Bell R.H.V. (1979) The assessment of elephant numbers and occupancy by means of droppings counts in the Kusungu National Park, Malawi. *African Journal of Ecology*, 17, 231-239
- Jenkins R.K.B., Corti G.R., Fanning E. & Roettcher K. (2002) Management implications of antelope habitat use in the Kilombero Valley, Tanzania. *Oryx*, 36, 161-169
- Johnson S.D. (1992) Plant-animal relationships. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 175-205. Oxford University Press, Cape Town
- Kay S. (1993) Factors affecting severity of deer browsing damage within coppiced woodlands in the South of England. *Biological Conservation*, 63, 217-222
- Kerley G.I.H., Pressey R.L., Cowling R.M., Boshoff A.F. & Sims-Castley R. (2003) Options for the conservation of large and medium-sized mammals in the Cape floristic region hotspot, South Africa. *Biological Conservation*, 112, 169-190
- Krug R.M., Krug C.B., Midoko Iponga D., Walton B.A., Milton S.J., Newton I.P., Farley N. & Shiponeni N.N. (2004) Reconstructing West Coast Renosterveld: past and present ecological processes in a Mediterranean shrubland of South Africa. In: *Proceedings of the 10th MEDECOS Conference* (eds. Arianoutsou M. & Papanastasis V.P.), pp. 120-131. Millpress, Rotterdam
- Landsberg J. & Stol J. (1996) Spatial distribution of sheep, feral goats and kangaroos in woody rangeland paddocks. *Rangeland Journal*, 18, 270-291
- Langley C.H. & Giliomee J.H. (1974) Behaviour of the bontebok (*Damaliscus D. Dorcas*) in the Cape of Good Hope Nature Reserve. *Journal of the Southern African Wildlife Management Association*, 4, 117-121
- Leopold B.D., Krausman P.R. & Hervert J.J. (1984) Comment: the pellet-group census technique as an indicator of relative habitat use. *Wildlife Society Bulletin*, 12, 325-326
- Letnie M. (2004) Cattle grazing in a hummock grassland regenerating after fire: the short-term effects of cattle exclusion on vegetation in South-Western Queensland. *Rangeland Journal*, 26, 34-48

- Loft E.R. & Kie J.G. (1988) Comparison of pellet-group and radio triangulation methods for assessing deer habitat use. *Journal of Wildlife Management*, 52, 524-527
- Luyt E. du C. (2005) *Models of Bontebok (Damaliscus pygargus pygargus, Pallas 1766) habitat preferences in the Bontebok National Park and sustainable stocking rates*. MSc. Thesis, Stellenbosch University
- Malan J.A., Viljoen J.H.A., Siegfried H.P. & Wickens H.d.V. (1994) *Geologie van die gebied Riversdale*. Government Printer, Pretoria
- Marques F.F.C., Buckland S.T., Goffin D., Dixon C.E., Borchers D.L., Mayle B.A. & Peace A.J. (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology*, 38, 349-363
- Massei G., Bacon P. & Genov P.V. (1998) Fallow deer and wild boar pellet group disappearance in a Mediterranean area. *Journal of Wildlife Management*, 62, 1086-1094
- Menard C., Duncan P., Fleurance G., Georges J. & Lila M. (2002) Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology*, 39, 120-133
- Milewski A.V. (2002) Elephant diet at the edge of the Fynbos Biome, South Africa. *Pachyderm*, 32, 29-38
- Moll E.J. (1987) Review of some new concepts in "Fynbos" ecology. In: *Papers in the Prehistory of the Western Cape. British Archaeological Reports International Series 332*, (eds. Parkington J. & Hall M.), pp. 120-131. BAR, Oxford
- Morrow P.A., Day J.A., Fox M.D., Frost P.G.H., Jarvis J.U.M., Milewski A.V. & Norton P.M. (1983) Interaction between plants and animals. In: *Mineral nutrients in mediterranean ecosystems* (ed. Day J.A.), pp. 111-124. CSIR, Pretoria
- Mucina L., Rutherford M.C. & Powrie L.W. (eds.) (2007) *Vegetation map of South Africa, Lesotho and Swaziland, 1:1 000 000, 2nd ed.*. SANBI, Pretoria
- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858
- Novellie P. (1987) Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe*, 30, 1-17
- Olf H., Ritchie M.E. & Prins H.H.T. (2002) Global environmental controls of diversity in large herbivores. *Nature*, 415, 901-904
- Owen-Smith N. (1982) Factors influencing the consumption of plant products by large herbivores. In: *Ecology of tropical savannas* (eds. Huntley B.J. & Walker B.H.), pp. 359-404. Springer-Verlag, Berlin
- Owen-Smith N. (1988) *Megaherbivores: the Influence of Very Large Body Size on Ecology*. Cambridge University Press, Cambridge
- Owen-Smith N. & Danckwerts J.E. (1997) Herbivory. In: *Vegetation of southern Africa* (eds. Cowling R., Richardson D. & Pierce S.), pp. 397-420. Cambridge University Press, Cambridge
- Plumptre A.J. & Harris S. (1995) Estimating the biomass of large mammalian herbivores in a tropical montane forest: a method of faecal counting that avoids assuming a 'steady state' system. *Journal of Applied Ecology*, 32, 111-120
- Quinn G.P. & Keough M.J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge

- Radloff F.G.T. & du Toit J.T. (2004) Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology*, 73, 410-423
- Rebelo A.G. (1987) Management implications. In: *A preliminary synthesis of pollination biology in the Cape flora* (ed. Rebelo A.G.), pp. 193-211. CSIR, Pretoria
- Rebelo A.G. (1992a) Preservation of biotic diversity. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 309-344. Oxford University Press, Cape Town
- Rebelo A.G. (1992b) Red Data Book Species in the Cape Floristic Region: threats, priorities and target species. *Transactions of the Royal Society of South Africa*, 48, 55-86
- Rebelo A.G. (1996) Renosterveld. In: *Vegetation of South Africa, Lesotho and Swaziland* (eds. Low A.B. & Rebelo A.G.), pp. 63-67. Department of Environmental Affairs and Tourism, Pretoria
- Rebelo A.G., Boucher C., Helme N., Mucina L., Rutherford M.C., Smit W.J., Powrie L.W., Ellis F., Lambrechts J.J., Scott L., Radloff F.G.T., Johnson S.D., Richardson D.M., Ward R.A., Proches S.M., Oliver E.G.H., Manning J.C., Jürgens N., McDonald D.J., Janssen J.A.M., Walton B.A., Le Roux A., Skowno A.L., Todd S.W. & Hoare D.B. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 52-219. SANBI, Pretoria
- Redfern J.V., Grant R., Biggs H. & Getz W.M. (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84, 2092-2107
- Rookmaaker L.C. (1989) *The zoological exploration of southern Africa 1650-1790*. A. A. Balkema, Rotterdam
- Rutherford M.C., Mucina L. & Powrie L.W. (2006) Biomes and bioregions of Southern Africa. In: *The vegetation of South Africa, Lesotho and Swaziland*. (eds. Mucina L. & Rutherford M.C.), pp. 31-51. SANBI, Pretoria
- Senft R.L., Coughenour M.B., Bailey D.W., Rittenhouse L.R., Sala O.E. & Swift D.M. (1987) Large herbivore foraging and ecological hierarchies. *BioScience*, 37, 789-799
- Shrestha M.K. (2004) *Relative ungulate abundance in a fragmented landscape: implications for tiger conservation*. PhD Thesis, University of Minnesota, Minneapolis
- Skead C.J. (1980) *Historical mammal incidence in the Cape Province. Volume 1: The Western and Northern Cape*. Department of Nature and Environmental Conservation of the Cape Provincial Administration, Cape Town.
- Skinner J.D. & Chimimba C.T. (2005) *The mammals of the southern African subregion*. Cambridge University Press, Cape Town
- Smith R. (2006) *De Hoop Nature Reserve helicopter game census October 2006*. Internal Report, CapeNature, Cape Town
- Specht R.L. & Moll E.J. (1983) Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In: *Mediterranean-type ecosystems: the role of nutrients* (eds. Kruger F.J., Mitchell D.T. & Jarvis J.U.M.), pp. 41-65. Springer-Verlag, Heidelberg

- Sponheimer M., Lee-Thorp J.A., DeRuiter D.J., Smith J.M., Van der Merwe N.J., Reed K., Grant C.C., Ayliffe L.K., Robinson T.F., Heidelberger C. & Marcus W. (2003) Diets of southern African Bovidae: Stable isotope evidence. *Journal of Mammalogy*, 84, 471-479
- Steinheim G., Wegge P., Fjellstad J.I., Jnawali S.R. & Weladji R.B. (2005) Dry season diets and habitat use of sympatric Asian elephants (*Elephas maximus*) and greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal. *Journal of Zoology*, 265, 377-385
- Teague W.R. (1999) Fynbos (macchia). In: *Veld management in South Africa* (ed. Tainton N.M.), pp. 327-333. University of Natal Press, Pietermaritzburg
- Telfer W.R., Griffiths A.D. & Bowman D.M.J.S. (2006) Scats can reveal the presence and habitat use of cryptic rock-dwelling macropods. *Australian Journal of Zoology*, 54, 325-334
- Van Zyl L.J. (1978) *Die waterbehoefte en drinkgewoontes van die Bontebok Damaliscus dorcas dorcas (Pallas, 1766) in die Bontebok Nasionale Park*. MSc. Thesis, Stellenbosch University.
- Wallington B.P., McKechnie A.E., Owen-Smith N. & Woodborne S. (2007) Stable carbon isotope analysis of eland (*Taurotragus oryx*) diet in the Suikerbosrand Nature Reserve. *Journal of Wildlife Management*, 37, 127-131
- Watson L.H. & Chadwick P. (2007) Management of Cape mountain zebra in the Kammanassie Nature Reserve, South Africa. *South African Journal of Wildlife Research*, 37, 31-39
- Watson L.H., Odendaal H.E., Barry T.J. & Pietersen J. (2005) Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire. *Biological Conservation*, 122, 173-180
- Watson L.H. & Owen-Smith N. (2000) Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology*, 38, 130-137
- Wilsey B.L. (1996) Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, 34, 32-38
- Young T.P., Palmer T.M. & Gadd M.E. (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation*, 122, 351-359
- Young T.P., Patridge N. & Macrae A. (1995) Long-term glades in Acacia Bushland and their edge effects in Laikipia, Kenya. *Ecological Applications*, 5, 97-108

STRONTIUM-ISOTOPE ANALYTICAL DETERMINATION OF THE HABITAT PREFERENCE OF LARGE HERBIVORES IN THE NUTRIENT DEPLETED SHRUBLANDS OF THE WESTERN CAPE, SOUTH AFRICA

Introduction

The mediterranean shrublands of the Fynbos Biome (Rutherford *et al.* 2006) at the SW tip of Africa are well known for their exceptionally high endemism, species richness, and species turnover among habitats (Cowling *et al.* 1996; Rebelo *et al.* 2006). The uniqueness of this region does not, however, rest only in the unique floral diversity, but also in the largely unappreciated fact that it hosted a diverse large mammal fauna before the onset of European settlement in the mid-17th century (Kerley *et al.* 2003).

Historical accounts leave little doubt that only 350 years ago the lowlands of the Fynbos Biome hosted a diverse large-herbivore (>20 kg) assemblage comprising of African elephant (*Loxodonta africana*), black rhino (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibius*), African buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), Cape mountain zebra (*Equus zebra zebra*), plains zebra/quagga (*Equus quagga*), red hartebeest (*Alcephalus buselaphus*), bontebok (*Damaliscus pygargus pygargus*), bush buck (*Tragelaphus scriptus*), grey rhebuck (*Pelea capreolus*), ostrich (*Struthio camelus*), and the extinct blue antelope (*Hippotragus leucophaeus*) (Du Plessis 1969; Skead 1980; Rookmaaker 1989; Boshoff & Kerley 2001). Preying on these large herbivores were lion (*Panthera leo*), leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*) (Du Plessis 1969; Skead 1980; Rookmaaker 1989; Boshoff & Kerley 2001). Rapid changes occurred in the Cape since the European settlers arrived and started to penetrate deeper inland. It is estimated that by the year 1700 there was no big game within 200 km of Cape Town left, and that by 1800 most of the mammals heavier than 50 kg had been driven close to extinction in the Cape Floristic Region (Rebelo 1992b).

The presence of the large herbivores in the Fynbos is also of considerable academic interest as it raises the question of how African herbivores of diverse size classes managed to survive in an area mostly (up to 67%; Rebelo 2006) covered by exceptionally nutrient-poor (Specht & Moll 1983; Campbell 1986) fynbos shrublands composed of fine-leaved ericoid shrubs, large-leaved proteoid shrubs, and tough-tissued restioids on mainly sandstone-derived soils (Rebelo *et al.* 2006). Most authors suggested that the herbivores concentrated in the renosterveld vegetation. This is a fire-prone asteraceous shrubland, often with an understory of grasses and a high diversity of geophytes. Renosterveld occurs predominantly on more nutrient-rich shale soils and covered about 30% of the region. Herbivores are thought to have avoided the extremely nutrient-poor fynbos shrublands (Bigalke 1979; Cody *et al.* 1983; Morrow *et al.* 1983; Campbell 1986; Moll 1987; Johnson 1992; Rebelo 1992a, 1996; Owen-Smith & Danckwerts 1997; Rebelo *et al.* 2006). This Renosterveld Preference Hypothesis has not been scientifically

tested and some authors claim that fynbos was utilised by the megafauna (Hendey 1983; Milewski 2002). The reviews of historical accounts (Du Plessis 1969; Skead 1980; Rookmaker 1989) are useful for determining the incidence of the native large mammal species. They are, however, vague in pinpointing the exact habitat preference of these species (Boshoff & Kerley 2001). Proper testing of this hypothesis has recently become a management and conservation priority as the Cape is experiencing a profound change in land use, with game farms being established across all types of habitats (Kerley *et al.* 2003; Briel & Nowers 2007). The establishment of the game farms involves the release of translocated large herbivores, which can negatively affect both plant and animal life of the target areas if inappropriate introductions are made (Castley *et al.* 2001).

The habitat preference of large herbivores is usually determined by direct (Jachmann 2002) or indirect (Marques *et al.* 2001) counts/observations, or by means of radio tracking (Millspaugh & Marzluff 2001). In this paper we test the hypothesis that large herbivores avoid habitats dominated by limestone and sandstone fynbos shrublands in favour of shale derived renosterveld vegetation in a novel way by using strontium (Sr) isotope analysis. We determined the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios in the bones of a number of different individuals from all the large herbivores species (eland, bontebok, Cape mountain zebra, grey rhebuck, and ostrich) present within De Hoop Nature Reserve (DHNR). These values were compared to the biologically available (*sensu* Price *et al.* 2002) $^{87}\text{Sr}/^{86}\text{Sr}$ ratio values obtained for the respective habitats on the different geological substrates present in the DHNR. Complete overlap between the biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ ratio values of the shale renosterveld and the ratio values obtained from the large herbivore bones can provide evidence for the predominant use of renosterveld areas by the large herbivores.

Background and methods

Strontium isotopes and habitat preference

Rubidium (Rb) and strontium (Sr) both occur in geological formations at varying ratios. Rubidium has two naturally occurring isotopes (^{87}Rb and ^{85}Rb), of which ^{87}Rb undergoes radioactive decay to stable ^{87}Sr with a half-life of 4.9×10^{10} years (Capo *et al.* 1998). Strontium has three naturally occurring stable isotopes (^{84}Sr , ^{86}Sr and ^{88}Sr) whose relative abundances in a rock mineral stays constant over time, while ^{87}Sr increases due to ^{87}Rb decay. The Sr-isotope ratios of geological formations thus vary due to their initial Sr-isotope composition, the original concentrations of Rb and Sr, and the time elapsed since rock formation for the decay of ^{87}Rb to ^{87}Sr (Capo *et al.* 1998). Strontium isotopes are usually measured and reported as the ratio of $^{87}\text{Sr}/^{86}\text{Sr}$ and this ratio is commonly referred to as the Sr-isotope ratio (Price *et al.* 2002).

Strontium does not undergo fractionation during biological processes (Blum *et al.* 2000; Bentley 2006), and consequently the strontium isotope ratio in the tissue of an organism matches that of its dietary Sr, which in turn reflects the biologically available strontium ratio of the environment where the organism lived (Price *et al.* 2002; Bentley 2006). In terrestrial systems biologically available Sr is predominantly a function of the geological

substrate plants grow on. It is, however, also to some extent influenced by the water and atmospheric depositions the area is exposed to (Price *et al.* 2002). The most accurate way to determine biologically available strontium ratio values is to use animal skeletal tissue, as skeletal formation acts as a powerful averaging mechanism for local $^{87}\text{Sr}/^{86}\text{Sr}$ variability (Price *et al.* 2002). This is done because bone or teeth incorporates the locally available $^{87}\text{Sr}/^{86}\text{Sr}$ ratios into its tissue as it is formed and, in the case of bone, remodelled over time over a range of ingested foodstuffs (Price *et al.* 2002). By using the bones of small herbivorous mammals with small home ranges restricted to the areas of interest, one can obtain reliable biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ values for different geological substrates in terrestrial studies (Price *et al.* 2002). Once the biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ values for the different substrates in an area are known, the organism can be linked to, or dissociated from, areas based on the Sr-isotope values of their respective body tissues. If the $^{87}\text{Sr}/^{86}\text{Sr}$ value of a herbivore's body tissue matches that of the biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ value for the area it has been found in, it suggest that the animal used the area as its predominant feeding ground. It is, however, also possible that the animal used another area with the same biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ value or alternatively used various areas with different $^{87}\text{Sr}/^{86}\text{Sr}$ values which average to the biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ value of the substrate the animal died in. The likelihood of these scenarios will differ from area to area pending on the nature of the biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ values of the specific substrates, as well as the $^{87}\text{Sr}/^{86}\text{Sr}$ values of the animals itself.

Study area

De Hoop Nature Reserve (34°26'S, 20°30'E), 323 km² in size, is situated on the South Coast of the Western Cape Province (Fig. 4.1). The southern border of the reserve is formed by the Indian Ocean and the eastern border it is marked by the inselberg of the Potberg Mountain (peak: 611 m). The western border comprises of the De Hoop Vlei (a lagoon cut-off from the sea by windblown sand dunes). The northern border (a game fence) separates DHNR from intensively cultivated private farms. DHNR shares its western border with the Denel Corporation Overberg Toetsbaan Conservancy Area (OTB) of 280 km². Together these two reserves cover an area of 603 km² that can be seen as one management unit (Greater De Hoop). When the De Hoop Vlei is filled with water (which was the case for the duration of this study) the movement of animals between the two areas is funnelled into a narrow corridor (\pm 300 m broad) between the southern end of the lake and the sparsely vegetated coastal dunes bordering the sea.

DHNR is composed geologically of a mosaic of three distinctly different geological substrates (Fig. 4.1, Coetzee 1993): Ordovician sandstones of the Table Mountain Group, Devonian shales of the Bokkeveld Group, and Pleistocene deposited marine and marine-related limestone of the Bredasdorp Group (Malan *et al.* 1994). The Potberg Mountain is predominantly composed of Table Mountain sandstone and supports Potberg Sandstone Fynbos vegetation (Rebelo *et al.* 2006). There is also a narrow shale band (< 200 m) running along the length of the Potberg supporting Western Coastal Shale Band Vegetation. The shales in the north-eastern corner of the reserve belong to the Ceres Subgroup (Coetzee 1993) and support Eastern Rûens Shale Renosterveld (Rebelo *et al.*

2006). The limestones of the Bredasdorp Group can be sub-divided into the Wankoe, Waenhuiskrans and Strandveld Formations (Malan *et al.* 1994). The Wankoe Formation consists of calcarenite (limestone), with aeolian cross-bedding and calcrete lenses and forms the dominant substrate of DHNR (Malan *et al.* 1994). The Waenhuiskrans Formation in the west of the Reserve next to the vlei consists of partly calcified dune sand with calcrete lenses (Malan *et al.* 1994) and is dotted with distinct karstic sinkhole depressions filled by light-grey to pale-red sandy soil. Both the Waenhuiskrans and Wankoe Formations support De Hoop Limestone Fynbos vegetation (Rebello *et al.* 2006). The karstic sinkhole depressions in the Waenhuiskrans sediments are, however, covered by short creeping grasses dominated by *Cynodon dactylon*. The Holocene Strandveld Formation occurs along the coastline and in the valley between the Potberg Mountain and Wankoe limestone hills. The Strandveld Formation along the coast consists of the light-coloured, lime-rich dune sand with shell fragments (Malan *et al.* 1994) and supports Overberg Dune Strandveld (Rebello *et al.* 2006). The highly leached light grey quartz sand of the Strandveld Formation in the valley is covered by Albertinia Sand Fynbos (Rebello *et al.* 2006) and is a product of the weathering of both the Table Mountain sandstone and the Bredasdorp limestone bordering it. A small section of Potberg Ferricrete Fynbos (Rebello *et al.* 2006) on the NW footslope of the mountain also falls within the boundaries of DHNR. The SW corner of the reserve is filled by windblown sand dunes supporting only sparse vegetation.

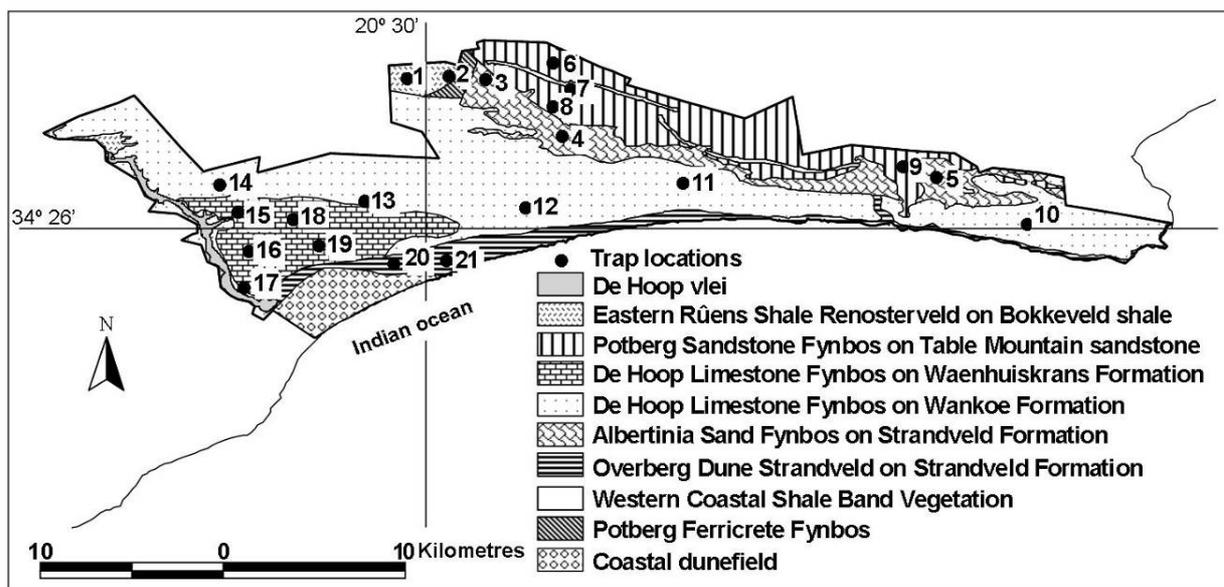


Fig. 4.1 The different vegetation types of De Hoop Nature Reserve as identified by Mucina *et al.* (2007) and its underlying geology as mapped by Coetzee (1993). The localities where rodents were captured for Sr-isotope analyses are also shown.

The mean annual precipitation (period: 1979–2007) as measured at the Driefontein weather station, situated 4.5 km directly north of the reserve is 473 mm (CV = 19%). Every month of the year contributes at least 30 mm of rain to the total, but most (65%) of the rain falls during the winter (April–October) when the evapotranspiration is the lowest.

The coldest month is July ($T_{\max} = 18.4^{\circ}\text{C}$, $T_{\min} = 6.3^{\circ}\text{C}$) and the warmest month is February ($T_{\max} = 27.2^{\circ}\text{C}$, $T_{\min} = 16.7^{\circ}\text{C}$). The driest months are November, December and January when the evapotranspiration exceeds 200 mm per month.

The complete helicopter game count done for Greater De Hoop in October 2006, close to the end of this study, gave the following numbers for the most common large herbivores: bontebok – 511, eland – 497, Cape mountain zebra – 76, ostrich – 460, and grey rhebuck – 10 (Smith 2006).

Biologically available Sr-isotope ratios

We restricted our study to the six major habitat types in DHNR as defined by the different geological substrates and the vegetation it supports: a) Eastern Rûens Shale Renosterveld on Bokkeveld shale (further renosterveld), b) Potberg Sandstone Fynbos vegetation on Table Mountain sandstone (further sandstone fynbos), c) De Hoop Limestone Fynbos on Wankoe limestone (further Wankoe limestone fynbos), d) De Hoop Limestone Fynbos embedded with scattered karstic sinkhole depressions supporting grazing lawns on Waenhuiskrans limestone (further Waenhuiskrans limestone fynbos), e) Albertinia Sand Fynbos on the Strandveld Formation sands in the valley at the base of the Potberg Mountain (further valley sand fynbos), and f) Overberg Dune Strandveld on the Strandveld Formation sands of the coastal dunes (further dune strandveld).

Vlei rats (*Otomys irroratus*) and striped mice (*Rhabdomys pumilio*) were collected in May 2006 to determine the biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ values of the habitats characterised by the different geologies. Vlei rats are strictly herbivorous (Davis 1973; Skinner & Chimimba 2005), and striped mice (although omnivorous to an extent) rely predominantly on plant matter for food and were therefore also considered suitable for the analyses (Davis 1973; Brooks 1974; Kerley 1989; Kerley *et al.* 1990; Skinner & Chimimba 2005). We attempted to collect fifteen specimens from five different localities (3 specimens per locality) in each of the six habitat types, but variability in trapping success resulted in some areas being sampled less thoroughly than others with a minimum of two locations and six specimens collected in the dune strandveld. The home ranges of vlei rats and striped mice are reported to be small but some migration does take place (Davis 1973; Brooks 1974). In order to prevent a migrant from influencing the data, trapping was conducted in locations more than 200 m away from the boundary of a habitat type. We aimed to catch three specimens per trapping locality in order to identify any outlying strontium isotope ratio value which might implicate a migrant. Collection localities were selected to be spread as widely as possible across the respective habitat types (see Fig. 4.1 for the exact locations where rodents were captured).

We used Sherman aluminium live traps (280 x 80 x 90 mm) to capture the rodents. Only the adult specimens of vlei rats and striped mouse were considered for euthanasia, while any other caught animal was released. Only three of the targeted rodents per trapping locality were euthanized by intra-peritoneal injection with Sodium Pentobarbitone (200 mg/kg). Ethical clearance for this procedure was obtained from the Stellenbosch University ethics committee (ref. no. 2006B01001). Euthanized individuals were frozen

separately in plastic bags till their incisors could be removed. The four incisor teeth of each euthanized rodent were removed and one of these was randomly selected to be analyzed for its Sr-isotope ratio value using laser ablation MC-ICP-MS. The Sr-isotope ratio values of the respective incisor teeth analysed was considered representative of the biologically available Sr of the habitat type the specimen was collected in. The incisors were washed and scrubbed in warm water to remove any superficial dirt and prepared for laser ablation by mounting them on microscope slides in groups of up to ten incisors per slide using double-sided tape.

Sr-isotope ratios in large mammals

Femur and tibia bones were collected from carcasses of grey rhebuck, mountain zebra, bontebok, eland and ostrich, all found opportunistically across the whole of DHNR with the help of rangers patrolling the area. We also obtained four mountain zebra bones from the neighbouring OTB Conservancy. The position of every sampled carcass was accurately mapped using handheld GPS devices. Only bones that were found above ground were collected, and only if they were considered to be from animals that had died within the last three years. We thus assume that the Sr-isotope ratio values of the bones we analyzed were not compromised by diagenetic alterations associated with burial – a well recognized problem in archaeological studies (Hoppe *et al.* 2003; Bentley 2006). In order to further minimize the chance for diagenetic alterations, we laser ablated only the internal section of the bone not exposed to direct weathering. This was achieved by making a cross-section into the shafts of the bones with a hack saw and removing a 2 mm thick slice which was then trimmed to be approximately 5 x 5 mm. The cross-sections were prepared for laser ablation by mounting them onto micro-slides in groups of up to 15 bone pieces per slide using double sided tape. As far as possible, only the shafts of femur bones were sampled, but in some cases (when femurs were not available) we also sampled from shafts of tibia bones.

Sr-isotope analysis

Sr-isotope ratios were obtained using the Nu Instruments NuPlasma HR multi-collector inductively coupled plasma-mass spectrometer (MC-ICP-MS) of the AEON EarthLAB, housed in the Department of Geological Sciences, University of Cape Town. *In situ* analysis of teeth and bone utilized a NewWave 213 nm laser ablation unit attached to the MC-ICP-MS unit using the procedure described in detail by Copeland *et al.* (2008). The laser parameters are listed in Table 4.1. The laser sample cell was flushed with helium (He) mixed with argon (Ar) before injection into the plasma. A so-called “pre-ablation” cleaning run was used to remove a thin surface layer of material, and so to eliminate any surface contamination. The constant background gas composition was measured for 30 seconds before each analysis with no laser firing, and subtracted from the signal measured during laser ablation. This procedure corrected for any potential isobaric interference of krypton (^{84}Kr and ^{86}Kr) in the argon gas supply on the measured Sr. During an analysis run, the ablated material was entrained by He flow and transported to the plasma where it was atomized and ionized before being accelerated into the mass spectrometer.

From each collection of incisors coming from a specific habitat type a single incisor was randomly selected to act as standard for that specific habitat type. A piece of eland bone was also randomly selected to act as standard for the bone analyses. These in-house laser ablation standards were analysed at the start and end of each laser ablation analytical session, typically bracketing 10 analyses of unknowns. Subsequent $^{87}\text{Sr}/^{86}\text{Sr}$ values obtained for these in-house standards by conventional solution analysis were further used to eliminate between session differences and to finally reference the laser ablation data to the international Sr isotope standard NIST SRM987.

Table 4.1: Laser parameters for both the cleaning run and the analysis of the bone and incisors. The wave length (213 nm), pulse rate (10 Hz) and scan length (0.75 mm) were the same for all procedures.

	Cleaning run (Bone & incisor)	Analysis (Bone)	Analysis (Incisor)
Spot size	250 μm	200 μm	200 μm
Energy density	0.04 J/cm	2.47 J/cm	0.9 J/cm
Energy	0.018 MJ	0.77 MJ	0.29 MJ
Scan speed	50 μs	5 μs	5 μs

For solution analysis the whole incisor of a rodent (weight 14–28 mg) was dissolved in 1 ml 65% HNO_3 , dried down and redissolved in lower molarity acid ready for the chemical isolation of Sr. The solution was passed through a calibrated cation exchange column, and a Sr fraction collected with no significant matrix elements or Rb present. This procedure took place at the Radiogenic Isotope Facility of the Department of Geological Sciences, University of Cape Town. The Sr fraction was again dried down and redissolved in 1.5 ml of 0.2% HNO_3 . This solution was further diluted, where necessary, to obtain a final 3 ml solution of 0.2% HNO_3 containing approximately 200 ppb Sr. This solution was then analyzed by free-aspiration into a micro-cyclonic spray chamber, with the resulting aerosol injected into the plasma. All Sr solution analyses were performed in batches of five, bracketed by analyses of the NIST SRM987 standard.

Previous testing of solution Sr isotope analysis has shown that when the Rb content becomes too high relative to the Sr content of a sample, the Sr isotope data are compromised. A solution of the NIST SRM987 Sr standard was analyzed repeatedly, with progressively more of a Rb concentration standard added. Each successive measured $^{87}\text{Sr}/^{86}\text{Sr}$ value was therefore the product of a more significant Rb correction. The proxy selected to monitor the level of Rb during a Sr isotope analysis was the measured ^{85}Rb voltage as a percentage of the total measured Sr voltage. It was found that correcting the ^{87}Sr signal for the interference of ^{87}Rb , by measuring the interference-free ^{85}Rb signal and applying a correction based on the natural isotope abundances of Rb, breaks down above approximately 0.3% ^{85}Rb as percentage of total Sr voltage. The procedure at this facility is therefore to consider the Sr isotope data compromised above this level of ^{85}Rb , and the data should then only be used with extreme caution if at all. These conditions were observed in this study only for a minority of laser ablation incisor analyses, and the

relevant samples were then tagged for solution analysis preceded by chemical purification of Sr.

All Sr isotope data reported in this study are referenced to the long-term $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.710255 for NIST 987 as measured in this facility, which agrees well with published values for this standard (Waight *et al.* 2002; Weis *et al.* 2006). The fifteen analyses of NIST SRM987 during this study yielded an average $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.710267, with an external 2sigma reproducibility of 0.00002. At least three to four repeated *in situ* analyses of each of the laser ablation in-house incisor standards yielded 2sigma external reproducibility typically better than 0.0001 for $^{87}\text{Sr}/^{86}\text{Sr}$ values (25 analyses, spread between 6 standards) after using the referenced solution data for each standard to correct for potential between session variability. Copeland *et al.* (2008) found that the mean difference in $^{87}\text{Sr}/^{86}\text{Sr}$ measured by laser ablation and by solution at this facility for modern rodent incisors were 0.0003 ± 0.0002 with a 2sigma external reproducibility of their in-house standards been 0.0003. Nine repeated *in situ* laser ablation analyses of our in-house bone standard yielded a 2sigma reproducibility of 0.00007 and a direct comparison between laser ablation and solution $^{87}\text{Sr}/^{86}\text{Sr}$ values for ten bone samples provided a mean difference of 0.00017 ± 0.00007 (F.G.T. Radloff unpublished data). All Sr isotope data were corrected for mass fractionation using a $^{86}\text{Sr}/^{88}\text{Sr}$ ratio of 0.1194 and the exponential law.

Results

Rodent Sr-isotope ratio values

The Sr-isotope ratios of the rodent incisor teeth collected from DHNR varied between 0.70906 and 0.71042 (Table 4.2 and Fig. 4.2). The Sr-isotope ratio values obtained for the dune strandveld showed the lowest variation and ranged between 0.70919 and 0.70933. The dune strandveld values could, however, not be separated from the values obtained from the Waenhuiskrans or Wankoe limestone fynbos habitats as both substrates have values overlapping with that of the dune strandveld. The range of Sr-isotope ratio values obtained from the Wankoe limestone fynbos vary between 0.70926 and 0.70955 and show complete overlap with the range of values obtained from the Waenhuiskrans limestone fynbos habitats. Incisors from Waenhuiskrans limestone fynbos provided the most diverse values and ranged from 0.70906 to 0.70988. The sandstone fynbos Sr-isotope ratio values provided a narrow range of values from 0.70982 to 0.71001 and are separated from the values obtained from the renosterveld on the shale, Wankoe limestone fynbos and dune strandveld values. The range of values from the sandstone fynbos does, however, overlap with some Waenhuiskrans limestone and sand fynbos Sr-isotope ratio values. The sand fynbos Sr-isotope ratio values obtained from trapping locations (Fig. 4.1) three (0.70992 and 0.70990) and four (0.70978) in the valley showed some overlap with the range of values obtained from the sandstone fynbos, and is higher than the values found from the incisors of location five (0.70941–0.70953) much further to the east. The incisors from the renosterveld on the shales had the highest Sr-isotope ratio values and showed no overlap with any of the other substrates (0.71009–0.71042).

Table 4.2 Sr-isotope ratio values of the incisor teeth of the 48 rodents caught in the respective habitat types of DHNR. The trap number corresponds to the trap location numbers in Fig. 4.1. Values in bold were ascertained by conventional solution analysis, while the rest of the values were determined with laser ablation MC-ICP-MS. The listed standard errors (2σ) represent the internal precision of individual MC-ICP-MS measurements.

Trap no.	Habitat type	Rodent species	$^{87}\text{Sr}/^{86}\text{Sr}$ ratio	$\pm 2\sigma$
1	Renosterveld on shale	<i>Rhabdomys pumilio</i>	0.71013	0.00001
	Renosterveld on shale	<i>Rhabdomys pumilio</i>	0.71028	0.00007
	Renosterveld on shale	<i>Rhabdomys pumilio</i>	0.71012	0.00010
2	Renosterveld on shale	<i>Otomys irroratus</i>	0.71009	0.00007
	Renosterveld on shale	<i>Otomys irroratus</i>	0.71020	0.00004
	Renosterveld on shale	<i>Rhabdomys pumilio</i>	0.71042	0.00005
3	Valley sand fynbos	<i>Rhabdomys pumilio</i>	0.70992	0.00001
	Valley sand fynbos	<i>Rhabdomys pumilio</i>	0.70990	0.00002
4	Valley sand fynbos	<i>Otomys irroratus</i>	0.70978	0.00004
5	Valley sand fynbos	<i>Otomys irroratus</i>	0.70941	0.00003
	Valley sand fynbos	<i>Rhabdomys pumilio</i>	0.70953	0.00006
	Valley sand fynbos	<i>Rhabdomys pumilio</i>	0.70949	0.00005
6	Sandstone fynbos	<i>Rhabdomys pumilio</i>	0.71001	0.00001
7	Sandstone fynbos	<i>Rhabdomys pumilio</i>	0.70996	0.00001
	Sandstone fynbos	<i>Rhabdomys pumilio</i>	0.70999	0.00001
8	Sandstone fynbos	<i>Rhabdomys pumilio</i>	0.70982	0.00001
	Sandstone fynbos	<i>Otomys irroratus</i>	0.70982	0.00006
9	Sandstone fynbos	<i>Rhabdomys pumilio</i>	0.70994	0.00001
10	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70929	0.00009
	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70955	0.00004
	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70942	0.00004
11	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70928	0.00001
12	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70926	0.00001
	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70930	0.00009
	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70926	0.00001
13	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70926	0.00001
	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70944	0.00007
	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70954	0.00004
14	Wankoe limestone fynbos	<i>Rhabdomys pumilio</i>	0.70930	0.00001
15	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70988	0.00007
16	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70957	0.00005
	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70935	0.00002
	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70975	0.00008
17	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70923	0.00001
	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70921	0.00005
	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70919	0.00002
18	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70937	0.00001
	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70994	0.00006
	Waenhuiskrans limestone fynbos	<i>Otomys irroratus</i>	0.70960	0.00005
19	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70940	0.00008
	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70942	0.00010
	Waenhuiskrans limestone fynbos	<i>Rhabdomys pumilio</i>	0.70906	0.00010
20	Dune strandveld	<i>Rhabdomys pumilio</i>	0.70919	0.00003
	Dune strandveld	<i>Rhabdomys pumilio</i>	0.70927	0.00005
	Dune strandveld	<i>Rhabdomys pumilio</i>	0.70927	0.00004
21	Dune strandveld	<i>Rhabdomys pumilio</i>	0.70933	0.00005
	Dune strandveld	<i>Rhabdomys pumilio</i>	0.70930	0.00004
	Dune strandveld	<i>Otomys irroratus</i>	0.70921	0.00007

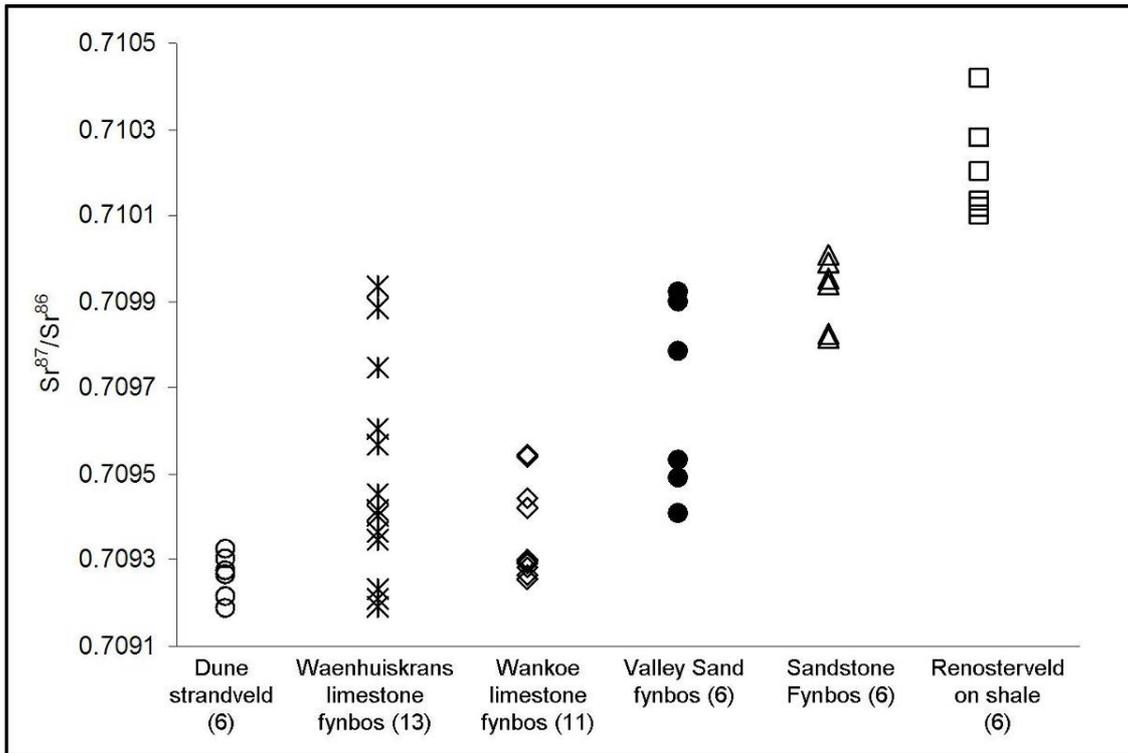


Fig. 4.2 Sr-isotope ratios of 48 rodents caught in habitats characterised by the respective geological substrates in the De Hoop Nature Reserve. The number of rodents sampled from each respective substrate is given in the brackets.

Large herbivore Sr-isotope ratio values

The Sr-isotope ratio values of the bones from the large herbivores covered a broader range (0.70920–0.71165) than that obtained from the rodent incisors (Table 4.3 and Fig. 4.3). The Sr-isotope ratio values obtained from the bones of five bontebok individuals that died in the shale renosterveld were higher and separated from the values ascertained from the bones of the five bontebok coming from the Waenhuiskrans limestone fynbos (0.70993–0.71011 vs. 0.70923–0.70957). The Sr-isotope ratio values of the bontebok from the Waenhuiskrans limestone fynbos were within the range of biologically available Sr-isotope ratio values determined for this habitat from the rodent incisor teeth. Only one of the five bontebok bones from the renosterveld shale habitat had a Sr-isotope ratio value (0.71011) falling within the biologically available Sr-isotope ratio range (0.71009–0.71042) determined for the renosterveld (as obtained from the six rodent incisor teeth from that habitat). The other four bones reflect values similar to that of the eastern section of the valley sand fynbos and sandstone fynbos.

Four of the five ostriches which died in Waenhuiskrans limestone fynbos had bone Sr-isotope ratios similar to those of the rodents that were collected from the same habitat type. One of the individuals, however, has a Sr-isotope ratio (0.71047) marginally higher than that of the highest rodent incisor value obtained from the renosterveld on the shale.

The Sr-isotope ratios in bones of two grey rhebuck individuals found in the Waenhuiskrans limestone fynbos habitats were much higher (0.71104 and 0.71165) than those of any rodent teeth measured in DHNR.

Table 4.3 The Sr-isotope ratio values of 32 large herbivores from DHNR as measured from their femur and tibia bones by laser ablation MC-ICP-MS. Habitat type refers to the specific habitat in which a bone was collected. Standard errors listed are internal precision of individual MC-ICP-MS measurements. The single value in bold was obtained by conventional solution analysis.

Large herbivore species	Habitat type	$^{87}\text{Sr}/^{86}\text{Sr}$ ratio	$\pm 2\sigma$
Bontebok	Renosterveld on shale	0.70993	0.00004
Bontebok	Renosterveld on shale	0.70994	0.00005
Bontebok	Renosterveld on shale	0.70992	0.00004
Bontebok	Renosterveld on shale	0.71011	0.00004
Bontebok	Renosterveld on shale	0.70997	0.00004
Bontebok	Waenhuiskrans limestone fynbos	0.70942	0.00004
Bontebok	Waenhuiskrans limestone fynbos	0.70932	0.00004
Bontebok	Waenhuiskrans limestone fynbos	0.70923	0.00003
Bontebok	Waenhuiskrans limestone fynbos	0.70957	0.00005
Bontebok	Waenhuiskrans limestone fynbos	0.70939	0.00005
Ostrich	Waenhuiskrans limestone fynbos	0.70921	0.00009
Ostrich	Waenhuiskrans limestone fynbos	0.71047	0.00005
Ostrich	Waenhuiskrans limestone fynbos	0.70945	0.00006
Ostrich	Waenhuiskrans limestone fynbos	0.70926	0.00003
Ostrich	Waenhuiskrans limestone fynbos	0.70920	0.00005
Grey Rhebuck	Waenhuiskrans limestone fynbos	0.71165	0.00005
Grey Rhebuck	Waenhuiskrans limestone fynbos	0.71104	0.00002
Mountain Zebra	Renosterveld on shale	0.70966	0.00007
Mountain Zebra	Waenhuiskrans limestone fynbos	0.70988	0.00004
Mountain Zebra	Renosterveld on shale	0.70982	0.00009
Mountain Zebra	Waenhuiskrans limestone fynbos	0.70992	0.00004
Mountain Zebra	Waenhuiskrans limestone fynbos	0.70997	0.00003
Eland	Waenhuiskrans limestone	0.71010	0.00007
Eland	Wankoe limestone fynbos	0.70957	0.00001
Eland	Waenhuiskrans limestone fynbos	0.70978	0.00007
Eland	Waenhuiskrans limestone fynbos	0.70924	0.00004
Eland	Valley sand fynbos	0.70929	0.00005
Eland	Waenhuiskrans limestone fynbos	0.70930	0.00004
Eland	Renosterveld on shale	0.70950	0.00004
Eland	Valley sand fynbos	0.70961	0.00003
Eland	Waenhuiskrans limestone fynbos	0.70938	0.00004
Eland	Waenhuiskrans limestone fynbos	0.70978	0.00004

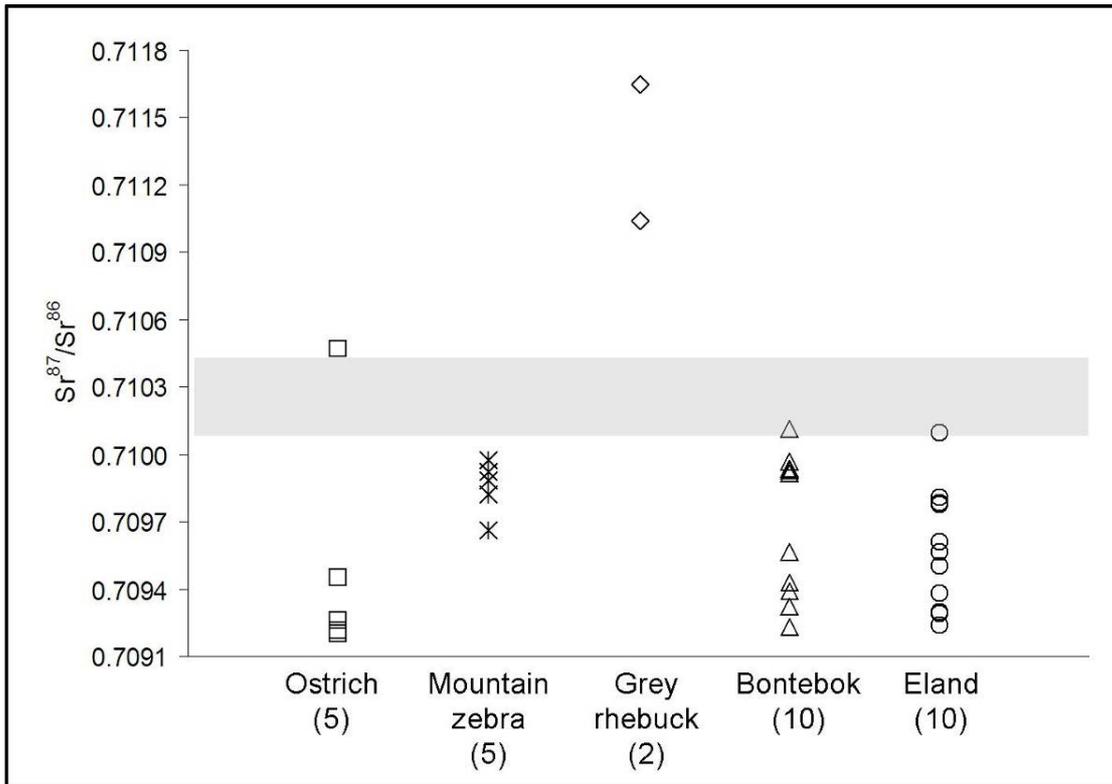


Fig. 4.3 Sr-isotope ratio values for 32 specimens of large herbivores that died in the DHNR. The number of individuals sampled for the respective species are indicated in brackets. The grey band shows the range of biologically available Sr-isotope ratio values for the renosterveld on the shale.

The five mountain zebra bones revealed a consistent span of Sr-isotope values (0.70966–0.70997), but these did not match the ratios of either the renosterveld or Waenhuiskrans limestone fynbos in which they were found. Eland bones were obtained from the largest number of different habitats and also showed diverse Sr-isotope ratio values (0.70924–0.71010). There is, however, no consistent match between the rodent incisor Sr-isotope ratio values for the habitats in which the eland died and the actual values obtained from the bones of the eland individuals

Discussion

Strontium isotope analysis has been used in palaeoecology to study the migration of mammoths and mastodons (Hoppe *et al.* 1999) to determine the landscape use of Holocene mammals (Feranec *et al.* 2007) and to map the origin of faunal assemblages (Porder *et al.* 2003). In modern day terrestrial mammal studies it has been used to trace the origin of ivory (Van der Merwe *et al.* 1990; Vogel *et al.* 1990) and to track the change in diet and habitat use of African elephants (Koch *et al.* 1995). It also has been used in a criminal investigation to verify the origin of white-tailed deer antlers (Beard & Johnson 2000). This study is, however, the first to our knowledge to attempt to use strontium

isotope analysis to indicate different extant large herbivore species habitat preferences within the same reserve.

Biologically available Sr-isotope ratio values

Analysis of the skeletal tissue of small animals is considered a reliable and robust method for the determination of the biologically available Sr value (further BAS value) of a particular geological substrate (Price *et al.* 2002). We are thus confident that our use of rodents is a reliable way of determining the BAS values for the geological substrates of the DHNR. The incisor teeth of these rodents grow continuously throughout their lives (Skinner & Chimimba 2005) and we were thus measuring the dietary Sr-isotope ratio that was ingested whilst the particular section of the teeth was produced. We also laser ablated the teeth down its length, which should present a reasonable time period of food ingestion that would have acted as an averaging mechanism for local $^{87}\text{Sr}/^{86}\text{Sr}$ variability.

The most recent geological map (Coetzee 1993; Malan *et al.* 1994) of the DHNR region was used as basis from which the different geological substrates and the respective habitats were identified and their boundaries determined. The six major habitat types could, however, not all be differentiated from each other on the basis of their respective BAS values. The incisor teeth of the rodents caught on the dune strandveld revealed a Sr-isotope ratio value that is very close to the modern day seawater value of 0.70918 (McArthur *et al.* 2001). This is not surprising considering that the strandveld shrublands are supported by Holocene shell-rich coastal dune sands (Malan *et al.* 1994). Sea-spray has also been shown to markedly influence the strontium isotope ratios of soils and plants immediate to some coastlines (Whipkey *et al.* 2000, Bentley 2006) and can very well be playing a role here as well. The limestone fynbos shrublands over older (Pliocene) Wankoe limestones (Malan *et al.* 1994) have, as expected, slightly higher Sr-ratios than the dune strandveld. There is, however, some overlap between the values obtained from these two habitats. The limestone fynbos habitat of the Pleistocene Waenhuiskrans limestones (Malan *et al.* 1994) has BAS values that overlap with both that of the dune strandveld and the Wankoe limestone fynbos. Surprisingly though is the three incisor values above 0.7096 that show no overlap with any of the values obtained from the Bredasdorp limestone habitats discussed so far. The closest substrate with BAS values that could potentially match these outlier values is more than six kilometres from the areas where the rodents with these values were caught. We thus exclude migration of these rodents from areas with high BAS values as a possible explanation for this conundrum. All three the teeth with the higher Sr-isotope ratios collected from the Waenhuiskrans limestone substrate were from *Rhabdomys pumilio* mice which is known to occasionally feed on insects. The remote possibility thus exists that these three striped mice consumed a diet of insects originating from areas with higher BAS values. Whether insects can travel the distances in excess of 6 kilometres from areas with higher BAS values and then be consumed in such quantities to elevate the Sr-isotope ratios of the rodents incisor teeth to the measured levels are doubtful. The reason for the three outlier values needs further investigation and will be omitted from further discussion.

The light-grey quartz sands supporting the valley sand fynbos at the base of the Potberg Mountain are mapped as part of the Strandveld Formation of the Bredasdorp Group (Coetzee 1993). Malan et al. (1994), however, described these sediments as a product of the weathering of both the Table Mountain sandstone and the Bredasdorp limestone bordering it, and this can explain the two very different groups of values obtained for this habitat. The rodent incisors collected from the western end of the valley have Sr-isotope ratios similar to sandstone fynbos BAS values possibly due to a larger deposition of weathered sandstone material in this area. The rodent incisors from the eastern end of the valley (trap location five, Fig. 4.1), in contrast, had Sr-isotope ratios resembling the BAS values of the Wankoe limestone fynbos bordering it. The sand in this section of the valley thus, most likely, has more weathered material of limestone origin in it.

The rodents caught on sandstone all have Sr-isotope ratios in a narrow range between 0.70982 and 0.71001. Ordovician sandstone of the Potberg Mountain, although older than the Bokkeveld shales of the Devonian age (Malan *et al.* 1994), has lower Sr-isotope values than those obtained from the renosterveld. The incisor teeth of the rodents caught on the shales of the renosterveld all had Sr-isotope ratios above 0.7109 and showed no overlap with any of the other substrates for which BAS values were obtained.

The measured biologically available Sr values revealed that it can only be used to distinguish between the three broader habitat units as defined by the three dominant geological substrate groups underlying the Reserve: Bredasdorp limestone = 0.70906 – 0.70960, Table Mountain sandstone = 0.70982 – 0.71001 and Bokkeveld shale = 0.71009 – 0.71042. The BAS values cannot be used to differentiate between the lime-rich habitats as subdivided to the formation level. We can, however, still proceed in testing whether the large herbivores preferred the shale since renosterveld had the highest BAS values and is clearly separated from the sandstone and Bredasdorp limestone BAS values. A large herbivore with a Sr-isotope ratio value between 0.71009 and 0.71042 thus presumably fed on vegetation supported by shale if it spent its entire life within the Reserve.

Sr-isotope ratio values of the large herbivores

The Sr-isotope ratios obtained from the large herbivore bones showed a much broader range of values than those of the BAS values found in the DHNR. The reason for this wider range is the two bone values (0.71104 and 0.71165) from the two grey rhebuck individuals that died in Waenhuiskrans limestone fynbos. When these two exceptionally high values are excluded, the BAS and large herbivore bone values are closely matched (rodent BAS: 0.70906–0.71042 vs. large mammal: 0.70920–0.71047) and fall within the range of instrumental measuring error.

The grey rhebuck values can be explained in two ways. Either we failed to recognize and sample an unknown geological substrate in the vicinity of the Waenhuiskrans limestones with very high BAS values, or these two individuals were recent migrants to the area from a substrate outside the Reserve. The first scenario is unlikely as the Bredasdorp limestones cover the area around the carcass locations for more than seven kilometres in

all directions both inside and outside the Reserve. The limestone substrate is easy to recognize as the white calcarenite protrusions are clearly visible across the landscape and we are thus confident that a non-limestone geological substrate in this area has not been overlooked. Migration from outside the reserve thus seems to be the only viable explanation for these values. Outside the DHNR just over seven kilometres to the north from where the carcasses of these animals were found, are shales of the Bidouw Subgroup (Malan *et al.* 1994). We did not determine the BAS values for these shales; the area is under intensive cultivation and is regularly and heavily fertilised. The possibility thus exists that these two individuals were recent immigrants from this shale area having possibly higher Sr-isotope ratio values than at least that of the Bredasdorp limestones. Grey rhebuck are territorial animals (Skinner & Chimimba 2005), but young non-breeding males and females are known to disperse before they form their own territories (Estes 1993). They are also accomplished leapers known to jump fences (Skinner & Chimimba 2005). Grey rhebuck individuals are periodically observed in the cultivated lands of the area surrounding DHNR (personal observation).

Sr-isotope ratios of the five ostrich bones reveal that four of these birds obtained the vast majority of their food from Bredasdorp limestone habitats as their bone values are well within the BAS value range for the habitats supported by Bredasdorp limestone. The fifth individual must, however, have moved onto the Waenhuiskrans formation area from the shale shortly before its death as it has a high Sr-isotope ratio (0.71047) that could only have been assimilated while this bird was feeding in the renosterveld underlain by the shale. These birds are effectively confined to the Greater De Hoop by the fence bordering the reserve. The value of 0.71047 is slightly higher than the highest BAS value (0.71042) recorded for the shale, but falls within the range of instrumental error associated with the Sr-isotope measurement.

The Sr-isotope ratio values of the mountain zebra bones fall within the BAS range values associated with sandstone fynbos. The mountain zebra in the greater De Hoop area have, however, never been recorded on or even close to the Potberg Mountain –the only sandstone habitat in the region (P. Lloyd, CapeNature, personal communication, Smith *et al.* 2007). The closest carcass, and the only one located in the DHNR, was also more than 15 km from the Potberg Mountain. The other four carcasses were found more than 30 km away in the OTB conservancy. The OTB conservancy is dominated by Waenhuiskrans limestone fynbos but also has island patches of shale within it. The four carcasses from OTB were found in, or in close proximity of, these shale islands and this can explain the given values. If the mountain zebra fed in both shale and Bredasdorp limestone habitats, they should have a Sr-isotope ratio somewhere in between that of the BAS values of both substrates. This is indeed the case with the average value for the carcasses being 0.70985 (SD = 0.00012), which is lower than the BAS values of shale (average: 0.71021), but still higher than the BAS values of Bredasdorp limestone (average: 0.70933).

Eland carcasses were found in all the habitat types except in sandstone fynbos and the dune strandveld. The bone Sr-isotope ratios of these eland then also cover a wide range of values from 0.7092 up to 0.71010. The seven individuals with values ≤ 0.7096 must have fed predominantly in the habitats underlain by the Bredasdorp limestone substrates. The

eland individual with the bone Sr-isotope ratio of 0.71010 most likely obtained the vast majority of its food from the renosterveld as it is the only area within the reserve with such high BAS values. It must, however, be kept in mind that some of the eland in DHNR occasionally leave the Reserve by jumping the nearly two meter high fence. The possibility thus exists that the eland obtain Sr from the fertilized agricultural fields on shales to the north of the reserve as well. A habitat preference study for eland and bontebok using traditional dung counts was run in conjunction with this project (see chapter 3 of this dissertation). The dung count study revealed that the eland prefer Waenhuiskrans limestone fynbos and the renosterveld, but that they also utilize valley sand fynbos and Wankoe limestone fynbos. Eland avoided Sandstone fynbos. It is thus not likely that the two eland with bone Sr-isotope ratios of between 0.7097 and 0.7099 obtained their fodder from the sandstone fynbos – but rather from both the renosterveld and the vegetation on the Bredasdorp limestone. Sr isotopes obtained from fodder coming from both the renosterveld and Bredarsdorp limestone vegetation can provide a bone Sr-isotope ratio value within the range associated with the sandstone fynbos BAS values.

Five bontebok bones were obtained from carcasses in renosterveld and five bones came from carcasses in Waenhuiskrans limestone fynbos. The dung count study revealed that these two habitats are also the two preferred areas of this antelope species and that they avoid sandstone fynbos and Wankoe limestone fynbos. The Sr-isotope ratio values of the 10 bontebok bones can also be split into two clearly separated groups based on the respective habitats they were found in. The five bones from the Waenhuiskrans limestone fynbos provided values that fell within the range of BAS values obtained for this habitat. However, only one of the bontebok bones collected from the renosterveld gave a Sr-isotope ratio value (0.71011) that fell within the BAS value range for this shale habitat (0.71009–0.71042). The other four bones gave very similar values (0.70992–0.70997) but were all lower than expected for these antelope that restrict their movements to the renosterveld in this part of the reserve. The bontebok population in the renosterveld is isolated from the population in the Waenhuiskrans limestone fynbos due to the more than eight kilometre barrier of avoided Wankoe limestone fynbos between them. The lower than expected Sr-ratios of the renosterveld bontebok can thus not be attributed to a mixture of fodder from both renosterveld and Waenhuiskrans limestone fynbos. We are familiar with the bontebok movements in and around the renosterveld area as it formed part of a renosterveld vegetation study entailing regular visits and game counts in this area (see chapter 5 of this dissertation). The ferricrete substrate to the immediate east of the renosterveld is only occasionally visited by a single group of seven bontebok, and the sand fynbos in the western part of the valley has a resident group of only five bontebok. There is no indication that the bontebok from the renosterveld population is visiting the ferricrete or valley sand fynbos areas on a regular basis. It is thus difficult for us to believe that the lower than expected Sr-isotope ratio values of the four bontebok from the renosterveld is due to a mixed diet coming from both renosterveld and vegetation from another habitat with lower BAS values.

The potential contribution of Sr from drinking water to body tissue Sr-isotope ratio values has to date been largely ignored in both archaeological and ecological studies

using Sr analysis. Åberg (1995) mentions that a reindeer from Iceland had an intermediate $^{87}\text{Sr}/^{86}\text{Sr}$ ratio between that of the volcanic soil it was found on and rainwater, but did not elaborate any further on this statement. In more recent articles both Hodell *et al.* (2004) and Knudson and Buikstra (2007) explicitly state that ingested water is also reflected in skeletal material, but provide no examples to illustrate this statement. Strontium in water has, however, been shown to have an influence on the formation of mouse bones in a metabolism study (Marie & Hott 1986). We consequently tested the water that is supplied to the artificial waterpoints in the renosterveld for its Sr-isotope ratio to establish if it could have any potential influence. The water revealed a Sr-isotope ratio of 0.709764 ($2\sigma = 0.000013$) that is lower than the Sr-isotope ratios of the four bontebok bones. It was also later established that the water supplied to the artificial drinking troughs is piped from a spring in the Potberg Mountain, which helps to explain the similarity of the water value to that of the sandstone fynbos BAS values. We thus have reason to believe that the lower $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in the drinking water of the bontebok residing in the renosterveld is reducing their skeletal tissue Sr-isotope ratios to below that of the renosterveld BAS values. Bontebok is very water dependant and drink daily (Van Zyl 1978).

An accidental opportunity to test the influence of drinking water Sr on ostrich bone $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in a more controlled environment did, however, not reveal any apparent influence. Five ostriches were raised on the Mariendhal Experimental Farm of the Stellenbosch University and only obtained food from natural vegetation growing on the Malmesbury shale soil (Rebelo *et al.* 2006) of their holding pen. The BAS values of this substrate were measured by the conventional solution analysis and were 0.71255 ($2\sigma = 0.00001$) and 0.71250 ($2\sigma = 0.00001$) as determined from the incisors of two herbivorous (Skinner & Chimimba 2005) Cape gerbils (*Tatera afra*) caught in the ostrich holding pen. The drinking water of the five ostriches was piped water from an irrigation scheme and had a Sr-isotope ratio of 0.71009. The Sr-isotope ratio values of the bones of these five ostriches after six months in the holding pen revealed an average value of 0.71232 ($n = 5$, $SD = 0.00021$) measured by laser ablation MC-ICP-MS. The Sr in the drinking water thus had very little if any influence on the bone values of the ostriches. The Sr concentration of the ostrich drinking water was, however, only 48 ppb which might be too low to significantly influence the Sr-ratios of the ostrich bone. The Sr concentration of the water provided to the bontebok in DHNR had a concentration of 220 ppb that is 4.5 times more than that in the water provided to the ostriches. The potential influence of different concentrations of strontium in drinking water may thus also play a role in the assimilation of Sr-isotope ratios in animal tissue.

Conclusions

The results from this study indicate that for the given geology of the DHNR it would have been very difficult to make accurate deductions concerning large herbivores' spatial use solely relying on Sr-isotope analysis. If we only relied on the Sr-isotope analysis, we might have concluded that the large herbivores avoid renosterveld of the shale substrate in favour of limestone and sandstone fynbos vegetation. Sandstone might even have been identified as an important habitat for bontebok, eland and mountain zebra. Our prior

knowledge on mountain zebra movements and the information from the study looking at the habitat preference of eland and bontebok using dung counts, however, clearly show that renosterveld is a preferred substrate of these large herbivores and that they actually avoid sandstone fynbos.

The potential contribution of the strontium in drinking water to the Sr ratios of animal tissue would also not have been recognized without the additional information. The influence of drinking water as an additional source of strontium to animal tissue needs more attention if this technique is to be used in future studies on contemporary animals' habitat preference, as well as in archaeological studies looking at human migration patterns. This is particularly important in studies where the area of interest have very different Sr-isotope ratio values in comparison to that of the water supply used within it.

Beard and Clark (2000) stated that the Sr-isotope composition of skeletal elements must be considered as a reflection of the "concentration-weighted average of the Sr that was ingested". Future studies will have to start considering the Sr concentrations of not only drinking water, as suggested by our preliminary ostrich study, but probably also that of the variety of foodstuff ingested from different habitats if we are to accurately predict the spatial use of animals.

Our study did, however, reveal that eland is more catholic in its spatial use compared to mountain zebra and bontebok, which appear to be much more habitat specific. Information of this nature can be valuable if used in conjunction with other stable isotopes in ecological niche dimensional studies as proposed by Newsome *et al.* (2007). The two bontebok populations in DHNR could be differentiated from each other based on their respective Sr-isotope values and indicate that the technique can be used to identify differences in feeding substrate selection between groups. Pinpointing the exact substrate might, however, be more difficult. In addition, the Sr-analysis also acted as an important hypothesis generating tool with the exceptionally high grey rhebuck Sr-isotope ratio values suggesting a significant dispersal event that merits further investigation. We believe that with some refinement this technique can be a valuable additional tool for ecologists looking at large mammals' spatial use – especially in areas with a less complex geology than DHNR.

References

- Åberg G. (1995) The use of natural strontium isotopes as tracers in environmental studies. *Water, Air and Soil Pollution*, 79, 309-322
- Beard B.L. & Johnson C.M. (2000) Strontium isotope composition of skeletal material can determine the birth place and geographic mobility of humans and animals. *Journal of Forensic Sciences*, 45, 1049-1061
- Bentley R.A. (2006) Strontium Isotopes from the earth to the archaeological skeleton: a review. *Journal of Archaeological Method and Theory*, 13, 135-187
- Bigalke R.C. (1979) Aspects of vertebrate life in Fynbos, South Africa. In: *Ecosystems of the World. 9A. Heathlands and related shrublands* (ed. Specht. R.L.), pp. 81-95. Elsevier, Amsterdam

- Blum J.D., Taliadro H.E., Weisse M.T. & Holmes R.T. (2000) Changes in Sr/Ca, Ba/Ca and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios between trophic levels in two forest ecosystems in the northeastern U.S.A. *Biogeochemistry*, 49, 87-101
- Boshoff A.F. & Kerley G.I.H. (2001) Potential distribution of the medium- to large-size mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *African Zoology*, 36, 245-273
- Briel S.C.P. & Nowers R.J. (2007) *Wildlife production in the Western Cape: a report on the quantification and qualification of wildlife production units*. Western Cape Department of Agriculture, Elsenburg
- Brooks P.M. (1974) *The ecology of the four-striped field mouse, Rhabdomys pumilio (Sparrman, 1784), with particular reference to a population on the Van Riebeeck Nature Reserve, Pretoria*. MSc. Thesis, Stellenbosch University.
- Campbell B.M. (1986) Plant spinescence and herbivory in a nutrient poor ecosystem. *Oikos*, 47, 168-172
- Capo R.C., Stewart B.W. & Chadwick O.A. (1998) Strontium isotopes as tracers of ecosystem processes: theory and methods. *Geoderma*, 82, 197-225
- Castley J.G., Boshoff A.F. & Kerley G.I.H. (2001) Compromising South Africa's natural biodiversity – inappropriate herbivore introductions. *South African Journal of Science*, 97, 344-348
- Cody M.L., Breytenbach G.J., Fox A.E., Newsome A.E., Quinn R.D. & Siegfried W.R. (1983) Animal communities: diversity, density and dynamics. In: *Mineral nutrients in mediterranean ecosystems* (ed. Day J.A.), pp. 91-110. CSIR, Pretoria
- Coetzee F. (1993) *1:250 000 Geological Series Map. 3420 Riversdale*. Government Printer, Pretoria.
- Copeland S.R., Sponheimer M., le Roux P.J., Grimes V., Lee Thorp J.A., de Ruiter D.J. & Richards M.P. (2008) Strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) of tooth enamel: a comparison of solution and laser ablation multicollector inductively coupled plasma mass spectrometry methods. *Rapid Communications in Mass Spectrometry*, 22, 3187-3194
- Cowling R., Rundel P.W., Lamont B.B., Arroyo M.K. & Arianoutsou M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, 11, 362-366
- Davis R.M. (1973) *The ecology and life history of the vlei rat, Otomys irroratus (Brants, 1872), on the Van Riebeeck Nature Reserve, Pretoria*. MSc. Thesis, Stellenbosch University.
- Du Plessis S.E. (1969) *The past and present geographical distribution of the Perissodactyla and Artiodactyla in southern Africa*. MSc. Thesis, University of Pretoria.
- Estes R.D. (1993) *The safari companion: A guide to watching African mammals*. Chelsea Green Publishing Company, Vermont.
- Feranec R.S., Hadly E.A. & Paytan A. (2007) Determining landscape use of Holocene mammals using strontium isotopes. *Oecologia*, 153, 943-950
- Hodell D.A., Quinn R.L., Brenner M. & Kamenov G. (2004) Spatial variation of strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) in the Maya region: a tool for tracking ancient human migration. *Journal of Archaeological Science*, 31, 585-601

- Hoppe K.A., Koch P.L., Carlson R.W. & Webb S.D. (1999) Tracking mammoths and mastodons: Reconstruction of migratory behavior using strontium isotope ratios. *Geology*, 27, 439-442
- Hoppe K.A., Koch P.L. & Furutani T.T. (2003) Assessing the preservation of biogenic Strontium in fossil bone and tooth enamel. *International Journal of Osteoarchaeology*, 13, 20-28
- Jachmann H. (2002) Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology*, 39, 841-852
- Johnson S.D. (1992) Plant-animal relationships. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 175-205. Oxford University Press, Cape Town
- Kerley G.I.H. (1989) Diet of small mammals from the Karoo, South Africa. *South African Journal of Wildlife Research*, 19, 67-72
- Kerley G.I.H., Knight M.H. & Erasmus T. (1990) Small mammal microhabitat use and diet in the southern Kalahari, South Africa. *South African Journal of Wildlife Research*, 20, 123-126
- Kerley G.I.H., Pressey R.L., Cowling R.M., Boshoff A.F. & Sims-Castley R. (2003) Options for the conservation of large and medium-sized mammals in the Cape floristic region hotspot, South Africa. *Biological Conservation*, 112, 169-190
- Knudson K.J. & Buikstra J.E. (2007) Residential mobility and resource use in the Chiribaya polity of southern Peru: strontium isotope analysis of archaeological tooth enamel and bone. *International Journal of Osteoarchaeology*, 17, 563-580
- Koch P.L., Heisinger J., Moss C., Carlson R.W., Fogel M., L. & Behrensmeyer A.K. (1995) Isotopic tracking of change in diet and habitat use in African elephants. *Science*, 267, 1340-1343
- Malan J.A., Viljoen J.H.A., Siegfried H.P. & Wickens H.d.V. (1994) *Geologie van die gebied Riversdale*. Government Printer, Pretoria.
- Marie P.J. & Hott M. (1986) Short-term effects of fluoride and strontium on bone formation and resorption in the mouse. *Metabolism*, 35, 547-551
- Marques F.F.C., Buckland S.T., Goffin D., Dixon C.E., Borchers D.L., Mayle B.A. & Peace A.J. (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology*, 38, 349-363
- McArthur J.M., Howarth R.J. & Bailey T.R. (2001) Strontium isotope stratigraphy: LOWESS version 3: best fit to the marine Sr-isotope curve for 0-509 Ma and accompanying look-up table for deriving numerical age. *The Journal of Geology*, 109, 155-170
- Millspaugh J. & Marzluff J.M. (2001) *Radio tracking and animal populations*. Academic Press, London.
- Moll E.J. (1987) Review of some new concepts in "Fynbos" ecology. In: *Papers in the prehistory of the Western Cape. British Archaeological Reports International Series 332*. (eds. Parkington J. & Hall M.), pp. 120-131. BAR, Oxford
- Morrow P.A., Day J.A., Fox M.D., Frost P.G.H., Jarvis J.U.M., Milewski A.V. & Norton P.M. (1983) Interaction between plants and animals. In: *Mineral nutrients in mediterranean ecosystems* (ed. Day J.A), pp. 111-124. CSIR, Pretoria
- Mucina L., Rutherford M.C. & Powrie L.W. (eds.) (2007) *Vegetation Map of South Africa, Lesotho and Swaziland, 1:1 000 000, 2nd ed.* SANBI, Pretoria.

- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858
- Newsome S.D., Martinez Del Rio C., Bearhop S. & Phillips D.L. (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5, 429-436
- Owen-Smith N. & Danckwerts J.E. (1997) Herbivory. In: *Vegetation of southern Africa* (eds. Cowling R., Richardson D. & Pierce S.), pp. 397-420. Cambridge University Press, Cambridge
- Porder S., Paytan A. & Hadly E.A. (2003) Mapping the origin of faunal assemblages using strontium. *Paleobiology*, 29, 197-204
- Price T.D., Burton J.H. & Bentley R.A. (2002) The characterization of biologically available Strontium Isotope ratios for the study of prehistoric migration. *Archaeometry*, 44, 117-135
- Rebello A.G. (1992a) Preservation of biotic diversity. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 309-344. Oxford University Press, Cape Town
- Rebello A.G. (1992b) Red Data Book Species in the Cape Floristic Region: threats, priorities and target species. *Transactions of the Royal Society of South Africa*, 48, 55-86
- Rebello A.G. (1996) Renosterveld. In: *Vegetation of South Africa, Lesotho and Swaziland* (eds. Low A.B. & Rebello A.G.), pp. 63-67. Department of Environmental Affairs and Tourism, Pretoria
- Rebello A.G., Boucher C., Helme N., Mucina L., Rutherford M.C., Smit W.J., Powrie L.W., Ellis F., Lambrechts J.J., Scott L., Radloff F.G.T., Johnson S.D., Richardson D.M., Ward R.A., Proches S.M., Oliver E.G.H., Manning J.C., Jürgens N., McDonald D.J., Janssen J.A.M., Walton B.A., Le Roux A., Skowno A.L., Todd S.W. & Hoare D.B. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 52-219. SANBI, Pretoria
- Rookmaaker L.C. (1989) *The zoological exploration of Southern Africa 1650-1790*. A. A. Balkema, Rotterdam
- Rutherford M.C., Mucina L. & Powrie L.W. (2006) Biomes and bioregions of Southern Africa. In: *The vegetation of South Africa, Lesotho and Swaziland*. (eds. Mucina L. & Rutherford M.C.), pp. 31-51. SANBI, Pretoria
- Skead C.J. (1980) *Historical mammal incidence in the Cape Province. Volume 1: The Western and Northern Cape*. Department of Nature and Environmental Conservation of the Cape Provincial Administration, Cape Town
- Skinner J.D. & Chimimba C.T. (2005) *The mammals of the Southern African Subregion*. Cambridge University Press, Cape Town
- Smith R. (2006) *De Hoop Nature Reserve helicopter game census October 2006*. Internal report, CapeNature, Cape Town
- Smith R.K., Marais A., Chadwick P., Lloyd P.H. & Hill R.A. (2008) Monitoring and management of the endangered Cape mountain zebra *Equus zebra zebra* in the Western Cape, South Africa. *African Journal of Ecology*, 46, 207-213
- Specht R.L. & Moll E.J. (1983) Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In: *Mediterranean-type ecosystems: the*

- Role of Nutrients* (eds. Kruger F.J., Mitchell D.T. & Jarvis J.U.M.), pp. 41-65. Springer-Verlag, Heidelberg
- Van der Merwe N.J., Lee-Thorp J.A., Thackeray J.F., Hall-Martin A., Kruger F.J., Coetzee H., Bell R.H.V. & Lindeque M. (1990) Source-area determination of elephant ivory by isotopic analysis. *Nature*, 346, 744-746
- Van Zyl L.J. (1978) *Die waterbehoefte en drinkgewoontes van die Bontebok Damaliscus dorcas dorcas (Pallas, 1766) in die Bontebok Nasionale Park*. MSc. Thesis, University of Stellenbosch.
- Vogel J.C., Eglinton B. & Auret J.M. (1990) Isotope fingerprints in elephant bone and ivory. *Nature*, 346, 747-749
- Waight T., Baker J. & Peate D. (2002) Sr isotope ratio measurements by double-focusing MC-ICPMS: techniques, observations and pitfalls. *International Journal of Mass Spectrometry*, 221, 229-244
- Weis D., Kieffer B., Maerschalk C., Barling J., de Jong J., Williams G.A., Hanano D., Pretorius W., Mattielli N., Scoates J.S., Goolaerts A., Friedman R.E. & Mahoney J.B. (2006) High-precision isotopic characterization of USGS reference materials by TIMS and MC-ICP-MS. *Geochemistry, Geophysics and Geosystems*, 7, 1-30
- Whipkey C.E., Capo R.C., Chadwick O.A. & Steward B.W. (2000) The importance of sea spray to the cation budget of a coastal Hawaiian soil: A strontium isotope approach. *Chemical Geology*, 168, 37-48

THE IMPACT OF HERBIVORY AND FIRE ON GRASS-SHRUB DYNAMICS OF MULTI-STRUCTURAL VEGETATION STATES OF THE CAPE RENOSTERVELD

Introduction

The nature of community assembly and the underlying dynamics involved in the co-occurrence of grass and woody plants in ecosystems across the world has received a lot of attention in the past (Scholes & Archer 1997; Jeltsch *et al.* 2000; House *et al.* 2003; van Langevelde *et al.* 2003; Sankaran *et al.* 2004, 2005). The competitive relationship between grass and woody plants is not merely of academic interest, but also of economic importance in areas where a sudden or unexpected increase in the cover of woody plants (see Skarpe 1990; Van Auken 2000; Roques *et al.* 2001 and references therein) is deemed undesirable due to the resulting trade-off in availability of grassy fodder for grazing animals (Kraaij & Ward 2006; Van Wieren & Baker 2008). Reasons for the increased cover of woody plants in grassland (often dubbed “bush encroachment”) has been sought in elevated CO₂ levels and climate change in general (Archer *et al.* 1995; Bond & Midgley 2000; Bond 2002), as well as in the interactions between nitrogen (nutrient), water availability (Ward 2002; Kraaij & Ward 2006), chronic high levels of livestock grazing, and change in fire frequency (Dublin *et al.* 1990; Van Auken 2000; Roques *et al.* 2001; Heisler *et al.* 2003; Van Langevelde *et al.* 2003).

The lowlands of SW Cape (Western Cape Province, South Africa) is one of the regions of the mediterranean-climate Fynbos Biome (*sensu* Rutherford *et al.* 2006) where shrub invasion is presumed to have replaced more extensive grasslands in the past. Whether this really happened is a contentious issue and has been a subject of debate for decades (Levyns 1956; Stindt *et al.* 1965; Joubert & Stindt 1979; Cowling 1984; Moll 1987; Stock *et al.* 1992; Rebelo 1995; Krug *et al.* 2004; Newton & Knight 2004). The main reason for the disparity of opinions is that the suggested change from grassland to shrubland coincided with the onset and expansion of European farming on the southern tip of Africa during the late 17th and most of the 18th century (Sparrman 1786; Rebelo 1995). Only casual reports on vegetation from historic documents (see Skead 1980 for a summary of historic vegetation descriptions) can thus be used to substantiate this presumed change. An attempt to verify the suggestions by means of isotope analysis of soils yielded no evidence that the West Coast renosterveld (asteraceous-dominated lowlands shrublands on shale soils) could have been dominated by C₄ grasses in recent times (Stock *et al.* 1992). There is, however, a possibility that the presumed grassland was dominated by C₃ grasses, which are found in vegetation of regions characterised by winter rainfall. C₃ grasses can not currently be distinguished from C₃ dicots by means of stable isotope analysis.

The supposed reason for the putative conversion of grasslands to shrublands in the Cape has been blamed on severe and continuous grazing of freshly burnt veld by domestic

stock (Sparrman 1786; Du Toit & Du Toit 1938; Stindt *et al.* 1965; Joubert & Stindt 1979; McDowell 1988), leading to an unwanted overgrazed state. With settled agriculture in the Cape, the disturbance regime was changed from an intense and localized, pulsed nomadic grazing system used by indigenous herbivores and domestic livestock, coupled with a variable fire frequency, to a system of continuous overgrazing and a fixed burning cycle (Cowling *et al.* 1986). More recently Rebelo (1995) and Krug *et al.* (2004b) suggested, however, that native large herbivores (or rather their absence for the last 300 years) might also have contributed to the presumed structural change in renosterveld. The removal of large browsers, such as African elephant (*Loxodonta africana*), black rhino (*Diceros bicornis*) and eland (*Tragelaphus oryx*), which all occurred across the lowlands of the Western Cape prior to European settlement (Skead 1980; Boshoff & Kerley 2001), could very well have been instrumental in keeping the overstory canopy more open – the same way as done by browsers in East African savannas (Dublin *et al.* 1990; Augustine & McNaughton 1998).

The question whether renosterveld was historically more grassy or shrubby at the landscape scale will most likely never be answered conclusively. It remains an important fact, however, that both shrubland and grassland states can be recognised in renosterveld today (Boucher 1981; Boucher & Moll 1981; Cowling 1984; Cowling *et al.* 1986; Rebelo *et al.* 2006). It is also widely accepted that the mechanisms governing the dynamics of these states need to be understood in order to implement proper conservation measures (Cowling *et al.* 1986; Rebelo 1995; Kemper *et al.* 1999). Renosterveld is a critically endangered vegetation type (Von Hase *et al.* 2003; Rouget *et al.* 2006) of which more than 80% had been transformed for agriculture in the lowland areas (Rebelo *et al.* 2006).

Renosterveld can be described as an evergreen, fire-prone shrubland or grassland dominated by small, cupressoid-leaved evergreen shrubs of the Asteraceae (very often dominated by renoster bush *Elytropappus rhinocerotis*), usually having an understory of grasses and containing many geophytes, which in places can become a major structural element. In addition to the shrubland and tussock grassland states, grazing lawn (grassland) and herb-dominated “bulbland” states have also been distinguished as the current physiognomic faces of renosterveld (Rebelo *et al.* 2006).

In this experimental study we subject three renosterveld vegetation states (shrubland, tussock grassland and grazing lawn) to both herbivory (grazing/browsing) and fire, which have been in the centre of discussions about the putative shrubland/grassland switches in renosterveld. We assume that by using native large herbivores still surviving in renosterveld today, we would not only gain a better understanding of present role in shaping vegetation dynamics renosterveld, but we also might gain insights into their historical role.

Conceptual model of predicted state changes

Before the onset of the experiment we developed a conceptual model of the predicted state changes (Fig. 5.1) based on current theory and the findings of similar experiments addressing vegetation-state changes in response to disturbance. Few studies on vegetation

dynamics have, however, incorporated multiple herbivore species, an episodic disturbance event, and multiple vegetation states into a single experiment (Wisdom *et al.* 2006) as has been done here.

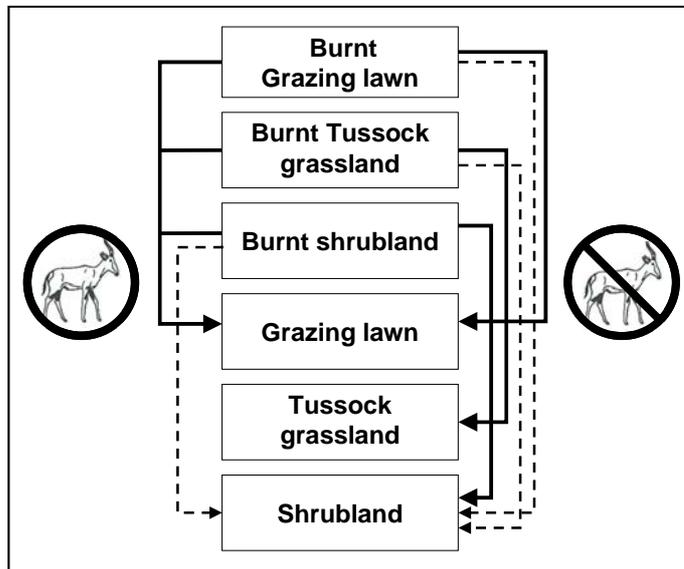


Fig. 5.1 Graphical model of the predicted changes between burnt and unburnt vegetation states in response to the presence (left side) and absence (right side) of large herbivores. Solid lines/arrows indicate predicted change, while the dashed lines/arrows indicate uncertain change.

We predicted that – as previously found (Beukes 1987; Novellie 1987; Luyt 2005) – herbivores will be attracted to recently burnt renosterveld veld due to the higher quality of forage appearing in short-lived, nutrient-rich post-fire habitats (Vinton *et al.* 1993; Hobbs 1996; Archibald *et al.* 2004). We argue that if the burnt area in this generally nutrient-poor environment (Joubert & Stindt 1979) is small, both browsers and grazers will gather in the post-fire recovering habitats in such numbers that only the most grazing and trampling resistant plant species will survive the intense disturbance, and consequently a grazing lawn might be formed (McNaughton 1984; Hobbs 1996; Olf *et al.* 1999; Archibald *et al.* 2005; Van der Wal 2005; Skarpe & Hester 2008). We further predict that even the unpalatable shrubs such as the common *Elytropappus rhinocerotis* would be removed just after they have germinated as a consequence of intensive and indiscriminate trampling and grazing by grazers (Hester *et al.* 2000), or through deliberate selection by browsers (Scholes & Archer 1997; Augustine & McNaughton 1998; Van Wieren & Baker 2008). Support for the suppression of shrub establishment was brought forward by Luyt (2005), who studied habitat preference of bontebok (*Damaliscus pygargus pygargus*), an endemic Cape antelope, in the Bontebok National Park (near Swellendam, Western Cape). He found that bontebok preferred recently burnt areas and that shrub establishment was suppressed in a small burnt area exposed to heavy grazing by the antelope population. There is, however, the remote chance that old

Elytropappus rhinocerotis shrubs might resprout from epicormic buds or roots (Cowling *et al.* 1986), which will result in the restoration of the shrubland vegetation state.

We suggest that in the absence of large herbivores, different vegetation states will revert to their former states after fire. Grasses are able to regulate woody plant recruitment through competitive exclusion in the absence of herbivory, but their effect may not be large enough to cause high mortality or bring about the exclusion of shrubs (Cowling *et al.* 1986; Scholes & Archer 1997; Brown & Archer 1999; DeSimone & Zedler 1999; Jurena & Archer 2003). If, in the absence of herbivory, shrub seedlings do manage to establish in the grasslands, it will most likely be directly after a fire when the competition for light and moisture is much reduced. Shrubs will also have a better chance to establish in tussock grassland rather than in grazing lawns due the highly competitive nature and fast and effective space conquest of the matt-forming *Cynodon dactylon* (Guglielmini & Satorre 2004), the dominating grass in the grazing lawns.

Methods

Study area

The study area is a patch of Eastern Rûens Shale Renosterveld (Rebello *et al.* 2006) in the De Hoop Nature Reserve (DHNR; 34°26' S, 20°30' E, 323 km²) located on the South Coast of the Western Cape Province, South Africa. It is situated on a gentle slope (< 6°) facing a shallow valley, at an altitude of 120 meter above sea level and separated from the coast (10 km to the south) by limestone hills and a broad valley filled with ferricrete and alluvial sediments. The mean annual precipitation (MAP; 1979–2007) at Driefontein Farm (a weather station situated 8.5 km directly west of the study area) amounts to 473 mm (CV = 19%). Every month of the year contributes at least 30 millimetres of rain to the total rainfall; the bulk of the rain, however, falls between April and October (65%) when the evapotranspiration is also at its lowest. The MAP for the two years of this study was 459 mm (Nov. 2005 – Nov. 2006) and 598 mm (Nov. 2006 – Nov. 2007), respectively. The coldest month is July (T_{max} = 18.4°C, T_{min} = 6.3° C), while the warmest month is February (T_{max} = 27.2° C, T_{min} = 16.7° C). The deep clayey soils of the study area are derived from Bokkeveld Group shales (Malan *et al.* 1994).

A large part of the approximately 200 hectares of the renosterveld had been cultivated (ploughed) for a number of years till 1980 – at which time it became incorporated into the De Hoop Nature Reserve (Heard *et al.* 2001). Since then the area was left undisturbed for 25 years and it turned into a mosaic of three distinctly different structural states: *Elytropappus rhinocerotis* shrubland, *Cymbopogon pospischilii* tussock grassland, and *Cynodon dactylon* grazing lawn.

The area is continuously grazed by a number of large herbivores (>20 kg). The most common species is the bontebok, which restrict their movements to this small patch of renosterveld. Bontebok avoids the neighbouring unpalatable and nutrient-deprived sandstone, ferricrete and limestone fynbos shrublands that surrounds the area (see Chapter 3 and 4 of this dissertation). An adult bontebok male weighs on average 61 kg,

while the females are slightly smaller at 55 kg (Owen-Smith 1988). Bontebok is almost exclusively a grazer preferring short grass (Beukes 1984, Skinner & Chimimba 2005). Eland is also present in the area, but this antelope is not restricted to the renosterveld patch as it is able to utilize limestone fynbos (see Chapter 3 and 4 of this dissertation). Adult eland males weigh anything between 425 kg and 840 kg, some being as heavy as 900 kg. Females tend to be smaller, weighing around 460 kg (Skinner & Chimimba 2005). Eland can be classified as a mix feeder with a preference for browse (Skinner & Chimimba 2005). An isotope analysis of eland bone collagen from DHNR revealed that their diet ($n = 6$) consist of around 16% C_4 grass, with the rest being made up of either C_3 grass or browse (see Chapter 2 of this dissertation). Ostrich (*Struthio camelus*) also frequent the renosterveld patch and weighs around 68 kg (Maclean 1984). The carbon isotope analyses showed that ostrich avoid C_4 grasses ($< 2\%$ of diet, $n = 6$) in DHNR, and focus on either C_3 grass or browse instead (see Chapter 2 of this dissertation). Ostriches seldom browse leaves from shrubs when forbs and green grass are available (Milton *et al.* 1994), and often pluck entire small plants (including roots) from the ground (Williams *et al.* 1993).

At the onset of the study (Nov. 2005) there were 128 resident bontebok individuals in the study area, but their numbers dropped to 62 by the end of the study (Nov. 2007). At any given time, the eland population in the area can count none to more than a hundred individuals as they move in and out of the area. The ostrich population size in the study area fluctuated between 18 and 44 during the study period. The October 2006 game census by helicopter for the whole of DHNR tallied the highest animal numbers in the history of the reserve (P. Loyd, CapeNature, personal communication) and was followed by a dramatic crash in both bontebok, eland and ostrich numbers as revealed by the February 2008 aerial count. This suggest that the reserve and study area were close to its carrying capacity and consequently subjected to intense grazing pressure for at least the first half of our study.

Study design

Within the studied patch of renosterveld, three sites (each representing one of the three structural vegetation states) were selected for experimental treatment. Each of the sites had to have a homogenous appearance (unbroken canopy cover and uniform physiognomy) on at least two hectares. The selected sites were also selected to be as close as possible to each other to assure habitat homogeneity (the same soil type, no obvious signs of soil surface damage, and grossly uneven drainage conditions).

A three hectare patch of a *Cynodon dactylon* grazing lawn and 6.2 ha patch of an *Elytropappus rhinocerotis* shrubland were found bordering on each other. The closest unbroken patch of *Cymbopogon pospischilii* tussock grassland (2.5 ha) was found 700 meters east of the former two sites. Each of these three sites were then sub-divided into two sub-sites, to yield six experimental blocks, with one of the blocks in each of the respective states earmarked for controlled burning intervention (Fig. 5.2).

Within each of the six experimental blocks, six plots (4 x 4 meters) were selected and permanently marked (Fig. 5.2). These plots (36 in total) were selected to be as similar as possible with regard to the biomass of the dominant species representing each structural state in each experimental block. Variation in slope and aspect between plots were also kept as uniform as possible with the average slope been 2.7 degrees (n = 36, SD = 1.5). Three subplots (0.5 x 0.5 meters) were permanently marked in a set manner within each of the 36 plots (108 in total) and located so as to be one meter from the border of the plot and one meter from each other. Three of the six plots within each experimental block were randomly chosen to serve as enclosure/ungrazed/unbrowsed replicate plots, while the remaining three replicate plots were left exposed to herbivory by large herbivores (further referred to as grazing).

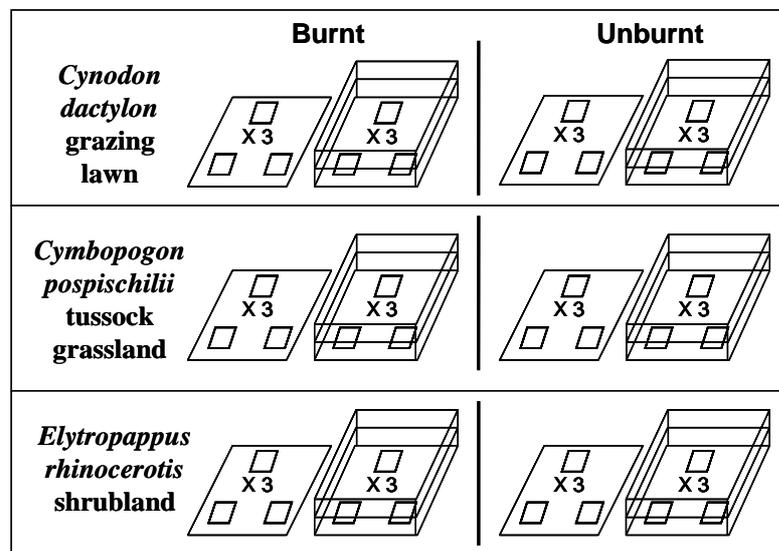


Fig. 5.2 A diagramme showing the experimental layout used in this study. Three areas of renosterveld comprising of three different vegetation states were each divided into two blocks of which one was burnt. Within each block six plots (4 x 4 meter) were selected of which three were grazed replicates and the other three replicates protected from grazing. Within each replicate plot there were three subplots (0.5 x 0.5 m) which were monitored for change in biomass and species composition.

Controlled burning was performed on the morning of 1 December 2005 to one experimental block of each vegetation state. The *Cymbopogon pospischilii* tussock grassland block was burnt between 08h20 and 10h00 a.m. (average air temperature during the burning period: 24.2° C, wind speed: 12.8 km/h). The *Cynodon dactylon* grazing lawn and *Elytropappus rhinocerotis* shrubland blocks were burnt simultaneously as they bordered on each other. The fire took place between 10h15 and 11h40 a.m. (average air temperature during the burning period: 27.5 °C, wind speed: 13.8 km/h). Five hectares of shrubland, 1.8 ha of grazing lawn, and 1.4 ha of tussock grassland were burnt. In the week following the burn, three enclosure camps were constructed in each of

the six experimental blocks. These exclosures (4 x 4 meters) were fenced with 1.8 meter high game-proof fence and topped by a double strand of barbed wire. The exclosures were deliberately kept small to discourage eland from entering, as this antelope is able to jump even two meter high fences with ease. The exclosures were designed to prevent access for all antelope species and ostriches for the duration of the study. Hares could have potentially entered the exclosures, but we found no evidence of their presence in the plots for the duration of the study.

Vegetation sampling

The biomass of all perennial plants present in the 108 subplots was estimated at the start of the experiment (November 2005) before the fire treatment, and then again repeatedly every six months for two years (May and November 2006, and May and November 2007). We used the Multipoint Minidisk Meter – a non-destructive sampling method developed for this particular purpose, which is able to cope with the structural complexity of the sampled vegetation (Radloff & Mucina 2007, or Chapter 6 of this dissertation). The method records the height of all perennial plants touching a mini-disk lowered into the vegetation at 25 fixed points within each of the 0.25 m² subplots.

All perennial plant species were identified, measured and classified into the following five growth forms: lawn grasses, tussock grasses, creeping shrubs, microphyllous shrubs, and nanophyllous shrubs. We measured height and harvested biomass for a representative (dominant) species of each growth form in order to calculate conversion (regression) equations to be used later for non-destructive biomass estimation in the permanent subplots. The regression equations were derived by using the calibration procedure of Radloff and Mucina (2007), whereby the biomass of a particular growth form is harvested in 12 plots and weighed after 25 height measurements have been taken in each plot. The total height (sum of the 25 height measurements) and biomass values of the 12 plots were then used to calculate the respective regression equations by expressing above-ground biomass as a function of total height (see Radloff and Mucina 2007, or Chapter 6 of this dissertation for details).

The biomass of a particular growth form within a subplot was determined by summing all the height readings of all the species of that particular growth form in the plot, and then recalculating those values to biomass using the appropriate regression equations. In this manner the change in the biomass of a growth form could be closely monitored over time. The biomass values of the three subplots in each plot were summed up to give a representative total biomass value (g/0.75m²) for a particular growth form in that plot. Biomass values for each of the five growth forms was calculated for each of the 36 plots at each measuring interval (n = 5), and these values entered the data analyses. We also kept track of individual species biomass changes as data were collected according to species and only later pooled according to growth form.

Data analysis

Non-parametric Mann-Whitney U tests were performed on the data collected before the fire and exclosure treatments were applied to test for significant differences between the biomass of growth forms present within the replicate plots to become exclosures ($n = 3$) and the replicates to be kept grazed ($n = 3$) in each of the six experimental blocks. The same tests were performed at the end of the experiment (after two years) to determine whether the exclusion of herbivores had a significant effect on the biomass of the five growth forms in both the burnt or unburnt blocks as measured in the replicate plots within each of the three vegetation structural states. The software package STATISTICA 8 (StatSoft 2007) was used to execute the tests.

An agglomerative hierarchical clustering method was used to classify the 36 plots individually both at the beginning and end of the experiment using the biomass data (pooled within growth-forms) collected at these times. We used minimum incremental sum of squares clustering (ISS; also known as Ward's Method) based on chord distance (for the continuous data) as the resemblance. Details of the method are found in Podani (1994, 2001). We choose the chord distance in order to normalise the biomass data due to large differences in the total biomass encountered among the different growth forms in the classified plots. The optimum number of clusters were determined using two methods: (1) optically, by judging for the internal homogeneity of the clusters from the topology of the dendrogram and, (2) using an *à posteriori* test based on information theory (Podani 1997) and calculated using the software package SYNTAX 5.02 (Podani 1994).

Ordinations of the data set (biomass of growth forms in 36 plots) were done using correspondence analysis [CA; see Lepš & Šmilauer (2003) for more detail] in order to confirm the results of the clustering and to judge on the importance of relative shifts in the positions of the plots in the theoretical ordination space. The ordination analyses were performed by CANOCO for Windows 4.52 (Ter Braak & Šmilauer 2002).

Results

The biomass calibration procedure revealed that there was a strong relationship between the height measurement values of all five the species selected to represent the respective perennial growth forms, and their actual biomass. In all cases the explained variance was above 90% and we consequently used these regression equations for the different growth forms to determine biomass non-destructively over the 2 year study period (Table 5.1).

Table 5.1 The coefficients of determination (r^2) and the slope of the respective regression lines (b) calculated from calibration measurements on species representing five perennial growth forms. The regression lines were forced through the origin.

Growth form	Representative species	r^2	b
Stoloniferous grass	<i>Cynodon dactylon</i>	0.924	0.323
Tussock grass	<i>Cymbopogon pospischilii</i>	0.973	0.416
Nanophyllous shrub	<i>Elytropappus rhinocerotis</i>	0.962	0.390
Microphyllous shrub	<i>Athanasia trifurcata</i>	0.982	0.189
Creeper shrub	<i>Galenia affinis</i>	0.904	0.340

The Mann-Whitney U test of the data collected with the establishment of the experiment revealed no significant differences ($p < 0.05$) amongst the biomass of the respective growth forms within the replicate plots to be left grazed and those to be protected from it, for both the grazing lawn and tussock grassland states (Table 5.2 and Fig. 5.3). There were, however, significant differences between the experimental blocks of the shrubland state. In the shrubland block to be left unburnt there was significantly more tussock grass biomass in the three replicate plots to be excluded from grazing (average 30.8 g/0.75 m²) than in the three replicate plots that were to remain grazed (average 4.7 g/0.75 m²). In the shrubland block to be burned there was significantly more nanophyllous shrub biomass in the replicate plots to be excluded from grazing (average 1 339 g/0.75 m²) than in the replicate plots that were to remain exposed to grazing (average 1104.9 g/0.75 m²).

The Mann-Whitney U tests for the biomass data collected after 24 months indicated (Table 5.2 and Fig. 5.3) that there was significantly more tussock grass biomass in the enclosure replicate plots than in the grazed replicate plots in both the burnt (average 140.1 vs. 422.3 g/0.75 m²) and unburnt (average 307.6 vs. 414.4 g/0.75 m²) tussock grassland blocks. There was also significantly more stoloniferous grass biomass in the enclosure replicate plots (average 236.8 g/0.75 m²) than in the grazed replicate plots (average 92.0 g/0.75 m²) of the burnt grazing lawn block. Within the burnt shrubland block there was significantly more nanophyllous shrub biomass in the grazed (average 0 g/0.75 m²) than in the enclosure replicate plots (average 66.1 g/0.75 m²). There was also significantly more microphyllous shrub biomass in the enclosure (average 225.0 g/0.75 m²) than in the grazed replicate plots (average 12.3 g/0.75 m²) of this burnt shrubland block.

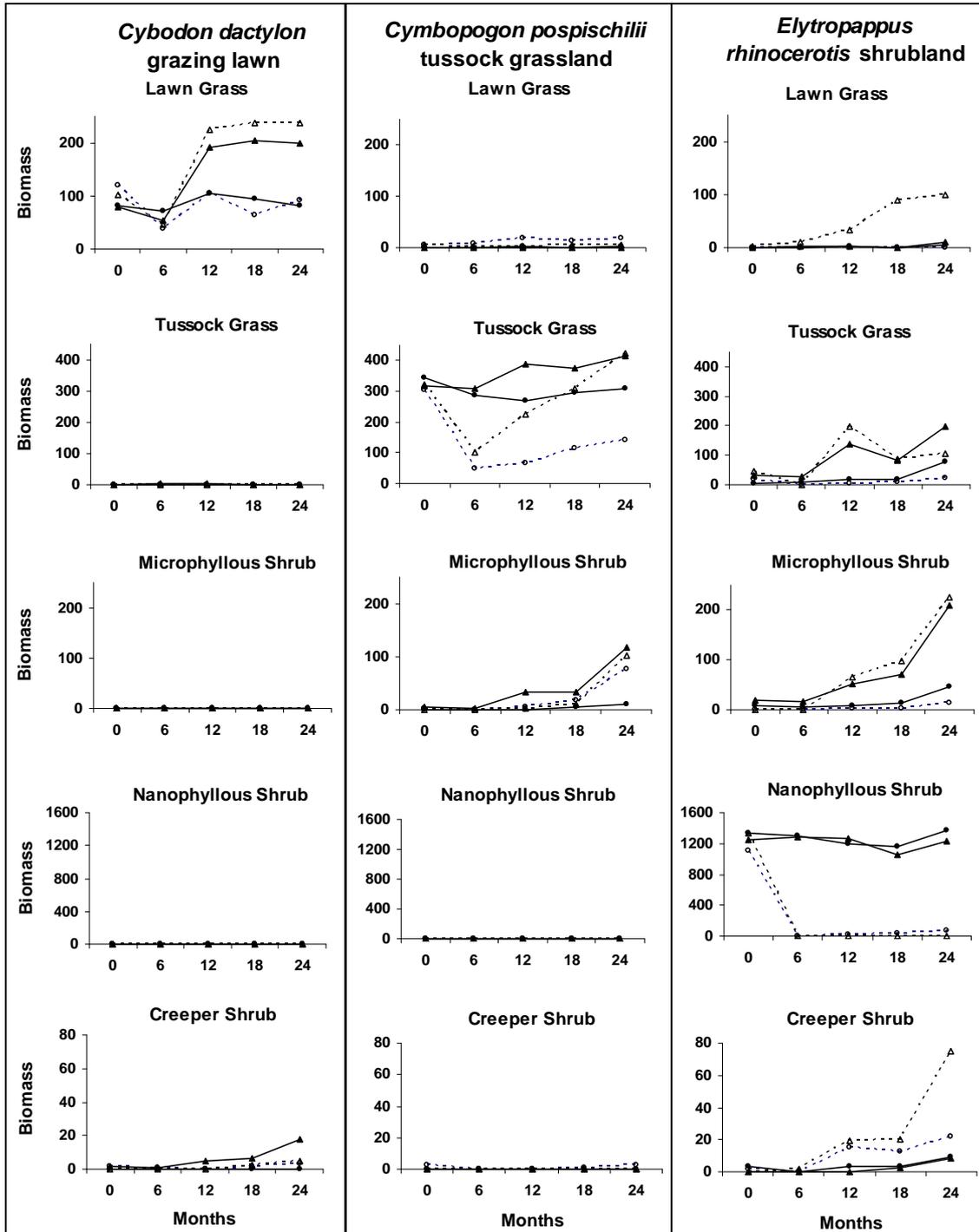


Fig. 5.3 Trajectories of change in the biomass of the five growth forms in each of the three structural vegetation states over the 24 month period following the experimental treatment. Dotted lines and open symbols represent the data of the burnt block in each state while the solid lines and filled symbols represent the data of the unburnt block. Triangles represent the values of exclosure plots and circles the values of grazed plots. The data points shown are the average biomass values (g/0.75 m²) calculated from the values obtained from the three replicate plots in each block.

Table 5.2 Results of the Mann-Whitney U test for the comparisons between the biomass values of five perennial growth forms measured in three enclosure and three grazed replicate plots within each of the six experimental blocks. We tested for difference in biomass at both the start of the experiment (0 Months), before application of any treatment, and again 24 months after the application of fire and the construction of enclosure camps. Numbers in bold denote the significant differences ($p < 0.5$).

Growth form type	Time of survey	Grazing lawn				Tussock grassland				Shrubland			
		Unburnt		Burnt		Unburnt		Burnt		Unburnt		Burnt	
		Z-value	P	Z-value	P	Z-value	P	Z-value	P	Z-value	P	Z-value	P
<i>Stoloniferous grass</i>													
	0 Months	0.218	0.8273	0.655	0.5127	-0.655	0.5127	0.655	0.5127	0.655	0.5127	-0.655	0.5127
	24 Months	-1.091	0.2752	-1.964	0.0495	0.655	0.5127	1.091	0.2752	0.218	0.8273	-0.873	0.3827
<i>Tussock grass</i>													
	0 Months	-0.655	0.5127	-0.655	0.5127	0.655	0.5127	0.218	0.8273	-1.964	0.0495	-1.091	0.2752
	24 Months	-0.218	0.8273	0.873	0.3827	-1.964	0.0495	-1.964	0.0495	-1.528	0.1266	-0.873	0.3827
<i>Nanophyllous shrub</i>													
	0 Months	0.000	1.0000	0.000	1.0000	0.000	1.0000	0.000	1.0000	1.091	0.2752	-1.964	0.0495
	24 Months	-0.655	0.5127	0.655	0.5127	0.000	1.0000	0.000	1.0000	0.655	0.5127	1.964	0.0495
<i>Microphyllous shrub</i>													
	0 Months	0.000	1.0000	0.000	1.0000	-0.218	0.8273	0.655	0.5127	-0.655	0.5127	0.000	1.0000
	24 Months	0.000	1.0000	0.000	1.0000	-1.528	0.1266	-0.218	0.8273	-1.091	0.2752	-1.964	0.0495
<i>Creeper shrub</i>													
	0 Months	-0.655	0.5127	1.309	0.1904	0.000	1.0000	0.218	0.8273	0.218	0.8273	0.655	0.5127
	24 Months	-0.655	0.5127	0.218	0.8273	0.000	1.0000	1.091	0.2752	-0.218	0.8273	-1.528	0.1266

The ISS clustering (corroborated by the CA ordination patterns on ordination plane of Axes 1 and 2) classified the 36 experimental plots at the onset of the experiment into three clusters based on the biomass of the five growth forms present in each plot (see inserts in Figs. 5.4 & 5.5). These clusters reflected the experimental layout, with the 12 plots of each structural vegetation state grouping together. The Axis 1 of the ordination plot (see inset in Fig. 5.5) separated the 12 grazing lawn plots from the shrubland and tussock grassland plots, and accounted for 50.7% of the variance. The Axis 2 separated 12 tussock grassland plots from 12 shrubland plots. Axis 1 and 2 together explained 98.2% of the variance.

The ISS cluster analysis of the biomass of the 36 plots (24 months after the fire and enclosure treatment were applied) differs markedly from the results of the analysis done on the pre-experimental data (Fig. 5.4). A formalised (information-theory based) analysis of the classification result of the 24-month data seeking the best separation of clusters, suggested the level of four clusters as the optimal non-hierarchical solution (total separation = 1.77; Podani 1997). At this level the 24-month data classification differs from the pre-experimental biomass classification with regards to the position of the shrubland plots that have been burnt and protected from grazing. After two years one of these plots cluster with the lawn grass plots and another with the tussock grassland plots. The third plot forms an outlier that separates from the tussock grassland plots to stand on its own.

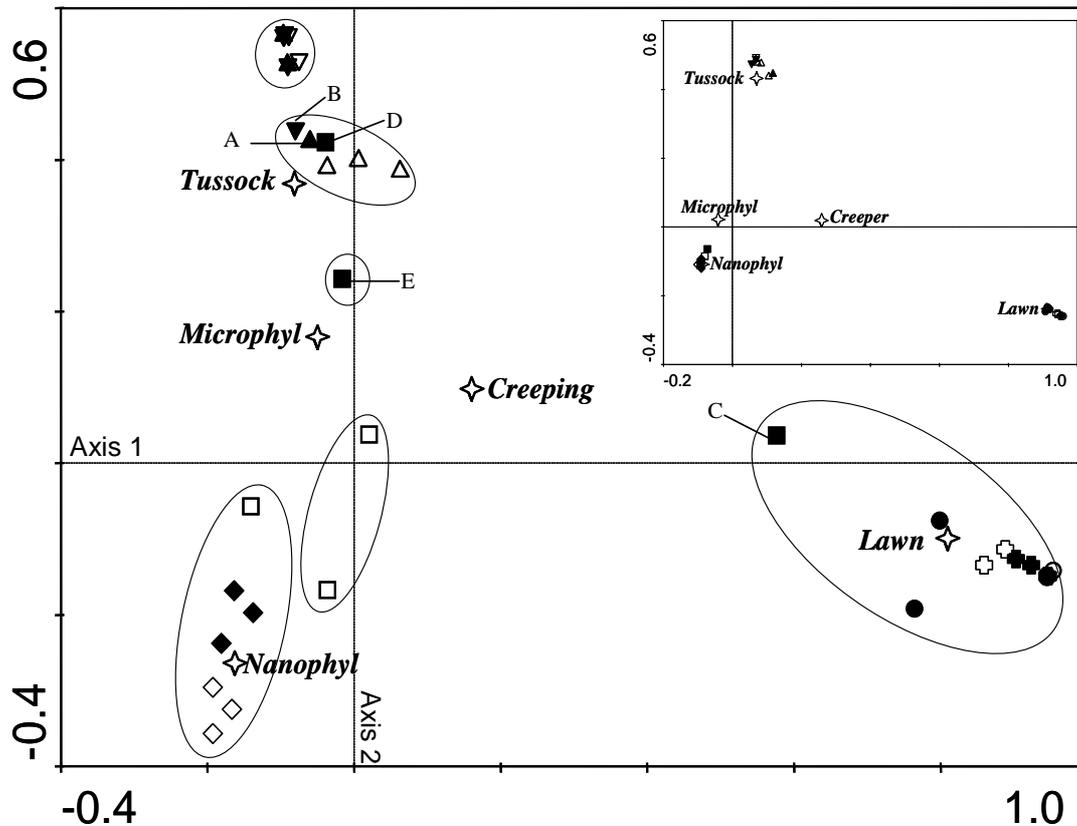


Fig. 5.5. CA ordination of the 36 sampling plots based on the difference in biomass between the five growth forms measured in each plot at the start of the experiment (the insert diagramme) and 24 months after the experimental treatments were applied (the full size ordination diagramme). The six groups identified by the ISS clustering are encircled. The growth forms are indicated with stars and their codes translate as follows: *Tussock* – Tussock grass, *Lawn* – stoloniferous grass, *Microphyl* – Microphyllous shrubs, *Nanophyl* – Nanophyllous shrub, and *Creeping* – Creeping shrub. Plot symbols: □ – Shrubland burnt and grazed, ■ – Shrubland burnt but ungrazed, ◇ – Shrubland unburnt but grazed, ◆ – Shrubland unburnt and ungrazed, ▽ - Tussock grassland unburnt but grazed, ▾ - Tussock grassland unburnt and ungrazed, △ - Tussock grassland burnt and grazed, ▲ - Tussock grassland burnt but ungrazed, ○ - Grazing lawn unburnt but grazed, ● - Grazing lawn unburnt and ungrazed, F – Grazing lawn burnt and grazed, G – Grazing lawn burnt but ungrazed. Letters A–E denotes specific plots referred to in the discussion.

Six ISS clusters were recovered on the CA ordination plane (Axes 1 and 2) of the 24-month dataset (Fig. 5.5). As in the ordination of the pre-experimental biomass data, the Axis 1 separated plots according to the abundance of lawn grasses and creeper shrubs, while the Axis 2 separated plots according to the abundance of tussock grass, microphyllous, and nanophyllous shrubs. The Axes 1 and 2 together accounted for 78.6% of the variance.

In accordance to the cluster analysis, the CA ordination also indicated that the plots most affected by the experimental treatments were the burnt and ungrazed shrubland plots. The three plots showed the biggest relative shift away from the nanophyllous shrubland plots they initially grouped with on the ordination plane featuring the pre-experimental biomass data set (insert Fig. 5.5). The group of plots that showed the second largest response to the experimental treatment were the burnt and grazed nanophyllous shrubland plots. These plots feature in the CA ordination (24-months data) much closer to the position of creeper shrub and microphyllous shrub growth forms than before the application of the experimental treatment.

The grazing lawn plots showed very little response to the experimental treatments, but two ungrazed and unburnt lawn plots were shown to become slightly outlying (Fig. 5.5) after the application of treatments. The tussock grassland plots showed reaction to the experimental treatments as indicated by five plots featured further from the other tussock grassland plots. The five plots are three grazed and burnt plots, a burnt but ungrazed plot and a plot both ungrazed and unburnt.

Discussion

Our results support the prediction of Hobbs (1996) that ungulates may exert minor effects on the structure and function of ecosystems years after disturbance, but immediately following a disturbance their effect can determine the trajectory of the system among alternative states. The vegetation states addressed in our study did, however, react differently to disturbance.

Cynodon dactylon grazing lawns

The grazing lawn state showed high resilience towards both burning and grazing treatments. After two years there was only a very weak indication of shrub establishment in both ungrazed and unburnt grazing lawn plots. This can be underpinned by the slight separation of two of these plots from the rest of the grazing lawn plots (Fig. 5.5) in the ordination space. One of these plots supports creeping shrub *Galenia affinis* and a single *E. rhinocerotis* individual was found to have germinated in the other plot. Although these observations can hardly be seen as an indication of shrub invasion, it has been shown elsewhere (Bazely & Jefferies 1986) that dicotyledons plants can invade grazing lawns once herbivores are removed. In their study Bazely and Jefferies (1986) were able to detect a change only after four years. We cannot, therefore, exclude the possibility that our study was too short to detect any sizable change.

The Mann-Whitney U test found no significant difference between the biomass of the ungrazed and grazed stoloniferous grasses in the unburnt grazing lawn replicate plots. This is despite the fact that the average biomass in the ungrazed replicate plots more than doubled (from 79.2 to 198.4 g/75 m²) in the two years of the study in comparison to hardly any change (81.1 vs. 80.8 g/75 m²) in the grazed replicate plots. The insignificant result can be attributed to the small sampling size and the substantial variation found amongst the three replicates of both the grazed and ungrazed plots, which was a product

of the initial plot selection. Despite the low sampling size a significantly higher stoloniferous biomass value was found in the plots protected from herbivory versus the exposed replicate plots in the burnt lawn grassland block. It shows that the grazing pressure in this area was sufficient to cause a grazing treatment effect (see Table 5.2 & Fig. 5.3). It appears that this vegetation state is too resilient to undergo a state change in response to fire followed by either grazing or the absence of it.

The grazing lawn state of renosterveld responded, given the time span of this study, as we hypothesized in reaction to the presence of herbivores with or without fire treatment by remaining a grazing lawn (Fig. 5.6). The state did not change towards a shrubland in reaction to a single fire and protection from grazing, which we postulated to be a remote possibility.

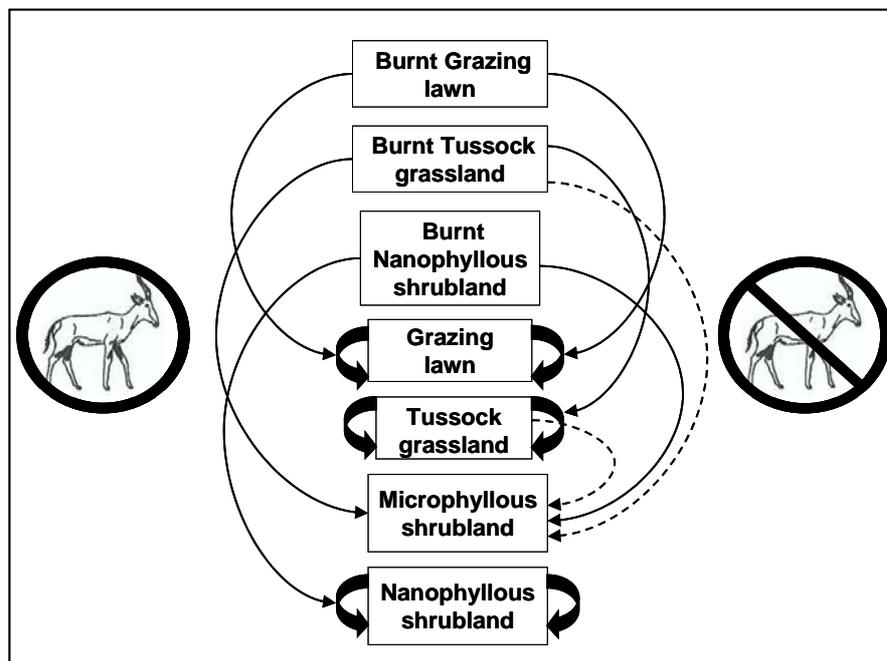


Fig. 5.6 Conceptual model of state changes experienced by renosterveld in response to presence/absence of both fire and herbivory. The solid lines show the prominent changes while the broken lines suggest changes experienced under unique conditions.

Cymbopogon pospischilii tussock grassland

The tussock grassland state showed less resilience to disturbance than the grazing lawn state. Five of the twelve experimental tussock grassland plots reacted to treatment (Figs. 5.4 & 5.5). All three grazed and burnt tussock grassland plots underwent a change and became *Athanasia trifurcata* shrubland with a *C. pospischilii* tussock grass understory. This observation supports the predictions that intense grazing of tussock grasslands following fire can facilitate shrub invasion in renosterveld (Sparman 1786; Du Toit & Du Toit 1938; Stindt *et al.* 1965; Joubert & Stindt 1979; Cowling *et al.* 1986; McDowell 1988). However, the shrub species involved here was not the nanophyllous *E.*

rhinocerotis, but the microphyllous *A. trifurcata*. It is interesting that this state change occurred after only a single fire followed by intense grazing, and that repeated fire is apparently not needed to initiate such change as suggested by Cowling *et al.* (1986). It is of added interest that bontebok was unable to convert any of the areas into grazing lawn, and that the browsing eland and ostrich were unable to keep the *A. trifurcata* seedlings from establishing. This indicates that these shrubs must be well resistant to trampling and grazing/browsing immediately following their germination. The significantly higher tussock-grass biomass in the exclosure plots in comparison to that of the grazed plots (see Table 5.2 and Fig. 5.3) is an indication that the grazing pressure was high enough to be implicated as the factor responsible for the state change.

The detected shrub invasion in tussock grasslands can be corroborated by a number of well documented cases of competition between germinating shrub seedlings and the regrowing grass layer (Strang 1969; Madany & West 1983; Knoop & Walker 1985; Skarpe 1990; Bullock *et al.* 1994; Van Auken 2000; Gillespie & Allen 2004). In our case the competition presumably occurred between the resprouting *C. pospischilii* tussock grasses and *A. trifurcata* shrub seedlings germinating after fire. Within the grazed plots the resprouting tussock grasses were grazed so extensively that they were unable to out-compete the germinating *A. trifurcata* shrubs, hence the area consequently converted to shrubland. In two of the exclosure plots the tussock grasses grew so vigorously that they prevented the shrubs from establishing and exclosures retained their tussock-grassland appearance after the fire. Midoko-Iponga *et al.* (2005) looked at influence of grass competition on transplanted renosterveld shrub seedlings and found that grass had a notable influence on *A. trifurcata* seedling growth. The third exclosure plot that converted to an *Athanasia* shrubland (Plot A in Fig. 5.5) actually supports the competition hypothesis. Closer inspection of this plot revealed that it had less tussock grass biomass compared to the other two replicate plots before the fire (213 vs. 373 & 382 g/0.75 m²) and more importantly the number of tussocks within the whole plot (as counted from photographs taken directly after the fire) was 55% and 57% less than that in the other two plots (88 vs. 153 & 160 tussocks per plot). We therefore hypothesise that the initial density of tussocks in this plot was too low to out-compete the germinating shrubs – even in the absence of grazing. This hypothesis hence implies that it is not only the effect of fire followed by heavy grazing that might cause a state change, but that the initial density of tussock grasses might also be of importance and can perhaps explain why Cowling *et al.* (1986) maintained that repeated fire followed by heavy grazing is necessary to bring about a state change. If the tussock density is above a certain threshold before a fire, it might actually be able to prevent shrub germination even in the presence of grazing following the fire. Repeated fire and intense grazing bouts might then be necessary to reduce the tussock density to a point where the shrubs can establish successfully (see Weber *et al.* 1998 on the threshold concept). This hypothesis is in direct conflict with the findings that the North American shrub *Prosopis glandulosa* can invade grassland irrespective of the herbaceous biomass present above (Brown & Archer 1999) or below ground (Jurena & Archer 2003). It might, however, be that *P. glandulosa* and associated grasses compete in a different manner for resources than is the case between *C. pospischilii* and *A. trifurcata*. The fact that no statistically significant difference could be detected between the microphyllous shrub biomass in the grazed and ungrazed burnt

plots can be attributed to the biomass in the enclosure plot that also converted to a microphyllous shrubland. This ungrazed plot accumulated more microphyllous shrub biomass (240 g/0.75 m²) than any of the three grazed plots (48, 58 & 121.5 g/0.75 m²).

The question still remains, however, why there were no *E. rhinocerotis* seedlings found in the burnt tussock grassland despite the fact that *E. rhinocerotis* form viable seedbanks (Du Toit & Du Toit 1938; Levyns 1956; Cowling *et al.* 1986). Isolated individuals of *E. rhinocerotis* were present in the area before the fire treatment and dense *E. rhinocerotis* stands occurred within 300 meters from this experimental block. This distance is short enough to assure that the wind dispersed seeds of *E. rhinocerotis*, known to travel fairly long distances (Cowling *et al.* 1986), reach the sites with ease. We hypothesise that *A. trifurcata* is a much better competitor at the seedling stage with the resprouting and grazed *C. pospischilii* grass than the shade and drought sensitive *E. rhinocerotis* (Cowling *et al.* 1986). The tussock grass density can thus be sufficient enough to prevent *E. rhinocerotis* establishment after a fire – even with the presence of grazing, but still the density might not be high enough to prevent *A. trifurcata* establishment.

Among the unburnt tussock grassland plots, which showed no apparent tendency for a state change, we detected an interesting anomaly: one of the ungrazed plots grouped with four burnt tussock grassland plots that converted to shrubland (Plot B in Fig. 5.5). Here we propose that the absence of herbivore trampling, a recognised disturbance effect (Zimmerman & Neuenschwander 1984; Hester *et al.* 2006; Hobbs 2006), could have caused the conversion to a shrubland state. Within this plot *Helichrysum crispum* is the shrub causing the regrouping. *Helichrysum* has high levels of secondary metabolites and are strongly aromatic (Van Wyk & Gericke 2003), making it unpalatable to herbivores. However, their young stems and leaves are soft, which makes them vulnerable to trampling. Small inconspicuous individuals of *H. crispum* were present within this plot before the experimental treatment took place and these flourished in the absence of herbivores/trampling during the two years. Similar sized individuals present within two of the grazed plots before the onset of the experiment did not increase in size and some even disappeared within the two years of the study. The significantly higher tussock grass biomass in the ungrazed replicate plots in comparison to that of the grazed replicates (Table 5.2 and Fig. 5.3) in this unburnt tussock grassland is again an indication that the grazing and trampling pressure were high enough to be implicated as factors in the state changes.

Our findings are in direct conflict with some of the predicted state changes (see Figs. 5.1 & 5.6). There is no evidence that the assemblage of herbivores present can change established tussock grassland to a grazing lawn – either with or without the help of fire in the time span of two years following a fire. Intense grazing after fire actually caused a change to microphyllous shrubland. Burnt tussock grassland did remain tussock grassland as predicted in the absence of herbivores where the initial density of tussocks were high enough, but it converted to a microphyllous shrubland where this requirement was not met. Unburnt tussock grassland changed to microphyllous shrubland where small trampling sensitive shrubs were present before the removal of herbivores. Our results suggest that in the absence of small established shrubs, the tussock grassland should

remain unchanged for the foreseeable future. When and how the trampling sensitive shrubs became established, remains unclear.

Elytropappus rhinocerotis shrubland

This vegetation state showed the most diverse reaction towards burning. All six plots in the burnt block showed marked change in their dendrographic and ordination positions after 24 months relative to their initial positions at the start of the experiment (Figs. 5.4 & 5.5). The three plots protected from grazing after the burn showed markedly different reactions to this treatment. One of the plots converted to *A. trifurcata* shrubland with a dense *C. dactylon* stoloniferous grass understory, another turned into *A. trifurcata* shrubland with dense *Ehrharta calycina* tussock grass understory, while the third became *Hermania flammula*–*Athanasia trifurcata* shrubland with a very sparse grass understory (Plots C, D and E in Fig. 5.5, respectively).

We choose to explain this disparate response according to the initial species composition present within the plots before the fire. The plot converted to a *C. dactylon* grazing lawn was the only one that had some *C. dactylon* present within its sub-plots before the fire. In similar fashion there were at least two small shrubs of *Hermania flammula* present within the plot (but not in the sub-plots) that converted into *Hermania*–*Athanasia* shrubland. There were, however, no *E. calycina* recorded in the plots before the fire. Important though is that none of these three plots contained any *E. rhinocerotis*, the nanophyllous shrub that dominated these plots before the fire. This is in direct contrast to the three burnt plots subject to herbivory in which *E. rhinocerotis* re-established and became the dominant biomass in two of the plots. We hypothesise that in the exclosures the rapid recovery and establishment of grass out-competed the light-demanding and drought-sensitive *E. rhinocerotis* seedlings. Within the burnt plots exposed to grazing, the herbivores removed the plants competing with the *E. rhinocerotis* seedlings. *Hermania* is known to be palatable (Walton 2005), which might explain why it is only present (and dominating) in an exclosure plot. *Hermania flammula* and *A. trifurcata* seedlings may be less sensitive to competition than *E. rhinocerotis* seedlings as they managed to establish in the exclosure plots despite competition with the grasses. Why the unpalatable *A. trifurcata* is not dominating this burnt experimental block, as observed in the burnt tussock grassland block, is unclear but it might be due to a difference in the seed bank densities at the time of the fire. The tussock grassland and shrubland experimental blocks are 700 meters apart, but *A. trifurcata* seeds are wind dispersed (Shiponeni & Milton 2006) and there were also some individuals present in the experimental block before the fire. The disparate response of the three replicate plots in reaction to fire and the absence of grazing explain the insignificant proof for grazing pressure in this shrubland block. The biomass of both tussock and lawn grasses are, however, visibly higher in the exclosure replicates than in the grazed ones (Fig. 5.3).

The biomass composition (growth forms) in the unburnt exclosure plots showed no significant difference from the grazed plots after two years. There is, however, a marked increase in both tussock grass and microphyllous shrub biomass in the exclosure plots relative to that of the unprotected plots (Fig. 5.3). This can be attributed to grazing and

trampling in the unprotected plots, but the impact is much less than that found in the tussock grassland and grazing lawn.

The predicted state changes of shrubland to grassland were refuted in most cases (see Figs. 5.1 & 5.6). Burnt shrubland in the presence of herbivory does not convert to grazing lawn, but returns to a nanophyllous shrubland state. This is not due to the resprouting of *E. rhinocerotis* from epicormic buds of roots (not a single burnt shrub was found to use this type of regeneration in the whole of the burnt block), but from the successful germination of seedlings. After the fire, none of the burnt ungrazed shrubland plots converted back to nanophyllous *E. rhinocerotis* shrubland. All three plots can now be classified as microphyllous shrubland, each having a very different understory (dense tussock grass layer, dense lawn grass layer, and creeping shrub layer).

Synthesis and application

This study corroborates the findings of Noy-Meir (1995) gathered in Mediterranean grasslands that fire and grazing have both distinct and interactive effects on vegetation communities and therefore should not be seen as two alternative mechanisms of disturbance. It also supports the conclusions of Weisberg and Bugmann (2003) that the effects of fire can not be understood without considering grazing as well. Herbivory by native grazers/browsers, or the release from it, can not by itself bring about vegetation-state changes in this herbivore-tolerant plant community. However, a combination of herbivory with fire can have major effects on the vegetation state dynamics. The processes involved are the direct and indirect effect of herbivory (Weisberg & Bugmann 2003) on seedling survival after fire. The physical removal of highly palatable and sensitive grass and shrub seedlings qualify as the direct effect while the indirect effect is defined as the reduction of the biomass of grazing and fire resistant grass species (and consequently a competition factor) that then indirectly affect unpalatable shrub seedling establishment.

The nature of the renosterveld state dynamics can be best approximated by the state and threshold model (Westoby *et al.* 1989; Laycock 1991), which postulates that a community can have alternative stable compositions after passing through a threshold triggered by past grazing management or episodic disturbance events (Cingolani *et al.* 2005). We suggest that the studied renosterveld patch in DHNR became a herbivore-resistant community composed of different structural states due to the persistent pressure of herbivores and can now only be altered by a drastic disturbance event such as fire.

Renosterveld patches still supporting shrub and grasses sensitive to grazing and browsing should only be exposed to herbivory at densities low enough to prevent their complete removal. The only way by which to convert renosterveld that is already in an unpalatable shrubland state to a palatable grassland and/or shrubland, is by removing herbivores completely after fire. This will provide the palatable shrubs and grasses (if there are viable meristem banks available) with the opportunity to re-establish. It might take some time before these species will be able to resist even light herbivory. Fire and grazing by native herbivores do not alter *C. dactylon* grazing lawn, but a possibility remains that

prolonged absence of grazing might result in a state change eventually. Tussock grassland in renosterveld can be converted to shrubland by heavy grazing after fire. These grasslands should be rested after fire to preserve their structure and texture (species composition), providing that the tussock density is high enough in the first place to prevent shrub seedling recruitment.

Our data and interpretations support the notion that a high fire frequency followed by intense grazing by livestock could have converted original renosterveld grasslands to unpalatable shrublands (Cowling *et al.* 1986). Native large herbivores of both the grazing (bontebok) and mix-feeding guild (ostrich or eland) are unable to remove unpalatable shrubs after fire. We must therefore conclude that the removal of herbivores from the system could not have contributed to the postulated vegetation change. We are, however, still uncertain about the impact black rhino and elephant might have had before they became extinct in the lowland landscapes of the Cape. Recent reports based on the diet of a captive black rhino suggests that these animals can utilise *E. rhinocerotis* (R. Erasmus, personal communication) but it is assumed that they never occurred on the lowlands in densities which could have caused massive state changes in the first place.

References

- Archer S., Schimel D.S. & Holland E.A. (1995) Mechanisms of shrubland expansion: land use, climate or CO₂? *Climate Change*, 29, 91-99
- Archibald S. & Bond W.J. (2004) Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13, 377-385
- Archibald S., Bond W.J., Stock W.D. & Fairbanks D.H.K. (2005) Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications*, 15, 96-109
- Augustine D.J. & McNaughton S.J. (1998) Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, 62, 1165-1183
- Beukes P.C. (1984) *Sommige aspekte van die ekologie van die Vaalribbok (Pelea Capreolus, Forster 1790) in die Bontebok Nasionale Park*. MSc. Thesis, University of Stellenbosch
- Beukes P.C. (1987) Responses of grey rhebuck and bontebok to controlled fires in coastal renosterveld. *South African Journal of Wildlife Research*, 17, 103-108
- Bond W.J., Woodward F.I. & Midgley G.F. (2002) Does elevated CO₂ play a role in bush encroachment? In: *Multiple use management of natural forests & woodlands: policy refinements and scientific progress. Natural Forests & Savanna Woodlands Symposium III* (eds. Seydack A.H.W., Vorster T., Vermeulen W.J. & Van der Merwe I.J.), pp. 202-208. Department of Water Affairs and Forestry, Pretoria
- Bond W.J. & Archibald S. (2003) Confronting complexity: fire policy in South African savanna parks. *International Journal of Wildland Fire*, 12, 381-389
- Bond W.J. & Midgley G.F. (2000) A proposed CO₂ controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology*, 6, 865-869

- Boshoff A.F. & Kerley G.I.H. (2001) Potential distribution of the medium- to large-size mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *African Zoology*, 36, 245-273
- Boucher C. (1981) Floristic and structural features of the coastal foreland vegetation south of the Berg River, Western Cape Province, South Africa. In: *Proceedings of a symposium on coastal lowlands of the Western Cape* (ed. Moll E.J.), pp. 21-25, University of the Western Cape, Bellville
- Boucher C. & Moll E.J. (1981) South African mediterranean shrublands. In: *Ecosystems of the world, 11, Mediterranean-type shrublands*. (eds. Di Castri F., Goodall D.W. & Specht R.L.), pp. 233-248. Elsevier, Amsterdam
- Brown J.R. & Archer S. (1999) Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology*, 80, 2385-2396
- Cowling R.M. (1984) A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. *Bothalia*, 15, 175-227
- Cowling R.M., Pierce S.M. & Moll E.J. (1986) Conservation and utilisation of South coast Renosterveld, an endangered South African Vegetation type. *Biological Conservation*, 37, 363-377
- DeSimone S. & Zedler P.H. (1999) Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. *Ecology*, 80, 2018-2032
- du Toit R. & du Toit E. (1938) Rhenoster Bush as a weed. *Farming in South Africa*, 1938, 429-445
- Dublin H.T., Sinclair A.R.E. & McGlade J. (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodland. *Journal of Animal Ecology*, 59, 1147-1164
- Guglielmini A.C. & Satorre E.H. (2004) The effect of non-inversion tillage and light availability on dispersal and spatial growth of *Cynodon dactylon*. *Weed Research*, 44, 366-374
- Heard H.W., Hoekstra T., Swanepoel R.B., Burgers C.J., Lloyd P.H. & Roets W. (2001) *Management plan for De Hoop Nature Reserve*. Unpublished report, Cape Nature Conservation, Cape Town
- Heisler J.L., Briggs J.M. & Knapp A.K. (2003) Long-term patterns of shrub expansion in a C₄-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. *American Journal of Botany*, 90, 423-428
- Hester A.J., Edenius L., Buttenschon R.M. & Kuiters A.T. (2000) Interaction between forests and herbivores: the role of controlled grazing experiments. *Forestry*, 73, 381-391
- Hobbs N.T. (1996) Modification of ecosystems by ungulates. *Journal of Wildlife Management*, 60, 695-713
- House J.I., Archer S., Breshears D.D., Scholes R.J. & Participants NCEAS Tree-Grass Interactions Participants (2003) Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*, 30, 1763-1777
- Jeltsch F., Weber G.E. & Grimm V. (2000) Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology*, 161, 161-171
- Joubert J.G. & Stindt H.W. (1979) The nutritive value of natural pastures in the district of Swellendam in the winter rainfall area of the Republic of South Africa. *Technical*

- Communication, Department of Agriculture, Technical Services, Republic of South Africa*, 156, 1-10
- Jurena P.N. & Archer S. (2003) Woody plant establishment and spatial heterogeneity in grasslands. *Ecology*, 84, 907-919
- Kemper J., Cowling R.M. & Richardson D.M. (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation*, 90, 103-111
- Kraaij T. & Ward D. (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, 186, 235-246
- Krug R.M., Krug C.B., Midoko-Iponga D., Walton B.A., Milton S.J., Newton I.P., Farley N. & Shiponeni N.N. (2004) Reconstructing West Coast Renosterveld: Past and present ecological processes in a Mediterranean shrubland of South Africa. In: *Proceedings of the 10th MEDECOS Conference* (eds. Arianoutsou, M. & Papanastasis, V.), pp. 120-132. Millpress, Rotterdam
- Lepš J. & Šmilauer P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge
- Levyns M.R. (1956) Notes on the biology and distribution of the Rhenoster bush. *Suid Afrikaanse Joernaal van Wetenskap*, 52, 141-143
- Luyt E. du C. (2005) *Models of Bontebok (Damaliscus pygargus pygargus, Pallas 1766) habitat preferences in the Bontebok National Park and sustainable stocking rates*. MSc. Thesis, Stellenbosch University
- Maclean G.L. (1984) *Roberts' Birds of southern Africa*. 5 edn. John Voelcker Bird Book Fund, Cape Town
- Malan J.A., Viljoen J.H.A., Siegfried H.P. & Wickens H.d.V. (1994) *Geologie van die gebied Riversdale*. Government Printer, Pretoria
- McDowell C.R. (1988) *Factors affecting the conservation of Renosterveld by private landowners*. PhD Thesis, University of Cape Town
- McNaughton S.J. (1984) Grazing lawns: Animals in herds, plant form, and coevolution. *American Naturalist*, 124, 863-886
- Milton S.J., Dean W.R.J. & Siegfried W.R. (1994) Food selection by ostrich in Southern Africa. *Journal of Wildlife Management*, 58, 234-248
- Moll E.J. (1987) Review of some new concepts in "Fynbos" ecology. In: *Papers in the prehistory of the western Cape. British Archaeological Reports International Series 332*, (eds. Parkington J. & Hall M.), pp. 132-163. BAR, Oxford
- Newton P.I. & Knight R. (2004) The Matrix: The development of coastal renosterveld. *Veld & Flora*, 90, 162-165
- Novellie P. (1987) Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe*, 30, 1-17
- Oloff H., Vera F.W.M., Bokdam J., Bakker E.S., Gleichman J.M., Maeyer K. & Smit R. (1999) Shifting mosaics in grazed woodlands driven by the alteration of plant facilitation and competition. *Plant Biology*, 1, 127-137
- Owen-Smith N.R. (1988) *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge
- Podani J. (1994) *Multivariate data analysis in ecology and systematics*. SPB Publishing, The Hague

- Podani J. (1997) Explanatory variables in classifications and the detection of the optimum number of clusters. In: *Data Science, classification, and related methods* (eds. Hayashi C., Ohsumi N., Yajima K., Tanaka Y., Bock H. & Baba Y.). Springer-Verlag, Tokyo
- Podani J. (2001) *SYN-TAX 2000. Computer programs for data analysis in ecology and systematics. User's manual*. Scientia Publishing, Budapest
- Radloff F.G.T. & Mucina L. (2007) A quick and robust method for biomass estimation in structurally diverse vegetation. *Journal of Vegetation Science*, 18, 719-724
- Rebello A.G. (1995) Renosterveld: Conservation and research. In: *The sustainable use and management of Renosterveld remnants in the Cape floristic region: proceedings of a symposium* (eds. Low A.B. & Jones F.E.), pp. 63-67. Botanical Society of South Africa, Cape Town
- Rebello A.G., Boucher C., Helme N., Mucina L., Rutherford M.C., Smit W.J., Powrie L.W., Ellis F., Lambrechts J.J., Scott L., Radloff F.G.T., Johnson S.D., Richardson D.M., Ward R.A., Procheş Ş.M., Oliver E.G.H., Manning J.C., Jürgens N., McDonald D.J., Janssen J.A.M., Walton B.A., Le Roux A., Skowno A.L., Todd S.W. & Hoare D.B. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 52-219. SANBI, Pretoria
- Rouget M., Jonas Z., Cowling R.M., Desmet P.G., Driver A., Mohamed B., Mucina L., Rutherford M.C. & Powrie L.W. (2006) Ecosystem status and protection levels of vegetation types. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 725-737. SANBI, Pretoria
- Roques K.G., O'Connor T.G. & Watkinson A.R. (2001) Dynamics of shrub encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38, 268-280
- Rutherford M.C., Mucina L. & Powrie L.W. (2006) Biomes and bioregions of southern Africa. In: *The vegetation of South Africa, Lesotho and Swaziland*. (eds. Mucina L. & Rutherford M.C.), pp. 31-51. SANBI, Pretoria
- Sankaran M., Hanan N.P., Scholes R.J., Ratnam J., Augustine D.J., Cade B.S., Ginoux J., Higgins S.I., Le Roux X., Ludwig F., Ardo J., Banyikwa F., Bronn A., Bucini G., Caylor K.K., Coughenour M.B., Diouf A., Ekaya W., Feral C.J., February E.C., Frost P.G.H., Hiernaux P., Hrabar H., Metzger K.L., Prins H.H.T., Ringrose S., Sea W., Tews J., Worden J. & Zambatis N. (2005) Determinants of woody cover in African savannas. *Nature*, 438, 846-849
- Sankaran M., Ratnam J. & Hanan N.P. (2004) Tree-grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, 7, 480-490
- Scholes R.J. & Archer S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28, 517-544
- Skarpe C. (1990) Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology*, 27, 873-885
- Skarpe C. & Hester A.J. (2008) Plant traits, browsing and grazing herbivores, and vegetation dynamics. In: *The ecology of browsing and grazing* (eds. Gordon I.J. & Prins H.H.T.), pp. 217-261. Springer, Berlin

- Skead C.J. (1980) *Historical mammal incidence in the Cape Province. Volume 1: The western and northern Cape*. Department of Nature and Environmental Conservation of the Cape Provincial Administration, Cape Town
- Skinner J.D. & Chimimba C.T. (2005) *The mammals of the southern African subregion*. Cambridge University Press, Cape Town
- Sparman A. (1786) *A voyage to the Cape of Good Hope, towards the Antarctic Polar Circle, and round the world: but chiefly into the country of the Hottentots and Caffres, from the year 1772, to 1776. Vol. 2*. Robinson, London
- StatSoft I. (2007) STATISTICA (data analysis software system), version 8.0. www.statsoft.com
- Stindt H.W., Celliers P.G., Joubert J.G. & Perold I.S. (1965) The nutritive value of natural pastures in the Humansdorp area in the South East Cape Province of the Republic of South Africa. *Technical Communication, Department of Agriculture, Technical Services, Republic of South Africa*, 45, 1-13
- Stock W.D., Bond W.J. & Le Roux D. (1992) Isotope evidence from soil carbon to reconstruct vegetation history in the south-western Cape Province. *South African Journal of Science*, 89, 153-154
- ter Braak C.J.F. & Šmilauer P. (2002) *Canoco Reference manual and CanoDraw for Windows User's guide: Software for canonical community ordination (version 4.5)*. Microcomputer Power, Ithaca, N.Y.
- Van Auken O.W. (2000) Shrub invasions of North American semiarid grasslands. *Annual Reviews in Ecology and Systematics*, 31, 197-215
- Van der Wal R. (2005) Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, 114, 177-186
- Van Langevelde F., van de Vijver C.A.D.M., Kumar L., van de Koppel J., de Ridder N., van Adel J., Skidmore A.K., Hearne J.W., Stroosnijder L., Bond W.J., Prins H., H. T. & Rietkerk M. (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84, 337-350
- Van Wieren S.E. & Baker P.J. (2008) The impact of browsing and grazing herbivores on biodiversity. In: *The ecology of browsing and grazing* (eds. Gordon I.J. & Prins H.H.T.), pp. 263-292. Springer, Berlin
- Vinton M.A., Hartnett D.C., Finck E.J. & Briggs J.M. (1993) Interactive effects of fire, Bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *American Midland Naturalist*, 129, 10-18
- Von Hase A., Rouget M., Maze K. & Helme N. (2003) *A fine-scale conservation plan for Cape Lowlands Renosterveld*. Technical Report, Botanical Society of South Africa, Kirstenbosch
- Ward D. (2002) Do we understand the causes of bush encroachment in African savannas? In: *Multiple use management of natural forests & woodlands: policy refinements and scientific progress. Natural Forests & Savanna Woodlands Symposium III* (eds. Seydack A.H.W., Vorster T., Vermeulen W.J. & Van der Merwe I.J.), pp. 189-201. Department of Water Affairs and Forestry, Pretoria
- Williams J.B., Siegfried W.R., Milton S.J., Adams N.J., Dean W.R.J., Du Plessis M.A. & Jackson S. (1993) Field metabolism, water requirements, and foraging behavior of wild ostriches in the Namib. *Ecology*, 74, 390-404

Wisdom M.J., Vavra M., Boyd J.M., Hemstrom M.A., Ager A.A. & Johnson B.K. (2006)
Understanding ungulate herbivory – episodic disturbance effects on vegetation
dynamics: Knowledge gaps and management needs. *Wildlife Society Bulletin*, 34,
283-292

DEALING WITH STRUCTURALLY DIVERSE VEGETATION: A QUICK AND ROBUST METHOD FOR BIOMASS ESTIMATION

Published as: Radloff, F. G. T. and Mucina, L. (2007) Dealing with structurally diverse vegetation: a quick and robust method for biomass estimation. *Journal of Vegetation Science*, 18, 719-724

Introduction

Above-ground plant biomass is widely used in ecological studies to quantify temporal and spatial changes controlled by both biotic and abiotic factors (Frank & McNaughton 1992; Knapp & Smith 2001; Olofsson *et al.* 2001; Augustine 2003). Agricultural and forestry research and practice also rely heavily on biomass estimates aiding decision-making processes with regards to animal, pasture, and fire management (Sanderson *et al.* 2001; Sah *et al.* 2004). The needs of both scientific research and science-user communities have been a major driving force of the continued development and evaluation of possibly quicker and more reliable non-destructive biomass estimation methods since the early thirties of the past century (Levy & Madden 1933; Goodall 1952; Haydock & Shaw 1975; Boutton & Tieszen 1983; Alaback 1986; Jonasson 1988; Frank & McNaughton 1990; Catchpole & Wheeler 1992; Harmony *et al.* 1997; Ter-Mikaelian & Parker 2000; Sanderson *et al.* 2001; Bråthen & Hagberg 2004).

Vegetation stands comprising of diverse growth forms such as stoloniferous grasses, tussock grasses, dwarf shrubs, and shrubs are particularly challenging environments for biomass estimation. Often each growth form requires a separate measurement technique to obtain accurate results, and those few available techniques able to handle a magnitude of growth forms tend to be very laborious (Jonasson 1988; Catchpole & Wheeler 1992).

This paper describes a new, quick and robust method able to estimate the biomass of various growth forms (< 1.5 m) present within a 0.25 m² plot, using a field apparatus specifically designed for this purpose.

Approach

The fire-prone shrublands of the shale-derived soils in the coastal lowlands of the Western Cape, South Africa (also called 'renosterveld'; see Mucina & Rutherford 2006 for a definition) contains a multitude of growth forms like stoloniferous grasses, tussock grasses and shrubs. The need to determine the impact large herbivores have on the renosterveld growth form dynamics prompted the search for a biomass-estimation method capable of fast, reliable and repeatable non-destructive sampling.

No technique adhering to the above prerequisites could be found and this led to the development of a new technique that combines the strengths of the well-known and widely-used *point-quadrat* (Goodall 1952) and *disk meter* (Bransby *et al.* 1977) methods. The point-quadrat method, also known as the canopy intercept (Frank & McNaughton

1990), point intercept (Jonasson 1988), or point contact method (Catchpole & Wheeler 1992), uses the number of plant contacts to a lowered pin to predict biomass for various growth forms. It is very effective provided many plots are sampled intensively (> 10 pin lowerings per plot of 0.25 m²) (Bråthen & Hagberg 2004). The use of this technique is, however, not without drawbacks. It is difficult to use the point-quadrat method in windy conditions, the high number of touches to fine branches and leaves may make it impractical (tedious and time-consuming), and it is inefficient in vegetation with a vertical branch structure (Stampfli 1991; Catchpole & Wheeler 1992; Bråthen & Hagberg 2004).

The disk meter method also known as the plate drop method (Schneider & Bell 1985) correlates plant biomass with the height (above ground level) of a metal or wooden disk (0.1 to 0.75 m²) lowered onto the top of the canopy of vegetation. It provides good correlations for both homogenous grass (Santillan *et al.* 1979) and legume stands (Harmony *et al.* 1997), and acceptable correlations for homogenous shrub layers (Schneider & Bell 1985). The predictive power of this method, however, drops where more than one growth form or vegetation layer co-occur (Schneider & Bell 1985; Harmony *et al.* 1997) and become impossible to use if species of different growth forms produce intertwined or overlapping stands.

Intensive sampling of plots, as with the point quadrant method, appears to be the only way to obtain a measure of biomass of different growth forms in a vegetation-structurally heterogeneous environment, but it is inevitably time-consuming. The sampling time can however be reduced if the parameter to be correlated to biomass is easy to measure. Disk height, as measured with the disk meter method, is a reliable and quick biomass correlation parameter, but only for homogenous stands of the same plant growth form. With the new technique this problem is overcome by reducing the size of the disk to such an extent (3 cm diameter, 0.0007 m²) that numerous disk-height readings can be taken of each of the different growth forms within the same sampling plot. The aim is not necessarily to compress the biomass underneath the disk but rather to use the multiple mini disk-height readings to form an image of each growth forms' vertical structuring within the plot. This image expressed as a total height value is then correlated to biomass.

The new technique measures the height of the different growth forms within a 0.25 m² plot with the mini disks at up to a 100 fixed, evenly spaced points. The field tests described below shows that the sum of these height values for each growth form correlates well to the targeted growth forms biomass within the plot. Obtaining these disk height values for various growth forms are quick with the newly designed field apparatus called the Multipoint Minidisk Meter (MMM) (see Appendix 6.1 for the design of the equipment) that is easy to use (see Appendix 6.2 for the measurement procedure). The field tests further indicate that the sampling intensity within a plot can be reduced to as few as 25 disk-height readings per plot, which make the method even more efficient and user-friendly.

Testing of the method

Field tests were performed to: (1) establish how accurate the new method predicts the biomass of different plant growth forms, and (2) determine the sampling intensity necessary for reliable results.

Field data collection

The data collection was done in the De Hoop Nature Reserve (Western Cape Province, South Africa) in a patch of renosterveld re-established on old fields abandoned since 1979. The renosterveld vegetation of the area is characterized by three distinct growth forms namely stoloniferous grasses, tussock (bunch) grasses, and shrubs (< 1.5 m). The stoloniferous grass layer is dominated by *Cynodon dactylon* (Poaceae) and the shrub layer by *Elytropappus rhinocerotis* (Asteraceae). The tussock grasses comprise mainly of *Cymbopogon pospischilii*, with some *Eragrostis curvula*, *Ehrharta calycina*, *Themeda triandra* and *Sporobolus africanus* (all grasses) also present.

To test how well the numerous disk-height measurements correlates with the biomass (confined within the plot) of the specific growth form measured, twelve sampling plots (0.25 m²), dominated by that growth form, were chosen for measurement. The 12 plots were selected to incorporate a wide spectrum of the targeted growth forms structural and biomass variation. Within each plot a 100 evenly spaced disk-height measurements were taken of the targeted growth form and the position of each disk-height measurement recorded relative to the grid reference number of the measuring apparatus (see Appendix 6.1 for more detail). Thereafter all the above ground biomass of the measured growth form within the plot was removed by clipping it at ground level. Where an individual plant – like a shrub – had branches and leaves protruding past the boundaries of a plot, only the biomass within the confinements of the plot were collected. This material was stored in paper bags and oven-dried (60°C) to a constant dry weight. The biomass of the targeted growth form within the plot was then determined by weighing the dried sample to the nearest 0.01 g.

Data analysis

The sampling of the 36 plots (12 per growth form) provided us, for each plot, with a 100 disk-height values for the targeted growth form, as well as, with the weight of the growth forms' above ground biomass within the plot. The 100 disk-height values were summed to provide a single “total height” value for that specific growth form within the plot. This left us with 12 “total-height” and 12 corresponding above ground biomass values for each of the three respective growth forms. A regression line forced through the origin was fitted to each growth forms' 12 pairs of data points, expressing above ground biomass as a function of total height. Goodness of fit was expressed by the coefficient of determination (r^2) and the standard errors calculated.

To determine whether the sampling intensity within a plot can be reduced and still provide a reliable biomass estimation value, the number of disk-height measurement values, used for the calculation of “total height”, was reduced and new regression lines fitted. This is per implication the same as simply taking less disk height measurements within a plot. The disk-height values were removed in a stratified manner, so that the remaining values still portrayed an image of the measured growth forms structural shape, which we believe is an essential factor for good correlation values. The disk-height values were removed in accordance to their original position within the measuring grid, so that the retained disk-height values still formed an evenly spaced grid across the sampling plot. Two datasets with reduced disk-height measurement values were created, one with 50 and another with 25 values (see Fig. 6.1 for a visual explanation).

New “total height” values were calculated for each of the new reduced data sets by summing the remaining 50 and 25 values separately. These new “total height” values were then used together with the unaltered above ground biomass values to create additional regression lines. For comparison, three regression lines were thus created per growth form, each using the same set of biomass values as dependant variable but different “total height” values as independent variable (obtained from summing up 100, 50, and 25 disk-height values, respectively).

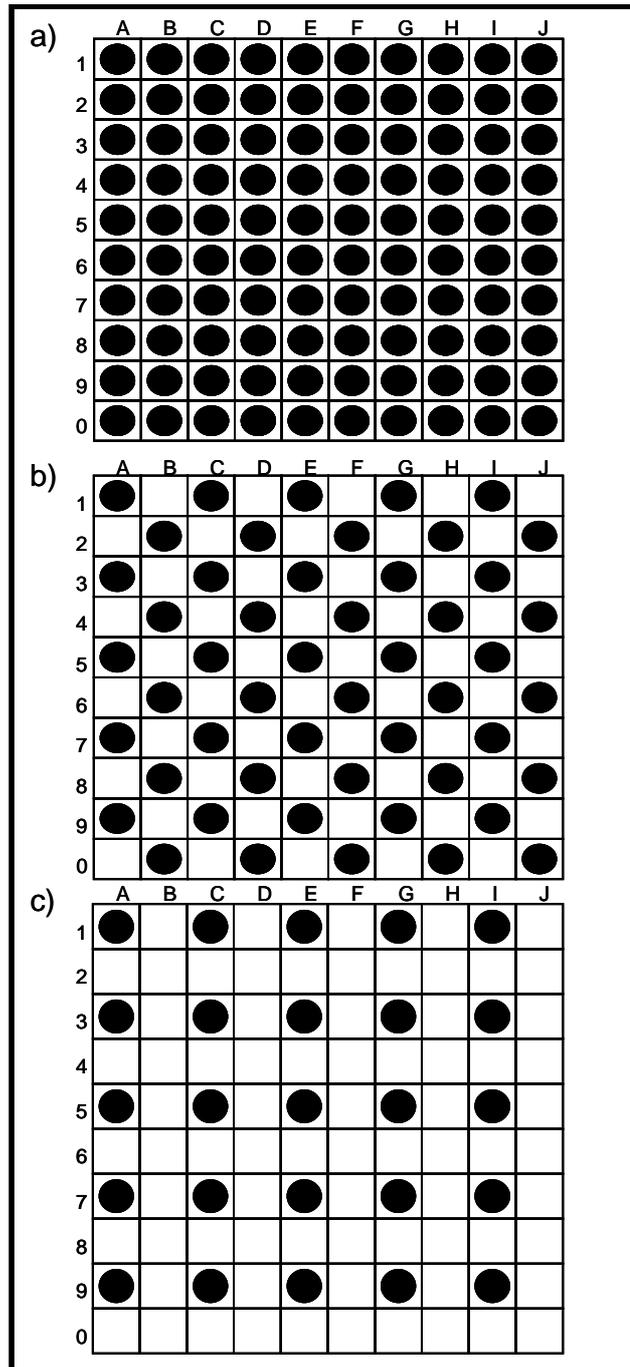


Fig. 6.1 The respective positions (•) of the mini disk height readings as used to determine separate “total height” (sum of the selected mini disk-height readings) values for the different sampling intensities: a) 100 points, b) 50 points and c) 25 points.

Results of the field tests

The relationship between “total height” (based on 100 measurements per plot) and the biomass present within the plot is highly significant for all three growth forms ($p < 0.00001$), with the explained variance above 90% in all cases (see Fig. 6.2 and Table 6.1).

The predictive power of this method varies little with regard to whether 100, 50 or 25 height measurements are used to calculate the “total height”. For each vegetation layer the difference in explained variance between the three regression lines is less than 1.6 % and remains above 88% in all cases (Table 6.1). The standard error is reduced with the reduction in disk-height measuring points to 25, for both lawn grass and shrubs. Only the standard error for the bunch-grass layer increases by 6% if the number of measurements is reduced to 25.

Table 6.1 Regression data for biomass based on three different “total height” values [sum of 100, 50, and 25 evenly spaced mini disk height readings (see fig. 6.1) as measured with the newly described apparatus (MMM)] determined for each growth form. $n=12$, r^2 = coefficient of determination, SE = standard error, b = slope of the regression line. All the regression lines were forced through the origin.

Growth-form	No. of measurements	r^2	SE	b
Stoloniferous grass	100	0.923	17.819	0.080
	50	0.918	18.219	0.161
	25	0.924	17.581	0.323
Tussock grass	100	0.903	58.040	0.111
	50	0.888	62.536	0.221
	25	0.890	61.980	0.432
Shrubs	100	0.959	78.016	0.102
	50	0.957	79.766	0.199
	25	0.962	74.844	0.390

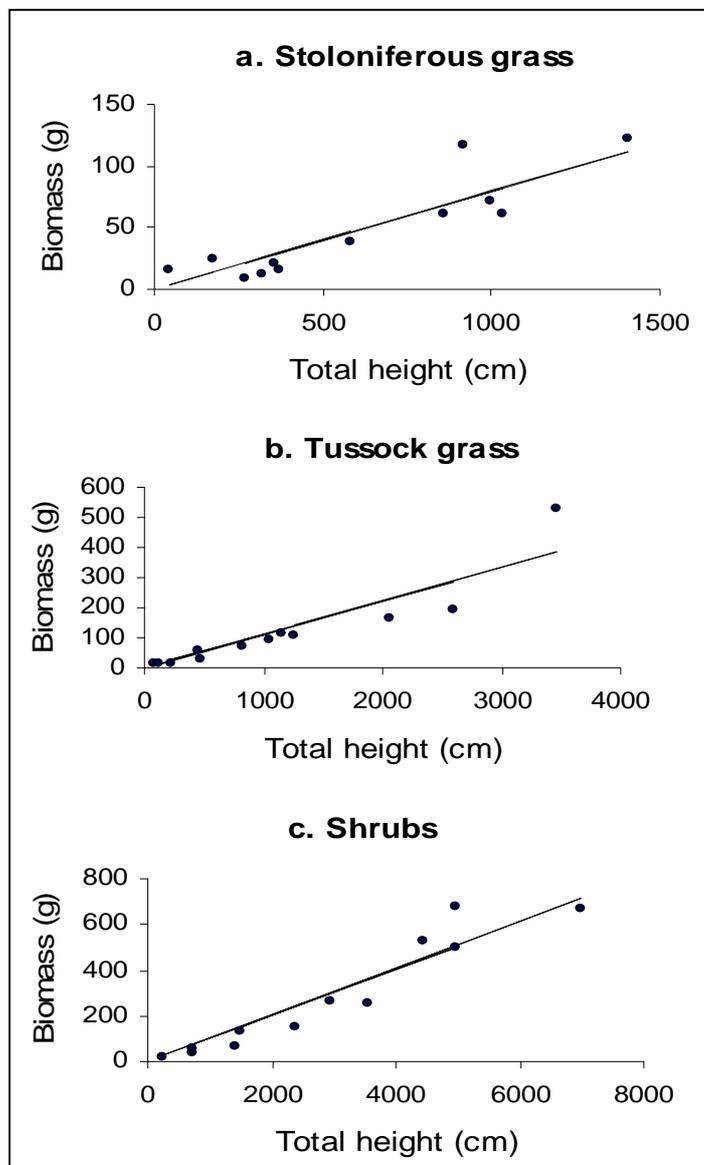


Fig. 6.2. Relationship between biomass and the sum of a 100 mini disk height values (“total height”) as measured with the newly described apparatus (MMM) in twelve 0.5 x 0.5 meter plots for each of the three respective growth forms: a) Stoloniferous grass: $y = 0.08x$, $n = 12$, $r^2 = 0.92$, b) Tussock grass: $y = 0.11x$, $n = 12$, $r^2 = 0.90$, c) Shrubs: $y = 0.10x$, $n=12$, $r^2 = 0.96$. The regression lines were forced through the origin.

Discussion

The explained variances for all regressions were very high (> 88 %) despite the small sample size (n=12). The new technique can thus be used with confidence to predict the biomass present within a 0.25 m² plot from total-height values as calculated from multiple evenly spaced disk-height measurements. Both the number of sampling plots and the sampling intensity within each plot have an influence on the standard error. Since the sampling intensity within plots has very little influence on the error values (Table 6.1), we conclude that the standard error will be reduced if the number of sampling plots are increased.

The field test described here measured only a single growth form in each plot. This was done because the plots were deliberately selected to be dominated by a particular growth form. This made it easier to select, for each growth form, plots with large variation in structure and biomass, which is important for calibration and test purposes. It also made harvesting much easier. Once the regression relations for all the respective growth forms are known the total biomass within plots with multiple growth forms can easily be measured at the same time. This is done by separately recording the height measurements of all the growth forms as they are encountered by the mini disk as it is manipulated through the vegetation till all the growth forms along a probes length have been accounted for (See Appendix 6.2 for more detail). The disk-height values recorded for each growth form are treated separately and “total height” values calculated for each. These separate “total height” values are then used in the regression equations of each growth form to predict the biomass within the plot. The process can be refined even further by calculating regression equations for particular species of interest. Disk-height measurements can then be taken for these species and their biomass within the plots determined.

The selective reduction of the number of disk-height measurements to 25 appears to have very little influence on the accuracy of the biomass prediction. The explained variance values remained high, irrespective of the amount of evenly spaced disk-height values used, as the standard error values either drop or increased only marginally. We believe that this is due to the stratified reduction of measuring points that enable a measure of the growth forms vertical structuring to be retained, albeit at a reduced resolution. If a limited number of random disk-height measurements are taken within a plot it is possible, purely by chance, that only particularly high or low parts of a growth form is measured. This can then lead to a under or over calculation of the growth forms “total height” and cause a consequent bias in biomass estimation. The chance of this happening with evenly spaced measurements is much reduced.

The amount of time saved by reducing the within plot sampling intensity from 100 to 25 points is quite substantial and makes the method very quick. A fieldwork session (involving three field workers), with only 25 evenly spaced disk-height readings, measured within a vegetation stand containing a mixture off all three growth forms , took on average only 8.07 minutes (\pm 2.25 minutes) per plot (n = 13) (this is without

harvesting). A further reduction of the number of height readings to 12 might still provide reasonable biomass predictive power, but we found that the species composition within a plot then starts to be under-represented (F. Radloff, unpublished data). Where the estimation of biomass per growth form is the sole aim, a further reduction in the number of height recordings may be considered.

If 25 height readings are found to be sufficient for biomass estimation within a specific vegetation type, alterations to the apparatus can be made to further reduce sampling time. Instead of using a plexi-glass box that needs to be moved five times within the frame in order to sample a single plot, a box capable of taking 25 evenly placed rods all at once can be used. A way to lower the rods and disks independently into the vegetation from such a box needs to be considered, and a multi-drawer system allowing each row of rods to be lower independently might be the solution.

The results of the field tests compare favourably to regression values published for similar tests done on the point-quadrat method (Jonasson 1988; Frank & McNaughton 1990), where 50 probes are used in 0.25 m². The MMM method is, however, less time consuming than the point-quadrat method as it is quicker to take a single disk-height measurement from a pin rather than counting the number of touches such a pin makes to the growth form it is lowered into. This argument is supported by Jonasson's (1988) statement that a 0.25 m² plot surveyed with the point-quadrat method should take around 45 min to complete in comparison to the 8 minutes taken for a plot surveyed with the MMM method (see above).

We are thus confident that the MMM method provides a good alternative biomass estimation method for vegetation composed of diverse growth forms, especially where sampling time is of essence. It will be especially useful to closely track changes in biomass within the same plot over time.

References

- Alaback P.B. (1986) Biomass regression equations for understory plants in coastal Alaska: Effects of species and sampling design on estimates. *Northwest Science*, 60, 90-103
- Augustine D.J. (2003) Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem. *Plant Ecology*, 167, 319-332
- Boutton T.W. & Tieszen L.W. (1983) Estimation of plant biomass by spectral reflectance in an East African Grassland. *Journal of Range Management*, 36, 213-216
- Bransby D.I., Matches A.G. & Krause G.F. (1977) Disk meter for rapid estimation of herbage yield in grazing trails. *Agronomy Journal*, 69, 393-396
- Bråthen K.A. & Hagberg O. (2004) More efficient estimation of plant biomass. *Journal of Vegetation Science*, 15, 653-660
- Catchpole W.R. & Wheeler C.J. (1992) Estimating plant biomass: a review of techniques. *Australian Journal of Ecology*, 17, 121-131
- Frank D.A. & McNaughton S.J. (1990) Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. *Oikos*, 57, 57-60

- Frank D.A. & McNaughton S.J. (1992) The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology*, 73, 2043-2058
- Goodall D.W. (1952) Some considerations in the use of point quadrats for the analysis of vegetation. *Australian Journal of Scientific Research, Series B: Biological Science*, 5, 1-41
- Harmoney K.R., Moore K.J., George R.J., Brummer C.E. & Russel J.R. (1997) Determination of pasture biomass using four indirect methods. *Agronomy Journal*, 89, 665-672
- Haydock K.P. & Shaw N.H. (1975) The comparative yield method for estimating dry matter yield of pasture. *Australian Journal of Experimental Agriculture and Animal Husbandry*, 15, 663-670
- Jonasson S. (1988) Evaluation of the point intercept method for the estimation of plant biomass, *Oikos*, 52, 101-106
- Knapp A.K. & Smith M.D. (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, 291, 481-484
- Levy B.E. & Madden E.A. (1933) The point method of pasture analysis. *New Zealand Journal Agriculture*, 46, 267-79
- Mucina L. & Rutherford M.C. (eds.) (2006) *The vegetation of South Africa, Lesotho and Swaziland*. SANBI, Pretoria
- Olofsson J., Kitti H., Rautiainen P., Stark S. & Oksanen L. (2001) Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, 24, 13-24
- Sah J.P., Ross M.S., Koptur S. & Snyder J.R. (2004) Estimating aboveground biomass of broadleaved woody plants in the understory of Florida Keys pine forests. *Forest Ecology and Management*, 203, 319-329
- Sanderson M.A., Rotz A.C., Flutz S.W. & Rayburn E.B. (2001) Estimating forage mass with a commercial capacitance meter, rising plate meter and pasture ruler. *Agronomy Journal*, 93, 1281-1286
- Santillan R.A., Ocumpaugh W.R. & Mott G.O. (1979) Estimating forage yield with a disk meter. *Agronomy Journal*, 71, 71-74
- Schneider B.H. & Bell D.T. (1985) A simple, effective technique for rapid measurement of fuels in low shrub communities. *Australian Forest Research*, 15, 79-84
- Stampfli A. (1991) Accurate determination of vegetational change in meadows by successive point quadrant analysis. *Vegetatio*, 96, 185-194
- Ter-Mikaelian M.T. & Parker W.C. (2000) Estimating biomass of white spruce seedlings with vertical photo imagery. *New Forest*, 20, 145-162

Appendix 6.1

The Multipoint Minidisk Meter (MMM)

The MMM consists of five different components that are easy to detach and transport (Fig. 6.3 A-E). These are four aluminium legs, a square metal frame, a plexi-glass box, 20 aluminium rods, and 20 small plexi-glass disks.

Plexi-glass disks

The transparent plexi-glass disks are 3 cm in diameter and 0.5 cm thick (Fig. 6.3A). The hole drilled through the centre of each disk is just wide enough to allow the disks free movement along the aluminium rods.

Aluminum rods

The rods are 6 mm in diameter and 1.5 m long (Fig. 6.3B). A nut has been secured to the end of each rod to prevent the disks from slipping off the bottom end of the rod. The edges of the nuts have been rounded to smooth the rods movement when lowered through the vegetation. Each rod has been marked at 1 cm intervals to assist accurate vegetation-height readings.

Plexi-glass box

The box is constructed of 1 cm thick transparent plexi-glass plates, and it is 50 cm long, 10 cm wide and 10 cm high (Fig. 6.3C). The short sides of the box are open, with two horizontal plates secured between the vertical sides, with one at the top and another 5 cm lower down. Each of these two plates has 20 evenly spaced holes in them that are aligned vertically in order to allow an aluminium rod to drop perpendicular through them to the ground. A third removable plate is positioned at the bottom of the box and can slide in and out like a drawer. This is used to secure the aluminium rods and plexi-glass disks in the box when it needs to be moved to a new position.

Metal frame and aluminium legs

The metal frame is a 50 x 50 cm hollow square with the sides 10 cm high (Fig. 6.3D). It has been designed to allow the plexi-glass box to slide freely into the frame at any of five adjacent positions, parallel to each other. There is a slit in two of the opposing sides of the frame to enable the free movement of the plexi-glass box's drawer plate.

Four metal brackets with adjustment screws are attached to the outside of the frame and each accommodates a square aluminium leg (3.8 x 3.8 x 150 cm) (Fig. 6.3E). The frame can be levelled at a comfortable height above the vegetation by independently adjusting each leg's height and securing it with the adjustment screws. The inside of the frame is marked to form a grid with alphabetical letters (a-j) on the one side, and numerals (0-9) on the side perpendicular to it. The inside of the frame is consequently divided into a 100 equally sized blocks, which coincide with the positions of the disks once the box and rods are secured in the frame. Each disk's position can thus be cross-referenced to a letter and number on the inside of the frame.

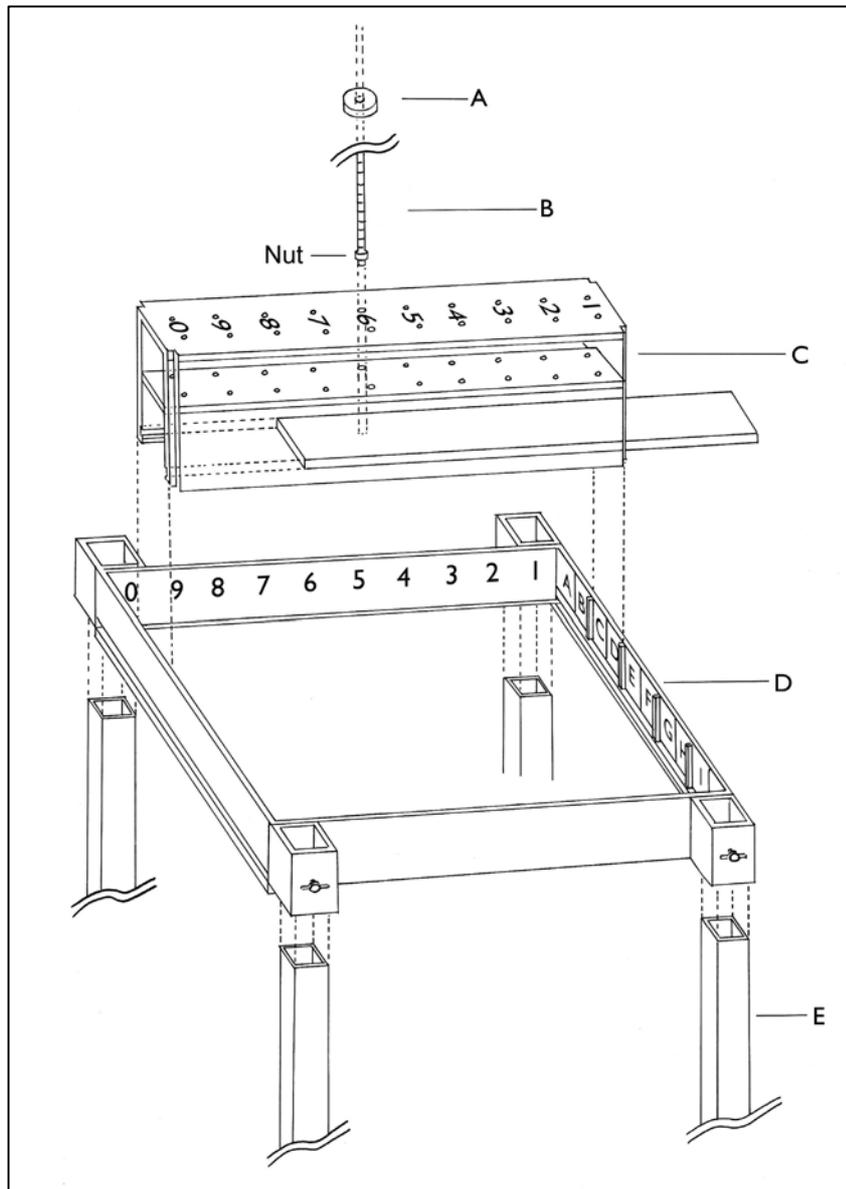


Fig. 6.3 The different components of the Multipoint Minidisk Meter. A – Plexi glass disk, B – Aluminum rod with nut, C - Plexi glass box with removable plate, D – Metal frame with leg brackets, E – Aluminum legs.

Appendix 6.2

Sampling procedure (Fig. 6.4)

A plexi glass disk is placed around each aluminium rod and moved down the length of the rod till it comes to rest on the nut attached to the bottom of it. The aluminium rods with their attached disks are then pushed into the aligned holes in the plexi-glass box from the bottom end after the removable plate has been removed. Once all the rods and their disks have been pushed into the box till they can go no further (the disk and nut at the end of each rod prevents it to be pulled through the box) the removable plate is replaced. The rods and disks are consequently secured into the box and can not move while the box is handled. The “loaded” box is then placed within the metal frame, which has been positioned horizontally above the vegetation.

The removable plate is slowly slid (through the slit in the side of the metal frame) out of the plexi-glass box in order to allow controlled lowering of the aluminium rods and the disks. The rods are allowed to slide through the vegetation stand onto the soil surface while the disks are held back (by hand) at the base of the box. Once a rod is firmly in contact with the ground, its disk is lowered along the rod and released on contact with the vegetation. The disk is then given time to settle and its height above-ground level is recorded to the closest half centimeter.

The resting height of each disk is recorded (with reference to the corresponding numeral and letter on the inside of the frame) together with the names of species the disk is touching. If the aluminium rod touches more than one growth form, the tallest growth forms' disk-height reading is taken first. Thereafter the disk is manipulated past this point and released on contact with the second growth form where its disk-height reading is also recorded. In this way disk-height readings of several growth forms can be recorded with minimum disturbance to the vegetation.

If all 20 aluminium rods are used in an analysis 100 disk-height values (20 readings at each of five positions within the frame) will be recorded for each growth form present within the 0.25 m².

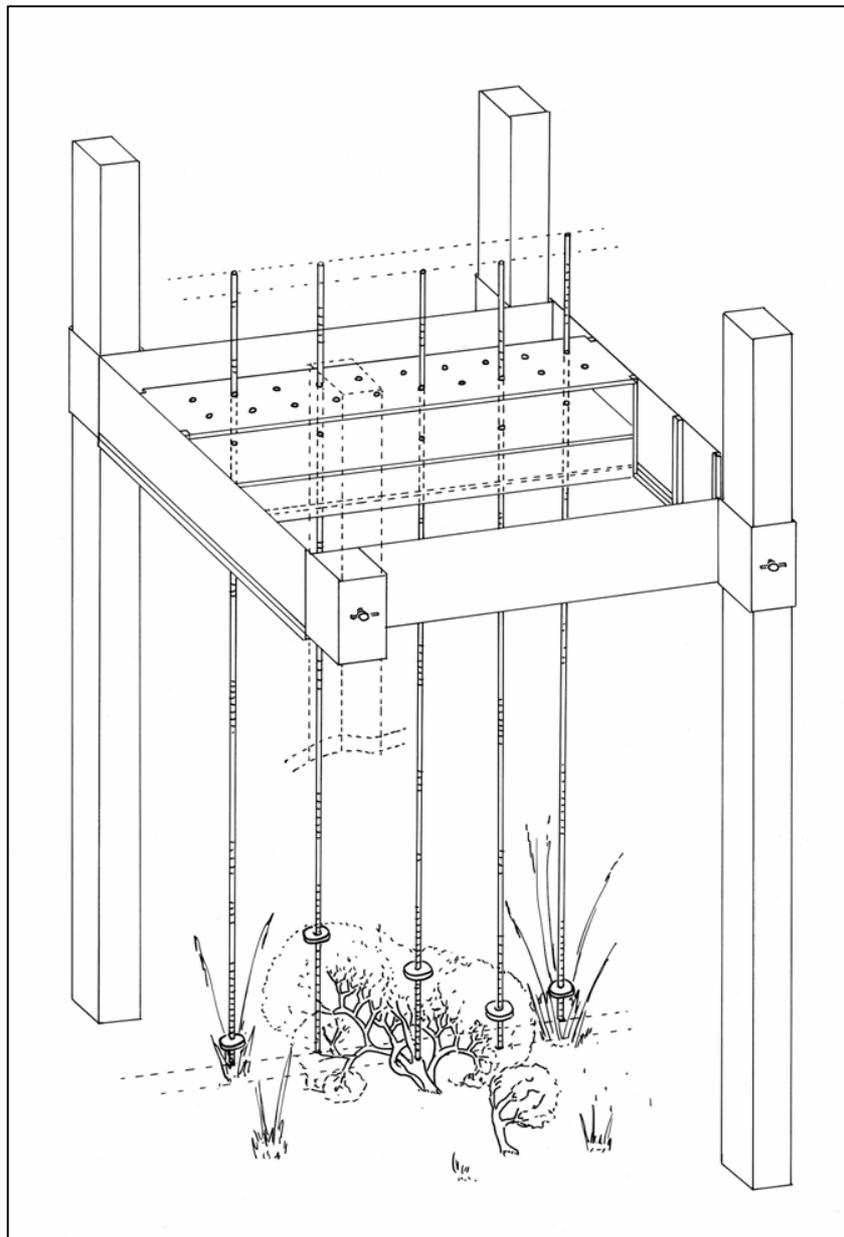


Fig. 6.4. The Multipoint Minidisk Meter assembled and in operation.

CONCLUSIONS WITH IMPLICATIONS FOR WILDLIFE MANAGEMENT AND SUGGESTIONS FOR FUTURE RESEARCH

Generating general theories that address the relationships between large herbivores and their environments is constrained by the complex nature of the interactions between animals, plants, and ecosystem components that varies across multiple spatial and temporal scales (Pastor & Cohen 1997). The coastal lowlands of the southwestern Cape is an area where diverse geology (Cowling *et al.* 1997; Rebelo *et al.* 2006) and variability in rainfall seasonality (Rebelo *et al.* 2006; Chase & Meadows 2007), together with overall climate stability (Cowling *et al.* 2005) have fostered the evolution of a complex, species-rich environment (Linder 2005). Large herbivore species native to the coastal lowland areas differ in their reaction to the spatial and temporal complexity of this environment and I therefore addressed questions relating to large herbivore ecology at different spatial scales.

At the scale of biome (Fynbos), I investigated the reasons for the absence of bontebok, buffalo and blue antelope from the western lowlands (Chapter 2). I hypothesised that these three species could not find enough sustenance to survive on the moribund C₃ grasses and very limited C₄ grass available to them on the western lowlands during the hostile summer months, when heat stress in this largely tree-less environment is highest and water availability is at its lowest. On the southern lowlands these large herbivores managed to survive because of an adequate supply of C₄ grasses that produced some green fodder of higher quality during the critical summer period. Evidence consistent with this Summer Nutritional Stress was found by means of carbon isotope analysis of late prehistoric, historic, and contemporary large herbivore remains. The analysis indicated that eland, elephant, grey rhebuck, ostrich and red hartebeest – all species that historically occurred on both the western and southern lowlands – can survive with as little as 15% C₄ grass in their diet. The diet of these species is in contrast to the bontebok, which utilizes a minimum of 26% and – in more natural environments – at least 43% of C₄ grass biomass. In summer carbon isotope analysis of bontebok dung revealed a diet of 73% C₄ grass. The samples of Cape mountain zebra (a non-ruminant grazer that occurred on both coastal lowlands) indicated a minimum C₄ grass consumption of 24%, but the samples were obtained from the southern lowlands where these animals had access to an adequate supply of both C₃ and C₄ grass. Further research on this topic could entail the carbon isotope analysis of the remains of the four blue antelope specimens in European museums which should reveal a high C₄ grass usage by these antelope to be consistent with the hypothesis. The evidence of a seasonal change in bontebok diet between C₄ and C₃ grass in De Hoop Nature Reserve also merits further investigation. This can be done elegantly by analysing bontebok tail hair increments isotopically, which should provide an accurate time sequence to the diet change (see Cerling *et al.* 2006, 2007). At the same time the quality of the available C₃ and C₄ fodder should also be analysed on at least a monthly basis across all seasons to confirm our postulated correlation between C₃ and C₄ forage quality and its intake by the bontebok.

Considering the evidence so far I postulate that obligate ruminant grazers (in particular bontebok) need access to an ample supply of C₄ grass during the stressful, dry summers characteristic of the southwestern Cape. The inappropriately introduced populations of obligate ruminant grazers on the western lowlands manage to survive by concentrating on anthropogenically transformed areas (e.g. fire breaks, old agricultural fields, recreational areas) hosting unnatural grazing lawns of C₄ pioneer species such as *Cynodon dactylon* (Langley & Giliomee 1974; Zumpt & Heine 1977; Walton 2005; Shiponeni & Milton 2006). These areas are kept in a grazing lawn state by the grazers that either prevent or prolong the time needed for the disturbed areas to convert back to their natural vegetation states (Walton 2005). The large herbivores also contribute to the dispersal of *C. dactylon* and alien grass seeds via endozoochory that further delay rehabilitation (Shiponeni & Milton 2006). The introduction of bontebok (or any other obligate ruminant grazer species) into remnant western lowland habitats, must therefore be discouraged if the main objective is to rehabilitate and preserve the natural vegetation of the western lowlands, such as the endangered renosterveld (Von Hase *et al.* 2003).

At a regional level I tested the Renosterveld Preference Hypothesis and found evidence in support of it (Chapters 3 and 4). Summer dung count surveys in De Hoop Nature Reserve showed that both eland and bontebok avoid sandstone fynbos and that limestone fynbos is only really utilised in micro-habitats such as karstic sinkholes filled with deep soils supporting grazing lawns. Renosterveld was, however, readily utilised by both species. The survey was done during a single summer for 84 consecutive days after which a prescribed burn forced its termination. The results of this survey might thus be considered too limiting for extrapolation to other seasons and years. However, considering the fact that the reserve was believed to be stocked close to its carrying capacity at the time of the survey (as substantiated by the October 2006 game census tallying the highest large herbivore numbers in the history of the reserve followed by a dramatic crash in the numbers of all large game) and that it was done at the peak of the dry season I am confident that the animals used all suitable habitat types. Whether additional surveys spanning multiple seasons and even years will provide contradicting results is doubtful. Personal communications with field rangers associated with the reserve for more than 20 years also supports this notion. Further support for my findings can be found in the work of Watson *et al.* (2005) and Watson and Chadwick (2007) who showed that even a non-ruminant species such as the Cape mountain zebra avoid sandstone fynbos, except after fire. Beukes (1987) and Novellie (1987) also found that the silcrete fynbos in the Bontebok National Park loses its appeal to grey rhebuck and bontebok four years after fire. All of these findings suggest that healthy large herbivore populations can only really be sustained on the coastal lowlands in areas that include a substantial part of the more nutrient-rich (Specht & Moll 1983) renosterveld habitats on shale. Limestone, sandstone and sand fynbos areas might be able to harbour some micro-habitats supporting small populations of large herbivores, but whether such areas will be able to support healthy and viable populations of large herbivores over the long term without serious management interventions such as rigorous burning programmes, remains to be seen. Unnaturally high fire frequencies can, however, lead to a loss of plant species diversity (Van Wilgen *et al.* 1992; Van Wilgen *et al.* 1994), which is undesirable in these

vegetation types rich in local endemics as well as rare and endangered species (Cowling *et al.* 1996; Goldblatt & Manning 2000).

The results of this study suggest that the model of Fritz and Duncan (1994) which predicts (for a given rainfall) the biomass of large herbivores that can be sustained in African savannas with low soil nutrient status, grossly overestimates the biomass of animals that can be supported on the limestone and sandstone substrates of the Fynbos Biome. This finding is, however, based on results from a herbivore assemblage that currently lack megaherbivores. Elephant and black rhino might have had slightly different habitat preferences than the mesoherbivores of the coastal lowlands. Theory predicts that megaherbivores should be able to cope with forage of very low quality as long as it is available in sufficient quantity (Fritz *et al.* 2002; Olff *et al.* 2002). The C-isotope analysis revealed an exceptionally low C₄ grass utilisation by elephants (Chapter 2) and, together with the work of Milewski (2002), this gives me reason to believe that elephants, and probably black rhino as well, might have been able to utilise a substantial amount of fynbos and strandveld in the lowlands. The two megaherbivore species might thus have been able to keep fynbos and strandveld more open than is currently the case and perhaps even caused it to harbour more grasses, as suggested by Hendey (1983). The low nutrient status of soils supporting the fynbos shrublands (Specht & Moll 1983) probably prevents grass persistence in the absence of regular fires. The fynbos species are better adapted to low nutrient levels and out-compete the grasses once the nutrient flushes induced by the fire recede (le Maitre & Midgley 1992; Cowling *et al.* 1997). Whether rhino and elephant could have provided the necessary nutrients for the maintenance of extensive grass patches through urine and dung deposition remains debatable. We will only really begin to grasp the historic role of megaherbivores in fynbos-grass dynamics when they are reintroduced into these habitats. The viable areas for such an experiment are presumably West Coast National Park, Agulhas National Park or the Greater De Hoop Area.

At a landscape level I investigated the interaction between fire and herbivory by native large herbivores in relation to renosterveld vegetation dynamics (Chapter 5). I conclude, given the scale and time span of the study, that the disappearance of the native herbivores probably had little to do with the putative change of renosterveld from a grassland to a shrubland, as was suggested by Krug *et al.* (2004) and Rebelo (1995). I did, however, find support for the notion that a high fire frequency followed by intense grazing by livestock could have converted original renosterveld grasslands to unpalatable shrublands (Sparrman 1786; Cowling *et al.* 1986; McDowell 1988). The results from this study suggest that herbivory by native grazers/browsers, or the release from it, cannot by itself bring about vegetation state changes in renosterveld that have already been altered to a herbivore-tolerant plant community. However, in combination with fire, the presence or absence of large herbivores seem to change the trajectory of the system among alternative states. Competition between germinating shrub seedlings and resprouting lawn or tussock grasses is suspected to be a key factor altering state trajectories. These findings and the consequent management suggestions can be seen as hypotheses that should be tested on a larger scale and at variable large herbivore population densities. Such experiments will, however, have to involve domestic stock as there is to my knowledge no lowland

renosterveld area other than in De Hoop Nature Reserve that is currently solely frequented by native large herbivores.

Renosterveld vegetation that still supports species sensitive to grazing must be carefully managed and only lightly grazed in order to avoid losing the sensitive species. Renosterveld areas of which the species composition has already been changed into a herbivore-tolerant community can be reverted to a state harbouring more grazing sensitive species by removing herbivores completely after fire. This will provide the palatable shrubs and grasses (if there are viable meristem banks available) with an opportunity to re-establish, but it might be some time before these species will be able to resist even light herbivory. How *C. dactylon* grazing lawns are established in the first place is not clear, as neither herbivory nor fire, or the combination of the two treatments, changed a tussock grassland or shrubland into a grazing lawn state. Established grazing lawns might, however, be converted to an alternative state if large herbivores are totally removed from the area, but this will probably be a slow process (certainly surpassing the two years of this study) that is in urgent need of further investigation. The tussock grassland state of renosterveld can be converted to a shrubland by heavy grazing following a fire; tussock grassland should be rested immediately after fire if such a change is undesirable.

The proper management of the few remnant renosterveld areas is crucial as only 5% and 12% of its original extent is still in a natural state on the western and southern lowlands, respectively (Von Hase *et al.* 2003). Even less areas enjoy proper protection (Rouget *et al.* 2003, 2006). I am of the opinion that if viable populations of the native large herbivores are to be successfully hosted on the lowlands, they will need access to large tracts of the more nutrient rich shale soils of the renosterveld areas. This will entail a considerable restoration effort of agricultural land, and whether these areas will ever resemble its original renosterveld state is debatable. It has been suggested that renosterveld had lost many plant species even before it has been explored botanically due to the detrimental farming practices of the Europeans (Rebello 1992). My results suggest that proper renosterveld restoration will only take place in the initial absence of large herbivores, at least until grazing sensitive plant species has been firmly established. Only then can the appropriate large herbivores be reintroduced and their numbers carefully managed to prevent these areas from converting to species poor grazing-tolerant communities.

A concerted effort needs to be made to either enlarge current reserves by including more remnant renosterveld, or to establish new reserves within this vegetation type. It is the only way we will ever be able to accommodate viable populations of the native large herbivores that used to roam this unique coastal environment only 350 years ago. Such an animal assemblage will, however, always miss one distinct species – the extinct blue antelope.

References

- Beukes P.C. (1987) Responses of grey rhebuck and bontebok to controlled fires in coastal renosterveld. *South African Journal of Wildlife Research*, 17, 103-108
- Chase B.M. & Meadows M.E. (2007) Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews*, 84, 103-138
- Cerling T.E., Wittenmyer G., Rasmussen H.B., Vollerath F., Cerling C.E., Robinson T.J. & Douglas-Hamilton I. (2006) Stable isotopes in elephant hair document migration patterns and diet change. *Proceedings of the National Academy of Science USA*, 103, 371-373
- Cerling T.E., Ayliffe L.K., Dearing D., Ehleringer J., Passey B., Podlesack D.W., Torregrossa A. & West A.G. (2007) Determining biological tissue turnover using stable isotopes: the reaction progress variable. *Oecologia*, 151, 175-189
- Cowling R.M., Ojeda F., Lamont B.B. & Rundel P.W. (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecology and Biogeography*, 14, 509-519
- Cowling R.M., Pierce S.M. & Moll E.J. (1986) Conservation and utilisation of South coast Renosterveld, an endangered South African vegetation type. *Biological Conservation*, 37, 363-377
- Cowling R.M., Richardson D. & Mustart P.J. (1997) Fynbos. In: *Vegetation of southern Africa* (eds. Cowling R., Richardson D. & Pierce S.), pp. 99-129. Cambridge University Press, Cambridge
- Cowling R.M., Rundel P.W., Lamont B.B., Arroyo M.K. & Arianoutsou M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, 11, 362-366
- Fritz H. & Duncan P. (1994) On carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society London*, 256, 77-82
- Fritz H., Duncan P., Gordon I.J. & Illius A.W. (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620-625
- Goldblatt P. & Manning J.C. (2000) *Cape plants. A conspectus of the Cape flora of South Africa*. National Botanical Institute & Missouri Botanical Garden Press, Pretoria & St Louis
- Hendey Q.B. (1983) Palaeontology and palaeoecology of the Fynbos region: an introduction. In: *Fynbos palaeoecology: a preliminary synthesis* (eds. Deacon H.J., Hendey Q.B. & Lambrechts J.J.N.), pp. 87-99, CSIR, Pretoria
- Krug R.M., Krug C.B., Midoko Iponga D., Walton B.A., Milton S.J., Newton I.P., Farley N. & Shiponeni N.N. (2004) Reconstructing West Coast Renosterveld: past and present ecological processes in a Mediterranean shrubland of South Africa. In: *Proceedings of the 10th MEDECOS Conference* (eds. Arianoutsou M. & Papanastasis V.P.), pp. 120-132. Millpress, Rotterdam
- Langley C.H. & Giliomee J.H. (1974) Behaviour of the bontebok (*Damaliscus d. dorcas*) in the Cape of Good Hope Nature Reserve. *Journal of the Southern African Wildlife Management Association*, 4, 117-121

- Le Maitre D.C. & Midgley J.J. (1992) Plant reproductive ecology. In: *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling R.M.). Oxford University Press, Cape Town
- Linder H.P. (2005) Evolution of diversity: the Cape flora. *Trends in Plant Sciences*, 10, 536-541
- McDowell C.R. (1988) *Factors affecting the conservation of Renosterveld by private landowners*. PhD Thesis, University of Cape Town.
- Milewski A.V. (2002) Elephant diet at the edge of the Fynbos Biome, South Africa. *Pachyderm*, 32, 29-38
- Novellie P. (1987) Interrelationship between fire, grazing and grass cover at the Bontebok National Park. *Koedoe*, 30, 1-17
- Olf H., Ritchie M.E. & Prins H.H.T. (2002) Global environmental controls of diversity in large herbivores. *Nature*, 415, 901-904
- Pastor J. & Cohen Y. (1997) Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. *Theoretical Population Biology*, 51, 165-179
- Rebello A.G. (1992) Preservation of biotic diversity. In: *The ecology of fynbos: nutrients, fire and diversity*. (ed. Cowling R.M.), pp. 309-344. Oxford University Press, Cape Town
- Rebello A.G. (1995) Renosterveld: Conservation and research. In: *The sustainable use and management of Renosterveld remnants in the Cape floristic region: proceedings of a symposium* (eds. Low A.B. & Jones F.E.), pp. 32-42. Botanical Society of South Africa, Cape Town
- Rebello A.G., Boucher C., Helme N., Mucina L., Rutherford M.C., Smit W.J., Powrie L.W., Ellis F., Lambrechts J.J., Scott L., Radloff F.G.T., Johnson S.D., Richardson D.M., Ward R.A., Proches S.M., Oliver E.G.H., Manning J.C., Jürgens N., McDonald D.J., Janssen J.A.M., Walton B.A., Le Roux A., Skowno A.L., Todd S.W. & Hoare D.B. (2006) Fynbos Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 52-219. SANBI, Pretoria
- Rouget M., Jonas Z., Cowling R.M., Desmet P.G., Driver A., Mohamed B., Mucina L., Rutherford M.C. & Powrie L.W. (2006) Ecosystem status and protection levels of vegetation types. In: *The vegetation of South Africa, Lesotho and Swaziland* (eds. Mucina L. & Rutherford M.C.), pp. 725-737. SANBI, Pretoria
- Rouget M., Richardson D.M. & Cowling R.M. (2003) The current configuration of protected areas in the Cape Floristic Region, South Africa – reservation bias and representation of biodiversity patterns and processes. *Biological Conservation*, 112, 129-145
- Shiponeni N.N. & Milton S.J. (2006) Seed dispersal in the dung of large herbivores: implications for restoration of Renosterveld shrubland old fields. *Biodiversity and Conservation*, 15, 3161-3175
- Sparman A. (1786) *A voyage to the Cape of Good Hope, towards the Antarctic Polar Circle, and round the world: but chiefly into the country of the Hottentots and Caffres, from the year 1772, to 1776. Vol. 2*. Robinson, London
- Specht R.L. & Moll E.J. (1983) Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In: *Mediterranean-type ecosystems: the*

- role of nutrients* (eds. Kruger F.J., Mitchell D.T. & Jarvis J.U.M.), pp. 41-65. Springer-Verlag, Heidelberg
- Van Wilgen B.W., Bond W.J. & Richardson D.M. (1992) Ecosystem management. In: *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling R.M.). Oxford University Press, Cape Town
- Van Wilgen B.W., Richardson D.M. & Seydack A.H.W. (1994) Managing fynbos for biodiversity: constraints and options in a fire-prone environment. *South African Journal of Science*, 90, 322-329
- Von Hase A., Rouget M., Maze K. & Helme N. (2003) *A fine-scale conservation plan for Cape Lowlands Renosterveld: Technical Report*. Botanical Society of South Africa, Kirstenbosch
- Walton B.A. (2005) *Vegetation patterns and dynamics of Renosterveld at Agter-Groenberg Conservancy, Western Cape, South Africa*. MSc Thesis, Stellenbosch University
- Watson L.H. & Chadwick P. (2007) Management of Cape mountain zebra in the Kammanassie Nature Reserve, South Africa. *South African Journal of Wildlife Research*, 37, 31-39
- Watson L.H., Odendaal H.E., Barry T.J. & Pietersen J. (2005) Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire. *Biological Conservation*, 122, 173-180
- Zumpt F. & Heine E.W.P. (1977) Some veterinary aspects of bontebok in the Cape of Good Hope Nature Reserve. *South African Journal of Wildlife Research*, 8, 131-134