A PLANT BASED STUDY OF THE FEEDING ECOLOGY OF INTRODUCED HERBIVORE GAME SPECIES IN THE CENTRAL FREE STATE

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A PLANT BASED STUDY OF THE FEEDING ECOLOGY OF INTRODUCED HERBIVORE GAME SPECIES IN THE CENTRAL FREE STATE

by

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I dedicate this thesis
to all who played a role
in making it possible

Psalm 147:7-9

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[1] Ortberg J 2008. Faith and doubt. Zondervan, Michigan, USA.

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CHAPTER 1
INTRODUCTION

INTRODUCTION

Game ranching can broadly be defined as the commercialization and utilization of wildlife by private landowners. It is an industry that is unique to southern Africa and should not be confused with game farming (definition in Chapter 2) that is also practiced in South Africa and various other parts of the world. While products from most of the traditional farming practices (e.g. cattle and sheep farming) can be produced in almost every country in the world, the rich wildlife resources of southern Africa are quite unique and its game product in relation to a specific natural environment is unrivalled in the world (Smit 2007). Exempted game ranches, where ownership of wildlife is vested in the owner of the property, further make South African game ranching unique (NAMC 2006).

By approximation there are 5 000 game ranches and 4 000 mixed game and livestock ranches in South Africa (NAMC 2006, Smit 2007). These cover some 17% of the country's total land area, compared with 6% for all officially declared conservation areas (NAMC 2006). The Free State province is less known as a game ranching area, but there are already an estimated 400 ranches with the number of traditional farms converting to game still increasing (Smit 2007). The value of wildlife is growing with a substantial potential of earning foreign capital (Du Toit 1995a), especially with the rapidly diminishing wildlife resources in other African countries (Smit 2007).

Formal conservation areas comprise a small percentage of the country (<6%), with more than 80% of South Africa available for agriculture and forestry (NAMC 2006). It is thus logical that land under private ownership is potentially important in conserving certain plant and animal species and unique ecosystems. Some people are of opinion that the conversion of a farming enterprise from cattle or sheep to game is synonymous to conservation, but this is not necessarily the case. Due to complexity of functional ecosystems, stocking of land with game cannot guarantee the maintenance of natural resources nor its sustainability (Smit 2007).

Game ranching is often perceived as an "easy farming system", mostly because there are no camps and thus no grazing system to be applied. Some owners practice game ranching solely as a hobby, while others strive towards economic existence over a short-term. Game ranching is, however, far more complex than generally anticipated. A broad knowledge base and an active rather than passive approach to management are required with such a multi-species system. Only a sound scientific approach that includes both economical and ecological principles will ensure long-term success and sustainability (Smit 2007).

In common with many game ranches in the region, some of the game species present in the study area did not historically occur in the central Free State. In this regard browser and mixed feeder species are of particular importance and they should preferably only be introduced in areas with adequate browse resources, something that is not generally associated with the Grassland Biome that covers most of the Free State province. Despite this limitation, browser and mixed feeder species are introduced in areas where trees are present, but which do not represent ideal habitat. As a consequence there is growing concern among some conservationists regarding aspects such as the impact of these introduced species on the habitat, as well as the ability of these species to adapt and survive in sub-optimal habitats. From the game ranchers' point of view, the optimal reproduction to the specific species' biological potential is essential to ensure maximum economic gain from these species. One of the general aims of nature conservation is therefore the formulation and implementation of effective management programs which will ultimately result in optimal land use, combined with effective land conservation (Bredenkamp and Brown 2001). Neither land use nor conservation objectives can be attained without a thorough knowledge of the ecology of a particular area (Edwards 1972, Bredenkamp and Brown 2001).

The main objectives of this study were to determine:

- Specific phenological patterns of woody species present in the study area through different seasons, including different weather seasons, i.e. wet and dry years;
- Seasonal changes in faecal nitrogen of four herbivore species, in order to make an assessment of their nutritional status and to indicate how phenology of woody species influence the quality of browse;
- Choice of habitat by different herbivore species (spatial separation) and any influence of leaf phenology of the woody species on local, seasonal movements of game species;
- Inter-species animal competition for space and food resources;
- The influence of the leaf phenology of deciduous woody species on browsing capacity; and
- The carrying capacity in order to compare it to current game numbers and make recommendations on the stocking densities.

The final objective was to combine all the information gained in a structural management plan that can also be applied to similar game ranches in the province.

CHAPTER 2

PRIVATE GAME RANCHES AND PROVINCIAL CONSERVATION AREAS IN THE FREE STATE PROVINCE

2.1 INTRODUCTION

Bothma *et al.* (2004) stated that: "wildlife ranching created a conservation revolution since the 1960's in South Africa." During the last half of the 20th century, establishment of numerous wildlife ranches on former livestock ranches, especially marginal agricultural land, has been the result of increasing costs and decreasing profit margins of stock farming. Consequently, South Africa now has more wildlife than in the early 1900's after the decimation of wildlife due to hunting and diseases such as rinderpest (Bothma *et al.* 2004). In 2006, wildlife ranching was practiced on 20.5 million ha and government protected areas covered 7.5 million ha of the approximately 122.2 million ha total land size of South Africa (NAMC 2006).

Commercial wildlife ranching on private land is becoming a significant earner of foreign exchange in South Africa (Du Toit 1995a, NAMC 2006). During 2009, sales of wildlife amounted to R183 million, which is an 11% increase from 2008 (Cloete and Taljaard 2010). In certain cases, private land owners are assuming increasing importance in the conservation of mammals and their habitats (Hanks *et al.* 1981, Du Toit 1995a) and may to some degree offset the conservation deficiencies of national parks (Du Toit 1995a). DEAT (2007a) stated in a report on the state of the environment: "It is encouraging that civil society and the private sector are increasing their participation in environmental management and accountability." However, this is mostly not the case in wildlife ranching. These privately owned game ranches are mainly used for commercial purposes, while conservation is usually not the main aim of these enterprises.

The objectives of this chapter were to:

i) quantify the number of privately owned game ranches in the Free State province in order to establish the importance and applicability of the main research of this thesis;
ii) compile a list of the large wildlife species present in the province; and
iii) identify those species not historically present in the province, as well as exotic species.

2.2 BACKGROUND

Only a small percentage of South Africa (6%) is covered by formal conservation areas. Land under private ownership can thus potentially be very important in the conservation of specific plant species, animal species and unique ecosystems (Smit 2007). In general, this is unfortunately not the case, since game ranching has become a commercially based activity. Over commercialisation of wildlife may in the long run have a negative impact on conservation of species and ecosystems. Some conservationists have growing concerns about some aspects of game ranching such as the cross-breeding of closely related species and sub-species, deliberate breeding of colour mutations, the impact of game on the environment, more specifically those species introduced into habitats where they did not occur naturally and the introduction of exotic species. The complexity of functional ecosystems in a multi-species system, where the number of variables that need to be considered is much higher than in stock farming, may result in the stocking of land in such a manner that neither the maintenance or improvement of natural resources nor its sustainability can be guaranteed (Smit 2007). The correct scientific approach and sound management can, however, ensure that game ranching contribute to the conservation of natural resources including threatened or rare wildlife species, while at the same time also contributing to the economic development and welfare of the country (NAMC 2006, Smit 2007).

DEAT (2007a) defines conservation as the maintenance of environmental quality and functioning. According to Owen-Smith (1988), in terms of the 'World Conservation Strategy' the objectives of conservation, are: i) to sustain life support processes; ii) to maintain biotic diversity; iii) to retain those species, or ecosystems of particular benefit or interest; and iv) to keep future options open. In the context of national parks and other designated conservation areas, these broad objectives tend to get translated into the more practical goal of retaining the full historic diversity of habitats and species in the region (Owen-Smith 1988). Further, game reserves, national- and provincial parks are often isolated from each other as 'islands in a sea' of expanding agriculture and human settlements (Hanks *et al.* 1981, DEAT 2007a). An increase in the creation of corridors between wildlife areas, where natural vegetation is still available on privately owned land, will greatly aid in connecting these ‘islands’ into a ‘continent’ again.

The South African human population increased to 46.9 million in 2004, with an average growth rate of 3.34%, having converted 18% of the land surface by 2002 into settlements and agricultural land (DEAT 2007a). A large part of the Free State province is covered by privately owned land and is particularly affected by cultivation (NAMC 2006, DEAT 2007a). Increasing population pressure and land-use change, over-exploitation, invasion by alien invasive plants, land degradation and the threat of climate change are threatening ecosystems. Of South Africa's terrestrial ecosystems, 34% are threatened (DEAT 2007a).

Countries in southern Africa have promulgated a large number of conservation areas. Most of the protected areas, including informal private landowner activities such as game farms and game ranches, are rather small and cover between 1 000 and 10 000 ha (DEAT 2007a). NAMC (2006) discusses certain aspects of the private sector game ranching industry and compares it to government owned areas where applicable. In the 1980's South Africa, Lesotho and Swaziland already had 155 state conservation areas >1 000 ha (Greyling and Huntley 1984). According to O'Connor and Krüger (2003), a number of these areas were established through the purchase of agricultural land, including rangeland for livestock, in order to conserve mammals. This resulted in a system of fragmented and relatively small reserves. Their efficacy in conserving mammals depends on whether the sizes of reserves are adequate to maintain viable populations. Population size of an antelope species depends on its habitat requirements and social system (*vid.* Chapter 7), as well as on the quantity and spatial distribution of resources (O'Connor and Krüger 2003).

According to Hanks *et al.* (1981), locally abundant herbivores have presented problems of habitat degradation in nearly every area due to these areas being small and isolated. This is usually a consequence of a lack of predation and prevention of dispersion caused by fences around reserves. Animal removal programs, by means of live capture, culling and/or hunting, attempt to prevent or reduce habitat degradation that results from persistent overabundance (Hanks *et al.* 1981). A specific example of dispersion of populations outside reserve boundaries is the Coleford Nature Reserve, situated in the foothills of the southern Drakensberg. Substantial movement of certain species in and out of the reserve was reported, indicating that these populations were resident over an area larger than the reserve itself. A species with such a connected meta-population can enhance the viability of an individual population within a small reserve (O'Connor and Krüger 2003).

NAMC (2006) defines wildlife ranching as "the management of game in a system with minimum human intervention in the form of the provision of water, supplementation of food, control of parasites, provision of health care or supplementation of wild prey populations." According to the International Union for Conservation of Nature's (IUCN) new definition, a protected area is: "A clearly defined geographical space, recognised, dedicated and managed through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley 2008). Du Toit (2010a) described ten types of protected natural areas present in South Africa, of which the following are relevant to this chapter:

National Park – "an extraordinary and unusual natural area that is managed by a nationally recognized conservation body for the specific purpose of protecting the ecological integrity and biodiversity of the area for the benefit of both the present and future generations";

Provincial Nature Reserve – "an area that is managed by the relevant province with recourse to the relevant ordinances and with various objectives";

Conservancy – “a conservation area legally owned and/or occupied by one or more landowners, but which is managed as a unit to achieve a common conservation goal”;
Extensive wildlife production unit (Game Ranch) – “a large fenced or unfenced privately owned or communal area on which wildlife is extensively managed for direct utilization of wildlife-related products, such as by hunting and live animal sales and tourism, and for indirect utilization such as ecotourism”;
Intensive wildlife production unit (Game Farm) – “a small fenced area on which wild animals are managed intensively for the production and harvesting of marketable products such as meat, hides, other products and live animals”;
RAMSAR site – “a wetland of international importance designated according to the guidelines of the International Convention for Wetlands.”

2.3 SURVEY OF PROVINCIAL AND PRIVATE GAME AREAS IN THE FREE STATE

Game ranching is is one of the fastest growing sectors in the conservation industry of southern Africa (Van der Waal and Dekker 2000), including the Free State province. With the expansion of the wildlife industry, the presence of woody plants as an essential food resource for browsing animals is of increasing importance. Woody plants create unique habitats that can support a greater diversity of species, than ecosystems without woody plants (Smit 2004). Therefore, the areas in the Free State that are distinguished by the presence of large woody plants that are characteristic of a rocky hill or koppie (Figure 2.1), a river and its drainage lines (Figure 2.2) are usually favoured for game ranching. No formal definition that distinguishes a hill from a mountain in South Africa could be found. Therefore, it was decided to use a local relief of <100 m elevation for koppies or hills and an elevation of >100 m as indicating a mountain in the generally flat Free State plains.

Data were obtained from Dave Hayter at the Provincial Department of Economic development, Tourism and Environmental Affairs (DETEA), previously known as Department of Tourism, Economic and Environmental Affairs and before that as Department of Environmental Affairs and Tourism (DEAT). Based on issued ‘Adequate Fencing Certificates’, as well as through personal communication, a database of all the privately owned game ranches was compiled by DETEA. These certificates are not obligatory to all game ranch owners in the province, but are necessary before certain other permits will be issued. Information in the supplied database included location of the game ranch in terms of the nearest town or city, game species present and their average numbers. From this database, game ranches in the vicinity of each town or city were counted and presented on a map of the Free State province (Figure 2.3) where these towns and the provincial conservation areas were already indicated (created by the Department of Geography, University of the Free State). Table 2.1 was also compiled from this data, listing the stated game species present in the province as well as their average, estimated numbers on private game ranches and provincial conservation areas up to August 2010.

There are 13 proclaimed and one non-proclaimed (Bathurst, southeast of Bloemfontein) provincial nature- and game reserves in total, managed by DETEA, and one national park managed by SANParks in the province (Figure 2.3). Eleven of the provincial conservation areas are located around a dam as indicated by their names, like Erfenis Dam Nature Reserve (NR), Gariep Dam NR, Kalkfontein Dam NR, Koppies Dam NR and Sterkfontein Dam NR, with Caledon NR including the Welbedacht Dam, Maria Moroka Park the Montloatse Setlogeb Dam, Rustfontein NR the Rustfontein Dam, Soetdoring NR the Krugersdrift Dam, Sandveld NR the Bloemhof Dam and Willem Pretorius Game Reserve (GR) the Allemanskraal Dam**.** Tussen-die-riviere GR is located at a confluence of the Caledon- and Orange Rivers and the Seekoeivlei NR is a floodplain ecosystem drained by the Klip River (Figure 2.4). The Seekoeivlei-wetland is a RAMSAR site, specifically due to breeding water birds. Additionally, there are 16 game areas in the Free State that are owned by municipalities, but are not in possession of an Adequate Fencing Certificate, therefore their data are not represented in the database. Some examples are the Franklin Nature Reserve inside Bloemfontein, Wolhuterskop NR in the Bethlehem area and Boshoff NR (D. Hayter, *pers. comm.*[1]). South African National Defence Force also owns a number of game ranching areas in the province.

There were a total of 343 private game ranches in the Free State up to August 2010, with Adequate Fencing Certificates from which the database was compiled (Figure 2.3). There are, however, a substantial number of game ranches that do not have such a certificate but still have large numbers of game on it. The highest numbers of game ranches that are incorporated in the database (Figure 2.3), occur in the vicinity of Boshof (49), Kroonstad (28), Bloemfontein (19), Fauresmith (16) and Hoopstad (16). In the vicinity of Vrede (13), Vredefort (13), Brandfort (12), Philippolis (12) and Heilbron (11) are also quite a number of game ranches. Private game ranches are present throughout the province, especially in areas with rivers and koppies (Figure 2.4), and in most of the vegetation types (Figure 2.5). Private game ranches, if well managed, can aid in the conservation of different vegetation types and certain game species, in association with the provincial conservation areas that conserve areas around dams and certain rivers (*vid.* the discussion on this topic under the heading ‘Background’ (2.2) in this chapter).

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[1] Dave Hayter, Chief Nature Conservator: Protected Area Planning & Stewardship Program, DETEA, Caledon Nature Reserve, Wepener.

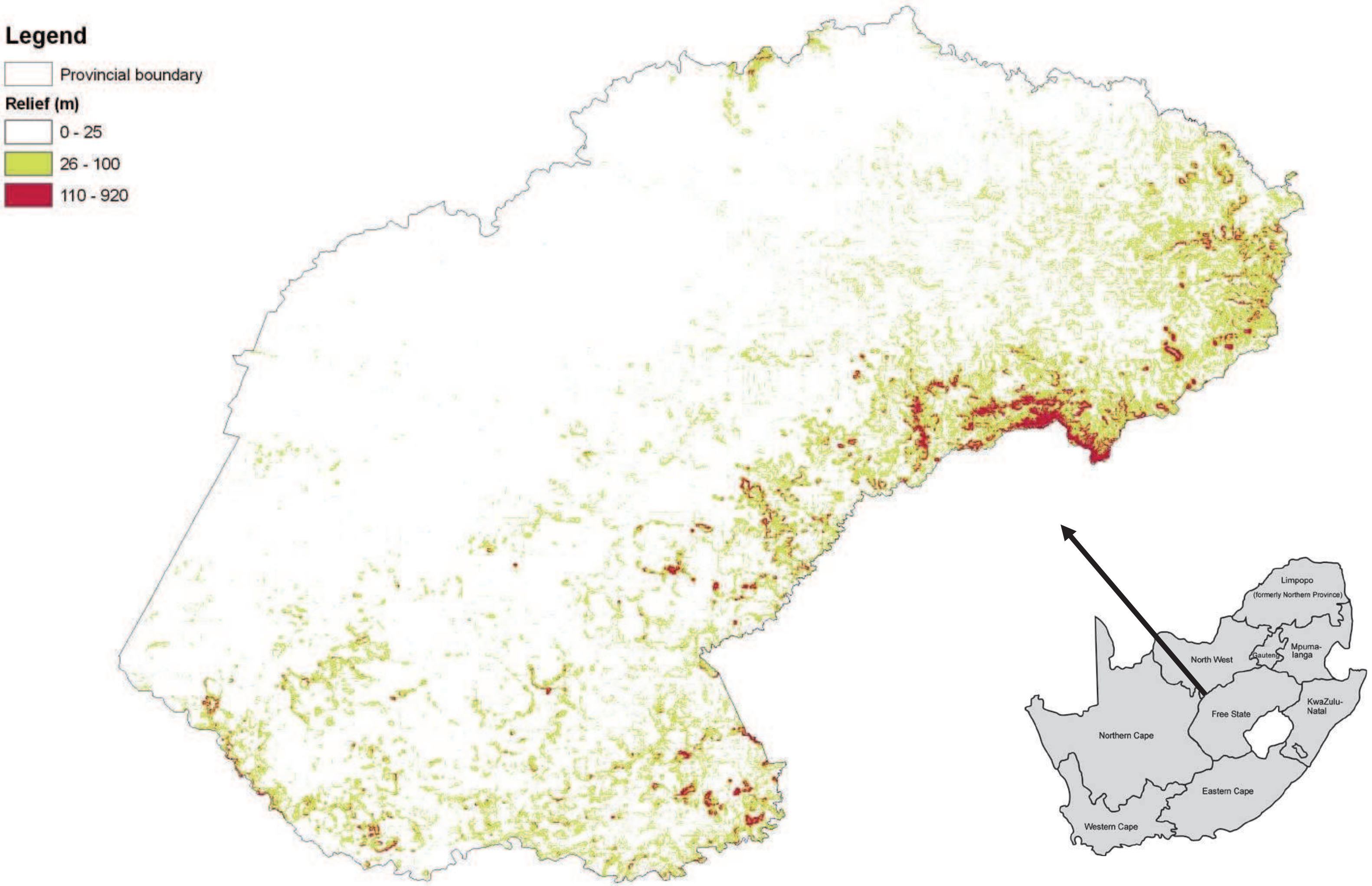

Figure 2.1 Rocky hills (koppies) and mountains present in the Free State Province. A hill is distinguished from a mountain by having an elevation of <100 m in the flat Free State plains and a mountain >100 m. Free State map is from Global Land Cover Facility (2004). The location of the Free State Province in the Republic of South Africa is from South African Provinces (2002).

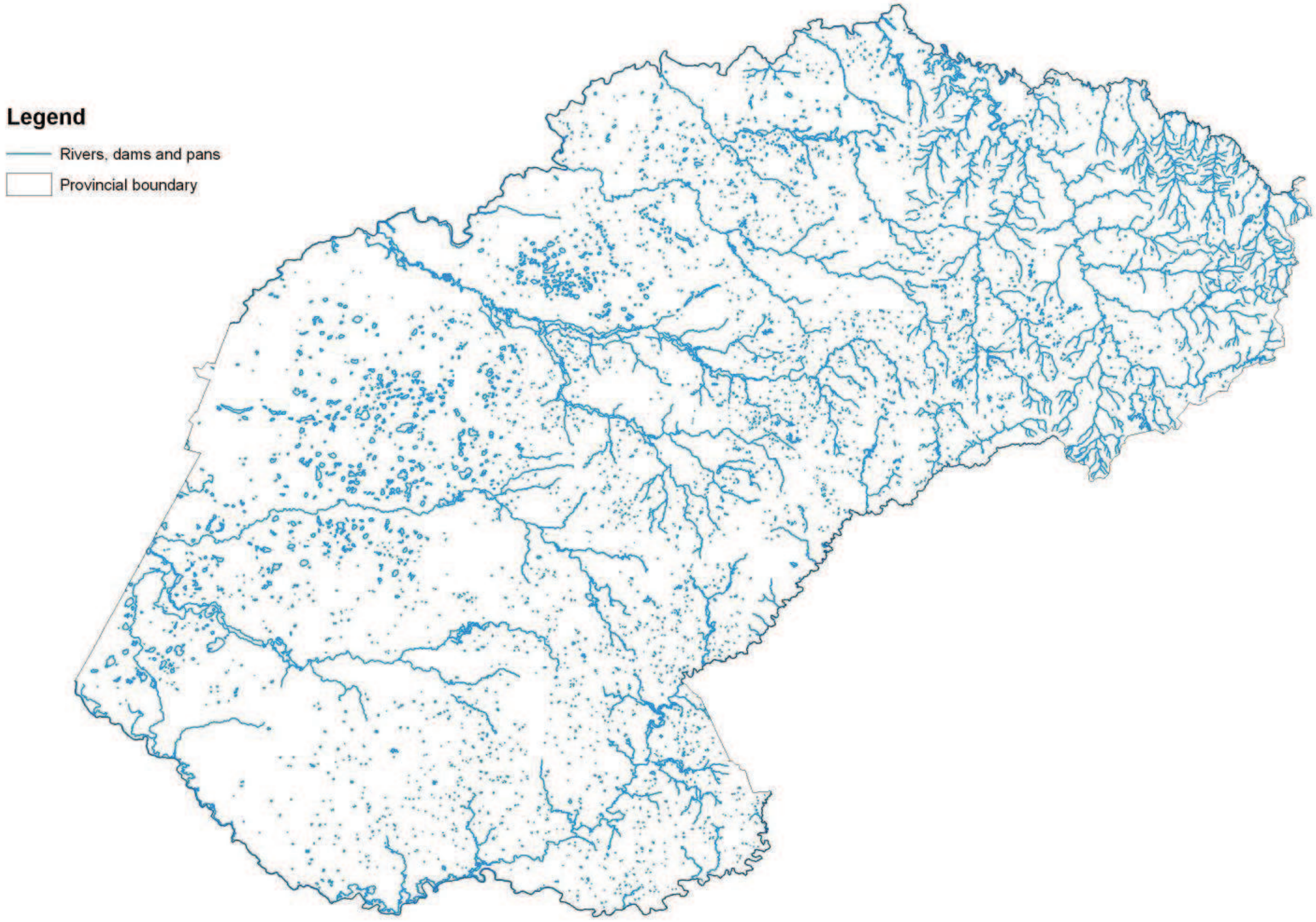

Figure 2.2 Rivers, dams and large wetlands present in the Free State province (from DEAT 1999).

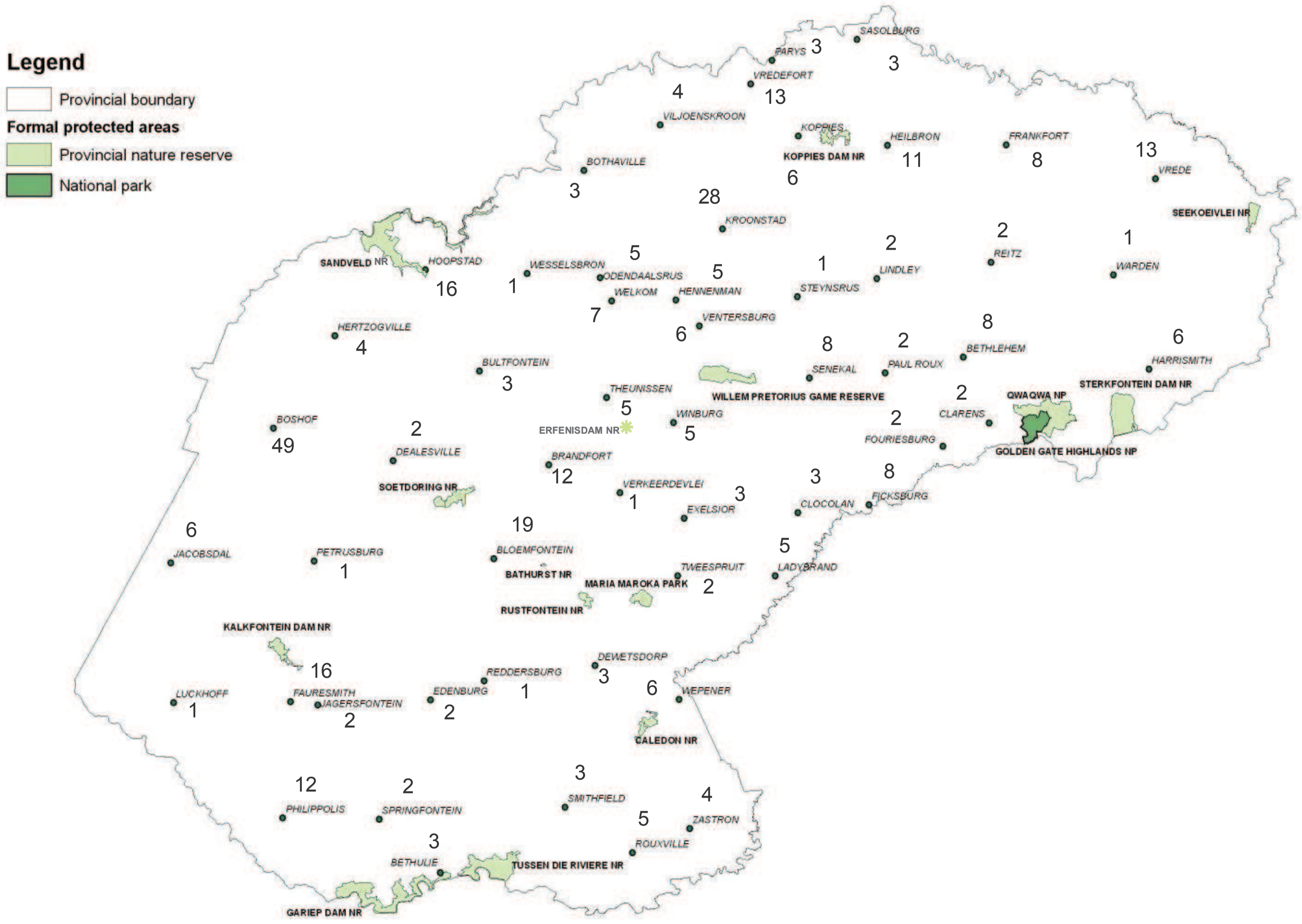

Figure 2.3 Map of the Free State, with some towns indicated and the known numbers of privately owned game ranches in the vicinity of that town. These numbers only include areas with Adequate Fencing Certificates and are not representative of all the game ranches present in the province. Proclaimed provincial nature reserves (except Bathurst NR) and national parks are also shown. Map created by Department of Geography, UFS.

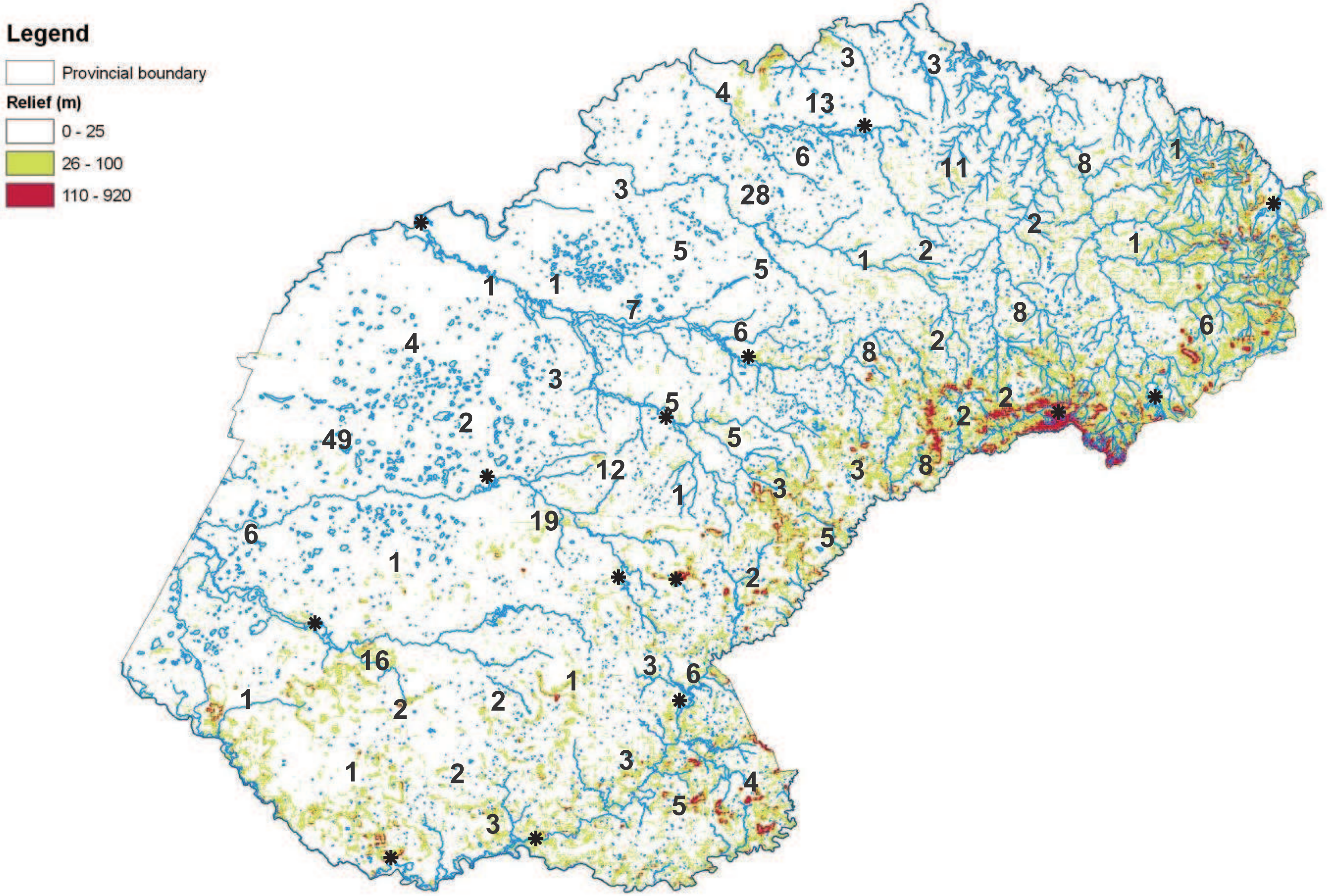

Figure 2.4 Rivers, dams, large wetlands (from Global Land Cover Facility 2004), small hills (koppies) and mountains (from DEAT 1999) in the Free State, along with the number of known private game ranches in the area and the provincial nature reserves and national parks (✱).

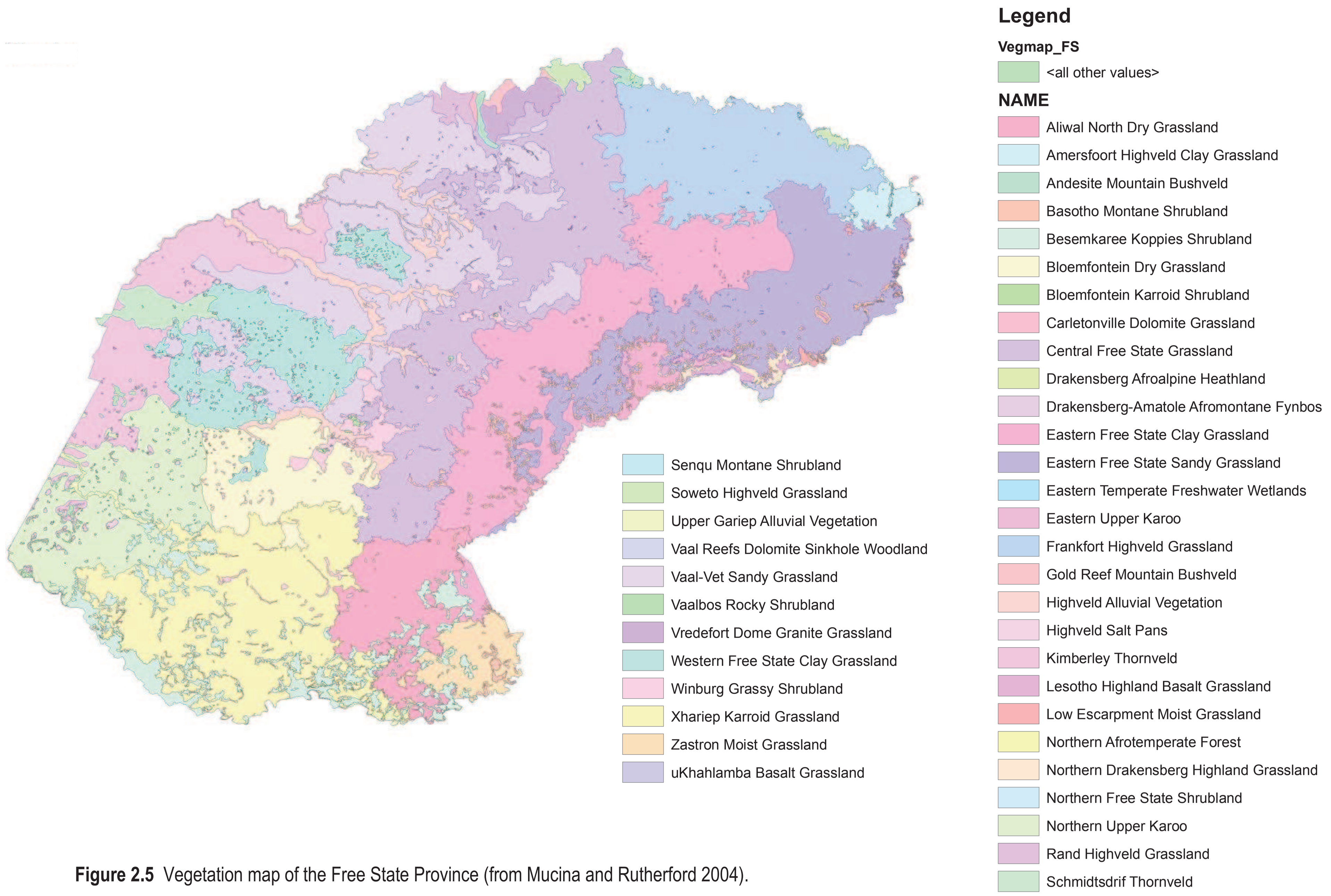

Figure 2.5 Vegetation map of the Free State Province (from Mucina and Rutherford 2004).

2.4 GAME SPECIES PRESENT IN THE FREE STATE PROVINCE

2.4.1 Absence and presence of game species

Some species have been introduced in areas in the country where they were previously absent (e.g. bontebok and sable antelope), while others (e.g. cheetahs, black- and white rhinoceroses) have disappeared in most of their former distribution ranges (Nel 2010). Table 2.1 lists 56 game species, including two flightless, large bird species and an additional seven colour variants of existing species present up to August 2010 in game ranches and conservation areas of the Free State. Of these species, only 25 are expected to occur in the province. Black- and white rhino's (*Diceros bicornis*, *Ceratotherium simum*) are present, but for security reasons their location and numbers may not be disclosed. Black-faced impala (*Aepyceros melampus petersi*) have been observed in the province, but they are not listed in Table 2.1 and their numbers in the province are not known.

Table 2.1 lists 16 game species that were not historically present in the Free State, as discussed by Skinner and Chimimba (2005). Some of these species, like impala and waterbuck, have been known to occur in the province for a long time and have adapted well to the available habitat. A discussion on historical presence of animal species follows in the next section. Skinner and Chimimba (2005) consider spotted hyaenas (*Crocuta crocuta*) as extinct in the Free State, except for vagrants, but the elusive, shy brown hyaena (*Hyaena brunnea*) is still occasionally sighted throughout the province.

The sitatunga and red lechwe are originally from Botswana and surrounding countries (Okavango Delta and Linyanti River) (Kingdon 2007), while an additional 14 species present in the Free State are exotic species (Table 2.1). A summary of the original distribution areas of these exotics as well as their natural habitats are provided in Table 2.2. Four of these species originate from north-west Africa (Kingdon 2007), whereas the other ten alien species do not originally occur on the African continent (Lever 1985). Their natural habitats range from dry deserts to tropical rainforests, also including woodland and grasslands (Table 2.2).

Numbers of animals indicated in Table 2.1 from the DETEA database are only averages, or in some cases estimates of the numbers present. These numbers are only an approximation of the wildlife present in the Free State and do not represent accurate numbers. Certain owners of game ranches were not keen on stating the game species present or their true numbers, while other areas are not included in the database because no Adequate Fencing Certificates were issued for them (D. Hayter, *pers. comm.*[1]).

[1] Dave Hayter, Chief Nature Conservator: Protected Area Planning & Stewardship Program, DETEA, Caledon Nature Reserve, Wepener.

Table 2.1 Game species present up to August 2010 in the Free State (FS) on provincial reserves and certain private game ranches (PGR) with their average, estimated numbers also indicated, as in the DETEA database. Exotic species are marked with a ❋ and species not historically present with a "not in FS" entry.

Exotic or not in FS	Game species	Scientific name	PGR Sp Total *	Provincial Sp Total	Sum Total
❋	Blackbuck, Indian	*Antilope cervicapra*	16		16
	Blesbuck	*Damaliscus dorcas phillipsi*	28 415	1 633	30 048
	Blesbuck (White)		1 999		1 999
	Blesbuck (Yellow)		208		208
not in FS	Bontebok	*Damaliscus dorcas dorcas*	618		618
	Buffalo, Cape	*Syncerus caffer*	1 194	331	1 525
❋	Buffalo, Water	*Bubalus bubalus*	10		10
	Bushbuck	*Tragelaphus scriptus*	355	15	370
not in FS	Bushpig	*Potamochoerus larvatus*	43		43
❋	Camel	*Camelus* species	1		1
	Cheetah	*Acinonyx jubatus*		4	4
not in FS?	Crocodile	*Crocodylus niloticus*	8		8
❋	Deer, European Fallow	*Dama dama*	2 354		2 354
❋	Deer, Hog	*Axis porcinus*	20		20
❋	Deer, Red	*Cervus elaphus*	19		19
❋	Deer, Sambar	*Cervus unicolor*	18		18
❋	Deer, Sika	*Cervus nippon*	1		1
	Duiker, Grey	*Sylvicapra grimmia*	3 157	473	3 630
	Eland	*Tragelaphus oryx*	5 204	1 041	6 245
❋	Emu	*Dromaius novaehollandiae*	19		19
	Gemsbok	*Oryx gazella*	7 340	1 037	8 377
not in FS	Giraffe	*Giraffa camelopardalis*	355	46	401
not in FS	Grysbok, Cape	*Raphicerus melanotis*	7		7
	Hartebeest, Red	*Alcelaphus buselaphus*	6 644	1 373	8 017
not in FS	Hippo	*Hippopotamus amphibius*	4	10	14
	Hyaena, Spotted	*Crocuta crocuta*	6		6
not in FS	Impala	*Aepyceros melampus*	11 179	804	11 983
not in FS	Impala (Black)		53		53
	Klipspringer	*Oreotragus oreotragus*	55	11	66
	Kudu	*Tragelaphus strepsiceros*	3 770	724	4 494
❋	Lama	*Lama glama*	29		29
not in SA	Lechwe, Red	*Kobus leche*	2 331		2 331
	Leopard	*Panthera pardus*	2		2
	Lion	*Panthera leo*	38	3	41
not in FS	Nyala	*Tragelaphus angasii*	1 360		1 360
	Oribi	*Ourebia ourebi*	134	24	158
❋	Oryx, Arabian	*Oryx leucoryx*	3		3
❋	Oryx, Scimitar-horned	*Oryx dammah*	117		117
	Ostrich	*Struthio camelus*	2 802	930	3 732
	Reedbuck, Common	*Redunca arundinum*	1 216	615	1 831
	Reedbuck, Mountain	*Redunca fulvorufula*	4 804	839	5 643
	Rhebok, Grey	*Pelea capreolus*	583	190	773
	Roan Antelope	*Hippotragus equinus*	353	39	392
not in FS	Sable Antelope	*Hippotragus niger*	1 118	234	1 352
❋	Sheep, Barbary	*Ammotragus lervia*	82		82

Continued on next page...

Table 2.1 continued

Exotic or not in FS	Game species	Scientific name	Private GR Sp Total *	Provincial Sp Total	Sum Totals
not in SA	Sitatunga	*Tragelaphus spekei*	13		13
	Springbok	*Antidorcas marsupialis*	31 746	8 236	39 982
	Springbok (Black)		2312		2 312
	Springbok (Copper)		497		497
	Springbok (White)		1 120		1 120
	Steenbok	*Raphicerus campestris*	4 383	265	4 648
not in FS	Suni	*Neotragus moschatus*	7		7
not in FS	Tsessebe	*Damaliscus lunatus*	486	207	693
not in FS	Warthog	*Phacochoerus africanus*	2 443	1 042	3 485
not in FS	Waterbuck	*Kobus ellipsiprymnus*	2 872	145	3 017
❋	Wild Boar (European)	*Sus scrofa*	41		41
	Wild Dog	*Lycaon pictus*	5		5
	Wildebeest, Black	*Connochaetus gnou*	10 073	1 861	11 934
	Wildebeest, Blue	*Connochaetus taurinus*	5 134	484	5 618
	Wildebeest (Red bred from blue)		49		49
	Zebra, Burchell's	*Equus burchelli*	3 232	1 082	4 314
not in FS	Zebra, Cape Mountain	*Equus zebra zebra*	8	104	112
not in FS	Zebra, Hartmanns	*Equus zebra hartmannae*	382		382
	Grand Totals		152 847	23 802	176 649

* Totals not accurate, because of withholding of information by some owners and certain game areas not included in the database due to lack of information

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As wildlife populations increase, it becomes necessary to set limits to their population sizes, in order to keep them in balance with their food resources and provide for their social needs (Bothma *et al.* 2004). This is extremely difficult to do as southern Africa has 23 types of large indigenous herbivore species that weigh > 100 kg and 22 that weigh < 100 kg. They have a range of diets; some migrate seasonally (blue wildebeest, buffalo, kudu, springbok, zebra) and others change their diet seasonally, like elephant, impala and eland (Bothma *et al.* 2004).

Table 2.2 Original distribution ranges of exotic species currently present in the Free State, as well as normal habitats that they occupy in their areas of origin. Information is from Lever (1985), supplemented by Gurung and Singh (1996) and Wikipedia Encyclopaedia (2010).

Common species name	Scientific name	Original distribution range	Normal habitat
Blackbuck, Indian	*Antilope cervicapra*	India, some parts of Nepal and Pakistan	Open plains, grasslands
Buffalo, Water	*Bubalus bubalus*	Southern Asia, south America, southern Europe	Tropical and subtropical forests, wetlands, swamps, grassland
Camel	*Camelus* species	West, central and east Asia (Two species: Arabian camel – 1 hump and Bactrian camel – 2 humps)	Dry deserts, mountains and arid places
Deer, European fallow	*Dama dama*	Europe, England, Wales	Mixed woodland, forest, open grassland
Deer, Hog	*Axis porcinus*	Pakistan to north India, southeast Asia, southwest China, western Thailand	Forests, clearings, grassland
Deer, Red	*Cervus elaphus* (± 7 subspecies exist)	Europe, western and central Asia, Atlas mountain region in northwest Africa between Morocco and Tunisia	Grassland, woodland, mountains
Deer, Sambar	*Cervus unicolor* (Indian sambar), *C. timorensis* (Sunda sambar), *C. mariannus* (Philippine sambar)	Southern Asia, China, Taiwan, Indonesia, India, Sri Lanka, Thailand	Damp woodlands, mixed coniferous forest, tropical forest, subtropical mixed forest, tropical rainforest, hills
Deer, Sika	*Cervus nippon*	Scotland, England, northern Ireland, east Asia from Vietnam to Russian far east, southern China, Japan, Taiwan	Coniferous woodlands and heaths on acid soils, patchy clearings of temperate subtropical forest
Emu	*Dromaius novaehollandiae*	Australia	Woods, scrubland, grassland, desert
Lama	*Lama glama*	South, central and North America, were common in California, Texas, New Mexico, Utah, Missouri, Florida	Domesticated animal; plains, grassland, mountains
Oryx, Arabian	*Oryx leucoryx*	Middle East: Syria, lower Palestine, Iraq, Saudi Arabia, Arabian peninsula	Gravel desert, hard sand areas of flats between softer sand dunes and ridges
Oryx, Scimitar-horned	*Oryx dammah*	Africa in Sahara, Chad, Niger, Tunisia	Steppe and desert
Sheep, Barbary	*Ammotragus lervia*	Northern Africa in Algeria, Tunisia, Libya, Egypt, Sudan, northern Chad, Niger, Mali, Mauritania, Morocco	Arid mountainous areas
Wild boar (European Bushpig)	*Sus scrofa*	Northern and central Europe, the Mediterranean region, including Africa's Atlas mountains, much of Asia.	Forest, broad-leaved woodland, grassland, scrub

2.4.2 Historical records

According to Boshoff and Kerley (2010), the value of historical distribution data has been widely recognised for aiding the reconstruction of animal assemblages for a region over a certain time period. The value placed on such data is demonstrated by one of the principles governing the re-establishment or removal of species into national parks, namely: ‘it should only take place where there is good evidence that the species occurred in the area in historical times.’ As Boshoff and Kerley (2010) stated: “These data have also provided the basis for determining national and regional policies and principles for translocation of indigenous and alien mammals, as embodied in the National Environmental Management: Biodiversity Act (Act 10 of 2004).”

It has been postulated that although there is a high level of accuracy attributed to historical distribution records from the past 100 years, this decreases between 100 and 500 years ago (Bernard and Parker 2006). Species-specific biases in the historical reporting frequency were indicated by Boshoff and Kerley (2010), where large charismatic species or more noticeable species had a higher number of records per species than inconspicuous species or species in rugged, mountainous areas. However, it is important to distinguish between the different types of historical records, like sight records, rock art, archaeological and ethnographic records, with the written records being the most widely used to reconstruct early distribution patterns of mammals (Bernard and Parker 2006, Boshoff and Kerley 2010). Boshoff and Kerley (2010) refer to “written records found in the diaries, journals and correspondence of people, most notably explorers, hunters, missionaries and naturalists during historical times.”

A discussion on the historical occurrence in the province of those game species present in the current study area follows. Kok and Opperman (1980) reported that giraffes were not historically present in the Free State. The importance of cover or shelter in the form of trees renders it unlikely that buffalo occurred in the open grass plains of the Free State, but their distribution map shows patchy occurrences in the province (Skinner and Chimimba 2005). Furstenburg (2006a) listed buffalo as occurring during the 1400 to 1700’s in the vicinity of the Vaal and Orange rivers and in the western corner of the province. It is often stated that blue wildebeest did not occur in the Free State, but historical evidence suggests that they did (Skinner and Chimimba 2005, Furstenburg 2006a). It is known that the black wildebeest is the species associated with the Free State grasslands and blue wildebeest usually with savannas of the Limpopo Province. According to Skinner and Chimimba (2005), other species that did not historically occur in the Free State are bontebok (originally from the southern Cape – blesbok is the common Free State species), impala, red lechwe (a Botswana and Namibian species), tsessebe (not occurring far south of the Vaal River) and waterbuck. Furstenburg (2006a) listed impala, waterbuck and roan to occur sporadically in the western Free State. Gemsbok distribution extended marginally into the Free State from the Northern Cape arid areas (Skinner and Chimimba 2005). Other species that are also present in the Free State province, but were historically absent are indicated in Table 2.1. Furstenburg (2006a) listed hippos to occur in the Vaal and Orange rivers on the borders of the province.

The historic occurrence of a species in a specific area is important, but there are other aspects that also need to be taken into consideration when determining the desired species composition of any wildlife area, namely habitat suitability, size of suitable habitat, veld condition, intra- and interspecies competition, conservation status of a species, carrying capacity, management implications, etc. Local climatic conditions, goals and objectives of the area, legal obligations and implications, as well as financial implications are also important aspects to consider (Nel 2010). There is still currently a huge controversy surrounding the historical presence or absence of species in certain areas.

2.4.3 Threatened or protected species (TOPS)

The TOPS regulations apply only to those species that are listed as Threatened (Critically Endangered, Endangered, Vulnerable) or Protected (section 56(1)) in terms of the National Environmental Management: Biodiversity Act (Act 10 of 2004), while provincial legislation continues to apply to all the other species (Carroll and Boshoff 2007, DEAT 2007 b). No restricted activity may be carried out involving a TOPS specimen without a TOPS permit. Restricted activity with regards to game species means "hunting, catching, capturing or killing by any means, method or device whatsoever, including searching, pursuing, driving, lying in wait, luring, alluring, discharging a missile or injuring with intent to hunt, catch, capture or kill any such specimen; conveying, moving or otherwise translocating the specimen; selling, or otherwise trading in, buying, receiving, giving, donating or accepting as a gift, or in any way acquiring or disposing of such a specimen" (Carroll and Boshoff 2007). Game farm hunting permits may only be issued if the game farm is registered (Carroll and Boshoff 2007, DEAT 2007 b).

Game species listed by the National Department of Environmental Affairs (Carroll and Boshoff 2007) to be 'Endangered', are African wild dog, black rhinoceros, mountain zebra, oribi and tsessebe. Species that fall in the 'Vulnerable' category include blue duiker, bontebok, cheetah, leopard, lion, pangolin, roan antelope, Samango monkey and suni. ‘Protected’ species are African elephant, black-footed cat, black wildebeest, brown hyaena, Cape clawless otter, Cape fox, honey badger, reedbuck, serval, Sharpe’s grysbok, spotted hyaena and white rhinoceros. Of the class Mammalia, no small rodents are listed here, nor any species from the classes Invertebrata, Amphibia, Pisces, Reptilia, Aves or Flora although they also fall in these categories. Of the listed species, tsessebe, bontebok, roan antelope and reedbuck are present in the study area, while African wild dog, cheetah and lion are present in another fenced off part of the Wag-‘n-Bietjie Private Nature Reserve. It is important to note that although the name of the farm on which the study was conducted includes the term ‘nature reserve’, it is for all practical purposes a typical game ranch used for commercial purposes.

2.5 FINAL REMARKS

The large number of private game ranches in the Free State emphasizes the necessity of the research reported in the thesis. Very few studies of this nature have been done in the Free State, since most research is focused on the savanna areas of the country. This statement is demonstrated by literature cited in the various chapters. Results of the research project presented in this thesis will be invaluable for the effective management of areas similar to that of the study area. Although not all vegetation types of the Free State are represented in the study area, the approach followed will still be applicable to other areas. The information in this chapter has highlighted the fact that there are a growing number of alien, exotic game species being introduced in the province. These aliens’ impact on local, indigenous species and the environment must be closely monitored and the aliens removed where deemed necessary. Further, once the law is passed, game ranchers will not be permitted to auction game species that were not historically present in the province and can only use these species for hunting or esthetic purposes. This is already the case for bontebok and lechwe.

CHAPTER 3
STUDY AREA

3.1 LOCATION

The study was conducted between March 2004 and December 2008 on the Wag-‘n-Bietjie Private Nature Reserve situated approximately 30 km north of Bloemfontein in the Brandfort district, central Free State (28°55`E, 26°18`S to 28°54`E, 26°19`S). The Modder River forms the southern boundary of the private reserve but due to the game fence positioned at the top of the river bank, there is no direct access to the river.

The private reserve with a total area of 750 ha is divided into two parts (Figure 3.1) by the gravel road to Soutpan, with a connecting tunnel underneath the road (Figure 3.2) allowing limited passage of game between sides. Game species in the northern part have free movement in the area with minimum human interference, while the gravel road restricts movement to the south. Only the northern part (437 ha) of the private reserve was used for the study. The smaller southern part was excluded due to the homestead, other buildings, predator camps, cultivated land and paddocks for domesticated animals that occupy the largest part of this section of the reserve (Figures 3.1 & 3.3). The northern part was undeveloped (Figure 3.3) with minimum disturbance of the game. As a result, the northern part presented the best habitat for the majority of the game present on the reserve. Game species on both parts of the private reserve were mostly sedentary and territorial, remaining in the part where they were introduced.

3.2 HISTORICAL BACKGROUND

Initially the Wag-‘n-Bietjie Private Nature Reserve was located on two farms: Roodeheuvel- and Veepost farms that were mainly used for grazing by Brahman cattle and only limited game ranching. During 1998 an ecological assessment of the northern part of the private reserve, then known as Roodeheuvel Private Nature Reserve, was executed to determine the potential for intensive game ranching and tourism. A second ecological assessment was undertaken in August 2000 in the southern part to include it as part of the already functioning private reserve in the northern part (Schulze 2000). During 2004 the established Wag-‘n-Bietjie Private Nature Reserve was sold to the current owner. At the time of the study it was used for commercial game ranching, with hunting (trophy hunting included) and live sales of game species (including rare species) being the main forms of utilisation. Predator camps have been built near the owner’s house on the southern side and house lions, wild dogs, Bengal tigers and other predators.

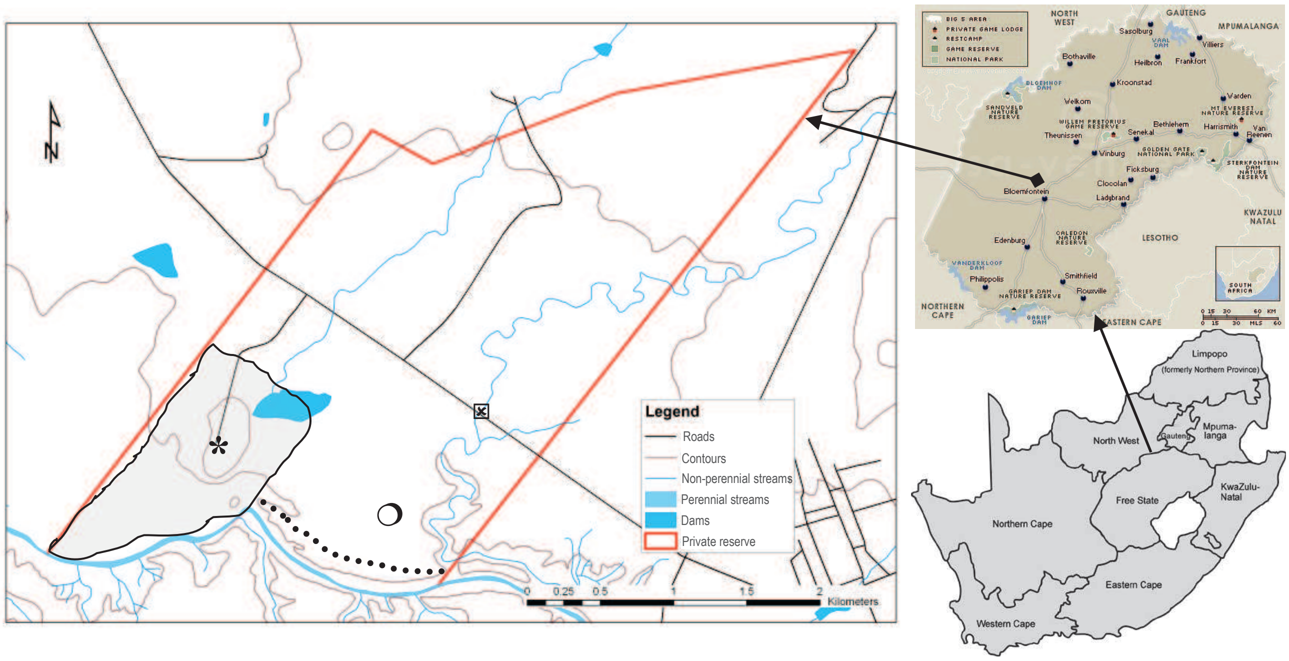


Figure 3.1 Topo-cadastral map of Wag-‘n-Bietjie Private Nature Reserve and surrounding area (Chief Director Mapping 1993). The shaded area is occupied by the owner’s house (*), other buildings, predator camps and cultivated lands, while ❍ is a disturbed area and ⊠ is the connecting tunnel underneath the Soutpan dirt road. The Modder River is fenced off (•••) and not accessible to game. The location in South Africa, Free State Province is also indicated, along with some of the larger nature reserves (from: South African Provinces 2002, Free State Province 2008).

Figure 3.2 The gravel road to Soutpan divides the reserve into two parts with a connecting tunnel underneath the road that allows limited passage of game between sides. The vehicle indicates the size of the tunnel.

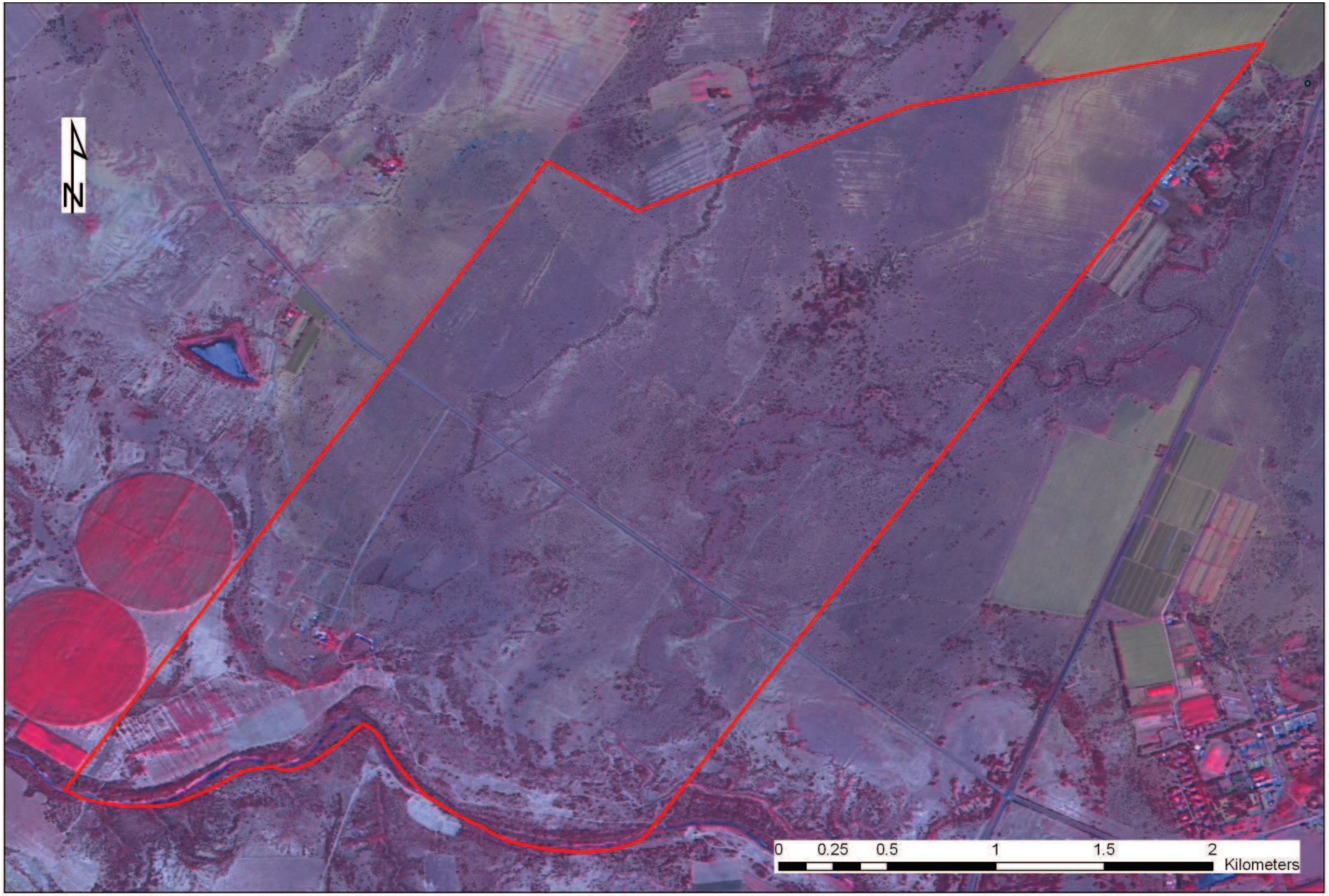


Figure 3.3 SPOT 5 satellite image of Wag-'n-Bietjie Private Nature Reserve (CSIR 2005) indicating buildings, predator camps, cultivated land, roads, fences, dry drainage lines and the dense vegetation on the banks of the Modder River. Glen Agricultural College is visible in the bottom right corner.

3.3 BIOTIC FACTORS

3.3.1 Vegetation

Geographically, the study area is located in the Grassland Biome (Rutherford and Westfall 1994) and the vegetation is described as Dry Sandy Highveld Grassland (Low and Rebelo 1996), or as Vaal-Vet Sandy Grassland (Mucina and Rutherford 2004). Although the study area falls in the Grassland Biome, the vegetation is more representative of *Acacia karroo* Riparian Thicket (Du Preez and Bredenkamp 1991), especially along the Modder River and between two dry drainage lines (or watercourses) located in the private reserve. Due to low game numbers and dominance of highly desirable perennial grasses, the veld of the private reserve appeared to be in a good condition at the start of the study. Rainwater collects in certain areas inside the drainage lines, but they are dry for most of the time. A detailed description of the vegetation types is presented in Chapter 4.

3.3.2 Animals

All the game species present in the study area during the time of study are listed in Table 3.1 and the scientific names conform to that of Skinner and Chimimba (2005). Ostriches (*Struthio camelus australis* Linnaeus, 1758) were quite abundant. Numbers of game species fluctuated over time and will be discussed in detail in Chapter 7. Giraffes were only found in the northern side (study area) of the private reserve. Only one or two Tsessebes were present in the study area, the rest of the herd was localised on the southern side. Other game species that were only found on the southern side were Black Impala, Black- and White Springbuck, Nyala (*Tragelaphus angasii* Angas, 1849) and Sable Antelope (*Hippotragus niger* Harris, 1838). Species that frequently travelled between the two sides of the private reserve were Buffalo, Eland, Kudu, Ostrich, Red Lechwe and Waterbuck. Most of the species present in the southern side were introduced there in order to keep them apart from species in the northern part of the private reserve, since they are sedentary.

Supplementary feed was given in the form of salt licks and game cubes throughout the year. Lucerne bales and game pellets were supplied from May/June to September each year on both sides of the private reserve. According to the manager, kudus occasionally helped themselves to lucerne after jumping over the fence surrounding the fields located behind the owner’s house (Figure 3.1). Two permanent earth dams provided water for game in the study area. A cement dam was filled with water by means of a wind pump located approximately 50 m from the main waterhole. A pump system distributed water from the cement dam to the waterholes. During 2007 a severe drought was experienced in the growing season and water was supplied in troughs from large green containers.

Table 3.1 Average numbers of game species present in the study area from 2004 to 2007.

Common name	Scientific name	Average number
Blue Wildebeest	*Connochaetes taurinus* (Burchell, 1823)	20
Bontebok	*Damaliscus pygargus pygargus* (Pallas, 1767)	25
Buffalo (African/Cape)	*Syncerus caffer* (Sparrman, 1779)	20
Burchell's Zebra	*Equus burchellii* (Boddaert, 1785)	10
Common Duiker	*Sylvicapra grimmia* (Linnaeus, 1758)	±10
Eland	*Tragelaphus oryx* (Pallas, 1766)	20
Gemsbok/oryx	*Oryx gazella* (Linnaeus, 1758)	20
Giraffe	*Giraffa camelopardalis* (Linnaeus, 1758)	6
Impala	*Aepyceros melampus melampus* (Lichtenstein, 1812)	40
Kudu	*Tragelaphus strepsiceros* (Pallas, 1766)	±20
Red Hartebeest	*Alcelaphus buselaphus* (Pallas, 1766)	10
Red Lechwe	*Kobus leche* (Gray, 1850)	20
Roan Antelope	*Hippotragus equinus* (E. Geoffrey Saint-Hilaire, 1803)	6
Southern Reedbuck	*Redunca arundinum* (Boddaert, 1785)	±6
Springbok	*Antidorcas marsupialis* (Zimmerman, 1780)	50
Steenbok	*Raphicerus campestris* (Thunberg, 1811)	±2
Tsessebe	*Damaliscus lunatus* (Burchell, 1823)	2
Waterbuck	*Kobus ellipsiprymnus* (Ogilby, 1833)	20

3.4 ABIOTIC FACTORS

3.4.1 Geology and Terrain model

Geology is described as the complex structure of rock formations which occurs in specific locations and sequences. It has a major influence on most other features of the landscape such as topography, land form, soil and thus also influences the vegetation (Van Riet *et al.* 1997). Alluvium outlines the area surrounding the drainage lines and the Modder River in the study area (Figure 3.4). Quaternary deposition underlies the area where the dry drainage lines are further apart and in areas with the absence of a drainage line. Dolerite, connected to a small rocky ridge just outside the study area (Figure 3.1), underlies Open Thicket next to the north-western boundary fence.

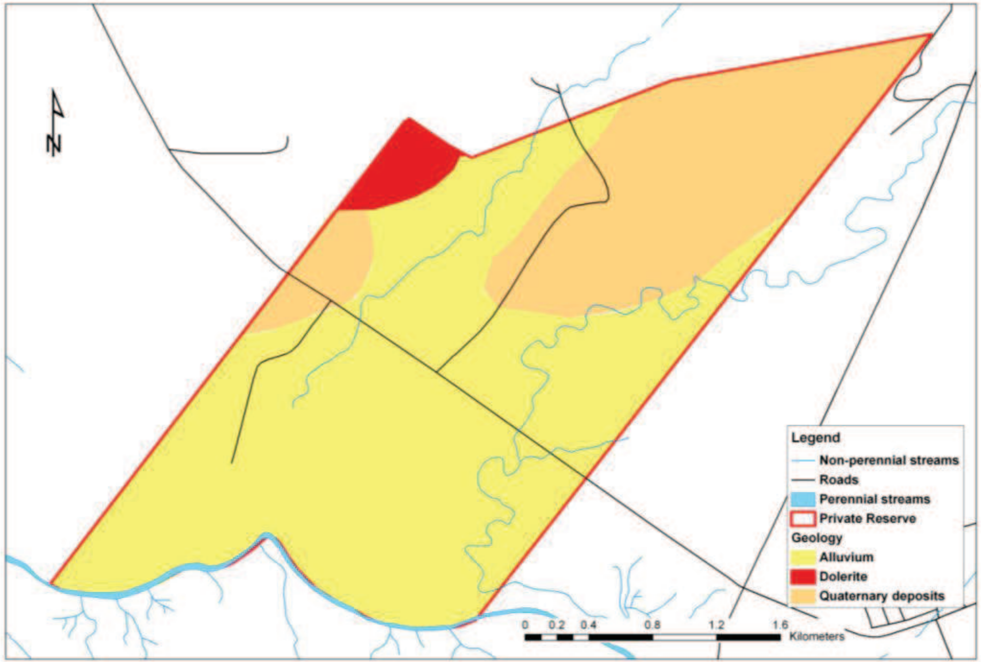


Figure 3.4 Geology of Wag-'n-Bietjie Private Nature Reserve (Chief Director Mapping 1998).

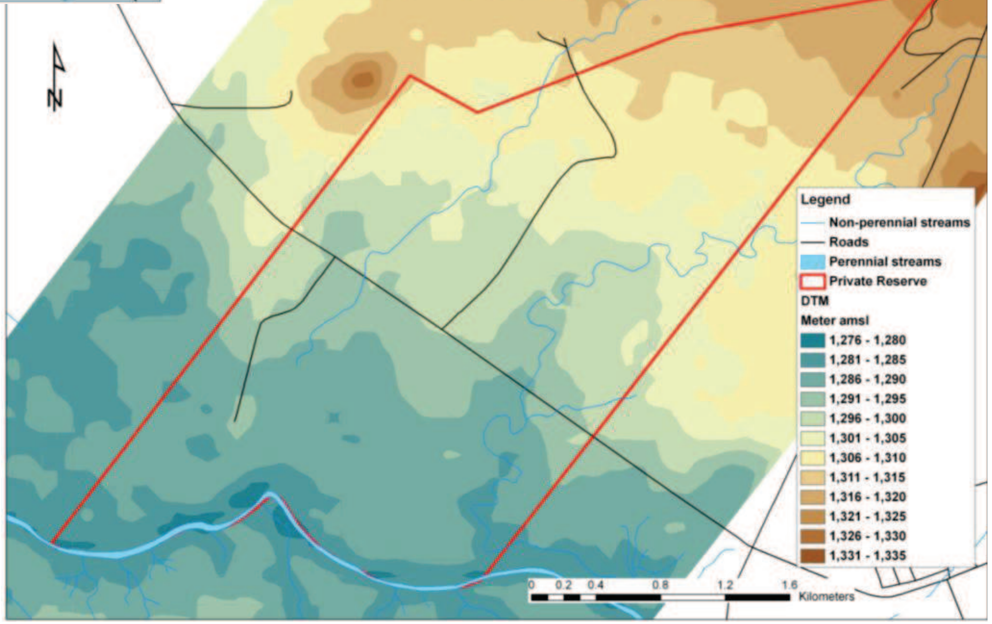


Figure 3.5 Digital Terrain Model of Wag-'n-Bietjie Private Nature Reserve (Global Land Cover Facility 2004) indicating the slight increase in altitude, 1276 m above mean sea level to 1335 m asl, from the Modder River northeast to the sharp corner in the grassland.

There is a difference in altitude from 1 335 m to 1 286 m asl in a north-eastern to south-western direction (Figure 3.5). There is also a slight decrease in altitude in the study area from the north-western corner to the bigger drainage line (connected to the river) next to the Soutpan Road, namely from 1 306 m to 1 286 m asl (Figure 3.5).

3.4.2 Land type and soil

A land type denotes an area that can be shown at a 1:250 000 scale and it displays a marked degree of uniformity with respect to terrain form, soil pattern and climate (Land Type Survey Staff 2001a). The total area of the Wag-‘n-Bietjie Private Nature Reserve falls in the Dc13 Land Type (Land Type Survey Staff 2001b). Terrain units 4 and 5 (footslopes and valley bottoms) are represented in the study area. The underlying rock formations of the Dc13 Land Type are mudstone, shale and sandstone of the Beaufort and Ecca Groups (Land Type Survey Staff 2001a).

Terrain unit 5 of the Dc land type consists of the following soil series or land classes: Oakleaf limpopo (40%), Dundee dundee (43%) and Stream beds (15%). The soil has a marked clay accumulation and is dark brown in colour. The Limpopo soil series consists of 15 – 30% clay in the A-horizon, 30 – 50% in the B-horizon and is described as fine sandy clay loam (Land Type Survey Staff 2001a). The Dundee soil series differs in clay content from 10 – 15% in the A-horizon to 20 – 30%, with no clay in the B-horizon and is described as loamy fine sand (Land Type Survey Staff 2001a). Alluvial soils are mainly of the Dundee soil form which are deposited along river banks (Van Der Merwe 1973) and classified as Fluvisols (FAO UNESCO 1987).

3.4.3 Climate

The study area falls in the summer rainfall region of South Africa. Normal annual rainfall of the central Free State ranges from 400 – 600 mm. The highest rainfall occurs from December to April, but is unpredictable and irregularly distributed (Figure 3.6). Long term mean rainfall (77 years) for the Glen Agricultural College, approximately 10 km from the study area, is 546.5 mm annually (Schulze 2000). Mean annual rainfall of the study period, 2004 – 2008, measured at the Glen Weather Station was 412 mm, but if the above average rainfall of 2006, causing flooding conditions, is omitted the mean rainfall was a low 359 mm. Total annual rainfall measured in 2006 was 612 mm (Figure 3.7) of which 179 mm was measured from January to February. In November 2006, 142 mm rain was measured, compared to 52 mm and 53 mm in November 2005 and

November 2007, respectively (Figure 3.6). Total seasonal rainfall (Table 3.2) of the growing seasons (July – June) was in range of the expected annual mean of between 359 and 412 mm.

Maximum temperatures during the summer months are known to reach 35ºC and more, but in winter months it gradually drops to between 12º and 21ºC, with June and July being the coldest months. Average maximum temperatures for winter and summer during the study period were 22°C and 33°C, respectively and average minimum temperatures were 2°C and 16°C, respectively. Average daily temperatures per month (calculated from daily minimum and maximum temperatures) ranged from 10°C to 22°C and roughly followed the same pattern through the study period (Figure 3.6). On average a 3°C warmer winter was experienced in 2005 than in other years. Black frost occurred on approximately nine nights in a row during May 2006 and May 2007 (Table 3.3), while trees still had mature, green leaves present.

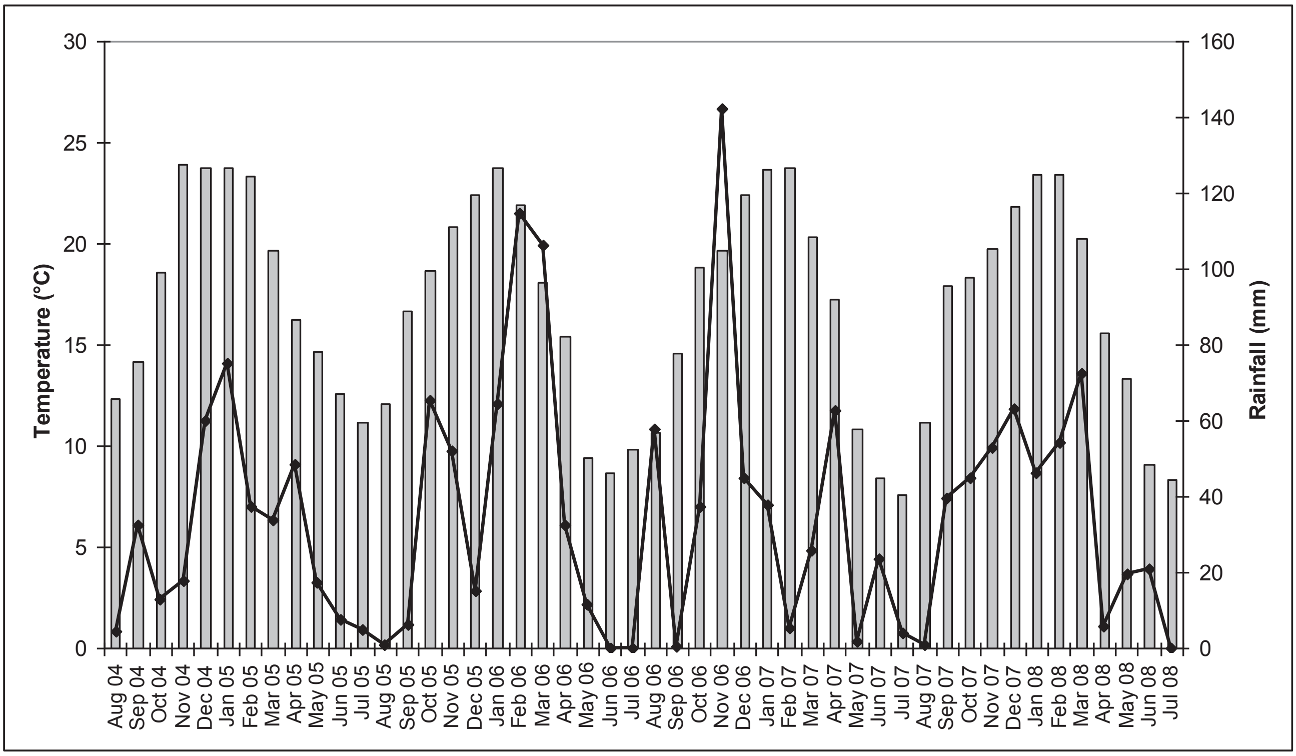


Figure 3.6 Average daily temperatures (bars) and rainfall totals (line) per month from August 2004 – July 2008. (Daily climate data supplied by the South African Weather Service).

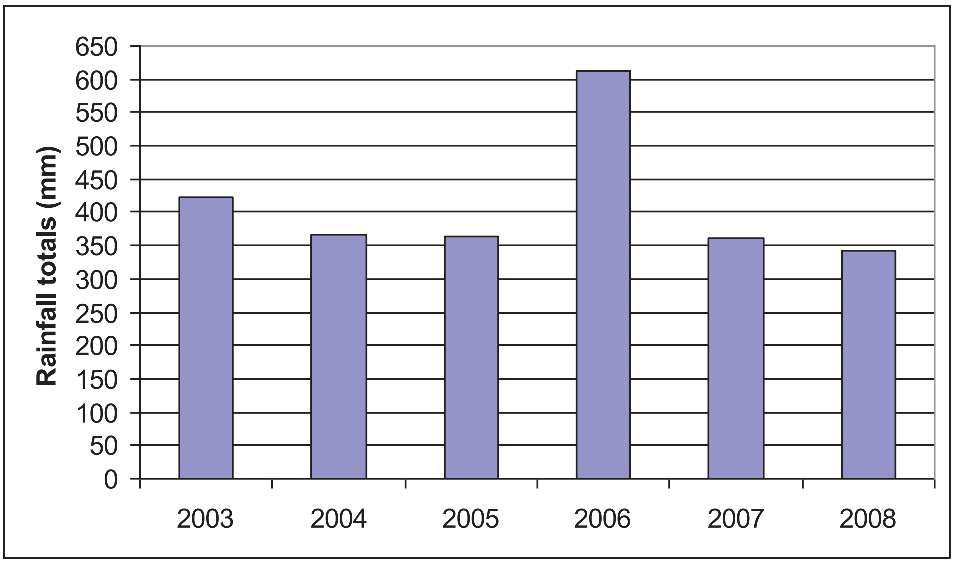


Figure 3.7 Annual rainfall totals from 2003 – 2008 as measured at Glen Weather Station, 10 km from the study area. Monthly totals supplied by the South African Weather Service.

Table 3.2 Total seasonal rainfall (mm) from July 2003 – June 2009 measured at the Glen Weather Station. (Daily rainfall totals supplied by the South African Weather Service)

Jul 2003 – Jun 2004	**Jul 2004 – Jun 2005**	**Jul 2005 – Jun 2006**	**Jul 2006 – Jun 2007**	**Jul 2007 – Jun 2008**	**Jul 2008 – Jun 2009**
378.8	349.4	474.2	439	424.8	377.4

Table 3.3 Daily minimum and maximum temperatures during the month of May, from 2005 – 2008. Temperatures in blue indicate when black frost occurred. (Source: South African Weather Service)

Date	**2005**		**2006**		**2007**		**2008**	
	Min	**Max**	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**
1	6.1	24.8	7	20	3.2	24.5	2.6	21.5
2	6.9	26.9	10.3	18.5	4.9	24.6	8.2	**15.1**
3	8.9	24.6	5.7	17.7	5.1	26	9.6	**13.3**
4	12.1	24.3	2.1	18.4	6.7	25.3	8.2	17.5
5	6.3	21.4	1.6	21	6.7	26.5	4.1	17.8
6	2.6	22.7	3.6	17.5	4.5	25.6	3.9	23.9
7	4.1	24.2	-1.2	16.1	3.2	26.7	2.9	23.7
8	2.7	25	-2.1	17.5	3.9	26.4	2.6	25.8
9	3.5	26.1	-0.8	19.6	3	25.7	5.6	26.7
10	4.5	27.9	-1.9	20.9	1.5	25.3	7.1	25.7
11	6.2	28.2	-2.6	21.8	3	25.2	1.9	22.2
12	6.3	26	0.5	22.4	0.8	25.3	0.5	22.2
13	6.1	26.5	0	22.3	1.9	25.7	1	22.9
14	8.1	25.8	1.3	22.9	4.2	27.6	2.4	25.2
15	6	16.2	2.9	21.9	1.5	19.2	5.1	26
16	3.5	21	2.4	22.5	0.5	20.7	6.6	26.3
17	4	24.5	7.1	19.8	-0.5	22.1	6.5	25
18	6.3	27.1	3.8	18.4	-1.7	25.5	8.6	22.6
19	5.7	26.4	6.9	14.7	3.5	26.2	5.4	23
20	6.3	25.1	2.9	10.7	4.2	16.6	5.7	21.9
21	6.7	25	**0**	11.6	**-2**	8.1	4.4	21.1
22	6.1	24.5	**-3.3**	13.2	**-4.2**	8.9	5	22.6
23	7.1	25	**-1.8**	11.9	**-6.1**	11	3.1	22.8
24	4.9	19.5	**-3.8**	10.9	**-7.7**	14	8.4	17.9
25	0.3	22	**-4.2**	14.7	**-7.2**	14.4	8.5	10.8
26	5.5	23.1	**-2.9**	18.1	**-5.8**	18.1	7	13.2
27	7.2	25.7	**-2.2**	19.3	**-5.5**	20.2	6.7	21.1
28	8.5	28	**-2.8**	16.3	**-3.2**	20.9	6.9	22.3
29	2.2	19.9	**-5.1**	18.2	**-2.6**	20.6	5.4	19.5
30	-0.8	17.7	**-1.9**	20.1	**-0.7**	22.9	7.3	22.6
31	0.5	23.2	0.9	22.7	3.6	23.6	2.4	18.3

CHAPTER 4
VEGETATION CLASSIFICATION OF THE *Acacia karroo* THICKET-GRASSLAND TRANSITION

4.1 INTRODUCTION

Geographically, the central region of the Free State province is located in the Grassland Biome, bordering on the Nama-Karoo Biome in the south (Rutherford and Westfall 1994). However, the vegetation of this biome does not only consist of homogeneous grassland. The grassland vegetation changes to riparian thicket where rivers run through the Grassland Biome, while koppies (rocky hills) support islands of woody vegetation. The study area is located in this central region and the vegetation ranges from grassland to riparian thicket areas.

The main objectives of this study were to provide a vegetation map, as well as classification of the vegetation (including two dry drainage lines that occur in proximity to the Modder River) and to compare the classification with other similar areas. These areas, where woody vegetation predominates, are an important habitat for animals that browse. As a result many game ranches and private reserves in the Free State province are located in proximity to rivers, dry drainage lines and other wetland areas. It was also attempted in this study to indicate the presence of a transitional zone between thicket and grassland that is found in most of these areas and to demonstrate its importance as a major unit of classification when developing management units for game ranches.

4.2 LITERATURE REVIEW

4.2.1 Vegetation overview

The Wag-‘n-Bietjie Private Nature Reserve (study area located in the northern part) is situated in the Grassland Biome. The conservation status of the Grassland Biome was very poor prior to 1996, with only 0.01% conserved, the reasons being that it is an excellent cattle and sheep farming area and many areas have been ploughed for the cultivation of maize (Bredenkamp and Van Rooyen 1996). Several game ranches and privately owned nature reserves have since been established in areas where some form of natural vegetation still exists (*vid.* Chapter 2). Private- and provincial nature reserves now constitute approximately 3.24% of the Free State province (D. Hayter, *pers. comm.*[1]).

The study area falls in the vegetation type described by Low and Rebelo (1996) as Dry Sandy Highveld Grassland and by Mucina and Rutherford (2004) as Vaal-Vet Sandy Grassland (Figure 2.5). This vegetation type includes the Western Bankenveld and Dry *Cymbopogon – Themeda* veld

[1] Dave Hayter, Chief Nature Conservator: Protected Area Planning & Stewardship Program, DETEA, Caledon Nature Reserve, Wepener.

of the Acocks classification system. Diagnostic grasses of the vegetation type include *Eragrostis lehmanniana*, *E. obtusa* and *Panicum coloratum*, as well as the common dwarf karroid shrub *Pentzia globosa*. Other prominent grass species are *Aristida congesta*, *Cymbopogon pospischilii*, *Cynodon dactylon*, *Digitaria eriantha*, *Eragrostis chloromelas*, *E. curvula*, *E. trichophora*, *Heteropogon contortis*, *Setaria sphacelata* and *Themeda triandra* (Du Preez and Bredenkamp 1991, Bredenkamp and Van Rooyen 1996, Mucina and Rutherford 2004). The vegetation type can be characterised by *Acacia karroo* trees occurring along water courses or drainage lines (Bredenkamp and Van Rooyen 1996). Du Preez and Bredenkamp (1991) listed the following species to be diagnostic in the riparian thicket of this area: *Acacia karroo*, *Asparagus laricinus*, *Diospyros lycioides*, *Lycium echinatum*, *L. hirsutum*, *Searsia pyroides* (previously *Rhus pyroides*) and *Ziziphus mucronata*. The lower strata of riparian thicket are characterised by *Setaria verticillata*, *S. incrassata*, *Melica decumbens*, *Bromus catharticus*, *Chloris virgata*, *Rubia horrida* (climber) and *Atriplex semibaccata* (Du Preez and Bredenkamp 1991).

The vegetation of the Grassland Biome follows a rainfall gradient, which generally corresponds to the relative contributions of ‘sweet’ and ‘sour’ grass species to the plant cover (Rutherford and Westfall 1994). Sweet grasses have lower fibre contents, maintain nutrients in the leaves in winter and are therefore palatable to grazers. The opposite is true for sour grass that prevails in colder areas than the study area, with higher rainfall (>625 mm) and at higher altitudes (Low and Rebelo 1996, Van Rooyen 2010). There is still a need for further research, but it seems that burning of the sweetveld is not generally recommended, especially in the semi-arid regions of the Free State (Tainton and Mentis 1984, Everson 1999, Janecke 2002). According to Everson (1999), “there should be no real need to remove accumulated ungrazed material by means other than grazing in these sweetveld areas.” Individual plants may become moribund if left unutilised for long periods, but these climatic climax grasslands are usually not subject to rapid degeneration if under-utilised (Everson 1999). Regular burning for many years in the dry season reduces the cover of these grasslands (*vid.* Chapter 9) and increases susceptibility of soil to erosion (Tainton and Mentis 1984).

4.2.2 Advantages of the Braun-Blanquet method

This classification method is based on total floristic composition and includes species with narrow ecological amplitudes. These species are not always the dominants, but indicate certain ecological factors. Classification of vegetation, particularly on groups of associated species which are restricted to certain sets of environmental conditions should thus be ecologically significant (Bredenkamp and Theron 1976, 1991).

Phytosociological tables summarise many of the communities in a single table that can be viewed in its entirety. The matrix of the table comprises quantitative data that indicate cover, abundance and fidelity of the individual species in the community. This quantitative data can be valuable in the determination of the grazing potential of the communities involved (Bredenkamp and Theron 1976, 1991). Results from additional stands can easily be incorporated into existing phytosociological tables and results obtained from other vegetation surveys can be compared with existing tables (Kent and Coker 1996).

Effects of mismanagement can be highlighted by the phytosociological table. Werger (1974) stated that "when field observations established that relevés summarised in a particular community always represent overgrazed stands, whereas closely related but less overgrazed stands are summarised in another community, that table would clearly show that the first community is just a degenerated version of the second. The table would show which floristic differences correspond to a particular degree of overgrazing and thus to the degeneration status of the community."

One of the most important advantages of the method is that it enables a hierarchical classification of vegetation. A phytosociological table indicates that some species are restricted to a community, or a smaller number of related communities. This demonstrates the relationship between communities and also provides the basis for the hierarchical classification. Floristically and environmentally related communities can be grouped. In this way numerous small vegetation units are grouped into successively larger more practical units. It is of considerable importance for management planners, for a management program can be adapted to and applied at different levels in the hierarchical system (Bredenkamp and Theron 1976, Kent and Coker 1996, Bredenkamp and Brown 2001).

Since the introduction of this method to South African ecologists, it has been successfully applied in numerous vegetation classification studies. A list of 41 references where the Braun-Blanquet method was applied in southern Africa, dating from 1973 to 2001, is provided by Janecke (2002). It includes studies done in the Eastern Cape Province, Gauteng Province, KwaZulu Natal, Limpopo Province, Mpumalanga Province, North-west Province, upper Orange River valley, Bophuthatswana and Botswana. Some examples of studies that were done in the Free State Province are: Rossouw (1983), Müller (1986), Du Preez and Bredenkamp (1991), Du Preez and Venter (1990, 1992), Kooij *et al.* (1992), Fuls *et al.* (1993), Malan *et al.* (1994), Dingaan *et al.* (2001), Malan *et al.* (2001a, 2001b), Janecke (2002), Janecke *et al.* (2003), Janecke and Du Preez

(2005). Results from these studies that are relevant to the study area will be referred to in more detail in the discussion of this chapter.

4.2.3 Some disadvantages of the Braun-Blanquet method

Much valuable work has been completed through application of the Braun-Blanquet method. Nevertheless, valid criticism of the method exists and centers on the following points, as described by Kent and Coker (1996):

- The subjectivity of the whole methodology and particularly the method of field sampling. Selection of ‘typical’ or ‘representative’ relevés of a vegetation unit is often highly biased. A substantial knowledge of the vegetation prior to any attempt at description is assumed.
- Non-homogeneous and transitional areas between typical and representative samples are not recorded under this method, yet are still clearly plant assemblages. Within any area there are a set of major plant communities that are characteristic and can be recognised consistently in the field. However between these major types there are zones of transition and ecotonal areas that should be recognised as such.
- The process of tabular rearrangement. The exact methodology of carrying this out varies from one worker to another. Species and relevés are grouped into a community or other unit according to the presence or absence of the species in relation to other communities. This can be a confusing concept for inexperienced researchers, since it has to be done by hand and by piecing it together like a jigsaw puzzle. Some computerised models can help with the initial groupings, but refinement is up to the researcher.
- The concept of ‘abstract’ communities. Species and relevés are blocked into a unit and if it does not fit into the block, some species or relevés should be discarded to prevent clutter in the table. The reason for doing this is ascribed to such a sample plot being badly chosen at the field description stage. Unfortunately, very little natural plant communities can fit into exact blocks, or are completely homogeneous. A homogeneous vegetation stand is therefore defined as one where the variation can be attributed to coincidence rather than environmental factors.
- The whole methodology is not well described in literature, has many variations and unnecessary terminology. The entire approach can only be applied and taught by very experienced workers in the field. Egler (1954) claimed that the method represented the forcing of a weak methodology on to a much more complex real world.

4.3 PROCEDURE

Classification of vegetation was done on the basis of the floristic-sociological approach, known as the Braun-Blanquet method. This method was used since it is internationally accepted and is almost exclusively used for classification research in the Free State. The essential viewpoint of the method is that plant communities are units of classification, based primarily on species composition (Kent and Coker 1996). According to Bredenkamp and Brown (2001): “A group of associated plant species with its particular habitat forms a plant community and this interrelationship between plants and the physical environment represents an ecosystem at the community level of organisation.” All plant species names conform to Germishuizen and Meyer (2003).

An 1:30 000 aerial photograph was used to distinguish between areas with obvious differences in vegetation, i.e. the presence and absence of woody species and the position of the drainage lines that indicate different vegetation units. The Global Positioning System (GPS) was used to draw the outline of each vegetation unit as well as the border fences onto a map by following it on foot or by vehicle where the terrain was accessible. The Garmin Mapsource computer program (Garmin 1999) was used to download the GPS information and from that the vegetation map was created.

Ninety five plots in total were dispersed over the above-mentioned vegetation units, covering all the vegetation units in accordance to their size. Plot sizes were fixed on 16 m^2 for the grassland and 100 m^2 for the woody communities, following Fuls *et al.* (1993), Dingaan *et al.* (2001) and Malan *et al.* (2001a). Areas next to dirt roads were avoided. Certain environmental aspects were noted in plots where applicable, like bare soil, percentage rock cover, presence of boulders or pebbles, animal presence in the form of footprints, trampling or droppings and visible disturbances.

In each sample plot all rooted plant species present were recorded and the cover abundance of each species was noted, according to the Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974)**:**
r : one or a few individuals (rare) with less than 1% cover of the total sample plot area;
+ : infrequent with less than 1% cover of total sample plot area;
1 : frequent with low cover, or infrequent with higher cover, 1 – 5% of sample plot area;
2a: abundant with 6 – 12% cover, irrespective of the number of individuals;
2b: abundant with 13 – 25% cover;
3: 26 – 50% cover;
4: 51 – 75% cover;
5: 76 – 100% cover.

4.3.1 Data analysis

As a first approximation, the data was classified using a Two-Way Indicator Species Analysis, or TWINSPAN. It is a computer program with a divisive-polythetic algorithm (Hill 1979a). Further classification refinements involved re-shuffling of species and relevés aimed at optimization of coincidence of groups of species with groups of relevés, in other words to achieve homogeneity in the clusters. Relevé (French for 'abstract') is the European equivalent for sample plot or vegetation sample. The set of floristic and environmental data is then collectively known as a relevé (Mueller-Dombois and Ellenberg 1974). Species with occurrences of three and less have been omitted from the main table, but listed underneath. Table manipulations were performed using the Megatab computer program (Hennekens 1996b).

The final groups (or blocks) of relevés and species were interpreted as plant communities characterised by diagnostic species. The vegetation types were not described as formal syntaxa, instead neutral terms were used, such as vegetation type, community and subcommunity. The following guidelines, as described by Pauw (1988), were used during the binomial naming of plant communities in the table. The first species name is preferably that of a diagnostic species that occurs in the community. The second species name is that of a visually prominent species or a dominant species with a high constancy in the community.

Ordination methods were applied to the data to illustrate relationships between plant communities. Ordination is a form of classification which involves the grouping of data on a scattergram by using numerical methods (Best 1988). Data was subjected to Detrended Correspondence Analysis, by making use of the computer program DECORANA (Hill 1979b, Hill and Gauch 1980).

4.4 RESULTS

The vegetation map is illustrated in Figure 4.1 and ordination of the vegetation data in Figure 4.2. Three vegetation types, including a transitional area, were recognised, with four communities and eight subcommunities collectively. The hierarchical classification (Table 4.1) is as follows:

1. *Acacia karroo – Asparagus laricinus* Thicket
1.1 *Ziziphus mucronata – Setaria nigrirostris* drainage line community
1.1.1 *Eragrostis curvula – Setaria nigrirostris* subcommunity
1.1.2 *Eragrostis curvula – Melica decumbens* subcommunity
1.1.3 *Bromus catharticus – Setaria verticillata* subcommunity
1.1.4 *Setaria nigrirostris – Ziziphus mucronata* subcommunity

1.2 *Acacia karroo – Cynodon transvaalensis* thicket community

1.2.1 *Cynodon transvaalensis – Acacia karroo* subcommunity

2. *Acacia karroo – Sporobolus fimbriatus* Thicket-grassland-transition

3. *Digitaria eriantha – Themeda triandra* Grassland

3.1 *Themeda triandra – Digitaria argyrograpta* community

3.2 *Digitaria eriantha* –smuts finger grass-variety community

3.2.1 *Themeda triandra – Digitaria eriantha*-variety subcommunity

3.2.2 *Eragrostis chloromelas – Digitaria eriantha*-variety subcommunity

3.2.3 *Eragrostis lehmanniana – Digitaria eriantha*-variety subcommunity

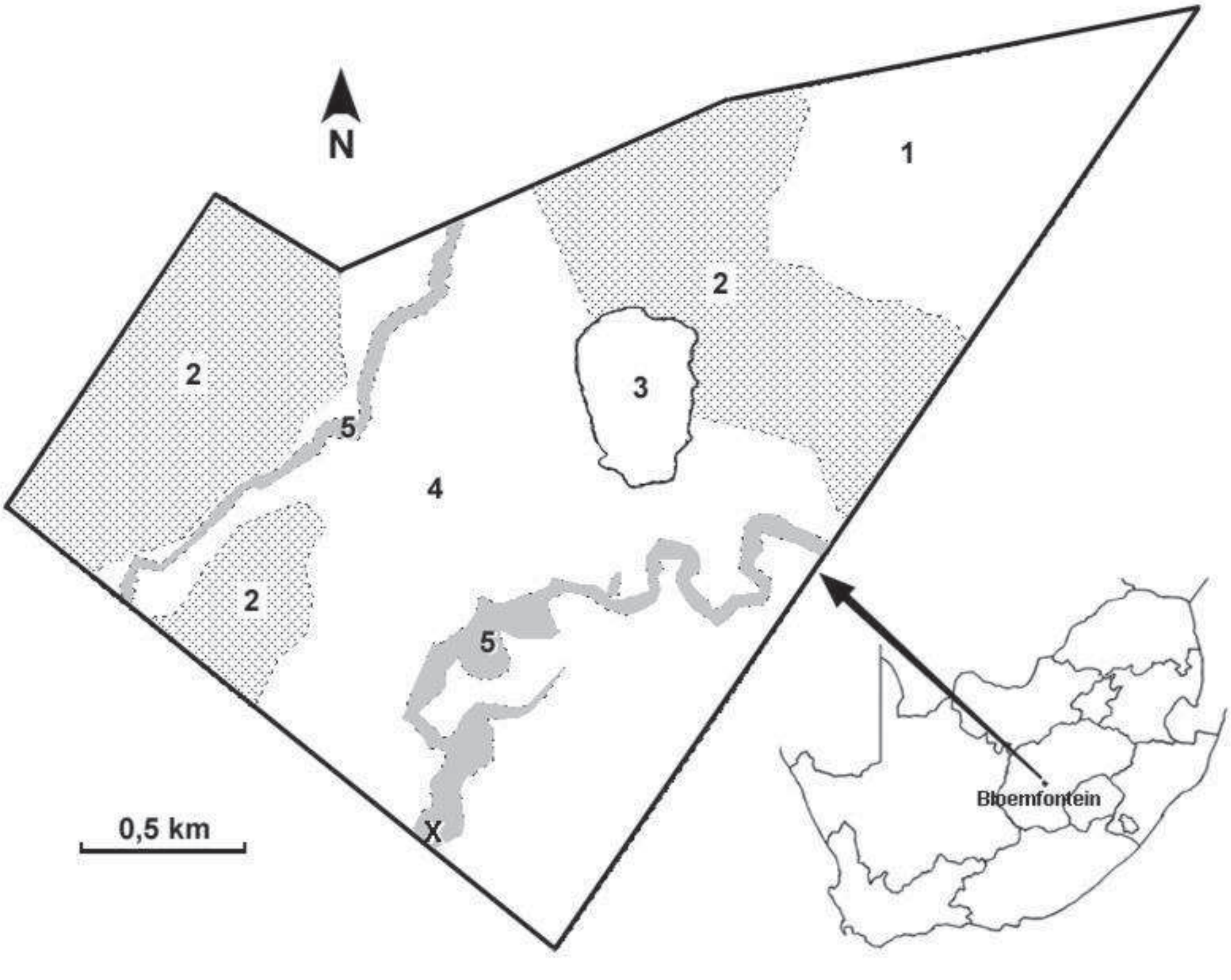


Figure 4.1 Vegetation map of the northern side of Wag-'n-Bietjie Private Nature Reserve, indicating the location just north of Bloemfontein. Legend: 1. Grassland; 1a. Smuts Finger Grassland; 2. Open thicket areas mostly representing the transitional area; 3. Disturbed area; 4. Dense thicket; 5. Dry drainage lines with the thicker area indicating a wetland; X. Connecting tunnel to the southern side of the private reserve.

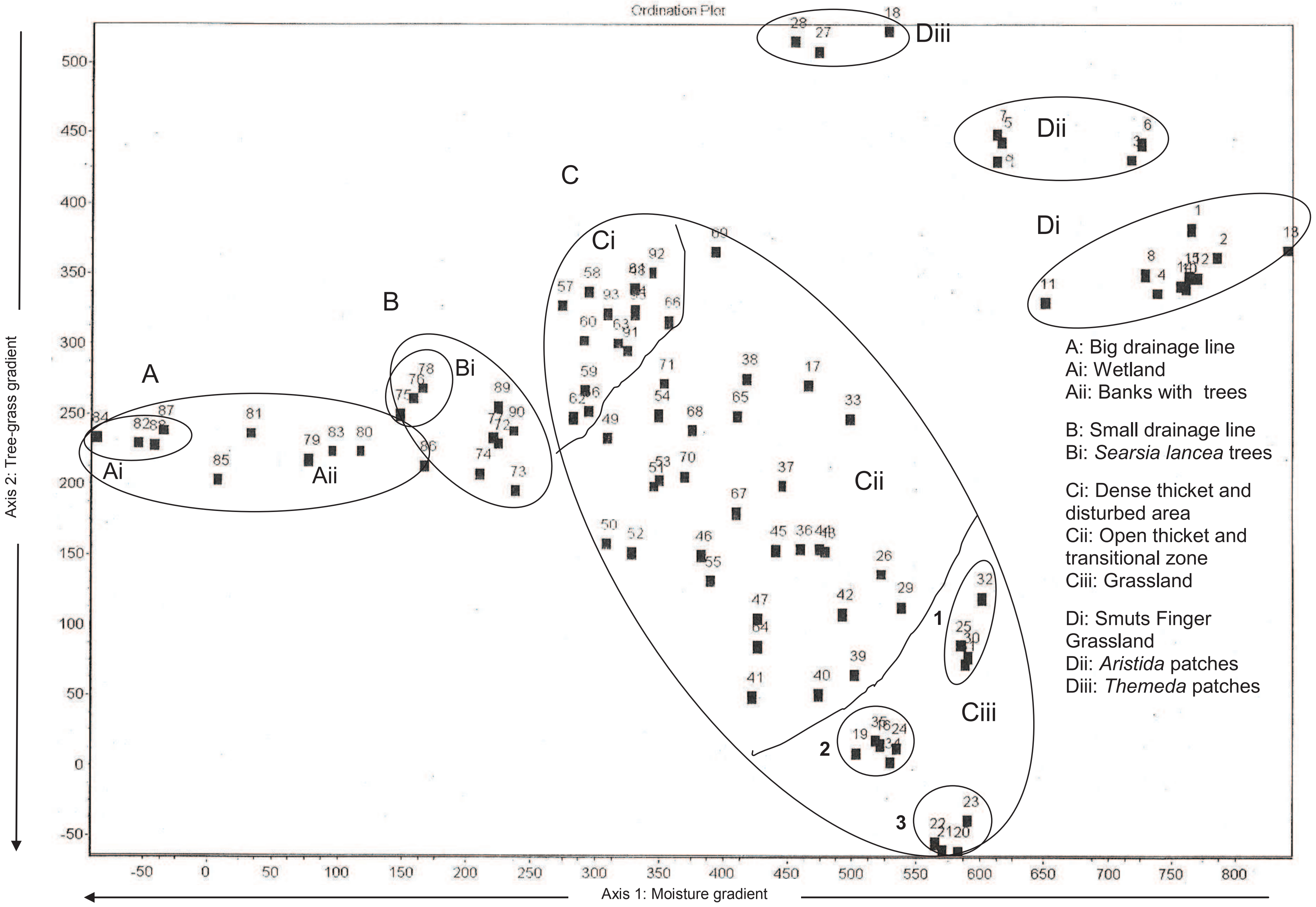


Figure 4.2 DCA-ordination plot of the vegetation (relevés) in the study area. Eigenvalue of axis 1 = 0.592 and of axis 2 = 0.292.

Table 4.1 Vegetation classification (phytosociology) of the woody and grassland vegetation of the study area. Abbreviations used: C: climber; D: dwarf karroid shrub; F: forb; G: grass; W: woody species, *: exotic species.

Releve Number												
Vegetation type		1						2	3			
Community		1.1				1.2			3.1	3.2		
Subcommunity		1.1.1	1.1.2	1.1.3	1.1.4	1.2.1				3.2.1	3.2.2	3.2.3
Species Group A												
Setaria nigrirostris	G	a a	a	. b a . a .	b b	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Eragrostis curvula	G			b . a	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Artemisia afra	F	. . . .	+ a a	a a . a . a	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Echinochloa holubii	G	. . . .	. .	. . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Bromus catharticus *	G	. . . .	. . . + .	+ b b	. . . . .	a a	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Convolvulus species	C	. . . .	. . . . .	a + .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Verbena brasiliensis *	F	. . . .	. . . . .	. . . . . .	r + b	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Alternanthera sessilis *	F	. . . .	. . . . .	. . . . . .	b . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Species Group B												
Cynodon transvaalensis	G	. . . .	. . . . .	. . . . . .	. . . . . .		b b . b	b b b b .	. . . .	. . . .	. . . .	. . . . . .
Aristida adscensionis	G	. . . .	. . . . .	. . + . . .	. . a . b	. . b . . .	. . . . a a . . a . .	a a	. . . .	. . . .	. . . .	. . . . . .
Chenopodium album *	F	. . . .	. . . . .	a b . . .	. . . . . .	+ b . a a .	. b . . . + . . .	. . a	. . . .	. . . .	. . . .	. . . . . .
Lycium horridum	D	.	. . . . .	. . . . . .	. . . . . .	. . . . . .	b + . + . + a . .	+ + r . . . . + . r	. . . . a	. . . .	. . . .	. . . . . .
Clematis brachiata	C	. . . .	. . . . .	. . . . . a	. + + . . .	. . . . . .	a . a . a + ...	. . . .	. . . .	. . . .	. . . .	. . . . . .
Opuntia ficus-indica *		. . . .	. . . . .	. . . . . .	. . . . + .	. . . . . .	. + . a	. . r . . r	. . . .	. . . .	. . . .	. . . . . .
Tagetes minuta *	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . + . . r	. . . . . . r . . r .	. . . .	. . . .	. . . .	. . . . . .
*Sphaeralcea bonariensis**	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . a	. + ...	. . . .	. . . .	. . . .	. . . . . .
Species Group C												
Acacia karroo	W	. . . .	. . . . .	. b	. . b b	b	. +	b	. . . .	. . . .	. . . .	. . . . . .
Asparagus laricinus	W	. . . .	. . a . .	a a a b	b a b . b a	a . + a	b b b	b a b a	. . . .	. . . .	. . . .	. . . . . .
Melica decumbens	G	a . . .	a a a	a . a	. b . . b .	. . . . . .	a b b a b	. . . .	. . . .	. . . .	. . . .	. . . . . .
Ziziphus mucronata	W	. . . .	. . . . .	b b	b	. . . . . .	a . . .	. a . b .	. . . .	. . . .	. . . .	. . . . . .
Diospyros lycioides	W	. . . .	. . . . .	. . b .	. b .	. . . . . .	. . b a a a b . . . b	a . b a . a . . . a .	. . . .	. . . .	. . . .	. . . . . .
Searsia pyroides	W	. . . .	. . . . .	.	. . .	. . . . . .	b . . b . . a	. . . . . b a . a . .	. . . .	. . . .	. . . .	. . . . . .
Setaria verticillata	G	. . . .	. . . . .	a a b b b	b b b a . .	. . . . . .	. . . . + .	. . . a . . . . + . .	. . . .	. . . .	. . . .	. . . . . .
Aristida diffusa	G	. . . .	. . a . .	a	. . . . . .	. . . . . .	. . . a	. . . . a a	. . . .	. . . .	. . . .	. . . . . .
Eragrostis biflora	G	. . . .	. . . . .	. . . . . .	b b a b .	. . . . . .	b . . . . b	. . . .	. . . .	. . . .	. . . .	. . . . . .
Chloris virgata	G	. . . .	. . . . .	. . . . . .	. b	. . . . . .	. . . .	. . r	. . . .	. . . .	. . . .	. . . . . .
Panicum maximum	G	. . . .	. . . . .	. . . . . .	a	. . . . . .	. . . .	. b . . . a a . . .	. . . .	. . . .	. . . .	. . . . . .
Species Group D												
Digitaria argyrograpta	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . b	. a a b . a . .	a . . . b a a a b a b b a . .	. . . .	. . . .	. . . . . .
Eragrostis obtusa	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . a . a	. + . . a . . a	. . a	. . . .	. . . .	. . . . . .
Helichrysum zeyheri	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . a . . .	. . . .	r . + . . . r + +	+ a . . + r . . a r . + + + r	. . . .	. . . .	. . . . . .

Continued on next page…

Table 4.1 Continued

Cymbopogon pospischilii	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . a	. . . + a	. . . . . . a . b . . a .	. . . .	. . . .	. . . . . .
Eragrostis superba	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . a	. . . .	. . . . a . . . . a a	. . . .	. . . .	. . . . . .
Tragus koelerioides	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. + ...	. . . . + ...	. . . .	. . . .	. . . . . .
Rosenia humilis	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	+ . . . . . + a	. . . . a	. . . .	. . . .	. . . . . .
Berkheya pinnatifida	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . r . . .	r r	. . . . + r . . . . + . .	. . . .	. . . .	. . . . . .
Pentzia globosa	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . . . a	. . . . a . . a	. . . .	. . . .	. . . .	. . +
Felicia muricata	D	. . . .	. . . . .	. . . . . .	. . . . a .	. . . . . .	. . . . + ...	a . . . . r +	. . a	. . . .	. . . .	. . . . . .
Hibiscus pusillus	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . . r . .	. . . + r + ... r . + . . r	. . . .	. . + + . .	. . . . . .
Species Group E												
D. eriantha (Smuts Finger)	G	. . . .	a . a . .	a a . a . .	. . . . . .	. . . . . .	. . . .	. . b . . . . . a a .	. . . . a	.		
Eragrostis chloromelas	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. a . . . a a b . b	b a	. . . b b b a a	. . a	. a a a . b	. . . . . .
Eragrostis lehmanniana	G	. . . .	. . . . .	. . . . . .	. . . . . .	. a a	. . . b a a . a a . .	. a . . . . b . . .	b b . . . . a .	a	a a	a a a b
Rhynchosia totta	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. r r .	r . + . r + r	+ + . a +
Aristida congesta	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	a . . . + a . .	. . . . a . . .	a	. . .	. . . . . . a	. .
Chrysocoma ciliata	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . a	. . . . + ...	. . . . a .	. . .	. . . .	. .
Species Group F												
Themeda triandra	G	. . . .	a a	. .	a a a b a	. . . . .	a a . .	a b b b a .	a b a b b a	a a a a	. . . . . .	. . . . . .
Sporobolus fimbriatus	G	a .	. b a b a	. a . . .	. b b	a a a	b a a	b a a a a b	b b . . . b . . a . . . b	. . . .	. . . .	. . . . . .
Panicum coloratum	G	. . . .	a a a	. b a a a	. . . a a a	. a . .	. . . . b a a a	a . a b b . b . a	. a . a . a a b b b b a b b	. . . .	. . . .	. . . . . .
Digitaria eriantha	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . .	. . . . . a a . .	. . . . .	. . . . a . a .	. . . .	. . . .	. . . . . .
Cynodon dactylon	G	. .	b b b	a . b b a	. b b	. . . . . a	a	. . a . b a . . . a .	b a a a . . b . a	a . . .	. . . .	. . . . . .
Species with low occurrence												
Searsia lancea	W	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Panicum schinzii	G	. . . .	. . . . .	. . . + .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Lycium cinereum	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . a	. . . .	. . . .	. . . .	. . . .	. . . . . .
Lycium species	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . b . . .	. . b	. . . .	. . . .	. . . .	. . . . . .
Ledebouria luteola	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . r .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Eragrostis trichophora	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Rubia horrida	C	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Aptosimum indivisum	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . . r +	. . . .	. . . .	. . . .	. . . . . .
Dipcadi viride	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . . r	. . . .	. . . .	. . . .	. . . . . .
Brachiaria eruciformis	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . . a . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Nenax microphylla	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . . . .
Salsola glabrescens	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	+	. . . .	. . . .	. . . .	. . . . . .
Pogonarthria squarrosa	G	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . .	. . . .	b . . . .
Hertia pallens	D	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	a	. . . .	. . . .	. . . . . .
Selago dinteri	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . . +	. . . .	. . . .	. . . . . .
Lantana rugosa	F	. . . .	. . . . .	. . . . . .	. . . . . .	. . . . . .	. . . .	. . . .	. . . . . . + ...	. . . .	. . . .	. . . . . .

4.5 DISCUSSION

4.5.1. *Acacia karroo – Asparagus laricinus* Thicket

This thicket is characterized by the dominance of woody species (Species Group C – Table 4.1) that occur along with grasses highly acceptable to game, like *Themeda triandra*, *Sporobolus fimbriatus*, *Panicum coloratum* and *Cynodon dactylon* (Species Group F). The vegetation type can be grouped into two communities, namely a drainage line community and a thicket community. Game frequents both these areas and includes the browsers, mixed feeders and even grazers like bontebok; red lechwe; red hartebeest; waterbuck and zebra (*vid.* Chapter 7).

4.5.1.1 *Ziziphus mucronata – Setaria nigrirostris* drainage line community

The vegetation of the two drainage lines present in the private reserve is represented by this community. *Searsia pyroides*, *Ziziphus mucronata* and *Asparagus laricinus* (Species Group C) are the more common woody species present on the banks of the drainage lines. *Acacia karroo* and *Diospyros lycioides* (Species Group C) were not so common. Only three *Searsia lancea* trees (previously *Rhus lancea*) are present and occur on the banks of the one drainage line. The species from Species Group A have a high fidelity in this community.

Du Preez and Bredenkamp (1991) classified the vegetation mostly found on the well developed river banks, floodplains, streams and smaller drainage lines in the Free State, as *Acacia karroo* Riparian Thicket. Malan *et al.* (2001b) reported the following species in the drainage lines (drainage channels) of the southern Free State, that concur with this study: *Acacia karroo*, *Artemisia afra*, *Asparagus laricinus*, *Diospyros lycioides*, *Searsia lancea*, *S. pyroides*, *Ziziphus mucronata*, *Sporobolus fimbriatus* and *Themeda triandra* on the banks of rivers and drainage lines; with *Chenopodium album* and *Setaria verticillata* in disturbed areas on the banks. *Celtis africana*, *Phragmites australis* and *Salix babylonica* were also conspicuous species listed by Malan *et al.* (2001b), but were not recorded in this study. This is probably because these species are more associated with wet areas, or rivers, while the drainage lines of the private reserve are mostly dry. The above-mentioned results also concur with that of Dingaan *et al.* (2001).

4.5.1.1.1 *Eragrostis curvula – Setaria nigrirostris* subcommunity

Around one drainage line, the topography changes to a large flattened area between the banks with the narrow drainage line itself sinking deeper into the earth's surface as it meanders through this wetland. The wetland covers about half of the length of this specific drainage line (Figure 4.1). It is dominated by *Eragrostis curvula* (Species Group A) that formed large tufts with 50 cm base diameter. *Setaria nigrirostris* (Species Group A) and *Sporobolus fimbriatus* (Species Group F) are the only other notable species.

4.5.1.1.2 *Eragrostis curvula – Melica decumbens* subcommunity

This subcommunity represents the basin of the larger drainage line, excluding the surrounding wetland (subcommunity 1.1.1). The vegetation is dominated by grasses, while tree species are absent. In areas where trees are absent from the bank as well, these same grasses are dominant. *Eragrostis curvula*, *Setaria nigrirostris* (Species Group A) and *Sporobolus fimbriatus* (Species Group F) are prominent in the basin of the drainage line, as in the wetland. Other species with high occurrences are *Melica decumbens* (Species Group C), *Artemesia afra* (Species Group A) and the species from Species Group F. The presence of the shade loving grass *Melica decumbens* can be ascribed to the banks casting a shadow early in the afternoons. Results of this study that corresponded to that of Dingaan *et al*. (2001) are the following: the dominance of graminoids in the ground layer on the banks (where the woody cover is not so dense); and the presence of *Bromus catharticus*, *Melica decumbens* and *Cynodon dactylon* on the banks.

4.5.1.1.3 *Bromus catharticus – Setaria verticillata* subcommunity

A significant species difference is noted on the banks of the larger dry drainage line where trees and shrubs are present, if compared to the *Eragrostis curvula – Melica decumbens* subcommunity (1.1.2). Species such as *Eragrostis curvula*, *Setaria nigrirostris* (Species Group A), *Themeda triandra* and *Sporobolus fimbriatus* (Species Group F) are still present, but not as prominent as in subcommunity 1.1.2**.** *Bromus catharticus* (Species Group A), *Setaria verticillata* and *Ziziphus mucronata* (Species Group C) dominate the vegetation on the banks. *Bromus catharticus* (an alien species) was only found where it was protected from grazers by woody species or densely growing grasses. It usually grows in moist to wet places, often in the shade (Gibbs Russel *et al.* 1990, Van Oudtshoorn 1999). The high presence of species from Species Group C and the presence of a

Convolvulus species (Species Group A) further contribute to the differentiation between this subcommunity and the previous one.

4.5.1.1.4 *Setaria nigrirostris - Ziziphus mucronata* subcommunity

This subcommunity represents the vegetation of the smaller, narrower, dry drainage line, with the absence of a wetland (Figure 4.1). The smaller size of the drainage line rendered it difficult to differentiate between the basin and the bank in sampling. The large woody species, along with other species from Species Group C, were mostly present on the banks, while species from Species Groups A & F were mostly found in the basin. *Setaria nigrirostris* (Species Group A) and *Ziziphus mucronata* (Species Group C) are dominant, while the prominent woody species are *Acacia karroo*, *Asparagus laricinus* and *Diospyros lycioides* (Species Group C). Species that are associated with this drainage line, but absent from the larger drainage line (subcommunities 1.1.2 & 1.1.3), are *Verbena brasiliensis*, *Alternanthera sessilis*, (Species Group A), *Eragrostis biflora* and *Chloris virgata* (Species Group C). The near absence of most of the other species in Species Group A is also diagnostic.

4.5.1.2 *Acacia karroo – Cynodon transvaalensis* thicket community

The species from Species Group B characterize this thicket community, which mostly occurs in the area between the two drainage lines (Figure 4.1). The dominant species are *Cynodon transvaalensis* (Species Group B), *Acacia karroo* and *Asparagus laricinus* (Species Group C)**.** *Melica decumbens*, *Ziziphus mucronata* (Species Group C) and *Sporobolus fimbriatus* (Species Group F) are prominent in the thicket community. *Diospyros lycioides* (Species Group C), *Panicum coloratum* and *Themeda triandra* (Species Group F), as well as the grass species from Species Group E, mostly occur with a 5 – 25% presence in these relevés. Woody species are dominant over graminoid species.

This thicket community (1.2), as well as the transitional community (2), is comparable with the *Acacia karroo* thicket class described by Du Preez and Bredenkamp (1991). Concurring diagnostic woody species were found, namely the dominant *Acacia karroo*, also *Ziziphus mucronata*, *Searsia pyroides*, *Diospyros lycioides* and *Asparagus laricinus*. Other conspicuous, corresponding species between the two studies were *Lycium hirsutum*, *Chenopodium album*, *Setaria verticillata*, *Melica decumbens*, as well as most of the species present in Species Group D and all of the species present in Species Groups E & F (Table 4.1). Rossouw (1983) listed similar species for the Bloemfontein area and Müller (1986) for the Willem Pretorius Game Reserve. They recorded all these species on the banks of rivers and dry drainage lines (watercourses), as well as on the plains.

4.5.1.2.1 *Cynodon transvaalensis – Acacia karroo* subcommunity

Acacia karroo (Species Group C) becomes co-dominant along with a carpet of *Cynodon transvaalensis* (Species Group B) in this subcommunity. Only four other species are prominent, namely *Chenopodium album* (Species Group B), *Asparagus laricinus* (Species Group C), *Eragrostis lehmanniana* (Species Group E) and *Sporobolus fimbriatus* (Species Group F). The absence of all other species from Species Group C is diagnostic. The area represented by this subcommunity is visibly disturbed, occurs next to ruins and an old paddock and is also characterised by the presence of a planted row of *Pinus* and *Eucalyptus* tree species. It is home to most of the grazers that prefer short and medium length grass in the private reserve (*vid.* Chapter 7). It is indicated as a disturbed area in Figure 4.1.

4.5.2. *Acacia karroo – Sporobolus fimbriatus* Thicket-grassland-transition

This area is considered transitional between the dense thicket (dominated by woody species) and the grassland (dominated by herbaceous species) (Figure 4.1), because woody species co-dominate with herbaceous species. Species of both of these mentioned vegetation types are present in this classification and only Species Group A is absent. This major community, or vegetation type, can also be grouped into the communities of both vegetation types on either side of it on Table 4.1, in other words the blocks of all the Species Groups can be elongated to include this vegetation type as a subcommunity of the new major unit that becomes Species Group F. However, this gives a wrong impression of the vegetation present and does not clearly distinguish between the two obvious, visible vegetation types, namely grassland and dense thicket.

Non-homogeneous and ecotonal (transitional) areas between typical and representative samples are not normally recorded under the Braun-Blanquet method. This is one of the big disadvantages of the method, since ecotones are clearly defined plant assemblages, are present throughout natural areas and should not be ignored. These relevés are mostly discarded from a data set, since the method implies that such relevés must have been badly chosen at the stage of field description and that disorder should be prevented on vegetation classification tables (Kent & Coker 1996). The relevés from this ecotone are, however, included in the data set, since it represents a large part of the study area that falls in a transitional zone and has distinct habitat characteristics. It represents areas between grass- and woody species dominated areas, called open thickets in this study. These areas are important for mixed feeders (feeding on grass and leaves from woody species), like impala and eland, as well as for grazers, especially blue wildebeest, that use trees for shelter (Table 7.1). Buffalo prefer a woody habitat but feed on grass (Estes 1997) and favour this habitat type, as do browsers from time to time, probably because the vegetation is not so dense.

Prominent species of the transitional zone are: *Acacia karroo*, *Asparagus laricinus*, *Ziziphus mucronata* (Species Group C), *Cynodon transvaalensis* (Species Group B), *Digitaria argyrograpta* (Species Group D), *Themeda triandra*, *Sporobolus fimbriatus*, *Panicum coloratum* and *Digitaria eriantha* (Species Group F). Species from Groups D & E are more prominent in this transitional community, than in the thicket community, and are separated on these grounds. These species are normally associated with grasslands of the semi-arid areas. *Sporobolus fimbriatus* and *Cynodon transvaalensis* are associated with the woody species and have a high occurrence, as is also the case in the thicket community (1.2)**.** *Sporobolus fimbriatus*, *Melica decumbens*, *Setaria verticillata* and *Eragrostis biflora* are known to occur in the shade under trees (Gibbs Russel *et al.* 1990, Van Oudtshoorn 1999).

There is a possibility that the presence of *Acacia karroo* in some of the transitional areas is as a result of encroachment from the drainage line into the grassland. It is known that a competition interaction for water exists between the trees and the herbaceous layer (Stuart-Hill *et al.* 1987, Smit and Swart 1994; Tainton 1999). Reduced density of the grass layer, and the associated reduction of water loss from the upper 60 cm of soil, may result in increased quantities of water penetrating to deeper soil layers despite increased rainfall run-off losses. Increased quantities of water in the deeper soil layers give deep-rooted woody species a competitive advantage (Tainton 1999). Tree thickening may also be linked to occasional periods of rainfall well above the average, known as episodic events, which give rise to pulses of germination and establishment. During these periods seedlings of woody species can withstand the competition for water from dense grass communities (Tainton 1999). This topic is discussed in more detail in Chapter 8.

4.5.3. *Digitaria eriantha – Themeda triandra* Grassland

The species that represent this vegetation type are normally associated with semi-arid grasslands of the area. The absence of woody species (Species Group C), associated with the thicket, is characteristic. None of the species characteristic of the drainage line (Species Group A) are present in this vegetation type. It is comprised of two communities and a subcommunity.

Digitaria eriantha is classified as a species complex including two varieties. The first variety is normally associated with the semi-arid grassland (Species Group F). It occurs in the thicket and grassland units of the private reserve. The other, purple coloured variety (Species Group E) occurs in the drainage line and as a dominant species in the sharp corner of the reserve (Figure 4.1), next to the characteristic grassland area. This latter variety is known as Smuts Finger Grass and probably has its origin as cultivated pastures.

4.5.3.1 *Themeda triandra – Digitaria argyrograpta* community

The species of Species Groups D, E & F are the more common forbs, dwarf karroid shrubs and grasses associated with the grassland (Tainton 1999). Palatable climax grasses, like *Themeda triandra*, *Panicum coloratum*, *Digitaria argyrograpta* and *D. eriantha*, have a high presence in the grassland. These grasses are abundant in good veld, but decrease in number when the veld is overgrazed (Van Oudtshoorn 1999). *Cymbopogon pospischilii* (previously *C. plurinodis*) is also a prominent species in the grassland. Only a few pioneer and subclimax grass species, that increase with underutilization or overgrazing (Van Oudtshoorn 1999), are present with a small percentage occurrence in the grassland, namely *Eragrostis obtusa*, *E. superba*, *Tragus koelerioides* (Species Group D), *Aristida congesta* (Species Group E), *E. chloromelas*, *E. lehmanniana* (Species Group E) and *Cynodon dactylon* (Species Group F). Several grazers are present in the study area, namely blue wildebeest; bontebok; buffalo; gemsbok; red hartebeest; springbok; tsessebe; waterbuck and zebra, but the herbaceous layer appeared to be in a good condition and not overgrazed when this vegetation study was done. Differences in grass production between wet and dry years are discussed in Chapter 8.

Themeda triandra (Species Group F) is dominant and reaches its highest percentage cover in this community. *Digitaria argyrograpta* (Species Group D), *Panicum coloratum* and *Digitaria eriantha* (Species Group F) are prominent in the grassland. The *Digitaria eriantha* variety that is present in this community differs from the Smuts Finger Grass that dominates in community 3.2 in Table 4.1. This variety is the one normally associated with the semi-arid grasslands of the area, with yellowish inflorescences and culms on average 500 mm tall.

Results concur with that of Soetdoring Nature Reserve, most notably with regard to the patches in the mosaic pattern of the grassland that are not overgrazed (Janecke and Du Preez 2005). These areas are dominated by palatable, decreaser grass species. Dwarf karroid shrubs and forbs are present, but not dominant. The *Eragrostis lehmanniana – Eragostis obtusa* vegetation class of Du Preez and Bredenkamp (1991) contains similar species for the grassland, but includes more of the dwarf karroid shrubs, pioneer and subclimax grasses, that increase with overgrazing. Results from Kooij *et al.* (1992), Fuls *et al.* (1993) and Malan *et al.* (1994) concur in terms of some grass species present, but also contain more pioneer grass species and dwarf karroid shrubs due to disturbances.

4.5.3.2 *Digitaria eriantha*-Smuts Finger Grass-variety community

This community is classified on its own, due to the different variety of *Digitaria eriantha*, Smuts Finger Grass (SFG, Species Group E), dominating the area. This variety has purple coloured inflorescences, culms that are on average 1 000 mm tall with the top half being purple coloured, as well as purple nodes on the bottom half of the culms. This is probably a cultivated pasture grass. Grazers, such as red hartebeest, springbok and blue wildebeest have been seen in the area, but it is not certain to what extend they graze this species. Few other plant species are present in this community, listed in Species Group E. The absence of most other species groups is also characteristic.

4.5.3.2.1 *Themeda triandra – Digitaria eriantha*-variety subcommunity

Themeda triandra (Species Group F) is diagnostic of this subcommunity, along with the noticeable dominance of the *Digitaria eriantha*-SFG variety (Species Group E). Only *Eragrostis lehmanniana* (Species Group E) is present in all the relevés, with *E. chloromelas* and the small forb *Rhynchosia totta* (Species Group E) in some of the relevés. Species that become dominant in the absence of the *Digitaria eriantha*-SFG variety are *Aristida congesta* (Species Group E), *Sporobolus fimbriatus* and *Cynodon dactylon* (Species Group F).

4.5.3.2.2 *Eragrostis chloromelas – Digitaria eriantha*-variety subcommunity

The absolute dominance of the *Digitaria eriantha*-SFG variety in this subcommunity is diagnostic. *Eragrostis chloromelas*, *E. lehmanniana* and the small forbs *Rhynchosia totta* (Species Group E) and *Hibiscus pusillus* (Species Group D) are the only species present in almost all the relevés. Small tufts of *Themeda triandra*, *Aristida congesta* (Species Groups E & F) and of *Pogonarthria squarrosa* are the only other plants associated with this subcommunity.

4.5.3.2.3 *Eragrostis lehmanniana – Digitaria eriantha*-variety subcommunity

Certain patches inside the area dominated by the *Digitaria eriantha*-SFG variety were not so densely covered and were bare compared to the surrounding areas. In these patches *Eragrostis lehmanniana, Aristida congesta*, *Chrysocoma ciliata* (Species Group E) and *Pentzia globosa* (Species Group D) are diagnostic. This subcommunity also differs from the other two in the complete absence of *Eragrostis chloromelas* (Species Group E). Signs of animal presence in the form of footprints and dung were found in some of these bare patches.

4.5.4 General discussion

Direct gradient analysis (canonical ordination methods) can be used to study the part of variation in community composition that can be explained by a particular set of environmental variables. In indirect gradient analysis the major pattern of variation in community composition is first determined and the environmental basis of this pattern is to be established later. Indirect gradient analysis has the advantage that no prior hypothesis is needed with regards to what environmental variables are relevant and informal field knowledge can be used to help interpret the patterns that emerge (Ter Braak and Pretence 1996, Lepš and Šmilauer 1999). In this thesis, indirect methods were used for Correspondence Analyses (CA) and Detrended Correspondence Analyses (DCA), while direct methods were used for Canonical Correspondence Analyses (CCA). The Monte Carlo permutation test was applied to the CCA-ordinations to indicate the statistical significance of the species-environment relation for the first and all canonical axes. According to Ter Braak and Prentice (1996): "Linear methods (Principle Components Analysis (PCA) and Redundancy Analysis (RDA) are appropriate to community analysis only when species data are quantitative abundances (with few zeros) and the range of environmental variation in the sample set is narrow". Consequently only non-linear methods were used in the thesis.

The DCA-ordination results of the vegetation data concur largely with that of the vegetation classification presented in Table 4.1. Ordination grouped the data on Axis 1 (Figure 4.2) according to a moisture gradient – from the wetland in the big drainage line to the grassland dominated by the *Digitaria eriantha*-Smuts Finger Grass variety, located in the sharp corner of the study area (Figure 4.1), the furthest distance from the drainage lines. It also grouped the data into the different vegetation units (A, B, Ci, Cii, Ciii, D) as indicated in Figure 4.1.

Axis 2 of Figure 4.2 represents the tree-grass gradient, from the dense thicket with a lower grass cover (Ci) to the grassland at the bottom with the highest grass cover (Ciii). The open thicket ecotone (Cii) is indicated in the centre of the plot and in between these two vegetation units. The grassland is divided into communities that contain similar herbaceous species than the thickets (Ciii), that are expected in the Grassland Biome, and the unique Smuts Finger grassland (D). Three groups can be observed in the grassland (Ciii), that each contain the following abundant species: 1) *Digitaria argyrograpta*, *Eragrostis superba*, *E. chloromelas*, *Themeda triandra*, *Panicum coloratum* and *Digitaria eriantha*.; 2) a high occurrence of *Themeda triandra*, along with *Eragrostis chloromelas* and all species from Species Group D (except *Eragrostis obtusa* and *Pentzia globosa* Table 4.1); and 3) *Cymbopogon pospischilli*, *Themeda triandra*, *Panicum coloratum* and *Digitaria argyrograpta*. A distinction was also made between noticeable white patches of *Eragrostis chloromelas* (Di) located in the purple coloured Smuts Finger dominated areas and disturbed patches (Dii) characterised by bare areas and pioneer species like *Aristida congesta* and *Chrysocoma ciliata*. Areas where *Themeda triandra* and *Sporobolus fimbriatus* became more prominent (Diii) were also grouped together.

A good comparison was found between data from this study area and that of authors who worked in similar areas in the Free State. Vegetation from the drainage lines corresponded to that reported by Du Preez and Bredenkamp (1991), Dingaan *et al.* (2001) and Malan *et al.* (2001b). Thicket vegetation that is further away from the drainage lines corresponded to results of Rossouw (1983), Müller (1986) and Malan (2001a). The grassland vegetation corresponded to results from Du Preez and Bredenkamp (1991), Fuls *et al.* (1993), Malan *et al.* (1994) and Janecke and Du Preez (2005).

4.6 CONCLUSIONS

The vegetation types of Wag-‘n-Bietjie Private Nature Reserve was found to consist of a dense thicket, a grassland and a thicket-grassland transitional area, or open thicket. The thicket is dominated by woody species normally associated with riparian thicket areas of the Free State province. The vegetation of the drainage lines was therefore grouped into the larger thicket unit. Species that can be associated with wet areas differentiated the drainage lines from the thicket vegetation. The grassland was found to be in relatively good condition and showed little evidence of overgrazing when this vegetation study was done. The open thicket was differentiated from the thicket and grassland by the co-dominance of woody species and species normally associated with grassland areas, instead of being dominated by either one of these two groups of species.

Vegetation units and the associated habitat gradients, as well as the floristic relationships between plant communities were explained by ordination. A moisture gradient and a tree-grass gradient were distinguished in the ordination results. Groups formed by ordination concurred with communities and subcommunities of the classification table. The transitional or ecotonal area, referred to as the open thicket, was clearly discernable in the ordination results as well.

The open thicket (transitional area) was found to be favoured by a large number of the study area's game species. A reason for this might be that it is not as dense as the thicket and allows for easy access of the woody vegetation and the grasses. It also provides shade and shelter in the form of trees. The difference in vegetation that was observed in the transitional area and its distinct habitat characteristics contributed to the inclusion of this area as a management unit of its own. The study area falls in a transitional zone because the presence of drainage lines of the Modder River results in riparian thicket vegetation occurring in the Grassland Biome.

The presence of *Acacia karroo* next to the grassland unit may be the result of encroachment from the drainage lines. If this is the case, care should be taken not to overgraze the grassland and transitional areas, because this may lead to increasing numbers of the species. A higher occurrence of *A. karroo* would in turn lead to denser thicket areas and may even reduce the size of the grassland unit if it intrudes into this unit.

Areas resembling the vegetation of the study area are popular for game ranches and nature reserves, because of the presence of woody species (*vid.* Chapter 2). However, care should be exercised when browsers and mixed feeders (that depend on the presence of leaves for food) are introduced into such areas (*vid.* Chapter 7), because of the deciduous nature of most species associated with this type of vegetation (*vid.* Chapter 5). The dominant woody species are *Acacia karroo*, *Diospyros lycioides*, *Searsia pyroides* (previously *Rhus pyroides*), *Ziziphus mucronata* and *Asparagus laricinus*. *Lycium* species are also mostly associated with riparian areas.

CHAPTER 5

LEAF PHENOLOGY (SEASONAL VARIATION) OF WOODY PLANT SPECIES

5.1 INTRODUCTION

The word phenology is derived from the relationship between a periodic biological phenomenon (for example breeding and migration patterns in animals) and climatic conditions: PHENO(MENON) + -LOGY (Wikipedia Dictionary 2008). Phenology as applicable to this study is defined as the study of periodic events in the life cycles of plants (such as leaf budding, leaf shedding and flowering) as influenced by the environment, especially seasonal variations in temperature, photoperiodism (day length) and precipitation (Wisiol and Hesketh 1987; Cleland *et al.* 2007; Wikipedia Dictionary 2008).

In winter when temperatures drop, daylight length is shorter and rainfall is limited all the woody species present in the study area are senescing leaves as part of their winter deciduous nature. The absence of vegetation types where evergreen species usually occur, i.e. rocky hills, in the study area, may create a lack of forage for browser game species during winter months. The objectives of this study were:

i) to quantify the plant phenology patterns of four tree- and three shrub species occurring in the study area; and

ii) to quantify the annual critical period in terms of available browse for browser- and mixed feeder game species, in order to establish if feed should be supplied to compensate for reduced leaf availability during this period.

5.2 LITERATURE REVIEW

5.2.1 Importance of studying plant phenology

Phenology is an important and often overlooked aspect of plant ecology. According to Cleland *et al.* (2007), the timing of the transition between vegetative and reproductive phases in plants that occurs in concert with flowering is crucial for optimal seed production of both individual plants and populations as a whole. Variation among plant species in their phenology is an important mechanism for maintaining species coexistence in diverse plant communities by reducing competition for pollinators and other resources. Timing of the onset of growth and senescence also determine the length of the growing season, thus influencing annual carbon uptake in terrestrial ecosystems. Cleland *et al.* (2007) stated that: “Phenological complementarity, such as nutrient capture and productivity, can also influence ecosystem processes. Thus, asynchronous responses among species to environmental changes could lead to altered community structure or ecosystem processes."

The importance of studying phenology is recognised world-wide and technology makes it possible to monitor plant phenology at a global scale. Satellite observations are increasingly important for studies of phenological and ecological responses to environmental change over space and time (Pettorelli 2005). Specific phenophases, such as flowering and fruiting, cannot be discerned on satellite images, but changes in the vegetation can be detected. The satellites' combination of comprehensive ground coverage and regularly repeated observations offer the opportunity for global phenological monitoring that is not possible with any other source (Cleland *et al.* 2007).

Plant phenology is very important in terms of availability of browse (shoots, leaves, fruits and flowers) for herbivores. In the eight plant communities researched by Dekker and Smit (1996) on the Messina Experimental Farm, Limpopo Province, the dominant tree species were all winter deciduous. The availability of browse in the Mopani Veld was at its lowest from September to November. They concluded that browser and mixed feeder game species selected different plant communities at different times of the year in order to find woody species that had longer leaf carriage periods. Availability of forage coupled to plant phenology is considered to be the most important factor influencing habitat selection by large herbivores (McNaugton 1987).

Despite the evident importance of phenology in terms of plant- and animal ecology, not many in-depth studies on phenology of southern African trees and shrubs are available. The studies of Hall-Martin and Fuller (1975); Guy *et al.* (1979); Skarpe and Bergström (1986); Van Rooyen *et al.* (1986); Milton (1987); Dunham (1991); Dekker and Smit (1996); Smit (2001) all involve the savanna biome. No published data on the phenology of woody plants in the central Free State could be found, emphasizing the importance of this study.

5.2.2 Leaf and shoot phenology

Some research on phenology of African vegetation (Hall-Martin and Fuller 1975, Skarpe and Bergström 1986, Van Rooyen *et al.* 1986, Abule *et al.* 2007), seasonal use of woody plants by browsers (Kok and Opperman 1980, Cooper *et al.* 1988, Buys 1990, Skinner and Chimimba 2005) and seasonal changes in the availability and palatability of browse (Pellew 1980, Cooper 1982, Dekker and Smit 1996, Sponheimer *et al.* 2003, Theron 2006) include information on the phenology of *Acacia* species as these are important browse plants for herbivores throughout the savannas of Africa. Milton (1987) reported that *Acacia karroo*, *A. luederitzii* and *A. burkei* in the Nylsvley Nature Reserve (near Naboomspruit or Mookgopong), Limpopo Province, had full leaf carriage in the third week of October and leaf buds had appeared on *A. tortilis*, *A. nilotica*, *A. mellifera* and *A. caffra*. Leaf fall commences in January for *A. mellifera* and in March for *A. burkei* and *A. caffra*. Leaf fall of *A. karroo* starts in April or May. Trees of all species other than *A. tortilis* were leafless for 2 – 3 months of the year (July to September). *Acacia* species that retain leaves into the winter may attract browsing ungulates, which feed on both leaves and pods and thereby disperse the seed. Milton (1987) concluded that the value of comparative studies of this type was that they facilitate predictions on the effects of seasonal browsing and management practices on various plant species.

Dekker and Smit (1996) found that despite the relative homogeneity of the Mopane bushveld vegetation in the Messina Experimental Farm, Limpopo Province, leaf carriage patterns and phenological states of leaves differed greatly between the eight plant communities studied. New-season leaves appeared either in November or December between the different communities. Other differences between communities were that leaf senescence started in April or in May and woody species were leafless for 1 or 3 months of the year. Exceptions were *Lannea schweinfurthii*, *Commiphora glandulosa* and *C. mollis* that were leafless for five to six months. Differences were also found between phenology patterns of the dominant tree species. In the case of *Colophospermum mopane* leaf flush started in September in some communities and in middle November in others. Results for *C. mopane* from a farm near Pontdrift, Northern Province concurred (Smit 2001). Dry leaves were recorded during June, August or September depending on the plant community and were retained from August to October in certain communities or not at all in other plant communities (Dekker and Smit 1996).

Most deciduous woody species in the short grass savanna of the western Kalahari of Botswana sprouted in September/October before the rains (Skarpe and Bergström 1986). Some *Acacia* species shed most of their leaves in the dry season as juveniles, but retained a major part as adults, suggesting a facultative deciduousness, presumably governed by the soil-water status. Age differences may account for differences in leaf retention over the dry season, while leaf retention by saplings may also be attributed to late summer shoot growth in response to damage by browsing mammals (Milton 1987, Smit 2001). Skarpe and Bergström (1986) concluded that in many species, leaves dried up but were retained until late in the dry season. According to Abule *et al.* (2007), "leaves retained on trees in a younger phenological state, followed by the early emergence of new season’s leaves, are likely to be of greater value to browsers than when trees are leafless for some time with only dry leaves available on the ground.”

Browsers usually utilise the tips of shoots and twigs, even in the absence of leaves (Abule *et al.* 2007). *Acacia* shoots were fully grown in February and in the process of becoming lignified in the Kalahari, Botswana. After late rains, some species, like *A. mellifera*, could develop a second shoot generation (Skarpe and Bergström 1986). Negi (1995) found that in certain tree species flowering followed shoot elongation and leaf expansion. *Acacia* species normally grow in a series of shoot flushes. The length of the shoot varies and gives the mature tree its characteristic form (Milton 1987). In the Nylsvley Nature Reserve, Limpopo Province rapid extension of *Acacia karroo* shoots occurred in September, October and December (Milton 1987).

5.2.3 Leaf phenology and climate

The definition of plant phenology (*vid.* Introduction) clearly states that climate influences periodic plant phenomena. Consequently, according to Cleland *et al.* (2007), global warming could significantly alter plant phenology because temperature influences the timing of development, both on its own and through interactions with other determinants, such as photoperiod (or day length). They further reported that the dates of the first leaf emergence had advanced globally at a rate of about 3 days per decade, while autumn had mostly been delayed due to global warming. This acceleration of spring has led to a longer growing season, predominantly by warming of the coldest days in late winter and early spring as opposed to consistent warming throughout the year.

It is generally believed that rainfall should also influence phenology. Skarpe and Bergström (1986), as well as Milton (1987) reported that in most woody species some activity, whether vegetative or reproductive, preceded the rains. Milton (1987) found that extension of *Acacia karroo* shoots occurred about six weeks before the rain. However, Dunham (1991) reported that neither the start of leaf production of *Faidherbia albida* trees in the Zambezi riverine woodlands, nor the duration of the leaf production period was directly related to rainfall. Rainfall was found to affect leaf drop in general (Rutherford and Panagos 1982). Leaf fall as a result of water stress is used by some woody species as a drought avoidance strategy (Smit 1994). Water stress also inhibits shoot growth. Milton (1988) reported that shoot production and basal increment of *Acacia tortilis* were positively correlated with rainfall and indicators of soil water.

5.2.4 Availability of browse and other food sources during winter months

Kok and Opperman (1980) and Theron (2006) listed deciduous trees, shrubs and climbers as the most important in the diet of giraffes during the wet season in the Willem Pretorius Game Reserve, Free State Province. When deciduous plants have shed their leaves and food reserves became scarce during winter, giraffes altered their food preferences. Less palatable, evergreen species that were not utilised during the wet season increased in importance as food reserve during the dry winter months. An increase in the utilisation of dry plant parts, like bark, pods, twigs and fruit (Kok and Opperman 1980) was also observed (*vid.* Chapter 6).

Owen-Smith and Cooper (1985) noted that kudus also increased their use of evergreen plants during the course of the dry season in the Nylsvley Nature Reserve, Limpopo Province. Consequently, *Strychnos pungens* was observed to be their staple browse species during this period. In addition to attached foliage, fallen leaf litter constituted a significant food source during the dry season. According to Van der Waal *et al.* (2003), competition for resources is expected to be the fiercest during October in the northwestern Limpopo Province due to the compound effect of leaf-fall and consumption. A shortage of foliage retained on woody plants have been experienced which might have led kudu to revert to dried forbs and fallen leaf litter. Smit (2001) noted that large scale mortalities of kudu were known for the mopane bushveld in the Northern Province from September to October, just before the onset of the rains, due to low leaf carriages of deciduous trees.

In the case of impala, Owen-Smith and Cooper (1985) observed a similar pattern where leaf litter constituted more than half of the total consumption of woody plant foliage during the dry season. Cooper (1982) noted that during autumn impalas spent 22% of their feeding time in the Nylsvley Nature Reserve, eating leaf litter of especially *Ziziphus mucronata*, *Strychnos cocculoides* and *Terminalia sericea* and this proportion increased even more during winter months. Impala browse and graze with the intensity depending on their locality and the season of the year (Van Rooyen 1992, Meissner *et al.* 1996). *Acacia* pods and some fruits of other species are also eaten when available. Plant species neglected at one time of the year may become favoured at another time, due to changes in food abundance and/or in relative leaf chemistry (Owen-Smith and Cooper 1988, Estes 1997, Van Essen *et al.* 2002).

Eland being a mixed feeder, was found by Buys (1990) to select large quantities of dicotyledons during the winter in the SA Lombard Nature Reserve, 16 km from Bloemhof in the Highveld of the North-West Province. Dry leaves from trees were also regularly taken in periods when preferred herbage was in short supply. They are known to break branches to reach browse at higher levels (Estes 1997, Skinner and Chimimba 2005). Eland will take full advantage of grazing when the nutritive quality of grass is high, but they are essentially browsers and will select a high quality diet in the form of browse during times of nutritional stress (Skinner and Chimimba 2005). According to Buys (1990), the period of highest nutritional stress for eland occurs during late winter.

5.2.5 Flowering and fruit bearing of plant species

A short description of the flowers and fruits of all the tree species occurring in the study area, namely *Acacia karroo*, *Diospyros lycioides*, *Searsia pyroides* (earlier *Rhus pyroides*) and *Ziziphus mucronata* will follow. Flowers of *A. karroo* are borne in scented, bright yellow, spherical heads (Venter and Joubert 1985, Smit 1999). When in full bloom trees are very conspicuous (Smit 1999). According to Milton (1987), flowers are only borne on green extending shoots throughout the growing season as new shoots are produced, but are most abundant between December and February in the Nylsvley Nature Reserve**.** Palgrave (2002) indicated that *A. karroo* flowers between December and January, but flowering is dependent on the rains of the season. Smit (1999) reported that flowers might be present between November and March. Pods occur in bunches, ripen in winter, are sickle-shaped, relatively thin walled and split while still on the tree, displaying the seeds which dangle from the pods by their funicles (Milton 1987, Smit 1999, Palgrave 2002).

Diospyros lycioides usually flowers from September to December (Palgrave 2002), with male and female flowers occurring on different plants (Van Wyk *et al.* 2000). Flowers are white to cream coloured (Venter and Joubert 1985), borne on slender stalks up to 2 cm long and are sweetly scented (Palgrave 2002). The fruit is a large, hard berry up to 20 mm in diameter, ripening from yellow through orange to dark red (Van Wyk *et al.* 2000, Palgrave 2002). Fruiting occurs between January and May and old fruit often remain on trees into the next flowering season (Palgrave 2002).

Small, greenish yellow flowers appear on *S. pyroides* from October to February (Palgrave 2002) with male and female flowers being borne on separate plants (Van Wyk *et al.* 2000). Fruit is a 4 – 5 mm spheroidal drupe (fleshy fruit with one or more seeds that are surrounded by a hard stony layer, like an olive) ripening from dull yellow to dark brown (Van Wyk *et al.* 2000, Palgrave 2002) and is present from November to May (Palgrave 2002). *Searsia pyroides* trees are frequently associated with *A. karroo* (Palgrave 2002).

Ziziphus mucronata flowers are small, yellowish green, inconspicuous and usually present in summer (November to February). Fruit is a 1.5 cm subglobose (semi-spherical) drupe, shiny reddish in colour (Van Wyk 2000, Palgrave 2002). Fruit often remains on the tree through winter, from March to August, until the leaves fall (Palgrave 2002).

5.3 PROCEDURE

Twenty plants of each of the tree and shrub species present in the study area were randomly selected and marked with cable ties and yellow, plastic markers usually used as cattle ear tags. Due to the abundance of *Acacia karroo* a total of 60 plants of this species were selected, with 20 plants in each of three height classes, namely 1 – 2 m; 3 – 4 m and >4 m, respectively. Each marked plant was numbered and its GPS location logged. Marked plants were widely distributed across the study area with representatives in each vegetation unit as determined from the vegetation map (*vid.* Chapter 4).

All the marked plants of *Acacia karroo* (60 plants), *Asparagus laricinus* (20 plants), *Diospyros lycioides* (20 plants), *Lycium echinatum* (10 plants), *L. hirsutum* (10 plants), *Searsia pyroides* (20 plants) and *Ziziphus mucronata* (20 plants) were as far as possible inspected every fortnight (following Dunham 1991) for a period of 4 years (Sept 2004 – Aug 2008). During every observation, each tree was allocated a leaf carriage score: 0 = no leaves; 1 = 1 – 15%; 2 = 16 – 40%; 3 = 41 – 70%; 4 = 71 – 90% and 5 = 90 – 100% of full leaf carriage. During 2006 unexpected excess growth of trees and shrubs was observed, therefore an extra score (or class value) was added, namely 6 = 101 – 120% of full leaf carriage. Leaves were also classified in different phenological states (phenophases):

- i) Newly formed buds (Budding leaves: BL);
- ii) Immature green leaves (IL)
- iii) Mature green leaves (ML);
- iv) Yellowing, senescing leaves (YL); and
- v) Dry, senescing leaves retained on the plant (DL).

The allocated total leaf carriage scores were subdivided into approximate estimates of the phenological composition (phenophase) of the leaves present (e.g. sum total of 3 may be consisting of 1 IL plus 2 ML). This was done in accordance to Dekker and Smit (1996) and Smit (2001).

5.3.1 Data and statistical analyses

Data of each species was entered into separate sheets of the Windows EXCEL program (Microsoft Corporation 2002). A median value for each phenophase of the 20 marked plants per species was determined per date and presented as stack bar graphs. Cleland *et al.* (2007) defined a phenophase as a particular stage of development, such as leaf budding, flowering, fruiting or leaf senescence and it is equivalent to 'phenological event' used in some publications. The sum total of these phenophase median values was calculated per woody species and indicated fortnightly and monthly (median) as class values (1 – 6), as well as in monthly average percentages of the specific class value (e.g. 1 = 1 – 15%, thus average 7%), hereafter referred to as leaf carriage percentages. From the sum total of class values (not the percentages), the median between the four tree species and the three shrub species were calculated and presented as line graphs.

Correspondence Analysis and Canonical Correspondence Analysis from the CANOCO 4.5 software (Ter Braak and Smilauer 2002) was used for ordination (Gauch 1982, Ter Braak 1986, 1987) of i) climatic parameters and each species' phenology totals, and ii) BL-phenophase values of each species. Significant differences, correlation and regression between data sets were analysed using the statistical programme GenStat® (Payne *et al*. 2009).

Analysis of variance (ANOVA) was used and where significance occurred, means were separated using Fisher's Protected Least Significant Difference procedure at 5% level of significance, unless otherwise stated (Snedecor and Cochran 1980, Vittinghoff *et al.* 2005). Standard error of means was calculated with SEM = S / √n where S is the standard deviation of the sample and n is the number of observations per variable. ANOVA was applied to test for differences in phenology between *Acacia karroo* trees in the various height classes, 1 – 2 m; 3 – 4 m and >4 m. The sum total of leaf carriage scores (ignoring phenophases, but indicating total percentage of leaves on *A. karroo* trees) was tested (5% level), as well as median values of the 20 individual trees for each phenophase at 1% level of significance, i.e. BL means for each height; IL means; etc. Differences between the other plant species' phenophases were also determined at 1% level of significance. These variables were acceptably normally distributed (distribution has a symmetrical bell-shape on a graph, McKillup 2006) with homogeneous variances. Differences between phenology sum totals of all the species, as well as averages between the four tree species and the three shrub species were also tested. Variances were heterogeneous and the 1% significance level was used. Differences in phenology sum totals between the four successive years and between similar seasons respectively

(ANOVA unbalanced design), were tested. Variables from this data were acceptably normally distributed with homogeneous variances.

Pearson's correlation coefficient was used as a measure of the linear relationship or association (Draper and Smith 1981, McKillup 2006, Fowler *et al.* 2006) between monthly leaf carriage percentages of two species. It was also used to test the relationship between climatic variables and leaf carriage percentages of each species. Linear regression analysis (Draper and Smith 1981, Vittinghoff *et al.* 2005) was applied to determine the relationship between total monthly average leaf percentages per species and minimum-, maximum temperatures and rainfall respectively.

5.4 RESULTS

5.4.1 Leaf phenology of tree- and shrub species

5.4.1.1 *Acacia karroo*

No significant differences ($p > 0.05$) were found between phenology class value totals of different tree heights (Table 5.1). SEM is the standard error of means, while CV is the ratio of the standard deviation to the mean (Fowler *et al.* 2006). Also, no significant differences ($p > 0.05$) were found between phenology class values of the different height classes' BL, IL and DL phenophases, respectively (Table 5.2).

Table 5.1 Results of the ANOVA test for differences in total leaf presence (sum of class values) between the height classes of *Acacia karroo* trees.

Height class of *A. karroo*	**Mean**
1 – 2 m	3.30
3 – 4 m	3.35
> 4 m	3.33
Summary statistics	
Standard error of means (SEM)	0.196
Number of replicates (n)	96
Probability ($p > 0.05$)	0.982
Coefficient of variation (CV%)	57.6%

Table 5.2 Results of the ANOVA test for differences between leaf presence (class values) in different phenophases of the height classes of *A. karroo* trees.

Height class (BL)	Mean	Height class (IL)	Mean	Height class (DL)	Mean
1 – 2 m	0.51	1 – 2 m	0.80	1 – 2 m	0.23
3 – 4 m	0.52	3 – 4 m	0.78	3 – 4 m	0.25
> 4 m	0.51	> 4 m	0.81	> 4 m	0.13
Summary statistics		**Summary statistics**		**Summary statistics**	
SEM	0.057	SEM	0.079	SEM	0.058
n	96	n	96	n	96
p	0.992	p	0.948	p	0.281
CV%	109.2%	CV%	97.1%	CV%	276.0%

The main difference that was observed in the veld between leaf carriage patterns of trees in the different height classes was that leaf fall of trees taller than 4 m was more rapid, shedding leaves quicker than smaller sized trees and no dry leaves were retained on big trees after June. Also, the leaf flush of these big trees were faster, reaching the immature leaf phase from budding leaves quicker in the first fortnight per season. However, these observed differences were small and not statistically significant, therefore only phenology results of the 3-4 m height class will be presented.

The phenology results of *Acacia karroo* are presented in Figure 5.1. New-season leaves appeared every year during the week of the 17th of September, between the third and fourth weeks of that month depending on which week the 17th fell for that year. Active growth was from September to the end of March or beginning of April. Leaf senescence started slowly from the end of April, except during 2006 when trees quickly shed approximately 50% of their leaves at the end of May. Dry leaves (about 2–10% of full leaf carriage) were retained on trees from May to June/July, except during 2007 when trees retained some leaves until budding leaves appeared in September. The leafless period of *A. karroo* trees varied annually and was from July to middle September (2½ months) during 2005, from August to middle September (1½ months) during 2006 and only in August during 2008.

5.4.1.2 *Diospyros lycioides*

The phenology results of *Diospyros lycioides* are presented in Figure 5.2. There were some similarities between the leaf carriage patterns of *Diospyros lycioides* and *A. karroo*: leaf flush

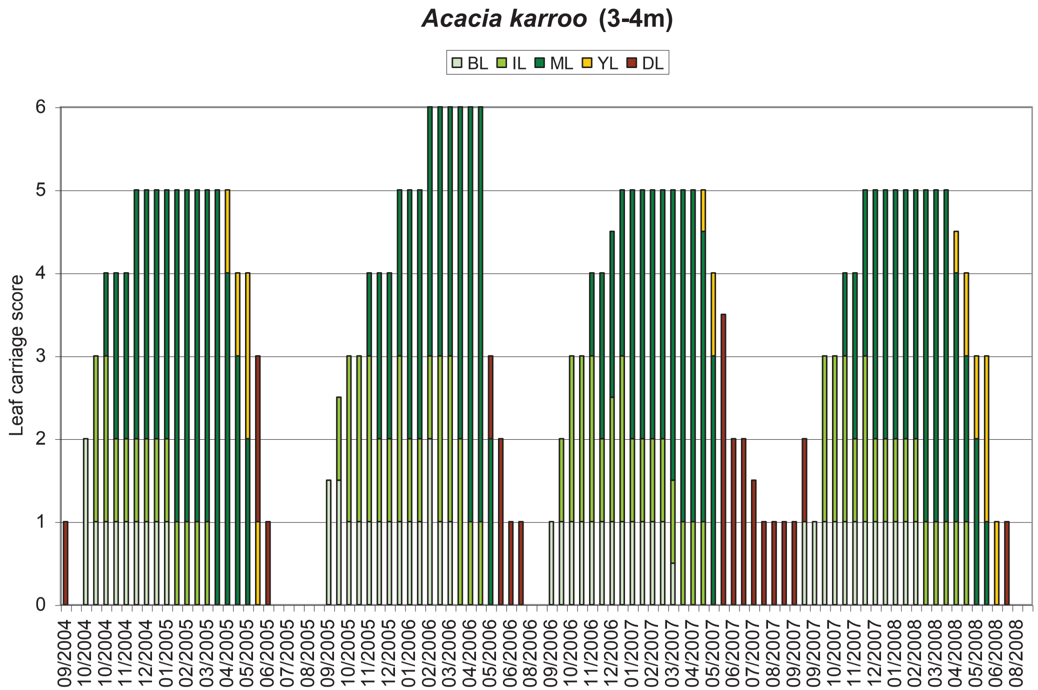
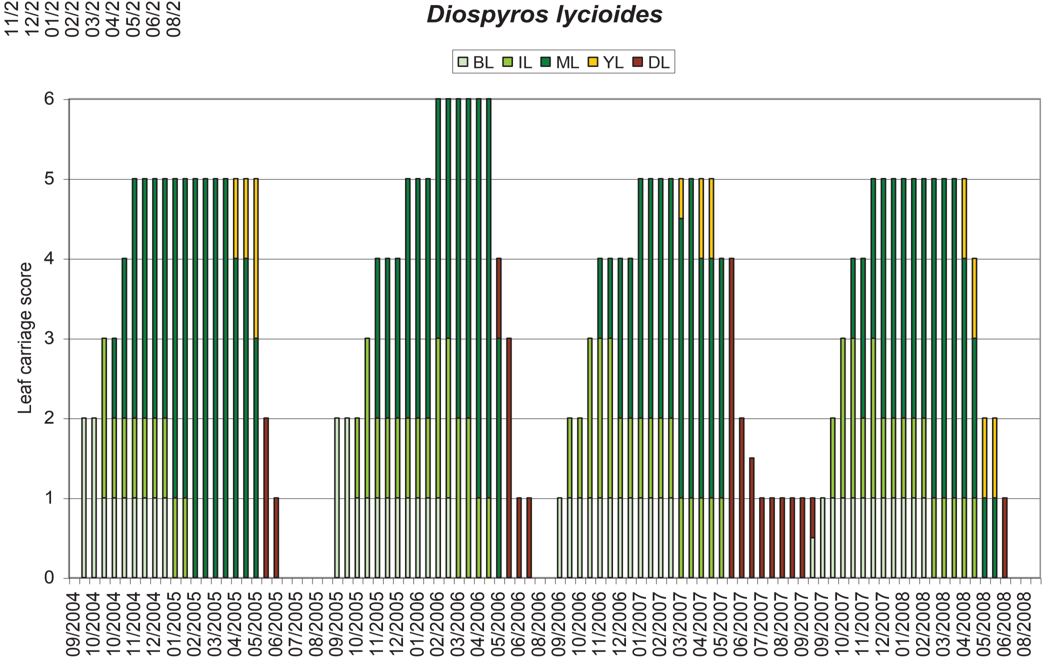


Figure 5.1 Phenology of *Acacia karroo* from September 2004 – August 2008. The phenology score on the y-axis indicates the percentage class of leaves present. The stack bars on the graph indicate median values per date for each phenophase of the leaves of 20 marked plants and the dates on the x-axis are the first, third and fifth week, where applicable, of each month.



<u>Legend</u>: BL Budding-, IL Immature-, ML Mature-, YL Yellow- and DL Dry leaves.

Figure 5.2 Phenology of *Diospyros lycioides* from September 2004 – August 2008 in fortnightly intervals.

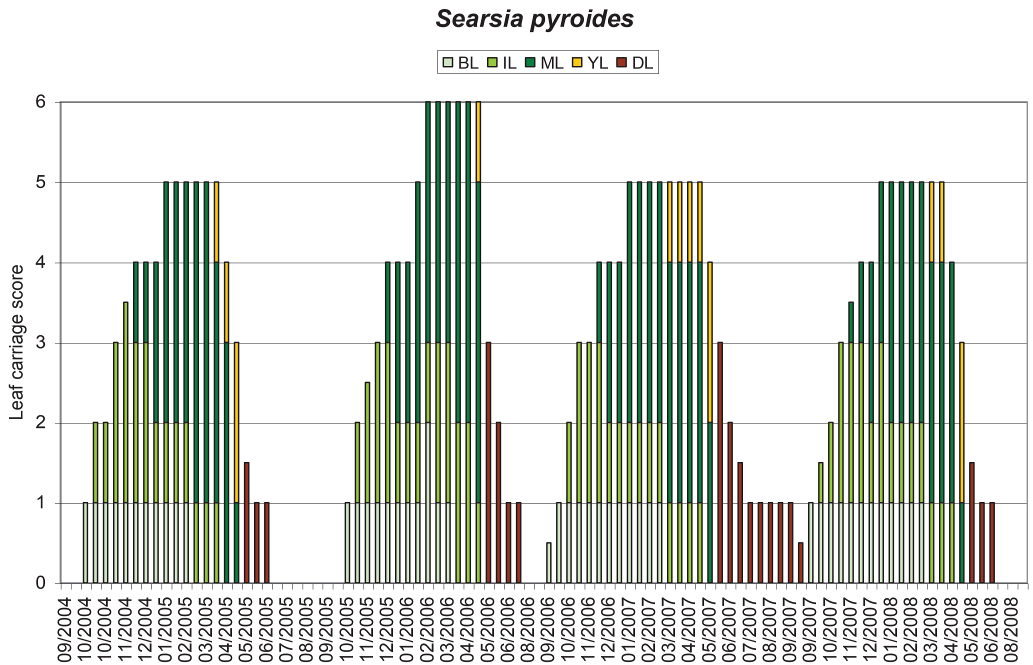


Figure 5.3 Phenology of *Searsia pyroides* from September 2004 – August 2008 in fortnightly intervals.

Legend: BL Budding-, IL Immature-, ML Mature-, YL Yellow- and DL Dry leaves.

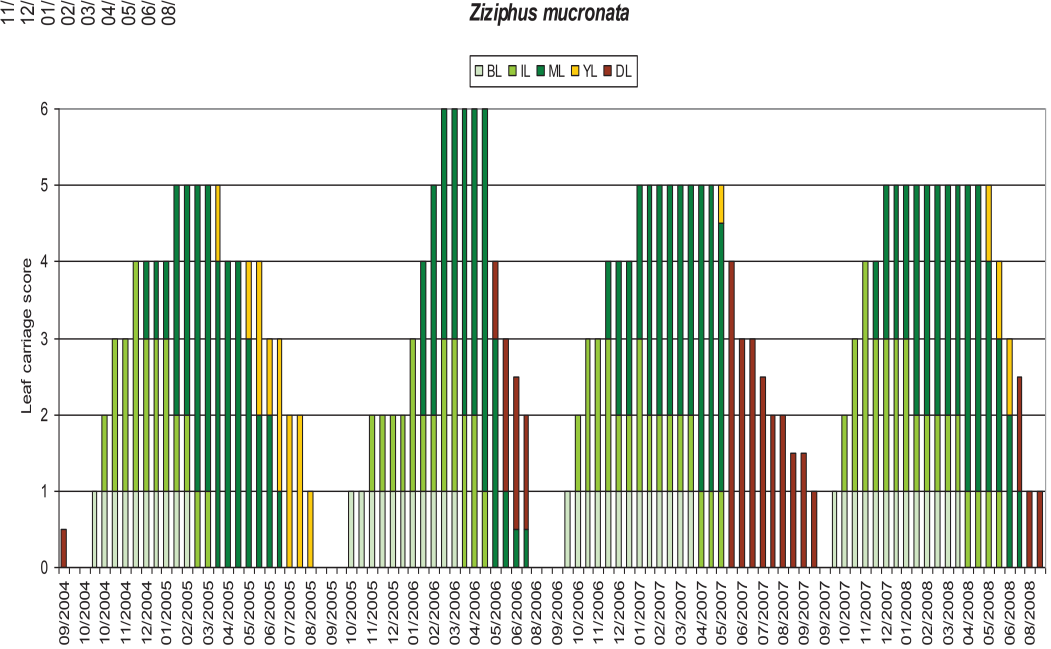


Figure 5.4 Phenology of *Ziziphus mucronata* September 2004 – August 2008 in fortnightly interv

started during the week of the 16th of September every season for *D. lycioides*, active growth ended in March, yellow leaves appeared in April (except during 2006 when leaf fall was rapid during May) and dry leaves were retained until June (except during 2007 when it was retained until September). The trees were leafless from July to middle September (2½ months). Excessive growth in response to flooding conditions in 2006 as observed in the other woody species (101 – 120%) was not observed in *D. lycioides*. Shoots of between 20 cm and 30 cm were abundant on all other woody species, while new shoots of *D. lycioides* mostly did not exceed 10 cm in length.

5.4.1.3 *Searsia pyroides*

The results of *Searsia pyroides* (previously *Rhus pyroides*) are presented in Figure 5.3. New-season leaves appeared in the first week of October. The active growth period was from October to the beginning of March. It was more difficult with *S. pyroides* to judge when leaves changed from immature, green leaves to mature leaves, thus giving the impression that these trees had a short mature leaf phase which might not be true. Yellow leaves were visible at the end of March and some dry leaves (1–5%) were retained on trees from May to June. Trees were leafless from July to the beginning of October 2005 (3 months), but only for 2 months in 2006 (August – September), while dry leaves were retained throughout the winter of 2007 until budding started in October.

5.4.1.4 *Ziziphus mucronata*

The phenology results of *Ziziphus mucronata* are presented in Figure 5.4. Leaf flush usually started in the second week of October (around 15 October) except for budding leaves appearing as early as 30 September during 2006. The active growth period was from October to March. *Ziziphus mucronata* trees were relatively slow to produce new leaves at the end of 2005 prior to the heavy rains of that specific summer season. The mature leaf carriage phase, however, was similar during that season compared to other seasons, namely from December to May. Leaves usually turned yellow in May and dry leaves were mostly retained from May to July (3 months), but in 2007 the leaf retention period was from May to September and from July to August in 2008. The trees were mostly leafless from September to middle October (1½ month), except during 2007 when trees were only leafless for a short period at the end of September.

5.4.1.5 *Lycium* species

The phenology results of *Lycium echinatum* are presented in Figure 5.5 and that of *Lycium hirsutum* in Figure 5.6. The leaf carriage patterns of shrubs in general were not as distinct as the patterns observed for the trees. The shrubs often shed a substantial quantity of their old leaves (up to 20%) at a time and produced new leaves shortly thereafter during the subsequent growing season. For example, both *L. echinatum* and *L. hirsutum* shed their leaves during December 2004 and March 2005**;** February 2006, May and June 2006**;** April and May 2007; and February to March 2008. New-season leaves of both *Lycium* species appeared in September. The end-of-season yellow leaves were visible from March to August on *L. hirsutum* and for the same period, but excluding May and July on *L. echinatum*. Leaf fall was rapid and dry leaves were not retained on shrubs for long periods. No leaves were present on *L. echinatum* during September 2004, as well as from September 2005 to the beginning of October (approximately 1 month for each of these seasons). *Lycium hirsutum* had up to 50% of its normal leaf carriage present during winter months in the form of mostly older mature leaves and some yellow leaves. The leaf carriage score of 6 for February 2006 was allocated to these shrubs, but new excessive leaves were quickly shed and replaced with new immature leaves, unlike trees where it was still present until leaf shedding in May.

5.4.1.6 *Asparagus laricinus*

It is acknowledged that "leaves" of *A. laricinus* are not considered to be true leaves, but rather phyllocladia – modified branches functioning as leaves (Venter and Joubert 1985). However, for the sake of comparison and to prevent possible confusion it will be referred to as leaves in this thesis.

Asparagus laricinus displayed a similar leaf phenology pattern (Figure 5.7) to the *Lycium* species (Figures 5.5 & 5.6) in that it shed its older mature leaves during the growing season and produced new leaves shortly thereafter. In *A. laricinus*, unlike the *Lycium* species, shed leaves were not immediately replaced with new leaves (Figure 5.7), for example from February – April 2005 and April – June 2006 and again from April – June 2007 and February to April 2008. New-season leaves appeared in October and end-of-season leaves that turn yellow from their tips were visible from April/May to September. *Asparagus laricinus* was leafless by middle October 2005 just before leaf flush started, but retained some mature- and yellow leaves into the winters of 2006, 2007 and 2008. Only 1 – 5% of these dry, yellow leaves were retained in September 2007, prior to the leaf flush. These shrubs also displayed excessive growth after the flood in February/March 2006 and

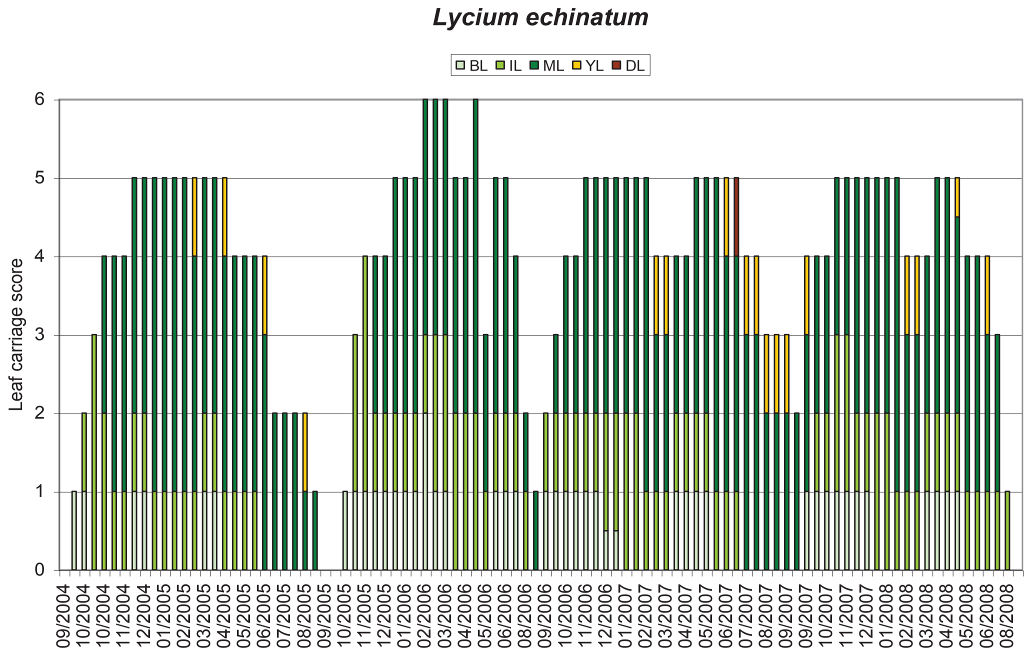


Figure 5.5 Phenology of the shrub *Lycium echinatum* from September 2004 – August 2008 in fortnightly intervals.

<u>Legend</u>: BL Budding-, IL Immature-, ML Mature-, YL Yellow- and DL Dry leaves.

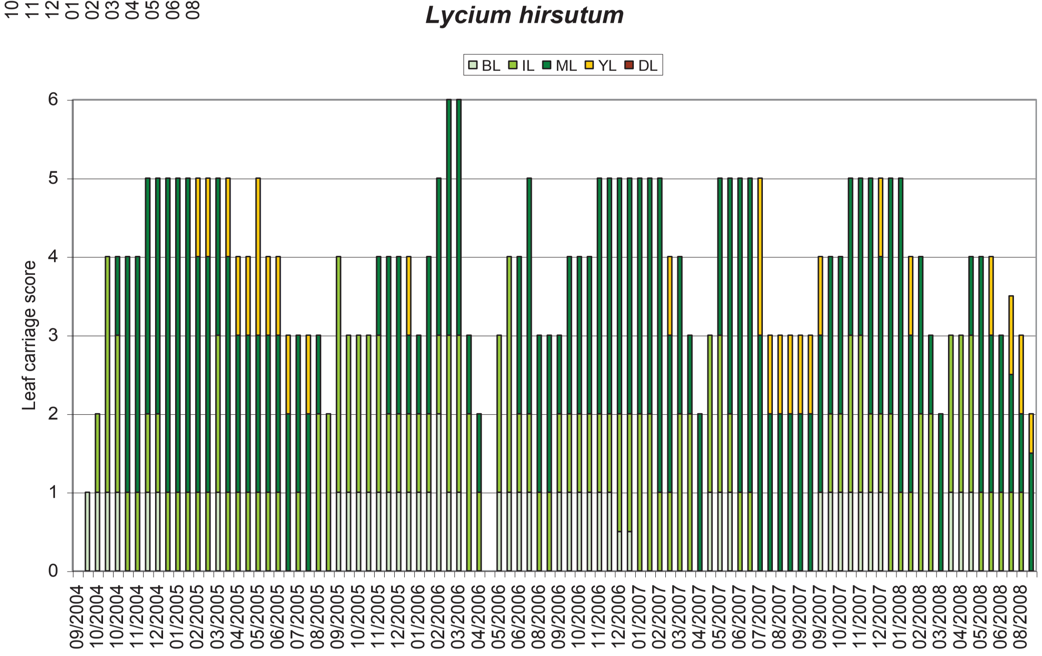


Figure 5.6 Phenology of the shrub *Lycium hirsutum* from September 2004 – August 2008 in fortnightly intervals.

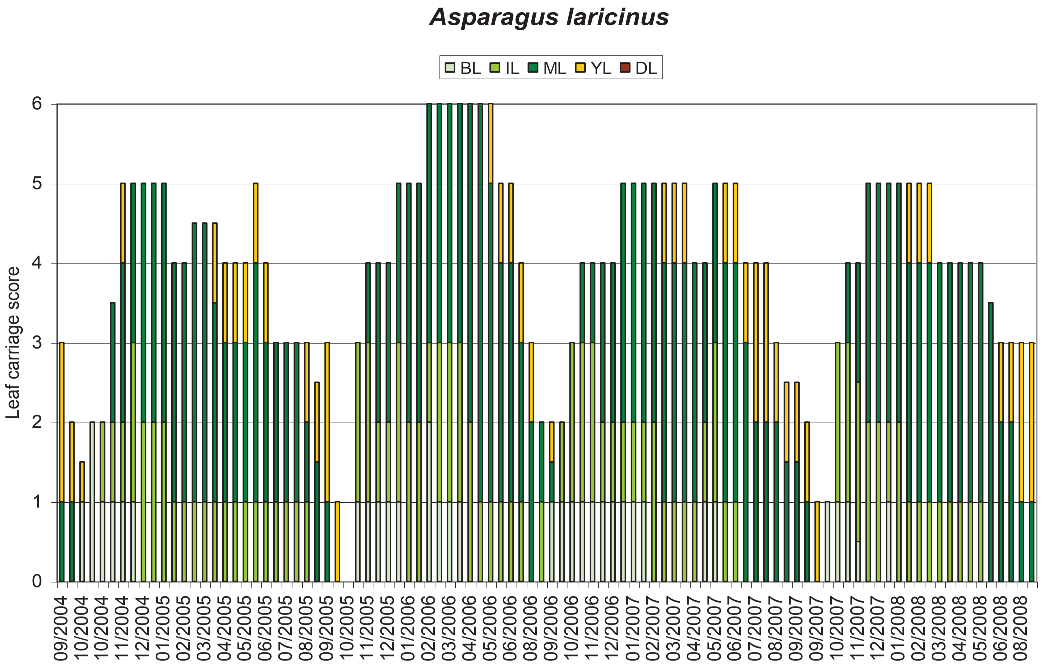
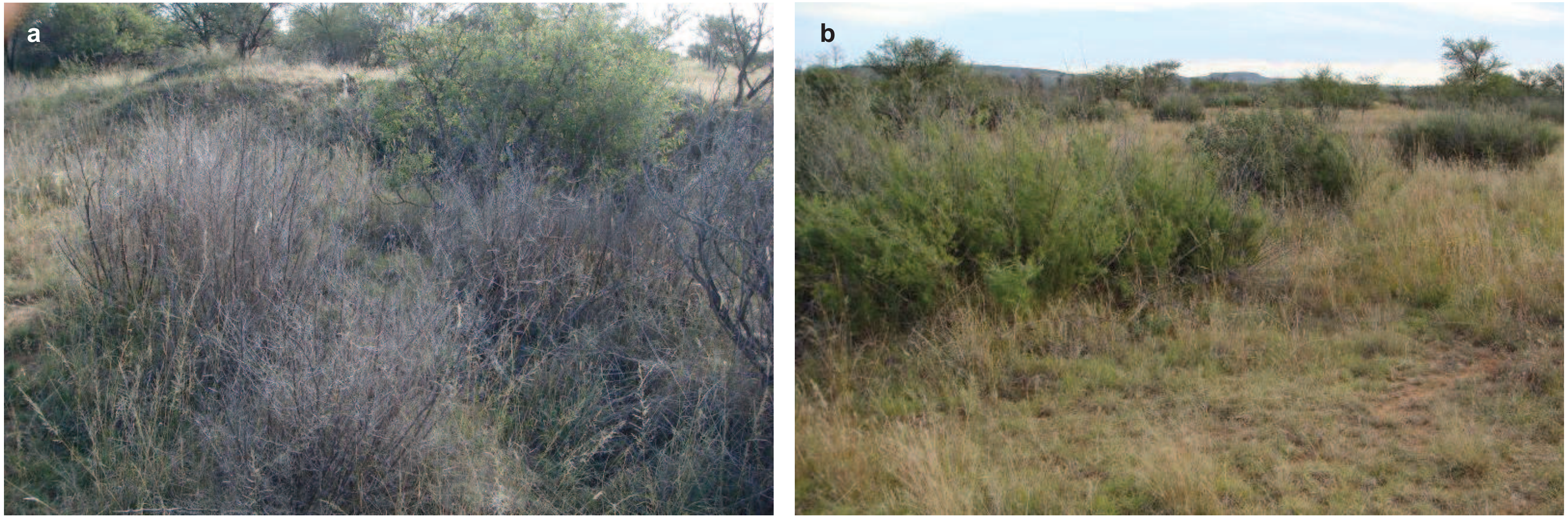


Figure 5.7 Phenology of the shrub *Asparagus laricinus* from September 2004 – August 2008 in fortnightly intervals.

Figure 5.8 *Asparagus laricinus* on 18 April 2008 in two different parts of the study area. All the plants of this shrub species were (a) leafless in an area between the drainage lines from the southern fence, while (b) this was not the case in the rest of the study area.



sprouted new shoots of approximately 15 cm in length. Unlike the *Lycium* species they retained this new growth until senescence started in June 2006. Mature leaves were mostly present from November to August (Figure 5.7) and leaves in an older phenological state with half of the leaf being yellow were observed from August to September. All the *A. laricinus* plants in a specific area around the smaller drainage line (Figure 4.1) were leafless from 18 April to 30 May 2008 (Figure 5.8), while this was not the case for any other plant in the rest of the study area. No obvious explanation can be offered for this phenomenon, except that soil moisture might have played a role.

5.4.2 Relationship between climate and leaf phenology

The results of the correlation analyses (Pearson's Correlation Coefficient, r) between average monthly temperatures or monthly rainfall totals and leaf carriage percentages for each species (average percentage of phenology class value totals), are presented in Table 5.3. The statisticians generally use "R" in regression modelling and "r" in correlation, while for probability "P" is used in regression modelling and "p" in ANOVA and correlation. A fairly strong correlation (r = 0.7 – 0.8) was found between minimum temperature and phenology of the tree species, except for *Z. mucronata* that had a moderate correlation (r = 0.5). The correlation was also moderate (r = 0.6) between these species' phenology and maximum temperatures. Correlations of r < 0.3 between temperature and the phenology of shrubs were poor.

Table 5.3 Results of correlation analyses between average monthly temperatures or monthly rainfall totals (independent variables) and leaf carriage percentages of each plant species (dependent variables).

	Acacia karroo	***Diospyros lycioides***	***Searsia pyroides***	***Ziziphus mucronata***	***Asparagus laricinus***	***Lycium echinatum***	***Lycium hirsutum***
Min temp							
r	0.806	0.735	0.762	0.453	0.365	0.390	0.368
p	<0.001	<0.001	<0.001	0.0018	0.0139	0.0081	0.0129
Max temp							
r	0.653	0.603	0.599	0.262	0.217	0.212	0.278
p	<0.001	<0.001	<0.001	0.0744	0.1277	0.1346	0.0603
Rainfall							
r	0.528	0.458	0.484	0.326	0.269	0.364	0.321
p	0.0001	0.0016	0.0008	0.0282	0.0675	0.0140	0.0306

No strong correlation was found between phenology and monthly rainfall totals (Table 5.3). Correlation analyses between weekly rainfall totals and weekly leaf carriage percentages of each tree species for September to October (Table 5.4), also delivered weak correlations that are statistically not significant ($p > 0.05$). It is clear from Figure 5.9 that *A. karroo* and *D. lycioides* started budding in the third week of September irrespective of time of rainfall. However, *S. pyroides* and *Z. mucronata* appear to have started budding after the first spring rains (Figure 5.10). Figures 5.11 and 5.12 illustrate phenology patterns of trees and shrubs in comparison with temperatures.

Table 5.4 Results of the correlation analyses between weekly rainfall totals (independent variable) and weekly leaf carriage percentages of tree species (dependent variable) from September to October.

	Acacia karroo	***Diospyros lycioides***	***Searsia pyroides***	***Ziziphus mucronata***
r	0.087	0.254	0.082	0.121
p	0.3420	0.1084	0.3480	0.293

CCA ordination of temperatures and rainfall superimposed on phenology of the different plant species are presented in Figure 5.13 (*vid.* page 53). The gradient lengths of the axes are short because the focus of the study was on testing the influence of certain parameters on species data and not on testing for gradients in the data. A high number of zero values were present in the dataset, therefore the downweighting option has been tested but due to very small differences between ordinations with and those without downweighting, that option proved omissible. Eigen-values (percentage variance of the axis) are low, because of all the zero values in the dataset, but since only associations are indicated and the eigen-value of Axis 1 is higher than the other axes, the results are still meaningful. Cumulative species variances, indicating variance of data across the four axes, are higher for the species climate relation than for the species data, probably because there are less zero- and similar values in the combined dataset. Phenology data is distributed along Axis 1, with *Z. mucronata* the furthest away and the other species in a similar broad horizontal plane. Distinct clusters of trees opposed to shrubs are evident, also with regard to the environmental vectors. Axis 1 is strongly associated with rainfall and Axis 2 with maximum temperatures (*vid.* section 5.5.1 for discussion).

No meaningful linear regressions could be found (Table 5.5) between the plant species' monthly leaf carriage percentages and mean monthly temperatures or monthly rainfall totals. The highest adjusted R-square value (coefficient of determination) was 64.2, but most R^2_a-values were < 35.

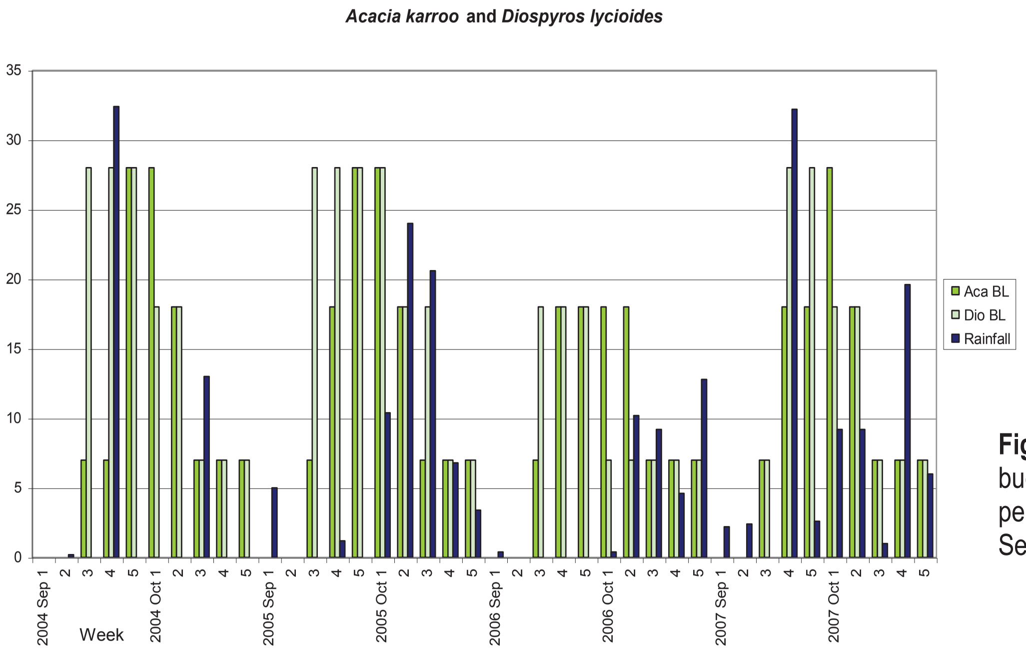


Figure 5.9 Weekly rainfall totals (mm) and budding leaf scores (average of the class percentage range) of *A. karroo* and *D. lycioides* for September and October of four years.

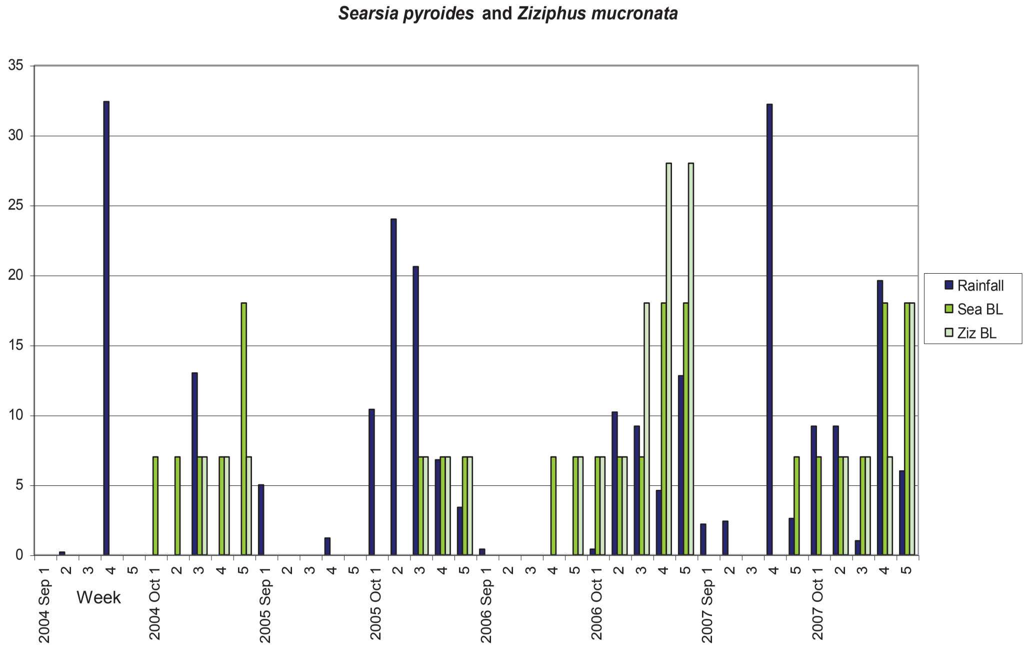


Figure 5.10 Weekly rainfall totals (mm) and budding leaf scores (average of the class percentage range) of *S. pyroides* and *Z. mucronata* for September and October of four years.

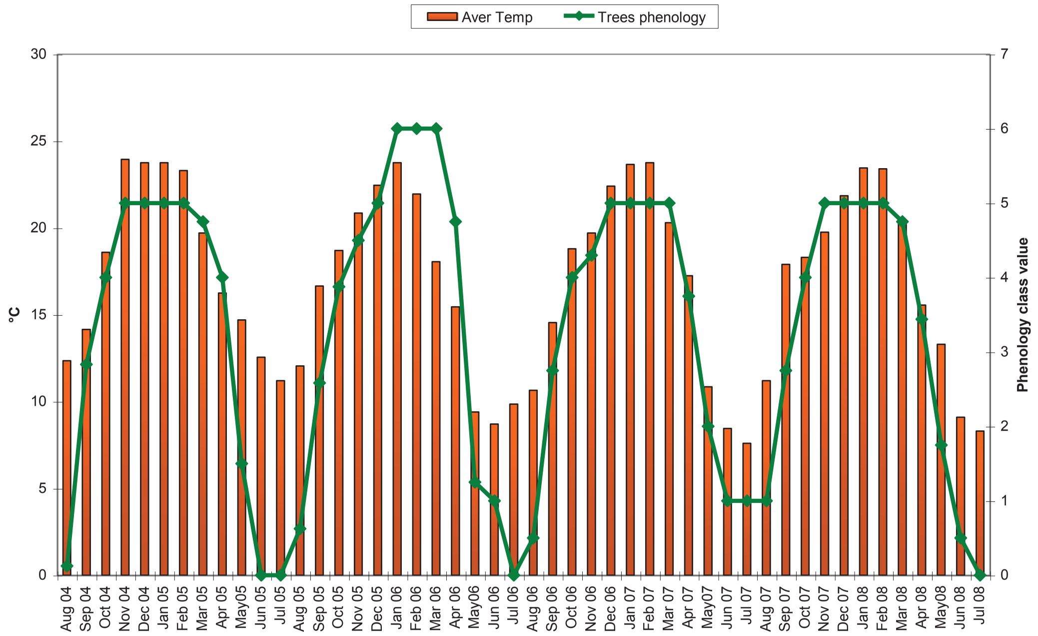


Figure 5.11 Median of leaf carriage sum totals for all the tree species from September 2004 to August 2008. Average temperatures per month (from daily average minimum- and maximum temperatures) are indicated for the same period.

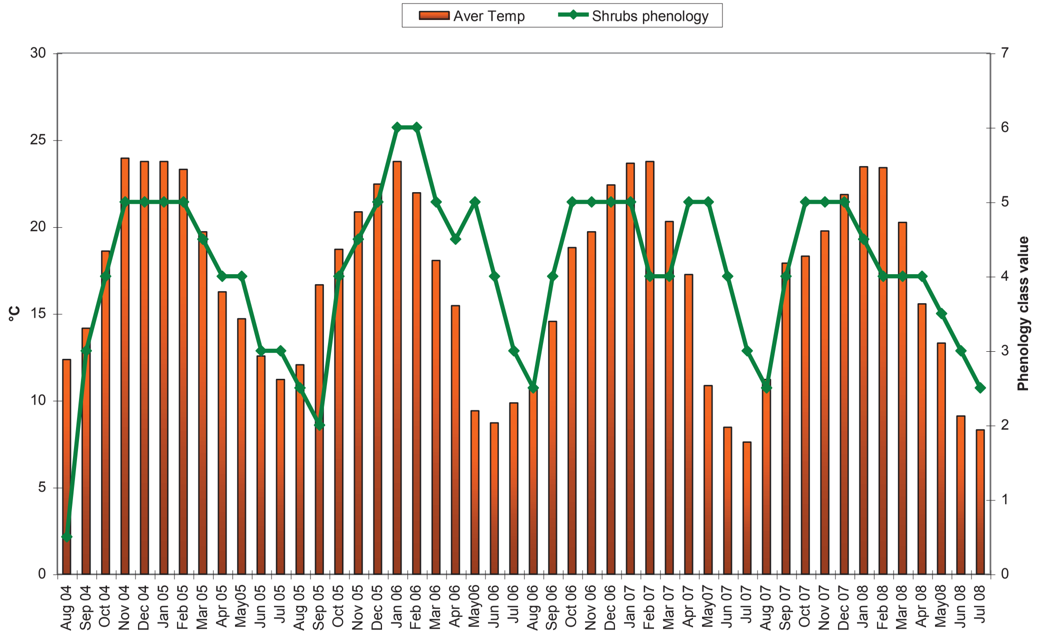
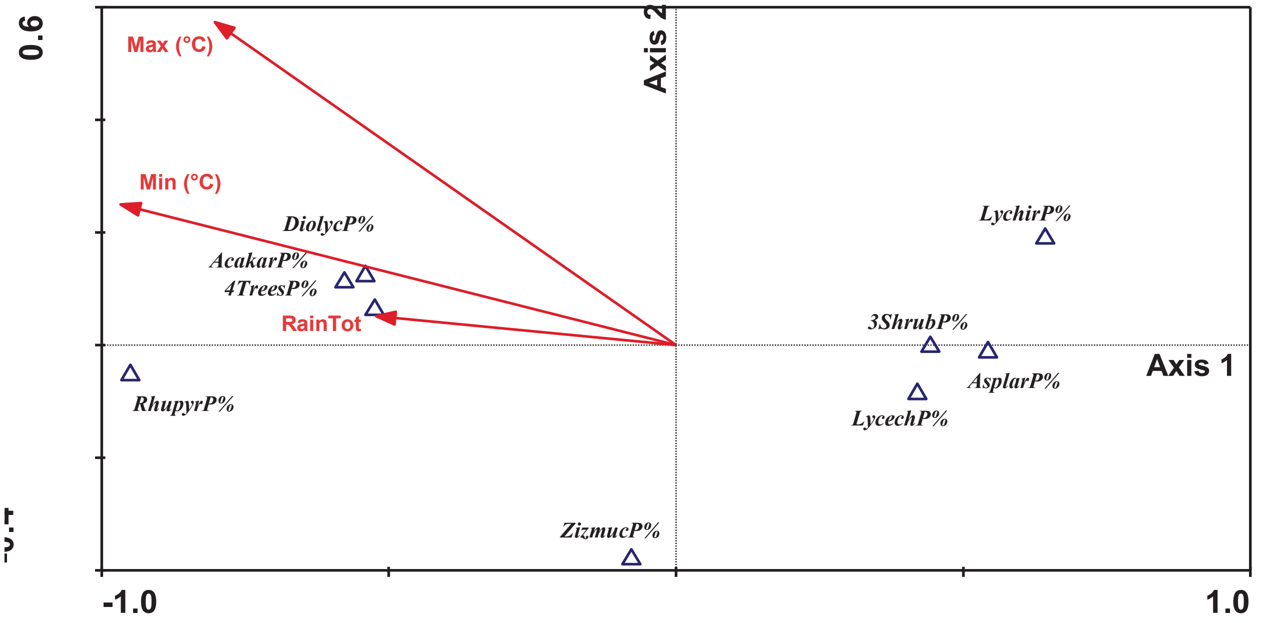


Figure 5.12 Median of leaf carriage sum totals for all the shrub species from September 2004 to August 2008. Average temperatures per month are indicated for the same period.



	Axis 1	Axis 2	Axis 3	Axis 4
Eigen-values	0.038	0.003	0	0
Sp-environment correlation	0.722	0.454	0.167	0
Cumulative % variance:				
of species data	32.8	35.3	35.5	70.5
of species-climate relation	92.4	99.4	100	0

Figure 5.13 Canonical correspondence analysis (CCA) of average percentages of phenology (P%) class value totals of each species and three climatic parameters superimposed. Median class values of the four tree species and three shrub species were also used in the ordination. Legend: Acakar = *Acacia karroo*; Asplar = *Asparagus laricinus*; Diolyc = *Diospyros lycioides*; Lycech = *Lycium echinatum*; Lychir = *L. hirsutum*; Rhupyr = *Searsia pyroides*; Zizmuc = *Ziziphus mucronata.* Monte Carlo permutation test of significance of first canonical axis indicated an Eigenvalue of 0.038 (F-ratio 21.492, P-value 0.0020) and of all canonical axes had a Trace of 0.041 (F-ratio 8.075, P-value 0.0020).

5.4.3 Leaf phenology between different years, seasons and species

No significant differences ($p > 0.05$) were found between the four years of study for phenology of individual species: *A. karroo* ($p = 1.00$); *D. lycioides* ($p = 0.921$); *S. pyroides* ($p = 0.969$); *Z. mucronata* ($p = 0.852$); *A. laricinus* ($p = 0.420$); *L. echinatum* ($p = 0.712$) and *L. hirsutum* ($p = 0.829$). There were also no significant differences ($p > 0.05$) between the four years for monthly total percentage leaves present on trees or shrubs grouped together (Table 5.6).

There were, however, significant differences ($p < 0.05$) between the four different seasons (similar seasons of the study period grouped together) for phenology sum totals of the individual species.

All the plant species had a F-probability value of less than 0.001. The sum totals of class values for each species were tested, not the phenophases separately, resulting in some seasons having similar totals. The grand sum total mean of trees and of shrubs grouped together significantly differed ($p < 0.05$) between the four seasons (Table 5.7).

Table 5.5 Summary of the linear regression analyses between mean monthly temperatures or monthly rainfall totals (independent variables) and each plant species' monthly leaf carriage percentages (dependent variables). R^2_a = adjusted coefficient of determination, P = probability, SER = standard error of regression.

	Acacia karroo	*Diospyros lycioides*	*Searsia pyroides*	*Ziziphus mucronata*	*Asparagus laricinus*	*Lycium echinatum*	*Lycium hirsutum*
Min temp							
R^2_a	64.2	53.1	57.1	18.8	11.4	13.4	11.7
P	<0.001	<0.001	<0.001	0.001	0.011	0.006	0.010
SER	23.3	28.2	26.8	35.0	24.4	28.7	21.3
Model	Y = 20.91 + 5.113x	Y = 21.60 + 4.917x	Y = 9.79 + 5.072x	Y = 35.98 + 2.863x	Y = 63.45 + 1.537x	Y = 59.09 + 1.955x	Y = 64.83 + 1.356x
Max temp							
R^2_a	41.4	34.9	34.5	4.9	2.6	2.4	5.7
P	<0.001	<0.001	<0.001	0.072	0.138	0.148	0.056
SER	29.9	33.2	33.1	37.9	25.6	30.4	22.0
Model	Y = -75.4 + 5.389x	Y = -72.6 + 5.240x	Y = -81.8 + 5.190x	Y = 4.1 + 2.160x	Y = 45.5 + 1.190x	Y = 39.7 + 1.382x	Y = 41.8 + 1.330x
Rainfall							
R^2_a	26.3	19.3	21.7	8.7	5.2	11.4	8.4
P	<0.001	0.001	<0.001	0.024	0.064	0.011	0.026
SER	33.5	36.9	36.2	37.2	25.2	29.0	21.7

Table 5.6 Results of the ANOVA test for differences between the four years' monthly total percentage leaves present on trees or shrubs.

Year (Trees)	Mean		Year (Shrubs)	Mean
1: 2004 – 2005	62.6		1: 2004 – 2005	76.1
2: 2005 – 2006	60.2		2: 2005 – 2006	79.2
3: 2006 – 2007	64.6		3: 2006 – 2007	79.2
4: 2007 – 2008	64.3		4: 2007 – 2008	75.2

Continued on next page...

Table 5.6 Continued

Summary statistics			Summary statistics	
SEM	11.93		SEM	7.29
n	12		n	12
p	0.994		p	0.970
CV	65.7%		CV	32.6%

Table 5.7 Results of the ANOVA test for an unbalanced design testing for differences between the four seasons of phenology sum totals of individual species, as well as for the grand sum total means of trees and of shrubs grouped together. Means followed by the same letter did not differ significantly.

Season (Trees)	**Mean (SEM)**		**Season (Shrubs)**	**Mean (SEM)**
Winter (Jun – Aug) (n=12)	14.58 a (4.8)		Spring (Sep – Oct) (n=8)	42.12 a (4.6)
Spring (Sep – Oct) (n=8)	27.00 a (5.9)		Winter (Jun – Aug) (n=12)	63.33 b (3.8)
Summer (Nov – Feb) (n=16)	93.75 b (4.1)		Autumn (Mar – May) (n=12)	91.67 ac (3.8)
Autumn (Mar – May) (n=12)	94.17 b (4.8)		Summer (Nov – Feb) (n=16)	95.00 c (3.3)
Summary statistics			**Summary statistics**	
p	<0.001		p	<0.001
Average L.S.D. (5%)	14.16		Average L.S.D. (5%)	22.37
CV for a single unit	26.33%		CV for a single unit	16.92%

Obvious differences can be observed in the line graphs between phenology sum totals of trees and shrubs grouped together (Figures 5.11 & 5.12). In testing for statistical differences, species variances were found to be heterogeneous, thus significance testing at 1% level was applied (Glass *et al.* 1972). Differences were highly significant (Table 5.8) between phenology sum totals of plants, both on an individual species scale and between the grand mean totals of trees and shrubs grouped together, supporting visual results from the line graphs.

Median class values of a specific phenophase of a species were tested for differences against other species and not against the specific date when leaves started to change into the next phase. Species variances were not homogeneous, thus significance testing at 1% level was applied (Glass *et al.* 1972). No significant differences ($p > 0.01$) were found between phenology class values of budding leaves present on different plant species, but for all the other phenophases (immature-, mature-yellow- and dry leaves) there were significant differences (Table 5.9).

Table 5.8 Results of the ANOVA test for differences between the phenology sum totals of plants, both on an individual species scale and between the grand mean totals of trees and shrubs grouped together. Means followed by the same letter did not differ significantly.

Species	**Mean**
Searsia pyroides	2.859 a
Ziziphus mucronata	3.208 ab
Diospyros lycioides	3.307 abc
Acacia karroo	3.354 abc
Lycium hirsutum	3.828 bc
Lycium echinatum	3.917 c
Asparagus laricinus	3.927 c
Summary statistics	
SEM	0.1706
n	96
p	< 0.001
L.S.D (1%)	0.6234
CV	48%

Woody plants Mean Total	**Mean**
Four trees	3.27
Three shrubs	4.01
Summary statistics	
SEM	0.162
n	96
p	0.002
L.S.D (1%)	0.597
CV	43.6%

Ordination of the phenology of different species was done separately from the climate values, but is not shown since groupings were very similar to the graph where climate was superimposed (Figure 5.13) with only cumulative species variances that increased to 65 – 78 and Eigen-values still remaining low (Axis 1 = 0.07, 2 = 0.01). CA ordination was also done on the budding leaf phenophase of different species for the duration of the four years of study (Figure 5.14). The gradient lengths of the axes are short because the focus of the study was on testing the influence of certain parameters on species data and not on testing for gradients in the data. The downweighting option to transform species data, due to a high number of zero values present in the dataset, has been tested, but was not used since omissible differences were found between ordinations with and those without downweighting. Low Eigen-values were again the result of a high number of zero and similar values (low variation) in the dataset. The trees separated around the second axis and the shrubs more on the first axis. Linear (PCA or RDA) ordination techniques could not be used due to all the zero values in the dataset (*vid.* page 53).

Table 5.9 Summary of ANOVA results in testing for differences between species' median class value totals of each phenophase (n = 96). Means followed by the same letter did not differ significantly.

Budding leaves	**Mean**
Acacia karroo	0.516
Diospyros lycioides	0.505
Searsia pyroides	0.484
Ziziphus mucronata	0.490
Asparagus laricinus	0.349
Lycium echinatum	0.448
Lycium hirsutum	0.469

Summary statistics (BL)	
SEM	0.0541
p	0.374
L.S.D (1%)	n.a.
CV	113.8%

Immature leaves	**Mean**
Diospyros lycioides	0.688 a
Searsia pyroides	0.745 ab
Acacia karroo	0.776 ab
Ziziphus mucronata	0.802 ab
Lycium echinatum	0.979 bc
Asparagus laricinus	1.000 bc
Lycium hirsutum	1.198 c

Summary statistics (IL)	
SEM	0.0745
p	< 0.001
L.S.D (1%)	0.272
CV	82.5%

Mature leaves	**Mean**
Searsia pyroides	1.203 a
Ziziphus mucronata	1.432 ab
Acacia karroo	1.688 abc
Diospyros lycioides	1.766 bc
Lycium hirsutum	1.922 bcd
Asparagus laricinus	2.115 cd
Lycium echinatum	2.307 d

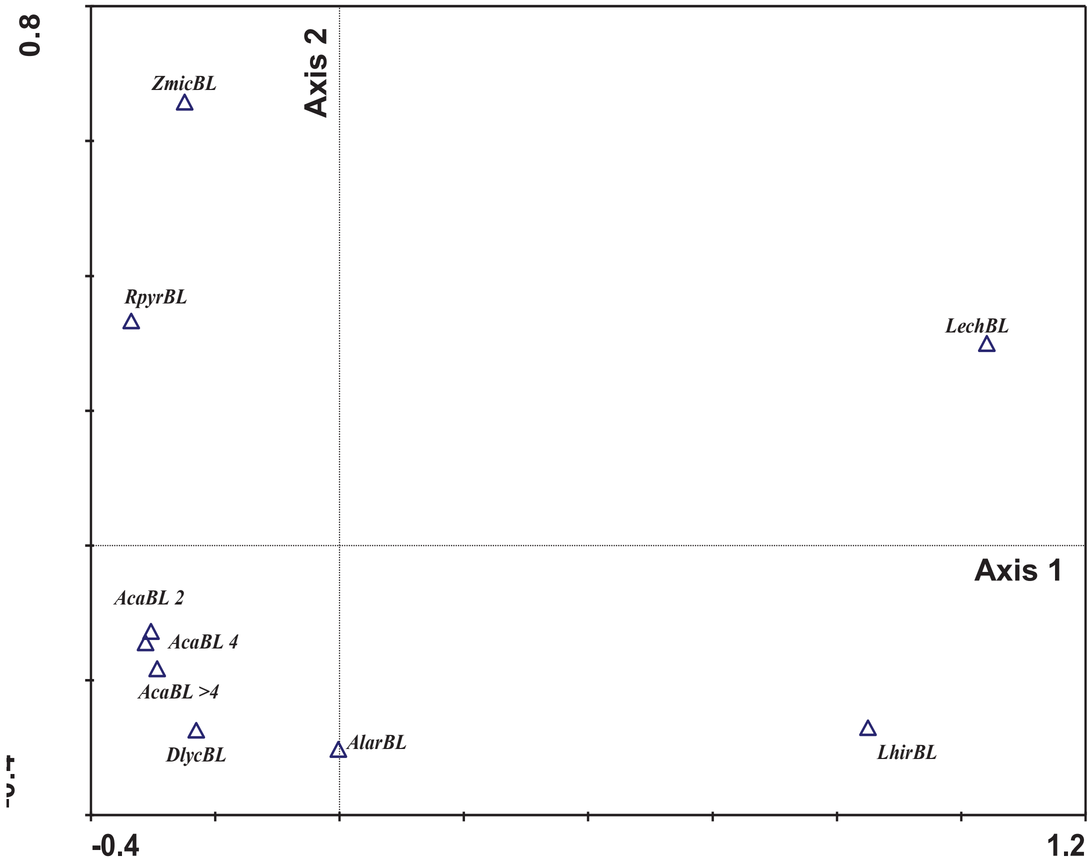
Summary statistics (ML)	
SEM	0.1437
p	< 0.001
L.S.D (1%)	0.5250
CV	79.3%

Yellow leaves	**Mean**
Diospyros lycioides	0.1094 a
Acacia karroo	0.1250 a
Searsia pyroides	0.1563 a
Ziziphus mucronata	0.1615 a
Lycium echinatum	0.1719 a
Lycium hirsutum	0.2708 a
Asparagus laricinus	0.4635 b

Summary statistics (YL)	
SEM	0.0460
p	< 0.001
L.S.D (1%)	0.1680
CV	216.3%

Dry leaves retained	**Mean**
Asparagus laricinus	0.0000 a
Lycium hirsutum	0.0000 a
Lycium echinatum	0.0104 a
Diospyros lycioides	0.2396 b
Acacia karroo	0.2500 b
Searsia pyroides	0.2708 b
Ziziphus mucronata	0.3229 b

Summary statistics (DL)			
SEM	0.0520	L.S.D	0.1901
p	< 0.001	CV	326.4%



	Axis 1	Axis 2	Axis 3	Axis 4
Eigen-values	0.252	0.104	0.089	0.054
Cumulative % variance:				
of species data	46.4	65.5	82.0	91.9

Figure 5.14 Correspondence analysis (CA) ordination of the budding leaf (BL) phenophase class values of each species and the different height classes of *Acacia karroo* (2 m, 4 m >4 m).

5.4.4 Flowering and presence of fruits or pods

Acacia karroo flowers were most abundant in November/December in the study area. Green pods were observed in February and brown, dry pods in March/April. Some pods were retained on trees until June, but not every year.

Flowering of *Diospyros lycioides* occurred between middle October and November. The large berries were observed between February and April. Some dry fruit were retained on trees until June.

Searsia pyroides was observed to flower mostly in November/December. Fruits (drupes) were observed between January and February. Dry fruits retained on trees were observed during May.

Ziziphus mucronata flowers were usually present in summer. Ripe fruits (drupes) were present on trees from March to April and dry fruits usually had a long retention period on trees mostly until July or in some individuals just before leaf budding in spring.

The small white flowers of *Lycium hirsutum* were only observed in June and those of *L. echinatum* in March and December, but were easy to overlook when these shrubs had full leaf carriage.

White flowers were observed on *Asparagus laricinus* in middle November, small, green berries in December and some red berries (~5 mm) in February/March.

5.5 DISCUSSION

5.5.1 Leaf phenology and the influence of climate

The definition of phenology in the introduction clearly indicates the influence of climate on periodic events in the life cycle of plants. Results of this study confirmed (Figures 5.11 & 5.12) that phenology follows the pattern of rising temperatures (budding in spring) and falling temperatures (shedding leaves in autumn). It is acknowledged that air temperature is probably not the only climatic factor that influences plant phenology – soil temperature, soil water content, time of spring rain, rainfall totals and daylight lengths (longer days in spring and shorter days in autumn, Cleland *et al.* 2007) should also play a role. Soil properties and daylight lengths were not measured as it falls outside the scope of this study. SA Weather Service supplied daily sunrise and sunset times from which the differences followed by average sunlight hours per month were calculated, namely**:**

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
13h55	13h27	12h40	11h49	11h01	10h27	10h20	10h44	11h28	12h21	13h12	13h50

When the highest temperatures and longest sunlight hours were experienced in summer, trees had full leaf carriage and when lowest temperatures and shortest sunlight hours were experienced in winter, trees were mostly leafless (Figure 5.11).

Rayner (1969) and Fowler *et al.* (2006) concluded that a correlation coefficient (r) of ±0.9 generally indicates a very strong correlation, ±0.7 a fairly strong correlation and in the region of ±0.5 the correlation is moderate. A fairly strong correlation (r = 0.7 to 0.8) was found between minimum temperature and phenology of tree species, but a moderate to poor correlation represented tree- and shrub species' phenology and maximum temperatures (Table 5.3). Ordination of this data (Figure 5.13) confirmed that minimum temperatures are more strongly associated with leaf phenology of *A. karroo* and *D. lycioides*, as well as with median phenology values of the four trees, than with maximum temperatures. Leaf phenology of *Z. mucronata* was poorly associated with temperatures (Table 5.3). Similarly, no strong association was found between shrub phenology and maximum temperatures (Figure 5.13). No statistically significant linear regressions (R^2_a-values ranged from 2.4 to 64%, with most values being below 35%) could be established (Table 5.5) between leaf phenology of any of the species and climate values (temperatures nor rainfall).

Only moderate to poor relationships (r < 0.5) were found between monthly rainfall totals and the different species' phenology (Table 5.3). Initially it was thought that the reason for this poor relationship was due to the fact that rainfall totals per month were used to determine the relationship with existing monthly phenology values of species. Weekly rainfall totals were therefore used against weekly phenology totals of the trees, but the relationships were even weaker with r-values ranging from 0.082 to 0.254 (Table 5.4). As an alternative, weekly budding leaf values were used (instead of phenology class totals including all the phenophases) against weekly rainfall totals. However, since BL-values were not continuous and rather sporadic, no relationship could be found with rainfall (data not shown). However, in Figures 5.9 and 5.10, weekly data for BL of tree species clearly illustrates the effect of the time of first spring rain on the time of budding. In this regard McKillup's (2006) statement that "a statistically significant result may not necessarily have any biological significance", holds true. If it was possible to statistically test phenology values on a finer scale against climatic values, i.e. with daily rainfall values, the relationship would probably be better. It falls outside the scope of this study.

In the study area, the spring rain usually occurs towards the end of September/October. *Acacia karroo* and *D. lycioides* budded in middle September, apparently unaffected by the time of spring rain (Figure 5.9). It was observed that *Searsia pyroides*, *Ziziphus mucronata* (Figure 5.10) and *Asparagus laricinus* were the only species that budded in October, about 2 – 3 weeks after the first spring rains. An exception was September 2006, when these latter two species were budding three weeks before the first spring rains. During the 2006 growing season, 57 mm rain was measured in vicinity of the study area in August and none in September (Figure 3.6). The earlier 'spring' rain probably contributed to the earlier budding of these three species of about two weeks, but it had no obvious effect on the other woody species. Another possible explanation for this is that the heavy rains and flooding that were experienced at the end of the hot season of 2006 might have increased the water table and thus provided enough soil moisture for the trees to bud before the first spring rains fell. The possible high availability of water (along with high levels of growing productivity earlier that year) might also have been responsible for the slow start of budding of *A. karroo* and *D. lycioides* during 2006 compared to other years (Figure 5.9).

Dekker and Smit (1996) found that some woody species in mopane bushveld produced new leaves before rains began and others came into full leaf very rapidly after the first rains fell. At the Nylsvley Nature Reserve, by the time the first heavy summer rains fell in December/January the density of leaves had already reached the level maintained during the wet season (Milton 1987). High soil water availability (rather than the time of rainfall occurrence) due to above normal rainfall and flooding conditions during February/March 2006, most probably resulted in the observed sprouting of new shoots and budding leaves in the study area. The most important factors that may determine phenology in general are temperature, day length and moisture availability rather than rainfall (Hall-Martin and Fuller 1975; Cresswell *et al.* 1982; Van Rooyen *et al.* 1986; Milton 1987), but the relative importance of these three factors varies seasonally and regionally (Cleland 2007).

The rainfall season of 2006 (Nov – Apr) yielded 113 mm more rain than the corresponding previous season (Figure 3.6) and an almost continuous downpour was experienced from late December to February. Consequently, the Modder River flooded the study area during February. The abundance of water during this time seemed to have stimulated all the species to bud again and sprout new shoots of up to 30 cm in length (Figure 5.15) resulting in excessive growth. *Diospyros lycioides* sprouted leaves and short shoots as well but only to the extent of a 10% increase in leaf carriage, compared to an increase of up to 20% as recorded in the other species. The reason for this might be that *D. lycioides* is a slow grower under conditions of high soil water availability compared to the other woody species.

Figure 5.15 Some of the woody species that sprouted new shoots of up to 30 cm in length after above normal rainfall was experienced in the rainfall season of 2006, resulting in the Modder River flooding its banks.

5.5.2 Phenology patterns and leaf carriage

No significant differences ($p > 0.05$) were found for leaf phenology of the different species between the four years of study (Table 5.6). There were significant differences in phenology ($p < 0.001$) between the seasons. In the case of trees, summer and autumn differed from winter and spring. In the case of shrubs, winter and summer differed from the other seasons (Table 5.7).

Similarities were observed between leaf phenology patterns of *A. karroo* and *D. lycioides* (Figures 5.1 & 5.2). A very strong correlation ($r = 0.96$, $p <0.001$) were found between their monthly leaf carriage percentages. Ordination also grouped these species together for total phenology over the four years (Figure 5.13), as well as for their BL-phenophase over the four years (Figure 5.14). Weekly BL-values for September to October of each year indicated a fairly strong correlation ($r = 0.707$, $p < 0.001$) between these species. In both species leaf flush started around 16 September, yellow leaves usually appeared in April and dry, brown leaves were mostly retained until June.

Phenology of *A. karroo* trees of different height classes were studied in order to represent phenology for different heights of preferred browsing (1.5 m, 2 m, 5 m – Du Toit 1990a). The main differences observed between phenology patterns of trees in these different height classes, were that in big trees taller than 4 m the leaf flush appeared to be faster than for smaller sized trees and leaf senescence was more rapid. No significant statistical differences ($p > 0.05$) were found between phenology class totals of *A. karroo* trees in height classes of 1 – 2 m, 3 – 4 m and >4 m ($p = 0.982$) nor for the phenophases separately (BL: $p = 0.994$; IL: $p = 0.948$; DL: $p = 0.281$).

Phenology patterns of *S. pyroides* and *Z. mucronata* (Figures 5.3 & 5.4) differed from those of the abovementioned two species in that they seem to have a shorter growing season. Ordination of total phenology grouped these species in a block, separate from the other species (Figure 5.13), but also not in close association with each other. New-season leaves of *S. pyroides* appeared in the first week of October, yellow leaves were already visible at the end of March and a small percentage of dry leaves were retained from May to June. Budding leaves appeared on *Z. mucronata* around 15 October, leaves usually turned yellow in May and dry, brown leaves were retained until July. Ordination results of the budding leaf phenophase for these two species (Figure 5.14) corresponded with ordination of the total phenology (including all phenophases) of the species. There was a fairly strong correlation between weekly BL-values during September to October of these two species ($r = 0.782$, $p< 0.001$). *Searsia pyroides* and *Z. mucronata* usually had mature leaves until May/June, unlike the other tree species that started shedding leaves in April. Kok and Opperman (1980) found that most of the deciduous species in the Willem Pretorius Game Reserve, Free State Province shed their leaves in May after the first frost.

Although mature leaves were still present on all the tree species during May, it was in an older phenological state. Dry, green leaves and not brown as expected, were observed in May 2006 and May 2007 giving the impression that leaves were still in its mature state (Figure 5.16). This might be due to sub-zero minimum temperatures (black frost) that were experienced during the last week of May (Table 3.3). Dunham (1991) reported that leaves of *Faidherbia albida* do not usually turn brown before dropping, but no other references specifically citing dry green leaves could be found. The autumn results of all the tree species over four growing seasons confirmed findings of Cleland *et al.* (2007), stating that end-of-season senescence is more variable than springtime budding.

Acacia karroo and *D. lycioides* trees were mostly leafless from July to middle September (1½ – 2½ months), while *S. pyroides* trees were mostly leafless from July to October (2 – 3 months) and *Z. mucronata* from September to middle October (1 – 1½ month). Dry leaves were retained on all tree species throughout the winter of 2007 until leaf budding occurred in spring. Mature trees of *A. karroo* were completely leafless from July to September at Nylsvley Nature Reserve, near Naboomspruit / Mookgopong, Limpopo Province (Milton 1987), which corresponded to results from this study. Thus, the leafless period of *A. karroo* is probably genetically determined, since the climate of these two areas differs substantially.

Phenology patterns of shrubs differed significantly ($p < 0.001$, Table 5.8) from that of trees on an individual species level (Figures 5.5 – 5.7), as well as on the means between trees and shrubs grouped together ($p = 0.002$) (Figures 5.11 & 5.12). Ordination also indicated no association between leaf phenology of the shrubs and trees (Figures 5.13 & 5.14). During the growing season, shrubs often shed up to 20% of their old leaves and produced new leaves shortly thereafter. New-season leaves of *Lycium echinatum* and *Lycium hirsutum* appeared in September and those of *Asparagus laricinus* in October. The end-of-season yellow leaves of the *Lycium* species were visible roughly from March to August and for *A. laricinus* from April/May to September. Kok and Opperman (1980) also reported that *A. laricinus* retained their leaves until July/August. Leaf fall in the study area was rapid and dry leaves were not retained on shrubs for long periods. *Lycium echinatum* was leafless for about a month from September. *Lycium hirsutum* had up to 50% of its normal leaf carriage present during the critical period, in the form of mostly older mature leaves and some yellow leaves. Ordination results also grouped *L. hirsutum* separately (Figure 5.13), indicating differences between this species and the other shrubs. No leaves were present on *A. laricinus* in middle October 2005 prior to the new leaf flush, but some mature- and yellow leaves were retained in the winters of 2006 and 2007. This was also the case for *L. echinatum*. A fairly strong correlation was found between the *Lycium* species (r = 0.70, $p < 0.001$) and also between *L. echinatum* and *A. laricinus* (r = 0.79, $p < 0.001$). Ordination confirmed an association between these last mentioned two species (Figure 5.13).

5.5.3 Browse availability

Plant defences against browsing (*vid.* Chapter 6), competition between trees, shrubs and the herbaceous layer, as well as bush encroachment and the interaction between woody species and herbivores all play a role in the availability of browse and were discussed in more detail in Chapter 8. All the tree and shrub species present in the study area are considered palatable (*vid*. Chapter 6). The observed seasonal leaf carriage patterns demonstrated the winter deciduous nature of all the tree species. Shrubs retained leaves for longer periods than trees (Figures 5.11 & 5.12), into the winter months when most trees were leafless. This might be one of the reasons why these shrubs were browsed (pruned down) to heights of about 1 m – 1.5 m (Figures 5.17 & 5.18). These species have reached heights of more than 2 m, even up to 3 m in the case of *L. hirsutum*, in other areas next to the Modder River where browsers were absent, or present in lower numbers (personal observation).

Availability of quality browse due to senescing leaves became progressively less from June to September (Figures 5.11 & 5.12) which represents a third of the year. The intensity of the critical period increases in time as the trees, followed by the shrubs shed their leaves until the critical period peaks in September when browseable leaves are almost absent in the study area. The critical period, when semi-deciduous trees and shrubs cannot sustain browsers and mixed feeders is thus from July/August to middle October (Figure 5.11). October is viewed as the most limiting period for impala in the Timbavati Private Nature Reserve, when browse is almost absent (Pietersen *et al.* 1993). According to Theron (2006), the critical period for giraffe in areas where evergreen species are available (i.e. rocky hills like in Willem Pretorius Game Reserve) is from August to October and not the dry season as a whole. Budding leaves, appearing in September/October, are considered to have a higher phenolic content than immature or mature leaves, rendering it more indigestible in some tree species (Cooper 1982, Cooper *et al.* 1988, Van Essen *et al.* 2002) and this probably aggravates the 'scarcity' of quality browse during the end of the critical period.

Figure 5.16 Dry, green leaves retained on trees at the end of May: a) *Acacia karroo*, b) *Diospyros lycioides*, c) *Ziziphus mucronata* with dry red berries and d) *Z. mucronata* in front and *Searsia pyroides* at the back.

Figure 5.17 *Lycium hirsutum* (a & c) and *Lycium echinatum* (b without leaves & d with leaves) in different locations have been browsed down to between 0.8 m and 1.5 m in height. This is evident throughout most of the study area. The red and white markers are 1 m high.

Figure 5.18 Examples of *Asparagus laricinus* that have been browsed down to less than 1 m in height (they seldom reach more than 1.6 m heights throughout the study area). The red and white marker is divided into 10 cm intervals and is 1 m in length.

The only evergreen species present in the study area are three *Searsia lancea* (previously *Rhus lancea*) trees of about 6 m tall, present on the banks of the smaller drainage line of the Modder River, and they show signs of severe browsing (Figure 8.17d). Evergreen and semi-deciduous shrubs, succulents, dry forbs, prickly pears, climbers, bark, leafless stems, fruits, pods and fallen leaf litter of especially *Ziziphus mucronata* may provide important food reserves to carry browsing ungulates in the central Free State through this difficult period of browse shortage (Kok and Opperman 1980, Cooper 1982, Owen-Smith *et al.* 1983, Theron 2006)**.** These food reserves do not appear to be abundant enough in the study area to sustain the number of browser- and mixed feeder species present for the full duration of the critical period. Consequently, feed was supplied from May/June to the beginning of October in the form of 10 bales of lucerne hay (*Medicago sativa*) and 10 bags of lucerne pellets twice a day. All game species present in the study area (browsers, mixed feeders and grazers) utilized the supplied feed during winter months (*vid*. Chapter 7). In other areas in the Free State where rocky hills (koppies) occur, or a permanent flowing river is present, the seasonal leaf availability may differ due to the presence of evergreen species associated with these areas. These, often less palatable evergreen species, will be utilized by game during the critical period (Owen-Smith and Cooper 1989, Estes 1997, Watson and Owen-Smith 2000). In areas where evergreen species are present it may not be necessary to give the same quantity of supplementary feed for the full duration of the critical period, but only from about August to October.

Dekker and Smit (1996) reported that availability of browse in mopane bushveld in the Limpopo Province was at its lowest from September to November and new-season leaves appeared from middle November – which differs completely from the results of this study. This emphasises the importance of determining the phenological patterns for a specific geographical area, since it differs between vegetation types and climate zones.

5.6 CONCLUSIONS

The following general conclusions can be drawn from this study:

i) Differences in phenological patterns were observed between the different years of study in the sense that phenophases change on different dates. This might be due to differences in climate between the years, specifically temperatures. New-season leaves mostly appeared on trees in September/October and leaf senescence started in April. It is important to annually monitor the phenological pattern of woody species for this area, especially the end of season pattern, starting from March, in order to know when it becomes necessary to give supplementary feed to the specific number of animals present in the area. Animal numbers should also be strictly regulated in the critical period. It is further important to determine phenological patterns of each palatable woody species in vegetation types of the same area, since differences were found by other authors between individuals of the same woody species that were located in different vegetation types.

ii) All the tree species are winter deciduous and were leafless for about 2 to 3 months, except where some dry leaves were retained on trees. Shrubs retained mature leaves for longer periods than trees and may become important browse reserves at the beginning of winter. The longer leaf carriage period of *Ziziphus mucronata* and the acceptance of this species' leaf litter to browsers during winter months should make it a valuable fodder tree. Ripe fruits and pods were available for game from March to May/June on the different tree species. Some dry fruits were retained on trees during most of the winter months and may be used as a form of supplementary feed.

iii) The critical period for browser and mixed feeder game species in the central Free State is from July/August to middle October, with a progressive decline of browse availability until the budding leaves become immature and should contain less tannins. Lucerne and game pellets were supplied from April/May to the beginning of October in an attempt to prevent game from losing condition during this period. It is concluded that the supply of feed is essential in similar areas in the central Free State where evergreen species are not available, since all the trees are deciduous and the shrubs and fruits are not abundant enough to sustain the numbers of browsers and mixed feeders during the critical period (also see Chapter 9 in this regard).

CHAPTER 6

ASSESSMENT OF FAECAL NITROGEN AS AN INDICATOR OF NUTRITIONAL STATUS OF FOUR GAME SPECIES

6.1 INTRODUCTION

An important component of wildlife management involves the monitoring of the nutritional status of wildlife populations, as this is related to their productivity, survival and fertility (Wrench *et al.* 1997). The quality of the diet available to ruminants can have a considerable influence on their feed intake and performance (Zimmerman 1980). Faecal nitrogen concentration (N_f) has been promoted as a non-destructive, inexpensive indicator of diet quality of ungulates in southern Africa (Erasmus *et al.* 1978, Buys 1990, Grant *et al.* 1995, Wrench *et al.* 1996). It may also be useful in estimating approximate stocking densities on game ranches (Grant *et al.* 2000), since availability of food resources often regulate animal population sizes (Wolff 1997).

The objectives of this study were:

i) to determine the nitrogen concentration of dung samples of four game species (2 browsers and 2 mixed feeders) in the study area;
ii) to compare faecal nitrogen concentration during different seasons over a period of two years (28 months) with the leaf phenology pattern (seasonal changes) of the animals' food species; and
iii) to compare N_f values of the game species to N_f values from the literature in order to determine the critical level where the animal will start to lose body condition.

6.2 LITERATURE REVIEW

6.2.1 Importance of faecal nitrogen

On game reserves stocked with several herbivore species, information on the quality of forage available to each species will greatly aid management decisions (Erasmus *et al.* 1978). Forage quality estimates have been used to determine nutritional status, but may not accurately reflect dietary quality due to selection (Cook *et al.* 1994). An alternative is to evaluate the chemical characteristic of faeces that is related to the quality and/or quantity of ingested diets. Faecal samples are easy to collect (Erasmus *et al.* 1978, Jhala 1997, Wrench *et al*. 1997) and especially useful because it has a relatively short turnover time (several days) and hence record subtle variations in diet as the seasonal cycle progresses (Codron *et al.* 2007b). By estimating forage quality from faecal indices, time consuming studies of food habits and chemical analyses of several plant species can be avoided (Jhala 1997). Faecal nitrogen has been shown to be positively correlated with the nitrogen (N) and protein content of the food, quality of food, the intake and dietary dry matter digestibility, as well as productivity and weight change in mature game species (Erasmus *et al.* 1978, Zimmerman 1980, Holechek 1982, Nunez-Hernandez *et al.* 1992, Grant *et al.* 1995, Wrench *et al.* 1997, Botha and Stock 2005). These relationships enable the use of chemical composition of faeces as an index of available forage (Erasmus *et al.* 1978, Grant *et al.* 1995, Wrench *et al.* 1997).

Monitoring and comparing certain faecal components of different species from various areas over several seasons can give an insight into their nutritional ecology, with possible indications of suitability of vegetation types, marginal areas and critical periods (Erasmus *et al.* 1978). This is important since, in certain areas and at certain times of the year shortages occur with N being the most limiting nutrient in winter (dry season) in Africa (Van Soest 1994, Wrench *et al.* 1997, Jacobs 2005). The positive correlations of faecal nitrogen (N_f) with intake and nitrogen in fodder are improved if N (most limiting nutrient) and phosphorous (most limiting mineral) concentrations in the faeces are considered together because their excretion is linked and when the season, locality and landscape are also defined (Grant 1989, Grant *et al.* 1995). Faecal indices have potential for evaluation of nutritive quality of the animals' diet particularly when relative differences over time, rather than absolute values are of primary concern (Holechek *et al.* 1982). When faecal nitrogen reflects intake, dietary protein and weight changes of animals, it becomes a viable index of relative inter-seasonal dietary quality fluctuation and within-season comparisons between different populations within similar habitats (Leslie and Starkey 1987, Stapelberg *et al.* 2008a).

Codron *et al.* (2007b) found a negative correlation between N_f percentage and body mass in the dry season and this correlation is stronger within the Bovidae. A significant negative relationship ($p<0.01$) between kudu density and N_f of samples collected from June to September was demonstrated by Van der Waal *et al.* (2003), while these relationships of samples collected in May and October to December were not significant ($p>0.05$). Owen-Smith (1990), Van Hoven (1991) and Grant *et al.* (1995) reported loss of condition and/or density dependant mortalities to have occurred especially during drought periods. N_f can be an effective way to monitor this in order to make timely decisions on the supplement of food before body conditions decline or mortalities occur. Despite inaccuracies in the prediction of protein intake from faecal nitrogen the method has potential for monitoring trends in ruminant dietary quality and could be used as a general indicator of qualitative seasonal changes (Erasmus *et al.* 1978, Buys 1990, Robbins 1993).

In seasonally stochastic environments where the availability of nutrient rich food varies widely, wild herbivores need to use resources in such a way as to maintain condition (Botha and Stock

2005). According to Botha and Stock (2005), knowing the critical N_f concentrations below which weight loss occurs is a useful indicator of an animal's nutritional status, yet few studies have used this approach for different herbivore species. These values may also be useful as an adjunct to determine appropriate stocking rates because of a negative correlation between density and N_f concentrations and also to base management actions on, such as supplementary feeding (Van der Waal *et al.* 2003).

6.2.2 Critique against the use of faecal nitrogen

Feeding experiments have established that the ingestion of phenol compounds (tannins) by herbivores interferes with the prediction of N_f from diet nitrogen concentration (Hobbs 1987, Robbins 1993, Van Soest 1994, Wrench *et al.* 1997). This is perceived to limit the usefulness of N_f as an indicator of the nutritive value of forage used by free ranging browsing species (Robbins 1993, Wrench *et al.* 1997, Grant *et al.* 2000). N_f is elevated whenever diets contain tannins (Hobbs 1987, Cook *et al.* 1994, Wrench *et al.* 1997, Botha and Stock 2005) resulting in a possible overestimation of fodder digestibility and available nitrogen (Holechek *et al.* 1982, Robbins *et al.* 1987, Nunez-Hernandez *et al.* 1992, Grant *et al.* 1995). Arman *et al.* (1975) suggested that increased N_f of diets containing dicotyledonous plant species might result from their higher digestibility, rapid fermentation in the rumen, formation of large quantities of bacterial nitrogen, and the presence of varying protein precipitants such as tannins or leucoanthocyanins.

Zimmerman (1980) mentioned that the relation between N_f and digestibility of feed is poor in the case of very fibrous diets, such as browse, since a higher faecal endogenous and bacterial excretion of nitrogen occurs. Holechek *et al.* (1982) is of the opinion that the N_f technique could render good results when the diet consists primarily of grasses and the objective is to compare forage digestibility between pastures. Arman *et al.* (1975) stated that for browsers and mixed feeders only very rough estimates of dietary crude protein would be possible. Hobbs (1987) and Nunez-Hernandez *et al.* (1992) considered N_f as an unreliable indicator of crude protein concentration and intake for different ruminants (grazers and browsers) on the same rangeland or if large shifts occurred in diet botanical composition of the same ruminant. Hobbs (1987) concluded that the N_f technique can only be used qualitatively to illustrate large differences in diet quality, like summer versus winter. Holechek *et al.* (1982), Wofford *et al.* (1985) and Robbins *et al.* (1987) found that faecal nitrogen was poorly correlated with forage intake and *in vivo* digestibility, because of higher tannin levels present in some of the forage plants. Botha and Stock (2005) were uncertain if the higher N_f levels of the mixed feeders in Hluhluwe-Umfolozi Park were due to the incorporation of woody species with relatively high nitrogen concentrations in the diet, or whether it was a consequence of higher tannin levels that resulted in undigested protein excreted in the faeces. It has also been argued that free-ranging herbivores avoid plants with high levels of phenolic compounds or low quality browse (Leslie and Starkey 1987, Grant *et al.* 2000, Botha and Stock 2005) that could interfere with faecal nitrogen determination.

Robbins *et al.* (1987) and Hanley *et al.* (1992) proposed equations that could be used to understand the defensive role of tannins relative to the effects of other major plant constituents that determine digestible protein and digestible dry matter. These equations may be used to yield an estimate of digestible protein and digestible dry matter in the absence of tannins. Faecal Acid Detergent Insoluble Nitrogen (ADIN), Acid Detergent Lignin (ADL) and non-fiber bound nitrogen concentration have been found to be better predictions of dietary N and intake than faecal nitrogen concentration (Wofford *et al.* 1985, Wrench *et al.* 1997). When faecal ADL is between 160 g/kg and 210 g/kg, indicating browse utilization, Wrench *et al.* (1997) suggested the use of ADL and ADIN in the prediction of dietary N. When faecal ADL is below 160 g/kg, indicating grass utilization, N_f should be used. However, results from Jhala (1997) related to the endangered Blackbuck (predominantly grazer that browse when appropriate browse is available), endemic to India, indicated that N_f showed positive correlations with crude protein content of the forage, digestibility of dry matter, digestibility of gross energy and digestibility of crude protein, while faecal acid detergent fiber and faecal lignin did nót show significant correlations with the above parameters. Further, the reciprocal relationship, % forage N regressed on N_f, had a good predictive capability and could be used to estimate forage quality of the Blackbuck from N_f.

Other methods used to determine nutritional status are fistulation and slaughtering of animals, which are impractical, expensive and may also be socially objectionable for wild animals (Wofford *et al.* 1985, Wrench *et al.* 1997). Faecal sample variation was also found to be much lower compared to samples collected with fistulated animals (Holechek *et al.* 1982). Another method is to use estimates of total faecal output via collection bags for forage intake estimation, which also requires large labour inputs (Wofford *et al.* 1985) and is not feasible for wild animals. Furthermore, the observer may accompany the animal in the veld and record its feeding preferences or may try to sample those plants and parts of plants that the animal selects (Erasmus *et al.* 1978, Botha and Stock 2005). According to Erasmus *et al.* (1978), this method is not only laborious and time-consuming, but tame animals are required and its effectiveness is still doubtful due to selective feeding of the animals. So basically none of these methods can be applied to wild, free roaming game species in order to estimate quality of feed, dietary protein, intake, dietary dry matter digestibility and productivity.

Despite all the critique against the N_f method not being as precise for browsers as for grazers, it has the advantage of limited disturbance to the wild animals. It allows sampling under natural conditions of any number of animals and the collection of faecal samples is often more economical in terms of cost and time when compared to techniques dependant on handling. Faeces are more representative of food eaten at different times and over different parts of the animals' range and the presence of other species of animals feeding in the same environment will not affect the analysis of the diet (Scotcher 1979). Determining the intake and diet nutritive quality of ruminants remains one of the most difficult aspects of range nutrition (Wofford *et al.* 1985). Faecal samples are inexpensive and easy to collect and until another method is developed for more accurate determining of the nutritional status of browsers and mixed feeders, the method of faecal nitrogen analyses will continue to be the only practical method for most researchers.

6.2.3 Woody plant - herbivore interactions

In response to defoliation caused by large herbivores, many plants alter growth hormone production and distribution for compensatory re-growth of damaged tissues (McNaughton 1983, Dangerfield and Modukanele 1996). According to Milewski and Madden (2006), through such compensatory growth, some plants tolerate extreme consumption rates in which a major loss of shoot and photosynthetic tissues has occurred. Some plants respond to destructive defoliation by increasing structural defenses that deter browsers (Milewski *et al.* 1991, Gowda 1997).

Defense mechanisms of plants against consumption by herbivores, such as small leaves, leaf toughness (Owen-Smith *et al.* 1983, Owen-Smith 1993), spines, thorns, prickles (Cooper and Owen-Smith 1986, Milewski and Madden 2006, Van Rooyen 2010) and chemical substances, especially condensed tannins, other polyphenols, alkaloids and toxins (Van Hoven 1984, Cooper and Owen-Smith 1985, Bryant *et al.* 1989, Van Soest 1994, Smit 2009, Van Hoven 2010) are well documented. A tannin is a phenolic compound of sufficient molecular weight that contains enough phenolic hydroxyls to form strong complexes with protein and other macromolecules (Van Soest 1994). According to Zucker (1983), soluble phenolics precipitate plant proteins and gastrointestinal enzymes, thereby reducing protein and cell wall digestion. Tannins are therefore known as anti-quality substances of woody species (Meissner *et al.* 1999). Fiber, lignin and cellulose also reduce the digestibility of food to ruminants and are considered an anti-feedant to them (Watson and Owen-Smith 2002, Vavra *et al.* 2007).

It has been reported that when a noticeable increase in tannin concentration of the leaves of trees occurs, there is a corresponding decrease of 50 – 60% in the voluntary utilization of such leaves by ruminants (Van Hoven 2010). The presence of high concentrations of tannin in plant species is associated with indigestibility and unpalatability (Milewski and Madden 2006, Van Hoven 2010). Concentration of tannins is lower in twigs than in leaves and flowers (Van Hoven 2010). According to Skarpe and Bergström (1986), in the western Kalahari, Botswana the crude protein content of leaves and twigs showed greater relative difference between the seasonal means for all the woody species than digestibility did. In February they found the leaves to contain 7.4% more crude protein than the twigs, while in June/July the difference was 5.5%. In both leaves and twigs the crude protein content decreased from the wet to the dry season. The *in vitro* dry matter digestibility of the leaves was higher than that of the twigs during both the wet and the dry seasons.

Owen-Smith (1993) concluded that a high variability in tannin levels in woody plant foliage exists among individual plants, between parts of the same plant and over time. It remains uncertain whether differences in tannin concentrations are genuine, due to changes in levels of non-tannin phenolics or degree of polymerization of tannin molecules, or indicative of altered concentrations of other metabolites. Fast-growing species are less defended and more heavily attacked by herbivores than slow-growing ones (Coley 1988). Evergreen trees with an extended leaf lifespan gain the most benefit and invest most heavily in tannins and lignins, which are metabolically inactive, large molecular weight compounds (Coley 1988, Owen-Smith 1993). Shorter leaf lifetimes would favour defense by low molecular weight mobile compounds such as alkaloids, cardiac glycosides or monoterpenes (Coley 1988). Deciduous and evergreen trees typical of nutrient-poor soils are generally unpalatable (Owen-Smith and Cooper 1987), commonly have high tannin levels (Cooper and Owen-Smith 1985) and show slow inherent growth rates (Bryant *et al.* 1989).

Changes in contents of tannins or other phenolics affecting nutritional value, can influence broader patterns of foraging behaviour. Kudus have a resting period during the predawn hours – the period in the diel cycle when tannin levels in leaves appear to be the highest (Owen-Smith 1993). Interestingly, kudus have been noted feeding for extended periods on the upper canopies of trees pushed over by elephants, which is the region where tannin concentrations are lowest. Feeding bouts of giraffe on individual trees commonly last 2 – 5 minutes, while those of kudus endure less than a minute on average, which is too short to be affected by subsequently rising tannin levels

(Owen-Smith 1993). Fitness of a herbivore is influenced by the efficiency of its foraging, which relates in various ways to the palatability of the food the herbivore selects (Owen-Smith and Novellie 1982, Milewski and Madden 2006). Even browsers such as giraffe with a specialized anatomy to deal with structural defenses, must physiologically contend with concentrated deposits of indigestible lignin and cellulose (Bryant *et al.* 1992, Milewski and Madden 2006).

According to Gordon and Illius (1994), for any given phenological stage, browse has higher levels of cell solubles and lignin, but lower levels of holocellulose (cellulose and hemicellulose) than grasses. Consequently browse has higher levels of the rapidly fermenting soluble component than grasses. However, because of the higher lignin content in the cell wall of browse, the absolute digestibility of browse tends to be lower (Meissner *et al.* 1999). Browsing ruminants show anatomical and physiological features distinguishing them from grazers, which may enable them to neutralize tannins or cope with their effects somewhat better than grazers. These include large salivary glands and large livers relative to grazers of similar body size (Hofmann 1973, Owen-Smith 1993). According to Gordon and Illius (1994), browsers are expected to have a digestive system adapted to the rapid excretion of the highly lignified, less digestible cell wall fraction, whereas grazers have adaptations to slow down the passage of plant material in the rumen, thereby increasing the extent of digestion of less lignified cell wall components.

There are also some potentially beneficial results of a browser feeding on a plant. The pruning action of large herbivores (*vid.* Chapter 8) can stimulate increased shoot growth and development (McNaughton 1983, Milton 1988, Du Toit *et al.* 1990, Milewski and Madden 2006). Giraffe feeding on *Acacia* species are known to stimulate increased shoot production (Owen-Smith 1988). Through their feeding habits, large herbivores may increase the overall vigour of the browsed vegetation (Sinclair and Norton-Griffiths 1979, McNaughton and Sabuni 1988). Large browsers may also facilitate seed dispersion and increase seedling recruitment (Miller and Coe 1993). Seeds of species like *Acacia erioloba* and *Faidherbia albida* germinate better after passing through the digestive system of a herbivore (Van Rooyen 2010).

Ruminants exist in a highly dynamic environment situation where their performance in terms of production and reproduction are determined by changes in nutrient requirements and also by the physical environment, including the quantity and quality of available feed (Jacobs 2005). Maintenance energy requirements of captive animals are often below what might be expected under free-ranging conditions since predation, activity and thermoregulatory requirements may be minimized. Due to the number of different biotic and abiotic variables affecting the animal's daily existence, the complexity of predicting requirements can be formidable (Roosendaal 2008).

According to Gallivan and Culverwell (1995): "Body condition indices may be useful in assessing the condition of individuals, but do not appear to be sensitive indicators of habitat condition. Body condition varies with season, age and reproductive status, and the temporal patterns may differ between age and sex classes. Individuals in poor condition can occur in habitat in good condition" and *vice versa*. According to Van Rooyen (1993), the body condition of impala is influenced by social status, reproductive state and nutrition. Environmental and animal physiological status, genotype, health status and social conditions can influence faecal nitrogen concentration (Wofford *et al.* 1985, Lewis 1992, Van Soest 1994). Grant *et al.* (1995) indicated that N_f concentrations were significantly affected by species, season and landscape in the Kruger National Park.

6.2.4 Proteins and nitrogen

Proteins are essential organic constituents of living organisms and are the class of nutrients in highest concentration in muscle tissues of animals. All cells synthesize proteins for part or all of their life cycle and without protein synthesis life would not exist. The percentage of protein required in the diet is the highest for young growing animals and declines gradually to maturity when only enough protein to maintain body tissues is required. Protein requirements differ for maintenance of adults, pregnancy, gestation, lactation and hair growth (Pond *et al.* 1995, Roosendaal 2008) and is also affected by sex (males tend to have higher requirements) and by species (Pond *et al.* 1995).

The animal obtains nitrogen in the form of crude protein from the plants that they feed on. In general a minimum of 7 – 8% crude protein is required by ruminants, but high producing animals require levels approaching 13 – 14%, while game species appear to have a lower requirement (Meissner *et al.* 1999). This crude protein fraction also contains variable amounts of non-protein nitrogen. Through extensive degradative and synthetic activities of the micro-organisms of the rumen, carbohydrates in the food are broken down to microbial protein (used for maintenance and growth of the rumen microorganisms) and into acetate, propionate and butyrate, which provide the major part of the energy requirements of the host animal. Bacteria acting on the structural carbohydrate fraction of the diet use only ammonia, whereas those acting on the non-structural fraction derive about 65% of their nitrogen from amino acids and peptides and the remainder from ammonia (Aharoni *et al.* 1991, McDonald *et al.* 2002). According to Aharoni *et al.* (1991), ammonia (NH_3) is the primary nitrogen source for the growth of rumen micro-organisms and is essential for the existence of several species of rumen bacteria.

All organisms can convert NH_3 to organic nitrogen compounds – that is substances containing C-N bonds, by means of the nitrogen cycle. Reduction of nitrate ion (NO_3^-), a soil constituent essential for the growth of most plants, to NH_3 is widespread among plants. NH_3 is converted to amino acids, which in turn are used to synthesize proteins. A protein is a polymer made of 20 different kinds of amino acid monomers (Mathews and Van Holde 1996) classified as indispensable (essential) and dispensable (non-essential). For food to be used with maximum efficiency, an animal must receive sufficient quantities of both amino acid types to meet its metabolic demands (McDonald *et al.* 2002).

Most of the nitrogen required by the animal is used for protein synthesis. Most of the food nitrogen is also present as protein and it is convenient and universal for the nitrogen requirements of animals, as well as the nitrogen status of foods to be stated in terms of protein (McDonald *et al.* 2002). According to Pond *et al.* (1995), some N is lost in faeces as a result of endogenous losses (metabolic faecal N from body tissues). The urinary loss of N involves both excess dietary N and end products of metabolism, such as urea, involving obligatory losses (Pond *et al.* 1995). In most animals the important nitrogenous excretion products are ammonia, urea and urinal acid. Thus, faecal nitrogen consists of unabsorbed dietary nitrogen, undigested microbial nitrogen and endogenous nitrogen, diluted by indigestible dry matter and endogenous material. N_f concentration increases with an increase in the N concentration of the herbivore’s diet (Leslie and Starkey 1987).

6.2.5 Differentiating between browsers, grazers and mixed feeders

Stable isotopic markers of animal tissues, of the rumen and faeces have been used to indicate whether animals are grazers, browsers or mixed feeders (Botha and Stock 2005, Codron *et al.* 2005). Botha and Stock (2005) described the advantages of this method to be that it requires no disturbance of the animals and it can indicate dietary intake over different time scales, from a few days to a few years. Giraffe and kudu in the Kruger National Park have been found to be pure browsers (90% woody plant diets - C_3) by means of the carbon isotopic composition of herbivore faeces, while impala has values intermediate (50% C_3 and 50% C_4 diet of herbaceous plants) between those of pure grazers and pure browsers (Grunow 1980, Codron *et al.* 2005). Codron *et al.* (2007b) indicated for the Kruger National Park that the protein percentage was highest for browsers (16.25%), lowest for grazers (8.13%) and intermediate for mixed feeders (13.75%).

Wild African herbivores can be divided into six main feeding types: obligate grazers with a diet of >90% grass; variable grazers with a diet of 60 – 90% grass; browser-grazer intermediates with a diet of 30 – 70% browse and grass and >20% wild fruits; generalists eating >20% of all the food types; browsers with a diet of >70% browse and frugivores eating >70% wild fruits (Gagnon and Chew 2000). A simplified classification of the feeding classes recognizes four basic types: low selective grazers with wide mouths that include >80% grass in the diet; high selective grazers with narrow mouths and >70% of their diet is grass; mixed feeders that use >30 – 70% grass and browse; and browsers that eat >80% browse and wild fruits (Bothma *et al.* 2004). Bothma *et al.* (2004) classified the species of a wildlife ranch (36 500 ha) in the Limpopo Province as follows: Low-selective grazers – African buffalo, bushpig, Cape mountain zebra, plains zebra, ostrich, white rhinoceros; high-selective grazers – blesbok, blue wildebeest, gemsbok, red hartebeest, waterbuck; mixed feeders – eland, elephant, impala, springbok, warthog; browsers – black rhinoceros, bushbuck, giraffe, grey duiker, grey rhebok, klipspringer, kudu, nyala and steenbok.

Although giraffe and kudu are known to be almost 100% browsers (Estes 1997, Skinner and Chimimba 2005), up to 2% of the total diet of giraffe constitutes grass (Kok and Opperman 1980, Theron 2006), 1% are forbs and 12% are shrub material when browse becomes scarce (Hofmann 1973) mainly in August and September (Theron 2006). Kudu will mostly take forbs, creepers and a little grass during the dry season to supplement their browse diet (Hofmann 1973, Owen-Smith *et al.* 1983, Owen-Smith 1994). All the other game species present in the study area, except eland and impala, are grazers that feed almost 100% of the time on grass, but also include a small percentage of browse and dwarf karroid shrubs when the quality of grass declines (Knight 1991, Estes 1997, Bodenstein 2000, Ryan *et al.* 2006, Codron *et al.* 2007b).

Impala and eland are mixed-, or intermediate feeders (Hofmann 1973) and considerable variation exists in relative contributions of graze and browse to their diet. Impala in Kruger National Park selected a wide range of mixed dicotyledon and monocotyledon plant material and consumed between 53% and 63% grass material (C_4 vegetation) (Wentzel 1990, Sponheimer *et al.* 2003). In the SA Lombard Nature Reserve near Bloemhof they consumed 46.2% grasses and 53.8% browse from shrubs and trees (Hofmann 1973). The ratio between grass and browse was 79.6% grass and 20.4% browse in the Timbavati Private Nature Reserve (Meissner *et al.* 1996). Impala in the Hluhluwe-Umfolozi Park, central KwaZulu Natal, consumed mainly grass throughout the year but it varied seasonally and declined from 80% in summer to 60% in winter when more browse (C_3 material) was taken after grass quality and availability declined (Botha and Stock 2005). Grass loses its nutritive value when maturing or becoming dormant, but browse maintains its nutritive value rendering the N_f values of browse higher than that of grass (Zimmerman 1980, Grant *et al.* 1995).

Eland eats mostly grass in the wet season (Hofmann 1973, Watson and Owen-Smith 2000), but is considered to be essentially a browser in the dry season. Free ranging eland in semi-arid areas, like the study area, consumes about 80% dicotyledon material such as forbs, shrubs and tree leaves, while the remaining 20% are grasses (Estes 1997). Watson and Owen-Smith (2000) found that shrubs and dwarf shrubs (70 browse species in total) constituted 94% and forbs 3% of their annual diet in the Mountain Zebra National Park, Cradock. Populations in savanna habitats, where browse is more readily available, include a larger browse component in their diet than those in grassland habitats (Wallington *et al.* 2007). In uKhahlamba-Drakensberg Park at Giants Castle, where 89% of the area is grassland, eland spend most of their time in open grassland areas, particularly during late spring and summer when grass is green and nutritious (Rowe-Rowe 1994). Buys (1990) found that during summer they fed mainly on grass, while in winter they made extensive use of patchily distributed browse, but grass never formed less than one third of dietary fragments identified in dung. Eland stomach structure is similar to that of browsers, so they probably digest mature grass less well than grazers do (Hofmann 1973, Watson and Owen-Smith 2000).

6.2.6 Food sources of giraffe, kudu, impala and eland

All the large woody species present in the study area are palatable, the trees being *Acacia karroo*, *Diospyros lycioides*, *Searsia lancea*, *S. pyroides*, *Ziziphus mucronata* and the shrubs are *Asparagus laricinus*, *Lycium echinatum* and *L. hirsutum* (Van Wyk *et al.* 2000). However, *S. pyroides* has been described to have a low acceptability, probably due to the strong resinous smell that is released when leaves are browsed (Van Wyk *et al.* 2000). Palgrave (2002) viewed *S. pyroides* as a very variable species in all respects. Owen-Smith and Cooper (1985) described *S. pyroides* in Nylsvley Nature Reserve as a semi-evergreen species that was well utilised by impalas and kudus during the dry season. In the study area, evidence of browsing was observed on all five above-mentioned tree species, including some individuals of *S. pyroides*. Results of Kok and Opperman (1980), Owen-Smith and Cooper (1987), as well as Buys (1990) confirmed that all the shrub and tree species present in the study area are palatable and utilised in other areas by giraffes, kudus, impalas and eland, respectively – giraffe favoured *Acacia* species and eland *D. lycioides*.

Searsia undulata, *A. karroo*, *Z. mucronata* and *A. laricinus* are considered to be the most important components in the diet of **giraffe** in the central Free State (Kok and Opperman 1980, 1985, Theron

2006). When deciduous species have shed their leaves, giraffes usually browse extensively on *A. laricinus* shrubs that retain leaves until late in the season and increasingly bite off shoot-ends of woody plants during the dry season (Kok and Opperman 1980, 1985). The usual feeding method that giraffes use is to bite on a shoot transversely with the stem passing over the incisors and then pull backwards, stripping the leaves off a hardened shoot and shearing off the shoot-end (Cooper and Owen-Smith 1986, Owen-Smith 1988).

Parker *et al.* (2003) listed the most important food species of giraffe in the Shamwari Game Reserve, Eastern Cape Province to be in order of importance: *Searsia longispina* (which is similar to *S. burchellii*), *Acacia karroo* and *Euclea undulata*. *Tarchonanthus camphoratus* was only consumed in summer, *Gymnosporia buxifolia* in winter and nine other species were also recorded in their diet. They concluded that giraffe foraging and preference corresponded to the availability of palatable browse. In the lowveld of Mpumalanga, woody species favoured by giraffes included *Ziziphus mucronata*, *Acacia nilotica*, *Dichrostachys cinerea* and *Combretum molle*, while species eaten mainly during the dry season included *Terminalea sericea*, *Peltophorum africanum* and *Ximenia caffra* (Oates 1973, Hall-Martin 1974). Kok and Opperman (1985) found that *Z. mucronata* was the most nutritional food plant of giraffes in the Willem Pretorius Game Reserve, Free State – its leaves had a high mineral content relative to other food plants, the highest crude protein, high *in vitro* digestibility of organic material and the lowest acid digestive fiber fraction. *A. karroo* is usually their most important food plant, but has a low average nutritional value in comparison to other plant species (Kok and Opperman 1985).

Giraffe prefers to feed on *Acacia* spp. (Mimosaceae) which are known for their high protein (nitrogen) content, up to 28% crude protein, that are fermented rapidly (Hofmann 1973, Petrides 1975). According to Owen-Smith (1993), with the exception of *Acacia karroo* and *A. nilotica*, members of the Mimosaceae generally have low levels of phenolics, including tannins. Caister *et al.* (2003) hypothesized that nursing giraffe females might avoid tannins as far as possible because they are not palatable to their young when passed on through the milk, while pregnant females have a high energy requirement that would benefit from higher quality forage of *Acacia* species. Pellew (1984) suggested that female giraffes seek a high energy browse and avoid browse with high fiber content in the dry season.

Giraffe and kudu will both expand their diet in the dry season to include evergreen and unpalatable deciduous woody species neglected during the wet season (Kok and Opperman 1980, Owen-Smith and Cooper 1987, Owen-Smith 1994, Theron 2006). Owen-Smith and Cooper (1985) reported evergreen species in Nylsvley Nature Reserve to display striking browse lines by August, indicating near complete utilization of all leaves within the reach of kudus by this time. Both species also feed on shoot-ends but nutritional value of shoot-ends decreases with increasing shoot diameter (Wilson and Kerley 2003). The proportion of woody material increases from 5% in the wet season to 15% of the rumen contents of giraffe (Owen-Smith 1988). Cropping of thicker shoots as a result of interspecies competition between kudu males and females, or re-browsing under a high browsing pressure consequently also results in a lower quality diet (Van der Waal 2005), along with the unpalatable and neglected evergreen species eaten during the dry season. Impalas usually pluck single leaves and avoid the woody shoot-ends of plants (Owen-Smith and Cooper 1985, Cooper and Owen-Smith 1986).

Additional food resources are utilised during periods of browse shortage or when deciduous species are leafless. According to Theron (2006), exotic plant species such as poplar-, pine-, eucalyptus- and willow trees as well as prickly pear, conyza weeds and cotoneaster are seasonally utilised by giraffe in the central Free State. Succulents, dry forbs and fallen leaf litter of especially *Z. mucronata* may also provide important food reserves for browsing ungulates during winter months (Cooper 1982, Owen-Smith *et al.* 1983)**.** Kok and Opperman (1980), Milton (1987), Owen-Smith and Cooper (1985, 1988), as well as Dunham (1991) reported that fallen pods and fruits were eaten by a variety of large herbivores, like impala, kudu and giraffe. Monro (1980) stated that the diet of impala in the Nylsvley Nature Reserve consisted almost entirely of fallen *Acacia* pods during the dry season. Owen-Smith *et al.* (1983) reported that fruits and pods were actively sought by kudus when available in the Kruger National Park and succulent euphorbias and aloes were also eaten. Palgrave (2002) indicated that fallen fruits of *Z. mucronata* were usually favoured by game and could provide useful fodder in times of drought, while Owen-Smith (1979) found *Z. mucronata* to increase in prominence as the dry season advanced in the Kruger National Park.

Kudus are known to eat a protein-rich concentrate food which is rich in water and easily digestible sugars and must then be subject to rapid fermentation (Hofmann 1973). They often shear off shoots with their cheek teeth and take leaf and stem material together (Cooper and Owen-Smith 1986). Koekemoer (2001) identified a total of 41 plant species in the diet of kudu in the Eastern Cape subtropical thicket. Owen-Smith and Cooper (1987) reported that kudus favoured the following species during the wet season in the Nylsvley Nature Reserve, in order of relative acceptability: *Grewia flavescens*, *Dichrostachys cinerea*, *Vitex rehmannii*, *Diospyros lycioides*, *Strychnos connuloides*, *Combretum molle*, *C. zeyheri*, *Acacia nilotica*, *A. karroo*, *Securidaca longipedunculata*, *Ziziphus mucronata*, *Lannea discolor* and six other species of intermediate acceptability. In the dry season *Searsia leptodictya*, *Strychnos pungens*, *Acacia tortilis*, *Dombeya rotundifolia* and *Ximenia caffra* were favoured when the availability of deciduous species declined. Other authors also listed some of these species to be favoured, namely *D. cinerea*, *Z. mucronata* in the Kruger National Park (Owen-Smith and Novellie 1982) and *D. lycioides* in Hwange National Park, Zimbabwe (Conybeare 1975). Kudu's staple woody species in the Kruger National Park include *Acacia nigrescens* and *Combretum hereroense* during the early wet season and *C. apiculatum* during the dry season (Owen-Smith *et al.* 1983).

Herbs, creepers and woody seedlings which are mainly derived from ground level feeding, made up approximately 40% of the year round diet of kudu in the Kruger National Park (Owen-Smith 1979). In Nylsvley Nature Reserve, they devoted considerable feeding time to forbs (non-graminaceous herbs) and weedy annuals like *Chaenopodium album*, *Schkuhria pinnata* and *Bidens* sp. where abundantly available (Owen-Smith and Cooper 1985). Kudu continued to feed on deciduous species in the dry season despite leaf loss (Owen-Smith 1994). Owen-Smith (1994) found that the overall proportion of the day devoted to foraging by the kudu was significantly higher over the dry season months than in the late wet season. Digestive capacity of kudu was apparently increased to accommodate a higher daily food intake, which compensated for reduced diet quality during the dry season (Owen-Smith 1994).

In deciduous savanna, the dry season is marked by a nutritionally restrictive period for kudu (Novellie 1983, Van der Waal *et al.* 2003). This contrasts with the apparent overabundance of browse during the rainy season (Owen-Smith and Cooper 1989). The availability of browse to kudu may become limiting because they compete with other browsers, while giraffe can avoid competition by virtue of their browsing height. Kudu showed a decline in condition in the Kruger National Park and suffered a substantial drop in total numbers during the drought in 1992, while giraffe condition was generally good and their numbers increased during this period (Grant *et al.* 1995). It appears that in times of resource scarcity, kudu opt for bulk by increasing the feeding time, rather than the time-consuming option of selecting for quality (Owen-Smith *et al.* 1983, Owen-Smith 1994, Van der Waal 2005). Kudus are expected to perform poorly in regions dominated by extremely small-leaved *Acacias*, or by tannin-rich trees and shrubs– unless more varied vegetation is available in localized places like rocky hill slopes or drainage lines (Owen-Smith 1985). The availability of browse during the dry season is thought to regulate kudu populations. Their low natural density can, however, be a major commercial limitation (Owen-Smith and Cooper 1985, Grossman 1994, Van der Waal *et al.* 2003).

Impala diets are believed to differ markedly between localities, reflecting changes in local vegetation (Sponheimer *et al.* 2003). Koekemoer (2001) indicated 38 plant species in the Eastern Cape subtropical thicket to occur in the impala diet, seven of which were grasses. *Digitaria eriantha* and *Themeda triandra* had the highest intake in the Timbavati Private Nature Reserve with the first mentioned constituting the largest part of the diet during the dry season and the latter during the wet season (Meissner *et al.* 1996). When sweeter grass species were not abundant in the Loskop Dam Nature Reserve, impalas relied heavily on *Setaria perennis* and *Cynodon dactylon* during the dry winter months (Pettifer and Stumpf 1981). They feed mostly on grasses in the wet season and on browse during the dry season (Dunham 1982). Dunham (1980) listed the principle woody species of wild impala in Zimbabwe as *Capparis tomentosa*, *Combretum mossambicense* and *Diospyros lycioides*, while a tame impala also utilized *Acacia tortilis*, *Colophospermum mopane*, *Dichrostachys cinerea*, *Diospyros senensis*, *Erythroxylum zambesiacum*, *Securinega virosa* and *Vangueria randii*. In the Nylsvley Nature Reserve 14 woody species were important in the diet, but the following eight were eaten constantly: *Acacia nilotica* (the most highly acceptable plant species), *Combretum molle*, *D. cinerea*, *Grewia flavescens*, *Searsia leptodictya*, *Strychnos pungens*, *Terminalia sericea*, and *Vitex rehmannii* (Cooper 1982). Matson *et al.* (2007) observed that *Terminalia prunioides* was an important browse species in the Ongava Private Game Reserve, Namibia because its new leaves appeared earlier than other species' in certain localities. Dunham (1982) made some observations of impala feeding on *A. tortilis* and *D. lycioides* in Zimbabwe.

Forbs are also included as part of the diet of impala, but certain forbs are not eaten until the post-flowering phase, probably due to a difference in the allocation of plant defense compounds (Cooper 1982). In the Nylsvley Nature Reserve, eight common forb species were recorded in the diet, of which *Waltheria indica* was the most acceptable throughout summer and autumn (Cooper 1982). The utilization of leaf litter by impala increased in winter and they sought out litter under *Strychnos cocculoides*, *Z. mucronata*, *T. sericia*, *A. nilotica* and *D. cinerea*, but ignored leaf litter of all other species in the Nylsvley Nature Reserve (Cooper 1982).

Small-mouthed ungulates like impala make better use of small-leaved *Acacias* than kudu (Owen-Smith 1985, De Garine-Wichatitsky *et al.* 2004) and eland and make better use of leaf litter (Owen-Smith 1985). Grasses have a more continuous dispersion pattern than browse plants which are usually more scattered. Thus the distance between food items for a browsing kudu would be greater than that for a grazing impala (Dunham 1982). Owen-Smith and Cooper (1987) concluded that impala favoured *A. nilotica*, *T. sericea* and *S. leptodactya* more than kudu did in the late wet season in the Nylsvley Nature Reserve. Over the dry season impala favoured *Euclea undulata* more than kudu did. The specialist browser, the kudu, selected an overall wider range of woody species in the Nylsvley Nature Reserve than impala (Owen-Smith and Cooper 1987). De Garine-Wichatitsky *et al.* (2004) found that the diet overlap between kudu and impala was low in the highlands of Zimbabwe, but a decrease in species selectivity of kudu during the dry season (stopping at a higher proportion of medium and small bushes) resulted in an increase in diet overlap for this period. In general, according to Grant *et al.* (1995), quality of diet as reflected in N_f concentrations was not limiting to impala in Kruger National Park.

Eland are rapid feeders, grasping the foliage with their lips or stripping the twig of leaves by drawing it through the lips and then cutting twigs up with the teeth (Skinner and Chimimba 2005). Buys (1990) identified six important browse species for eland in the SA Lombard Nature Reserve, Bloemhof, namely *Searsia lancea*, *Grewia flava*, *D. lycioides*, *Tarchonanthus camphoratus*, *Z. mucronata* and *A. karroo*. Eland in the Waterberg Plateau Park, Namibia ate *T. sericea* in large quantities during the wet season, while *Dombeya rotundifolia* was eaten in the dry season only and *Burkea africana* and *Ochna pulcra* only when new leaves emerged (Jankowitz 1982). Owen-Smith and Cooper (2002) divided woody species, including dwarf karroid shrubs, with regard to acceptability over the seasonal cycle into two groups: i) *Felicia muricata*, *Grewia occidentalis*, *Pentzia sphaerocephala*, *Searsia erosa* and *Walafrida geniculata* were favoured as long as they retained leaves, while ii) *A. karroo*, *Chrysocoma ciliata*, *D. lycioides*, *Felicia filifolia*, *Maytenus heterophylla*, *Pentzia incana*, *Searsia longispina* and *S. pallens* were neglected for part of the seasonal cycle, even though they retained leaves, with shoot phenology strongly influencing acceptability.

The following were the most abundant shrubs included in the eland's diet in Suikerbosrand Nature Reserve (50 km southeast of Johannesburg),: *Lippia javanica*, *Mundulea sericea* and *S. pyroides*; the forbs were *Hibiscus calyphyllus*, *Tagetes minuta*, *Bidens pilosa*; and *Aloe marlothii* was also included (Wallington *et al.* 2007). Kerr *et al.* (1970) listed among perennial species eaten in Zimbabwe: *Tricholaena monachne*, *Urochloa mosambicensis*, *Schmidtia pappophoroides* and the annuals *Brachiaria deflexa*, *Cenchrus biflorus* and *Chloris virgata*. Buys and Dott (1991) indicated that eland utilized more grass during the rainy season, but turned to browse in winter months. Buys (1990) concluded that consumption of dicotyledons increased from February to May and then remained static until the end of winter. Botha and Stock (2005) stated that nitrogen concentration of faeces could prove a useful means of indicating whether opportunistic feeders that are able to switch to eating browse in the drier months are able to maintain their nutritional condition better than pure grazers.

The large muzzle and high absolute food requirement of the eland reduce its ability to select for leaves (Watson and Owen-Smith 2000, 2002). Eland have a high metabolic rate, a narrow thermal neutral zone and lose much urea in the urine (Taylor and Lyman 1967). These characteristics necessitate the intake of food with high protein content and the chemical contents of faeces indicate that eland make optimal use of the available protein resources, although this is done at the cost of a reduction in fiber digestibility (Arman *et al.* 1975, Buys 1990). Peak levels of fiber in eland dung at the end of winter when fiber contents of browse was declining do not indicate a change to grazing, but was probably caused by a faster rate of passage which is associated with a high quality diet that gives shorter time for fermentation. Although eland select a high quality diet during nutritional stress periods, they concentrate on abundant species and cannot afford to spend too much time searching for less abundant species (Buys 1990). Dry tree leaves will be taken when preferred herbage is in short supply (Petrides 1975).

6.2.7 Quality and digestibility of forage

According to Grant *et al.* (1995), in the case of selective feeders, browsers and short grass feeders, the critical level in faecal nitrogen (N_f) would seldom occur and because N_f is positively correlated to fodder digestibility, the influence of drought on them is mainly lack of food rather than quality. Mild drought conditions may cause increased phenol levels in woody plants (Bryant *et al.* 1991) which can be reflected in the diets of browsing animals (Grant *et al*. 2000). Browsers should not normally be affected by a short term or seasonal drought as long as shrub and tree leaves are still available (Grant *et al.* 1995).

An inverse relationship exists between protein and fiber content of food plants. When protein content of a food plant falls below 4 – 8% it becomes uneconomical for herbivore digestion (MacLeod *et al.* 1996). Hofmann (1973) noted that giraffe, for example, spent a progressively greater proportion of time on chewing the cud as the season advanced. When lush green foliage was available, giraffe needed less time to feed and consequently had more leisure time to chew their cud in the daytime**:** seasonally changing quality, varying hardness and fiber content of feed were influencing the intensity of rumination. Forage quality is closely connected with that of fiber, which is needed in coarse form to maximize rumen function. Poor-quality forages that are too high in total fiber tend to have fermentation rates barely adequate to feed rumen bacteria (Van Soest 1994).

It appears that larger animals consume relatively poorer quality foods regardless of diet type (Gordon and Illius 1994, 1996, Du Toit 1995, Codron *et al.* 2007b). Smaller species require higher energy yields from their food through selection in order to maintain higher metabolic rates (Bell 1970, Jarman 1974, Demment and Van Soest 1985, Owen-Smith 1988, Du Toit 1995). Decreased diet quality with increasing body size complements expectations that fiber-digestion efficiency increases with body size (Owen-Smith 1988, Gordon and Illius 1994, 1996, Robbins *et al*. 1995). In principle, larger animals are predicted to have longer digesta retention times than smaller species, allowing for more complete microbial fermentation. Novellie (1990), Du Toit (1995), and Gordon and Illius (1996) hypothesized that such adaptations enabled larger animals to cope with poor quality diets and thereby avoid competition with smaller species by having a wider resource-tolerance range, especially during limiting periods. The importance of diet quality and its implications for body size is a fundamental nutritional adaptation (Codron *et al.* 2007b).

Productivity of the large herbivores depends basically on the intake of digestible energy and nutrients, thus not only on the biomass and species composition of the forage available, but also on nutritive composition and digestibility of the fodder species at any particular time (Skarpe and Bergström 1986, Meissner *et al.* 1999). The animals generally cannot compensate for low quality forage by increasing their intake. On the contrary, according to Skarpe and Bergström (1986), the voluntary intake is positively correlated with the nutrient content and digestibility of forage. Protein and dry matter digestibilities are critical factors in the nitrogen and energy economics of animals and tannins present in browse reduce both in ruminants (Hanley *et al.* 1992). According to Robbins *et al.* (1987), wild animals have increased detoxification capabilities, but they must still balance the rate of intake with the rate of detoxification if they are to successfully consume forages containing absorbable phenolics, such as tannins. Van Soest (1994) concurred with this statement.

There appears to be differences between crude protein values in the wet and dry seasons. Kok and Opperman (1985) found an increase in the percentage crude protein and *in vitro* digestibility of organic matter of deciduous plants in the early wet season in the Willem Pretorius Game Reserve. Zimmerman (1980) showed that crude protein and digestibility were both higher during the hot, wet season in the mixed bushveld of the Nylsvley Nature Reserve. The crude protein content peaked in the beginning of the wet season in October, whereas the digestibility peaked in the middle of the wet season (November/December). While nitrogen concentration of mature vegetation falls dramatically in a dry season, the cellular content of plants is still relatively high (Zimmerman 1980). Owen-Smith (1994) indicated that in the Nylsvley Nature Reserve, crude protein levels in leaves dropped abruptly at the onset of the dry season by 15 – 30% of their wet season concentrations, followed by a slow further decline. Kok and Opperman (1985) concluded that the total nutritional values of woody plants were higher in a wet year than in a dry year with less rainfall. There was some evidence, according to Hofmann (1973) that nitrogen or protein availability was the critical factor in survival of some groups of ruminants subjected to natural starvation during dry seasons.

6.3 PROCEDURE

6.3.1 Collection of dung samples

Dung of eland, impala, kudu and giraffe were collected every fortnight from September 2005 to December 2007 and each species' dung/faeces were then pooled per month and stored in a paper bag. Fresh dung, less than 24 hours old, was required (Erasmus *et al.* 1978, Grant *et al.* 1995, Wrench *et al.* 1996, Codron *et al.* 2005) and only recently deposited, fresh or moist dung was subsequently collected. The GPS position of the collected dung and the vegetation unit (Figure 4.1) where it was collected per date was noted.

In accordance with the recommendation by Cook *et al.* (1994), where possible, the dung from several individuals of both sexes were collected, but not from suckling juveniles. However, Wrench *et al.* (1996) found no significant faecal nitrogen differences between impala males and females. Following Van der Waal *et al.* (2003), it was assumed that the same also applied to the other species. Following Codron *et al.* (2005), droppings from different dung piles encountered on the same day were taken to represent a different individual of the relevant species.

Samples were collected after locating the animals with a vehicle or on foot. If dung were not found in the vicinity of the first encounter, fleeing animals were tracked. Erasmus *et al.* (1978) and Zimmerman (1980) found no differences in crude protein, crude fat or neutral detergent fiber between dung excreted during the day or night, and the time of sampling was therefore not considered critical.

Leaves of each phenophase, i.e. Immature-, Mature-, Yellow- and Dry leaves of woody species were collected once-off at the end of March 2007. During May 2007, green leaves dried on all tree species without turning yellow and this was also collected in paper bags. Leaves were collected to establish if the nitrogen (N) concentration differed between phenophases. Dry fruits and pods of tree species were collected once-off during June 2007 to determine their crude protein content.

Figure 6.1 a) Leco Nitrogen Analyzer b) Dried, powdered dung/faeces and leaves were weighed in aluminium foil containers and c) the weight entered into the computer. d) The foil container was closed and e) loaded into the rotary wheel of the nitrogen analyzer. f) A sample fell in the combustion chamber of the analyzer and was incinerated at 900°C until only gasses remained that were used in determining the percentage of nitrogen present in the sample.

6.3.2 Drying of samples and nitrogen analysis

The collected dung, leaves, fruits and pods were air dried at room temperature whereafter they were dried in an oven at 70°C for 48 hours (Wrench *et al.* 1996, Milis *et al.* 2007). Wrench *et al.* (1996) indicated that dried samples can be kept for up to a year before analyzing. Wrench *et al.* (1996) found a significantly lower N concentration in samples that developed mould, thus dung samples from the study area were dried in thin layers to avoid fungal growth.

After oven drying, all samples were grounded with a Tecator mill through a 1 mm mesh screen to a homogeneous powder (Wrench *et al.* 1996, Codron *et al.* 2005, Milis *et al.* 2007). The mill was thoroughly cleaned after each session to prevent contamination of other samples. Each sample was thoroughly mixed and two sub samples of 0.4 g were weighed off in small glass bottles. These samples were dried again in an oven at 70°C for 24 h. A Leco FP 528 Nitrogen Analyzer located at the Department of Animal, Wildlife and Grassland Sciences, UFS was used to determine the nitrogen concentration of the prepared plant and faecal samples (Figure 6.1).

Chemical protein content was calculated from the determined nitrogen concentration by a modification of the Kjeldahl technique as performed by the Nitrogen Analyzer. It gives a value which includes most forms of nitrogen, although nitrites, nitrates and certain cyclic nitrogen compounds require special techniques for their recovery (McDonald *et al.* 2002). Two assumptions are made in calculating protein from nitrogen concentration: 1) all nitrogen in the sample is present as protein, and 2) all protein contains 160 g N/kg. The nitrogen concentration of food is then expressed in terms of crude protein: CP (g/kg) = g N/kg x 1000/160, or more commonly as CP (g/kg) = g N/kg x **6.25** (McDonald *et al.* 2002).

Average nitrogen values were calculated between duplicate dung samples of each species per month as determined by the Nitrogen Analyzer. Nitrogen percentages were then multiplied with a factor of 6.25 in order to obtain the percentage protein in each sample, as was done by Allen (1974), Erasmus *et al.* (1978), Zimmerman (1980), Negi (1995) and Milis *et al.* (2007). The mass of nitrogen present in dung (g N/kg dung) was calculated from percentages since the exact weight (g) of each sample that was loaded into the Nitrogen Analyzer is known (Figure 6.1), as well as the percentage nitrogen recorded in that sample. These faecal nitrogen- (N_f) and percentage protein values were used in comparison to related values found in the literature.

6.3.3 Data and statistical analyses

Nitrogen and protein data were computerized in a Windows EXCEL file (Microsoft Corporation 2002) and separated into sheets according to species. Descriptive statistics include bar graphs that were created of the N_f values (g N/kgDM) per month for each species and N_f values of species were also combined as lines on a single graph. Average N_f values were calculated between the two browsers and between the two mixed feeders and indicated as line graphs with 2-point moving average trend lines added. These graphs also include median leaf phenology values (*vid.* Chapter 5) of the four tree and three shrub species (bars). Further, a dataset was created listing the species' N_f values for each vegetation unit, according to the GPS position where fresh dung was collected on a specific date for each of the game species concerned.

All data were analysed using the statistical programme GenStat® (Payne *et al*. 2009). One-sample t-test (A minus B) at 5% level (Rayner 1969) was used to test for differences between duplicate dung samples of each species. Analysis of variance (ANOVA) was applied to test for equality of several means simultaneously (McKillup 2006, Fowler *et al.* 2006) and where significance occurred, means were separated using Fisher's Protected Least Significant Difference procedure at the 5% level of significance (Snedecor and Cochran 1980, Vittinghoff *et al.* 2005). Standard error of means for ANOVA was calculated with $SEM = S / \sqrt{n}$ where S is standard deviation of the sample and n is the number of observations or data points per variable (Fowler *et al.* 2006).

Factorial ANOVA for an unbalanced dataset was applied to test for differences in giraffes' and in impalas' faecal nitrogen values (g N/kgDM), respectively, between different years, seasons and the year-by-season interaction. For kudu and eland dung, differences between years and seasons were tested separately due to incomplete data for the year-by-season model. All data were acceptably normally distributed (determined by means of graphs) with homogeneous year and season variances. ANOVA for an unbalanced design was used to test for differences between N_f-values collected in different vegetation units.

Pearson's correlation coefficient was used as a measure of the linear relationship (Draper and Smith 1981, Fowler *et al.* 2006) between monthly N_f percentages of the animal species and monthly phenology class values of the plant species. Multiple linear regression analysis (Vittinghoff *et al.* 2005), in particular forward selection stepwise regression, was applied to determine which measurements influenced the percentage protein measured in giraffe, kudu, eland and impala dung. In this procedure, the measurement most correlated to percentage protein is first introduced in the regression model, secondly the next measurement most correlated to the residuals from the model is included in the model, etc. The "best" model is determined when the adjusted R-square value does not increase by more than 1% (Draper and Smith 1981). The statisticians generally use "R" in regression modelling and "r" in correlation. The same applies to probability, "P" is used in regression modelling and "p" in ANOVA and correlation.

Canonical Correspondence Analysis from the CANOCO 4.5 software (Ter Braak and Smilauer 2002) was used for ordination (Gauch 1982, Ter Braak 1986, 1987). The monthly percentage faecal protein of the four game species was superimposed on the monthly leaf carriage percentages of trees and shrubs.

6.4 RESULTS

6.4.1 Faecal nitrogen of the four game species

A quick overview of the faecal nitrogen (N_f) concentration of all four species (Figure 6.2) reveals a seasonal pattern with the highest concentrations mostly occurring in summer months (November to February) and the lowest concentrations during winter (June to August). Differences in nitrogen concentration were mostly $< 0.04\%$ between duplicate dung samples of each species that were pooled per month. Therefore, no significant differences were found with the t-test between nitrogen concentration of each species in duplicate samples used for nitrogen analysis ($p = 0.405 > 0.05$ for $n = 74$, mean = 0.008324 with a standard error of mean = 0.00994).

Difficulties were experienced when comparing nitrogen concentration from this study with values reported in the literature, because all values were not in the same format. Some authors indicated nitrogen concentration in dung or faeces as g N/kg DM (Gates and Hudson 1981, Wofford *et al.* 1985, Grant *et al.* 1995, Wrench *et al.* 1997, Van der Waal *et al.* 2003), while others have indicated it as percentage protein (% N x 6.25) or as percentage nitrogen (Buys 1990, Pietersen *et al.* 1993, Botha and Stock 2005, Roosendaal 2008). It proved difficult to convert values indicated as percentage nitrogen to g N/kg DM since the original mass of samples on which the analysis was done was not known. Therefore, both units of comparison had been used to incorporate values from the literature in the comparison. Figures 6.2 to 6.6 and Table 6.1 indicate N_f in g/kg DM, whereas Table 6.2 indicates ranges and minimum values of faecal nitrogen as percentage protein. Table 6.3 summarises nitrogen values found in leaves of woody species in both units. Figures 6.7 and 6.8 indicate average values of N_f in g/kg DM for the browsers and mixed feeders, respectively.

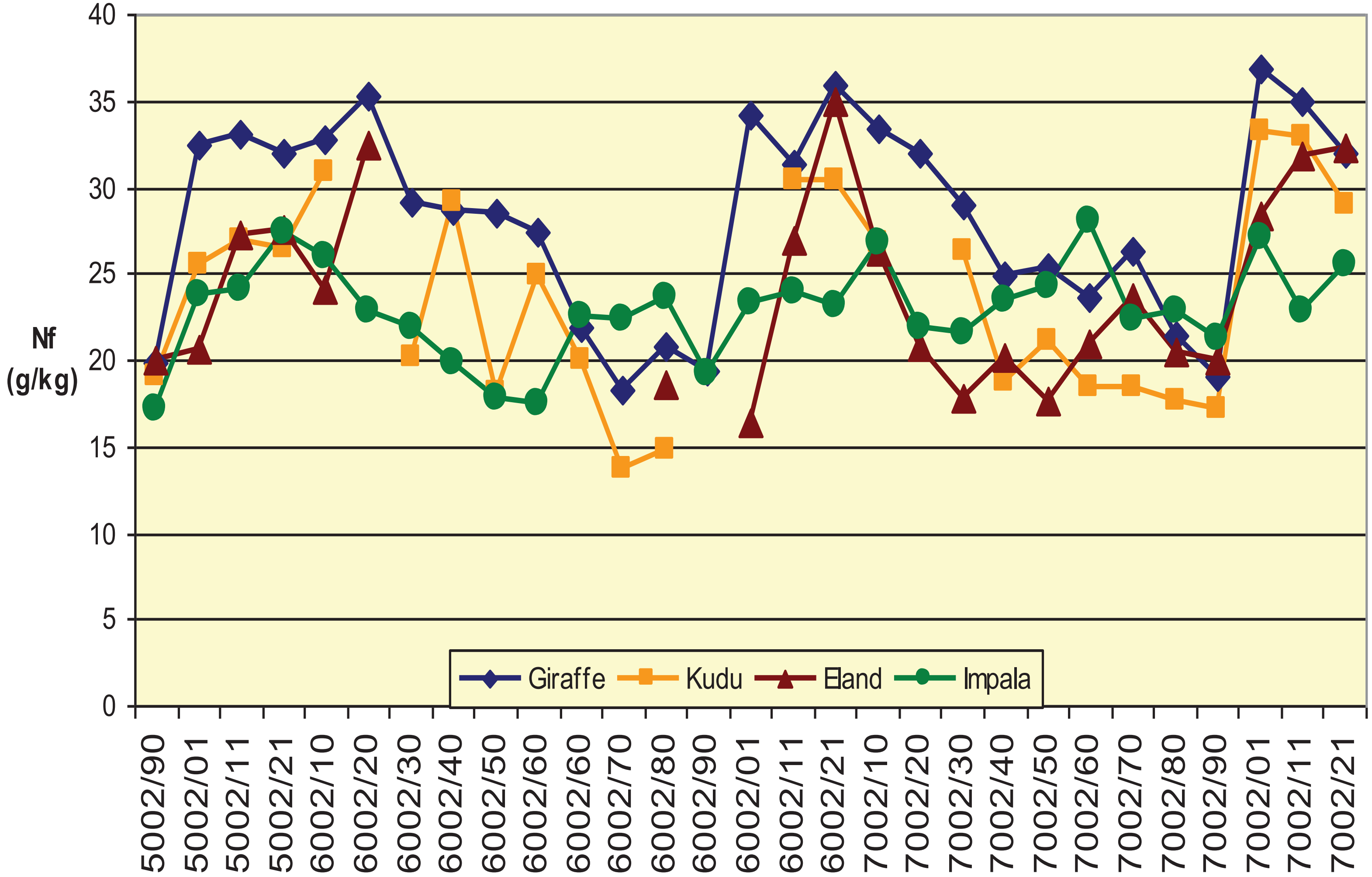


Figure 6.2 Faecal nitrogen concentrations from September 2005 to December 2007 of the four studied game species.

Table 6.1 Comparison of minimum Nf concentrations (g N/kg DM) recorded during winter in the study area, with critical levels where animals start to lose body condition, as reported in the literature.

Species	Minimum Nf (g/kg)	Critical levels (g/kg)	Source of critical levels
Giraffe	2006: **18.31** 2007: **19.02**	---	
Kudu	2006: **13.64** 2007: **17.23**	18.1	Grant *et al*. 1995, Van der Waal *et al*. 2003
Impala	2006: **16.86** 2007: **21.25**	16.6	Grant *et al*. 1995
Eland	2006: **16.30** 2007: **17.58**	---	
Browsers	---	15 - 16	Stoltz 1999 {Landbouweekblad:CC Grant}
Grazers	---	13 - 14	Wrench *et al.* 1997, Stoltz 1999
Cattle	---	10 - 12	Grant 1989, Woffard *et al*. 1985
Elk	---	± 16 (1.6 %N)	Gates and Hudson 1981

Table 6.2 Protein percentages (not necessarily critical values) as reported in the literature compared to values from this study. (Ranges from winter to summer are average values of corresponding seasons)

Species	% Protein (this study)	% Protein (literature)	Geographical region (literature)	Comment from literature	Source of protein percentage
Giraffe	Range: 11.4 - 22.9	12 - 22	Kenia	Range from winter to summer	Roosendaal 2008
Kudu	Range: 8.6 - 20.8	< 10	NW Limpopo	Mortalities in populations	Van Der Waal 2003
Impala	Range: 10.5 - 17.5	11	Hluhluwe-Umfolozi		Botha and Stock 2005
		± 10	Kruger NP	Dry season	Grant *et al.* 1995
		9.38	Timbavati		Pietersen *et al*. 1993
Eland	Range: 10.2 - 21.8	8 - 12	North-west Province	Fluctuated around means	Buys 1990
Browsers	---	14 - 16		Maintenance	Roosendaal 2008
		18		Lactation	Roosendaal 2008
Grazers	---	10		Crude protein deficiencies	Wofford *et al*. 1985
Grass	---	± 6 *		Necessary for microbial activity	Wrench *et al*. 1997

* 11 - 12 g N/kg DM

Table 6.3 Nitrogen and protein content of different phenophases of the woody species present in the study area as collected at the end of March and DGL at the end of May 2007. IL = Immature-, ML = Mature-, YL = Yellow-, DL = Dry-, DGL = Dry green leaves.

Species	Unit	IL	ML	YL	DL	DGL
Acacia karroo	g N/kg DM	23.25	22.17	---	19.83	25.72
	% protein	14.53	13.86	---	12.39	16.08
Asparagus laricinus	g N/kg DM	15.11	15.93	14.40	---	---
	% protein	9.45	9.95	9.00	---	---
Diospyros lycioides	g N/kg DM	20.37	19.62	18.27	14.96	17.08
	% protein	12.73	12.26	11.42	9.35	10.67
Lycium echinatum	g N/kg DM	67.81	52.33	23.95	---	---
	% protein	42.38	32.70	14.97	---	---
Lycium hirsutum	g N/kg DM	---	27.06	20.34	---	---
	% protein	---	16.91	12.71	---	---
Searsia pyroides	g N/kg DM	17.04	17.09	8.90	12.19	---
	% protein	10.65	10.68	5.56	7.62	---
Ziziphus mucronata	g N/kg DM	23.14	22.77	---	18.69	26.38
	% protein	14.46	14.23	11.68	---	16.49

6.4.1.1 GIRAFFE (*Giraffa camelopardalis*)

N_f values of giraffes followed an annual trend through the 2 years and 4 months study period (Figure 6.3). It increased in October, ranged from 30 to 35 g N/kg DM during summer, whereafter it decreased in autumn (March – May) to between 24 and 30 g/kg and in the winters it decreased further to between 18 and 23 g/kg. N_f concentration was slightly higher in the winter of 2007 than in 2006. Peaks in N_f concentration were observed during February 2006 and December 2006 and can be linked to higher rainfall that was experienced (Figure 3.6). The highest N_f concentration recorded was 36.8 g N/kg (23% protein) in October 2007 (Figure 6.3).

6.4.1.2 KUDU (*Tragelaphus strepsiceros*)

On occasion, due to their preference for the riverine vegetation, it proved difficult to locate the kudus to collect dung samples, hence some missing values in Figure 6.4. N_f concentrations averaged 16 g/kg in August, increased to 27 – 30 g/kg in December and fluctuated from March to June. A gradual increase in N_f concentration was observed from spring to summer of 2005, while it almost doubled from September to October 2007. Relatively little differentiation was found from April to September 2007, from 17 to 18 g/kg and 21.2 g/kg in May, respectively. The highest N_f concentration of kudu dung was 33.2 g N/kg (21% protein) in October 2007.

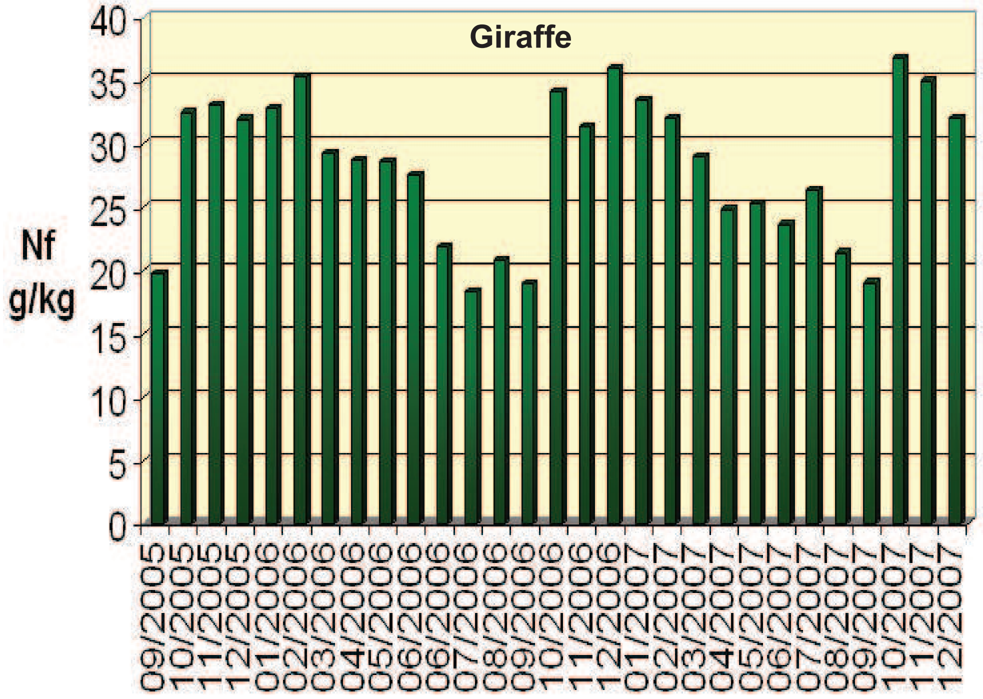


Figure 6.3 Faecal nitrogen concentrations of giraffe from September 2005 to December 2007. The first and last week of June 2006 are presented to indicate the differences in nitrogen concentrations when trees still have leaves and have shed most of their leaves after excessive growth.

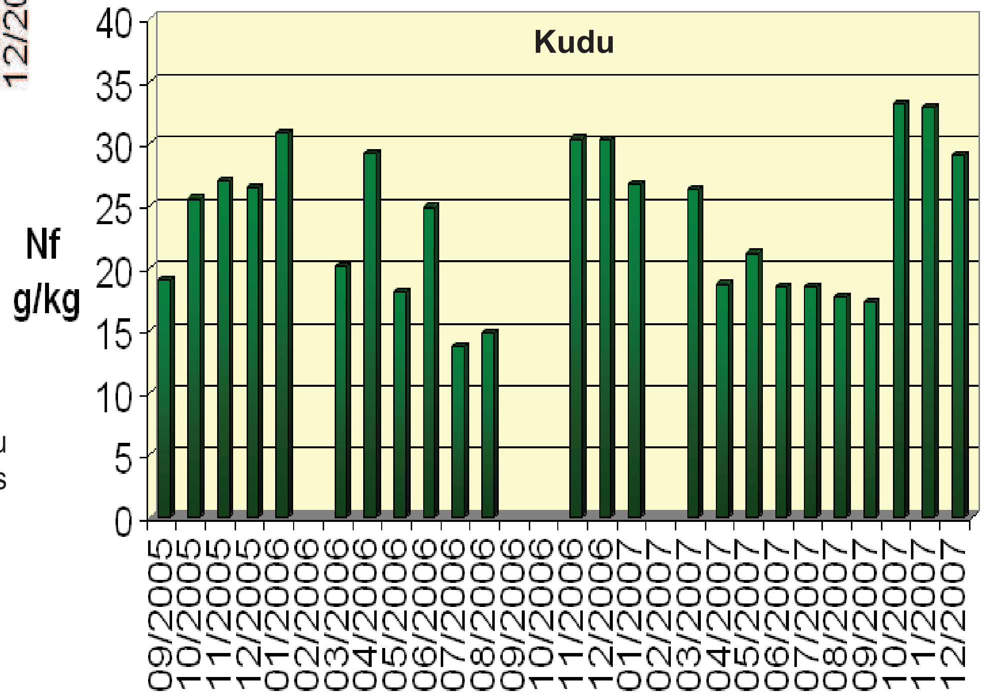


Figure 6.4 Faecal nitrogen concentrations of kudu from September 2005 to December 2007. No data is available in months when kudus could not be found.

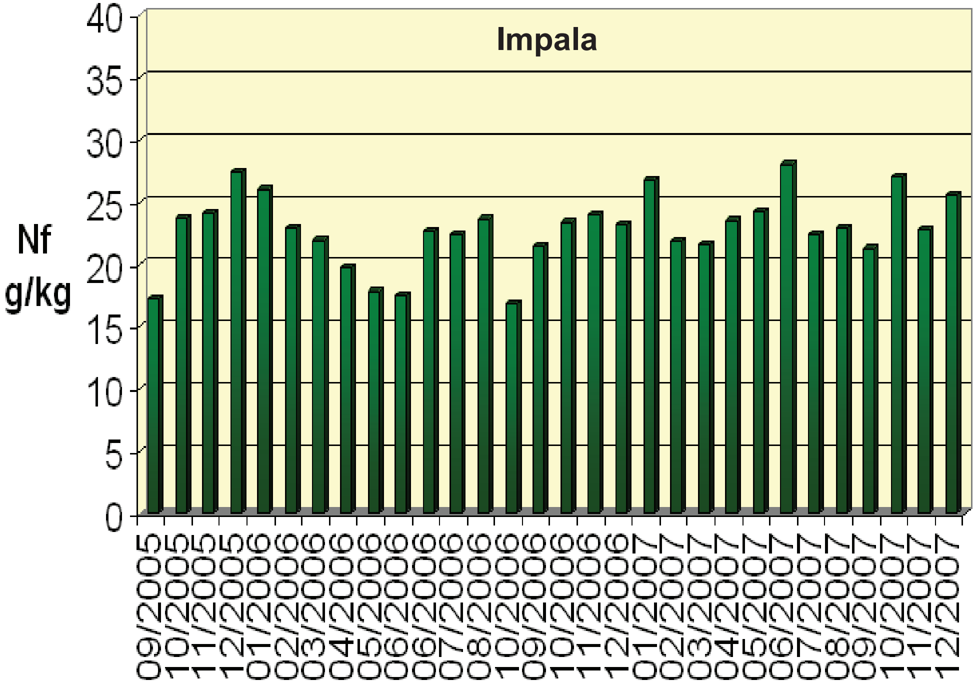


Figure 6.5 Faecal nitrogen concentrations of impala from September 2005 to December 2007. The first and last week of June 2006 are presented to indicate the differences in nitrogen concentrations when trees still have leaves and have shed most of their leaves after excessive growth.

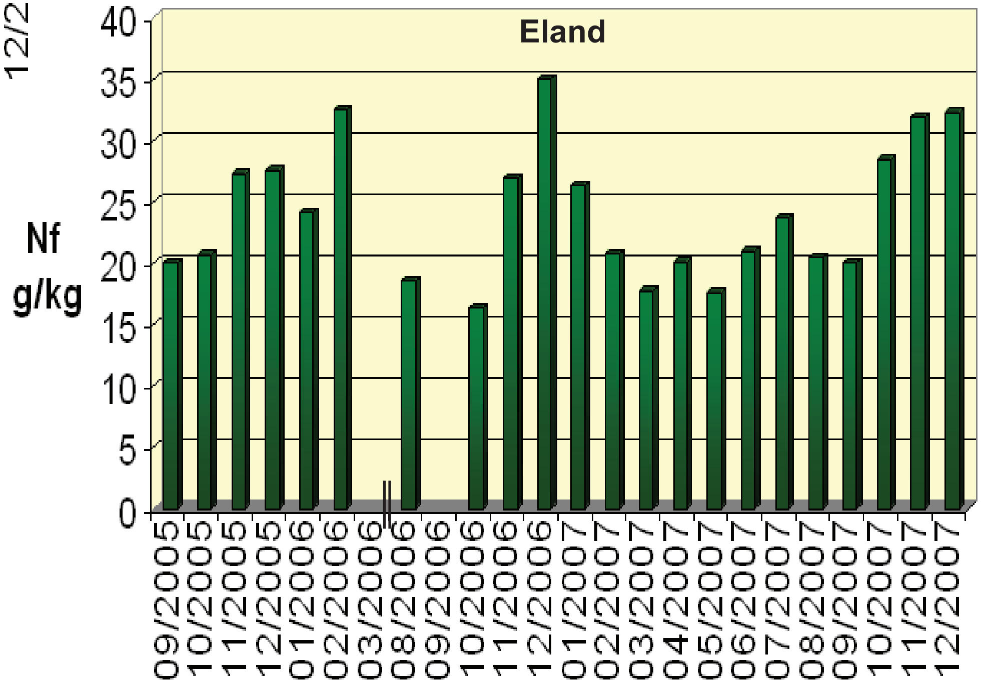


Figure 6.6 Faecal nitrogen concentrations of eland from September 2005 to December 2007. No data is available from March to July, or for September.

6.4.1.3 IMPALA (*Aepyceros melampus*)

N_f concentration of impala did not show a specific seasonal trend over the study period (Figure 6.5). N_f concentrations varied from a low of 17 g/kg in September to a high of 23 – 27 g/kg in December. From June to August 2006, N_f concentration increased from 17 to 23 g/kg and lowered again to 17 g/kg in September 2006. From October 2006 to November 2007 the concentrations fluctuated between 22 and 24 g N/kg, except during January, June and October 2007 when it averaged 27 g/kg. The highest N_f concentrations were 27.9 g/kg (17.5% protein) recorded during June 2007, and 27.1 g/kg during October 2007.

6.4.1.4 ELAND (*Tragelaphus oryx*)

Unfortunately the eland had been relocated in March 2006 and the study could only resume again in August 2006. A seasonal trend was distinguished in the form of higher N_f concentrations observed during the summer, that decreased during winter and increased again during late spring. N_f concentration was 20 g/kg during September (Figure 6.6) and fluctuated around 30 g/kg in December, thereafter it decreased to between 17 and 21 g/kg during autumn and winter. In December 2006, the highest N_f concentration of 34.9 g/kg (21.8% protein) was recorded.

6.4.2 Faecal nitrogen between different years, seasons and habitats

N_f values of giraffe and impala, separately yielded no significant differences ($p > 0.05$) between different years (Table 6.4), but significant differences ($p < 0.001$) between seasons (similar seasons grouped together) were evident. For giraffe ($p < 0.001$) there were differences between summer and all other seasons as well as between winter and autumn. For kudu ($p = 0.061$) there were differences mostly between winter and summer (some data missing), while spring1 x summer2 had a probability of 0.054 and winter2 x summer1 had a $p = 0.052$ which was treated as not significant. There were no significant differences ($p > 0.05$) between the year-by-season interaction and N_f values of either of these species. Too much data of kudu is missing in spring and of eland in autumn, thus the year-by-season interactions are not complete and therefore not presented. Monthly averages between browsers and mixed feeders are illustrated in Figures 6.7 & 6.8, along with leaf phenology values.

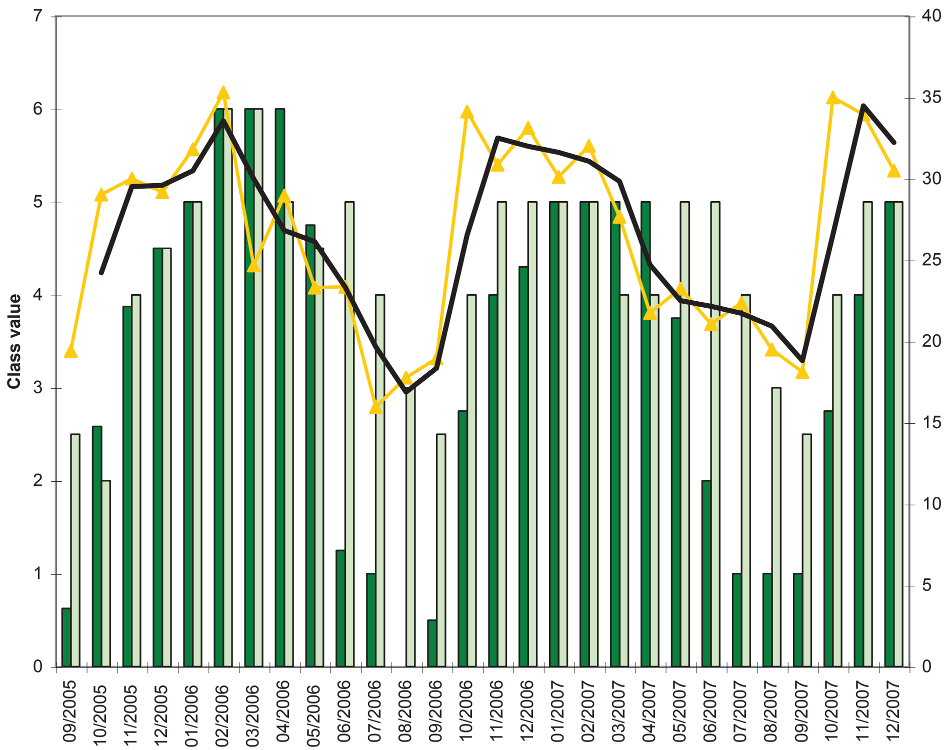


Figure 6.7 Average Nf values of giraffe and kudu are indicated on a monthly basis, along with phenology totals of trees and shrubs.

Legend for phenology class values:

0 = no leaves;
1 = 1 – 15%;
2 = 16 – 40%;
3 = 41 – 70%;
4 = 71 – 90%
5 = 90 – 100%
6 = 101 – 120%
of full leaf carriage

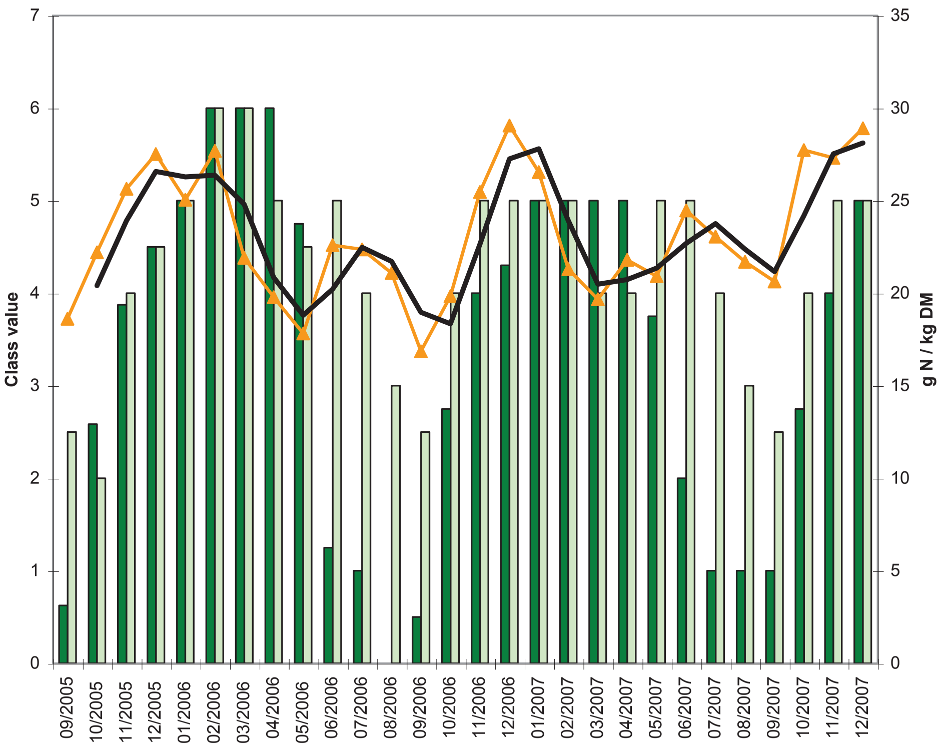


Figure 6.8 Average Nf values of impala and eland are indicated on a monthly basis, along with phenology totals of trees and shrubs.

Table 6.4 Results of the Factorial ANOVA for an unbalanced dataset (5% level) in testing for differences in faecal nitrogen of giraffe and impala (g N/kg DM) between years, seasons (similar seasons grouped together), as well as the year-by-season interaction. Least Significant Differences (LSD) are not applicable where no significant differences were found. Means followed by the same letter did not differ significantly.

Year: Giraffe	**Mean (SEM)**		**Year: Impala**	**Mean (SEM)**
1: 09/2005 – 08/2006(n=12)	27.72 (1.13)		1: 09/2005 – 08/2006(n=12)	22.46 (0.72)
2: 09/2006 – 08/2007(n=12)	28.02 (1.13)		2: 09/2006 – 08/2007(n=12)	23.23 (0.72)
Summary statistics			**Summary statistics**	
Probability (p)	0.853		p	0.463
L.S.D	n.a.		L.S.D	n.a.
Season: Giraffe	**Mean (SEM)**		**Season: Impala**	**Mean (SEM)**
Winter (n = 6)	22.04 a (1.59)		Spring (n = 4)	20.31 a (1.25)
Spring (n = 4)	26.33ab (1.95)		Autumn (n = 6)	21.48 ab (1.02)
Autumn (n = 6)	27.60 b (1.59)		Winter (n = 6)	23.65 bc (1.02)
Summer (n = 8)	33.23 c (1.38)		Summer (n = 8)	24.53 c (0.88)
Summary statistics			**Summary statistics**	
p	<0.001		p	0.043
Average L.S.D.	4.909		Average L.S.D.	4.436
Year x season	**Mean (SEM)**		**Year x season**	**Mean (SEM)**
Winter x Year 1 (n = 3)	20.31 (2.25)		Spring x Year 1 (n = 2)	20.52 (1.76)
Winter x Year 2 (n = 3)	23.77 (2.25)		Spring x Year 2 (n = 2)	20.12 (1.76)
Spring x Year 1 (n = 2)	26.13 (2.76)		Autumn x Year 1 (n = 3)	19.84 (1.44)
Spring x Year 2 (n = 2)	26.54 (2.76)		Autumn x Year 2 (n =3)	23.11 (1.44)
Autumn x Year 1 (n = 3)	28.81 (2.25)		Winter x Year 1 (n = 3)	22.86 (1.44)
Autumn x Year 2 (n = 3)	26.38 (2.25)		Winter x Year 2 (n = 3)	24.44 (1.44)
Summer x Year 1 (n = 4)	33.27 (1.95)		Summer x Year 1 (n = 4)	20.11 (1.25)
Summer x Year 2 (n = 4)	33.19 (1.95)		Summer x Year 2 (n = 4)	23.96 (1.25)
Summary statistics			**Summary statistics**	
p (Interaction)	0.637		p (Interaction)	0.409
L.S.D.	n.a		L.S.D.	n.a.
Coefficient of variance (CV)	14.00%		CV	10.92%

There were no significant differences ($p > 0.05$) in N_f values of kudu or eland between different years (Table 6.5). Significant differences ($p < 0.1$) were found in N_f values of these two species between the seasons of different years (Table 6.6). For eland, there were significant differences ($p = 0.015$) between summer, spring and autumn (some winter data is missing) and for impala there were differences ($p = 0.043$) between summer and autumn, summer and spring, winter and spring. Higher seasonal variation was present in kudu N_f values when year 3 was included, thus a 10% significance level was used for the kudu. Significant seasonal differences were also found ($p = 0.029$, average LSD = 7.48, CV = 17.92%) when a 5% significance level was used on the kudu data excluding the last four months of 2007 (year 3).

Table 6.5 Results of ANOVA for an unbalanced dataset (5% level) in testing for differences in N_f values of kudu and eland (g N/kg DM) between different years.

Year: Kudu	**Mean (SEM)**		**Year: Eland**	**Mean (SEM)**
1: 09/2005 – 08/2006 (n=12)	22.69 (1.78)		1: 09/2005 – 08/2006 (n=12)	24.37 (2.01)
2: 09/2006 – 08/2007(n=12)	23.14 (1.97)		2: 09/2006 – 08/2007 (n=12)	22.34 (1.61)
3: 09/2007 – 12/2007 (n=4)	28.10 (2.96)		3: 09/2007 – 12/2007 (n=4)	28.13 (2.66)
Summary statistics			**Summary statistics**	
p	0.291		p	0.199
CV	22.15%		CV	24.87%

Table 6.6 Results of ANOVA for an unbalanced dataset in testing for differences in N_f values (g N/kg DM) of kudu (10% level) and eland (5% level) between seasons of three years. Means followed by the same letter did not differ significantly.

Season: Kudu	**Mean (SEM)**		**Season: Eland**	**Mean (SEM)**
Winter 1 (n = 3)	17.76 a (2.81)		Autumn 2 (n = 3)	18.48 a (2.17)
Winter 2 (n = 3)	18.19 a (2.81)		Spring 1 (n = 2)	20.32 ab (2.66)
Autumn 2 (n = 3)	22.06 ab (2.81)		Winter 2 (n = 3)	21.70 ab (2.17)
Spring 1 (n = 2)	22.32 abc (3.44)		Spring 3 (n = 2)	24.21 abc (2.66)
Autumn 1 (n = 3)	22.48 abc (2.81)		Summer 2 (n = 4)	27.22 bc (1.88)
Spring 3 (n = 2)	25.22abcd (3.44)		Summer 1 (n = 4)	27.84 c (1.88)
Summer 1 (n = 3)	28.08 bcd (2.81)		Summer 3 (n = 2)	32.06 c (2.66)
Summer 2 (n = 3)	29.16 cd (2.81)			
Summer 3 (n =2)	30.99 d (3.44)			

Continued on next page...

Table 6.6 Continued

Summary statistics		Summary statistics	
p	0.061	p	0.015
Average L.S.D. (10%)	9.11	Average L.S.D. (5%)	7.07
CV	20.45%	CV	15.23%

Significant differences ($p < 0.05$) were found between the N_f values of giraffe dung collected in different vegetation units / habitats (Table 6.7). Differences in N_f values of giraffe were present between the disturbed area, open thicket and dense, riparian thicket. No significance ($p > 0.05$) was found between vegetation units for the other three species' N_f values (Table 6.7).

Table 6.7 Results of ANOVA for an unbalanced design (5% level) in testing for differences between N_f values of the species' dung (g N/kg DM) collected in different vegetation units. Means followed by the same letter did not differ significantly.

Giraffe habitat	**Mean (SEM)**
Disturbed area (n = 10)	21.48 a (0.8)
Open thicket (n = 4)	29.08 b (1.3)
Dense thicket(n = 8)	32.44 c (0.9)
Big drainage line (n= 6)	33.51 c (1.1)
Summary statistics	
p	<0.001
Average L.S.D	4.157
CV	9.33%

Kudu habitat	**Mean (SEM)**
Disturbed area (n = 5)	22.91 (2.79)
Dense thicket (n = 7)	23.58 (2.36)
Big drainage line (n = 12)	24.22 (1.80)
Summary statistics	
p	0.923
L.S.D	n.a.
CV	26.28%

Eland habitat	**Mean (SEM)**
Big drainage line (n = 8)	21.69 (1.97)
Dense thicket (n = 4)	24.49 (2.79)
Open thicket (n = 5)	25.07 (2.49)
Disturbed area (5)	26.40 (2.49)
Summary statistics	
p	0.491
L.S.D	n.a.
CV	23.20%

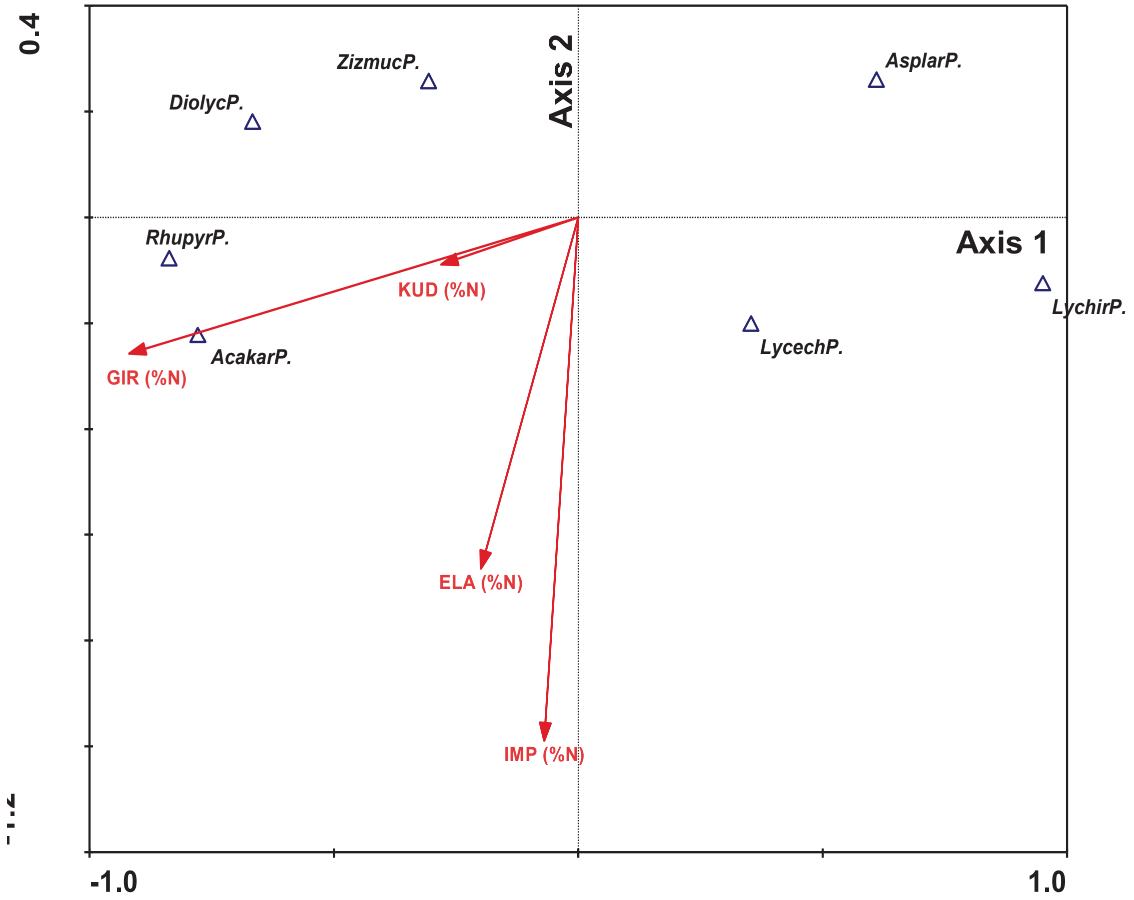
Impala habitat	**Mean (SEM)**
Dense thicket (n = 12)	21.92 (0.79)
Big drainage line (n = 5)	23.73 (1.22)
Disturbed area (n = 11)	23.93 (0.82)
Summary statistics	
p	0.196
L.S.D	n.a.
CV	11.86%

Protein percentages of giraffe and of kudu, respectively (Table 6.8), had a fairly strong correlation with leaf carriage percentages of *Acacia karroo* (r = 0.7), moderate with *Diospyros lycioides* and *Searsia pyroides* (r = 0.6), with a low r-value of 0.3 to 0.5 for the leaf carriage percentages of the other woody species. A moderate correlation was found between eland protein percentages and leaf carriage percentages of *A. karroo* (r = 0.5), *Lycium hirsutum* (r = 0.6) and *L. echinatum* (r = 0.5); and also between impala protein percentages and leaf carriage percentages of *L. echinatum* (r = 0.6). *Lycium hirsutum* had a moderate correlation (r = 0.5) with Nf of three game species, excluding impala. Impala protein percentages had an overall low correlation (r = 0.3) with leaf phenology of the woody species. Figures 6.7 & 6.8 give a visual explanation of why above-mentioned low correlation values between N_f values and leaf phenology of the woody plants were found.

Table 6.8 Results of correlation analyses between leaf carriage percentages of the plant species (independent variables) and protein percentages in dung of game species (dependent variables).

	Acacia karroo	***Diospyros lycioides***	***Searsia pyroides***	***Ziziphus mucronata***	***Asparagus laricinus***	***Lycium echinatum***	***Lycium hirsutum***
Giraffe							
r	0.730	0.624	0.561	0.393	0.361	0.517	0.478
p	<0.001	<0.001	<0.001	0.008	0.015	<0.001	<0.001
Kudu							
r	0.726	0.635	0.553	0.370	0.327	0.457	0.550
p	<0.001	<0.001	<0.001	0.012	0.028	0.002	<0.001
Eland							
r	0.513	0.377	0.360	0.262	0.305	0.451	0.603
p	<0.001	0.011	0.015	0.074	0.040	0.002	<0.001
Impala							
r	0.373	0.227	0.326	0.300	0.248	0.567	0.386
p	0.012	0.115	0.028	0.043	0.089	<0.001	0.009

CCA-ordination (*vid.* page 53) results of faecal protein and leaf carriage percentages (Figure 6.9) also yielded weak or no associations. The influence of certain parameters on species data was tested, rather than gradients and therefore gradient lengths of axes are short. The shrubs were grouped on the right side of the graph on Axis 1 and the trees on the left side. Giraffe's faecal protein had a strong association only with *A. karroo*, supporting the correlation data. Kudu had a stronger opposite association than giraffe with *Acacia karroo* and *Asparagus laricinus*. This is probably because browsers rely on the semi-deciduous *A. laricinus* when the deciduous *A. karroo* is leafless. The faecal protein of the browsers is stronger correlated with trees than with shrubs, while no such correlation is evident for the mixed feeders. These tree species are the browsers' favourite, preferred food, rather than *Lycium* species. Mixed feeders are more selective in preferred food sources and will also include grass. Faecal protein of giraffe and kudu (browsers) were weakly associated, as well as faecal protein of eland and impala. Faecal protein of the browsers is strongly associated with Axis 1 and that of the mixed feeders is strongly associated with Axis 2.



	Axis 1	Axis 2	Axis 3	Axis 4
Eigen-values	0.033	0.003	0.002	0.0
Sp-environment correlation	0.652	0.491	0.306	0.209
Cumulative % variance:				
of species data	27.4	29.7	31.2	31.4
of species-climate relation	87.2	94.7	99.4	100

Figure 6.9 Canonical correspondence analysis (CCA) of the monthly percentage faecal protein, related to nitrogen (N), of giraffe, kudu, eland and impala superimposed on the monthly leaf carriage percentages or phenology (P) of the woody plant species. Legend: Acakar = *Acacia karroo*; Asplar = *Asparagus laricinus*; Diolyc = *Diospyros lycioides*; Lycech = *Lycium echinatum*; Lychir = *L. hirsutum*; Rhupyr = *Searsia pyroides*; Zizmuc = *Ziziphus mucronata.* Monte Carlo permutation test of significance of first canonical axis indicated an Eigenvalue of 0.033 (F-ratio 8.669, P-value 0.014) and of all canonical axes had a Trace of 0.038 (F-ratio 2.631, P-value 0.014).

Forward selection stepwise linear regression analysis (FSSR) of protein in giraffe dung was applied to the following data sets: phenology of plant species (total % leaf carriage); browse production at feeding heights of 1.5 m, 2 m, 5 m for each plant species and for sum totals of each feeding height (kg leaf dry mass/ha x monthly phenology totals); feed supplied at different heights (1 m, 2.5 m) in the form of lucern or game pellets (kg/month); and total browser units sustainable per month.

The best correlated term included in the giraffe %protein model (Table 6.9) was:
Ig) *A. karroo* phenology sum totals per month (*vid*. Chapter 5); then added were
IIg) *S. pyroides* leaf dry mass (DM) of trees less than 5m tall (BECVOL model, *vid*. Chapter 8) multiplied by the species' monthly phenology total;
IIIg) *L. echinatum* leaf DM of shrubs less than 5m tall multiplied by monthly phenology totals; and
IVg) *Z. mucronata* phenology sum totals per month.

FSSR analysis of percentage protein in kudu dung (Table 6.10) was done on the same above-mentioned data sets as used for giraffe. The best correlated term included in this model was:
Ik) *A. karroo* leaf DM on trees < 5m tall multiplied by monthly phenology totals; then added were
IIk) *S. pyroides* phenology totals per month;
IIIk) Median monthly phenology values of the three shrubs (*vid*. Chapter 5); and
IVk) Median monthly phenology values of the four trees.

FSSR analysis of percentage protein in eland dung (Table 6.11) was applied to the same data sets as for giraffe, but also including total grazer units present per month in the study area; and total grass production per month (kg DM / ha). The best correlated term included in the model was:
Ie) Total browser units present per month; then added were
IIe) *L. hirsutum* leaf DM of shrubs < 5m tall multiplied by monthly phenology totals;
IIIe) Total grass production;
IVe) Median monthly phenology values of the three shrubs;
Ve) *D. lycioides* leaf DM of trees < 5m tall multiplied by monthly phenology totals; and
VI e) *Z. mucronata* leaf DM of trees less than 5m tall multiplied by monthly phenology totals.

FSSR analysis of percentage protein in impala dung was also done on the same data sets as for giraffe, but including total grazer units present per month in the study area; and total grass production per month (kg DM / ha). The only fitted term was total browser units present in the study area (Table 6.12). Since impala is a mixed feeder, this term alone cannot be used to accurately predict protein content in impala dung.

Table 6.9 Summary of results of forward selection stepwise linear regression analysis (FSSR) of protein (%) in giraffe dung applied to phenology, browse production, feed supplied and browser unit totals. Ig) *A. karroo* phenology per month; IIg) *S. pyroides* browse production; IIIg) *L. echinatum* browse production; IVg) *Z. mucronata* phenology per month; R^2_a = adjusted R-square value, SER = standard error of regression; P = probability of final model at each step.

Giraffe N_f	**Ig**	**IIg**	**IIIg**	**IVg**
R^2_a	53.0	64.4	66.0	68.1
P	<0.001	<0.001	<0.001	<0.001
SER	2.46	2.15	2.10	2.03
Model	$Y = 13.421 + 0.070X_1$	$Y = 12.481 + 0.165X_1 - 0.0057X_2$	$Y = 11.060 + 0.166X_1 - 0.0066X_2 + 0.0408X_3$	$Y = 10.77 + 0.158X_1 - 0.0047X_2 + 0.064X_3 - 0.038X_4$

Table 6.10 Summary of results of FSSR analysis of protein (%) in kudu dung applied to phenology, browse production, feed supplied and browser unit totals. Ik) *A. karroo* browse production; IIk) *S. pyroides* phenology per month; IIIk) Median monthly phenology values of the three shrubs; and IVk) Median monthly phenology values of the four trees.

Kudu N_f	**Ik**	**IIk**	**IIIk**	**IVk**
R^2_a	38.2	48.8	53.9	58.6
P	<0.001	<0.001	<0.001	<0.001
SER	2.94	2.68	2.54	2.41
Model	$Y = 10.94 + 0.00034X_1$	$Y = 10.02 + 0.00087X_1 - 0.099X_2$	$Y = 5.38 + 0.0009X_1 - 0.141X_2 + 0.076X_3$	$Y = 1.66 + 0.0017X_1 - 0.156X_2 + 0.131X_3 - 0.140X_4$

Table 6.11 FSSR analysis of protein (%) in eland dung applied to phenology, browse production, feed supplied, browser unit totals, grazer unit totals and total grass production per month. Ie) Browser unit totals; IIe) *L. hirsutum* browse production; IIIe) Total grass production; IVe) Median monthly phenology values of the three shrubs; Ve) *D. lycioides* browse production; and VI e) *Z. mucronata* browse production.

Eland N_f	**Ie**	**IIe**	**IIIe**	**IVe**	**Ve**	**VI e**
R^2_a	37.2	51.3	63.1	69.0	74.0	78.8
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
SER	2.73	2.40	2.09	1.92	1.76	1.59
Model	$Y = 8.18 +$ $0.084X_1$	$Y = 3.65$ $+ 0.065X_1$ $+ 0.140X_2$	$Y = 7.92$ $+ 0.050X_1$ $+ 0.134X_2$ $- 0.0006X_3$	$Y = 8.48$ $+ 0.034X_1$ $+ 0.097X_2$ $- 0.0008X_3$ $+ 0.043X_4$	$Y = 6.00$ $+ 0.057X_1$ $+ 0.103X_2$ $- 0.0008X_3$ $+ 0.080X_4$ $- 0.004X_5$	$Y = 10.12$ $+ 0.046X_1$ $+ 0.061X_2$ $- 0.0012X_3$ $+ 0.074X_4$ $- 0.006X_5$ $+ 0.002X_6$

Table 6.12 FSSR analysis of protein (%) in impala dung applied to phenology, browse production, feed supplied, browser unit totals, grazer unit totals and total grass production per month. Ii) Browser unit total.

Impala Protein %	**Ii**
R^2_a	12.9
P	0.034
SER	1.62

6.5 DISCUSSION

6.5.1 Seasonal variation in faecal nitrogen

A seasonal pattern in nitrogen concentration in the dung of all four studied game species was observed (Figure 6.2), with the highest values mostly recorded from November to February (hot-wet season, summer) and the lowest values from June to September (cool-dry season, winter). From the literature it is clear that a similar pattern (increasing N_f values in summer and decreasing in winter) is evident even when animals occur in different vegetation biomes. Grant *et al.* (1995) also recorded the lowest N_f concentrations from July to September (dry season) in the Kruger National Park, while January to March (wet season) had the highest N_f concentrations. Zimmerman (1980), Kok and Opperman (1985) as well as Owen-Smith (1994) found a decrease in crude protein**,** which included nitrogen values and digestibility values, from the wet to the dry seasons. Erasmus *et al.* (1978) reported that N_f was higher in summer than in winter in the Mountain Zebra National Park.

It is noteworthy that a lower N_f concentration was also reported in the Kruger- and the Mountain Zebra National Parks during winter, even though evergreen woody species should be available for game to browse when deciduous species were leafless, which was not the case in the current study area. Evergreen species are usually not easily digestible due to higher tannin content (Coley 1988, Owen-Smith 1993) and higher intake of these species should elevate N_f concentration. It is possible that animals making use of evergreen species may have to search for it due to patchy distribution thereof and thus selected other available browse like shoots of deciduous trees and semi-evergreen palatable shrubs instead. Wilson and Kerley (2003) and Van der Waal (2005) indicated the use of leafless shoots by browsers. The selection of leafless shoots and shrubs that retain some leaves could explain the decrease in N_f values in winter, as was found in this study, due to a reduced intake of leaves with high phenolic compounds. It would, however, increase competition for these resources due to much less readily available browse for the same number of animals. According to Melton (1987), when food availability increased animals fed more selectively to optimise nutritional quality intake, but as food availability decreased animal selectivity of food decreased.

No significant differences ($p > 0.05$) were found in N_f values of the four game species between the different years of study (Tables 6.4 & 6.5). There were significant differences between N_f of different seasons. N_f of all four species in summer mostly differed from that of the other seasons (Tables 6.4 & 6.6). Trees have full leaf carriage in summer, so animals have the best browsing available compared to the other seasons when browse quality declines, as was reflected in N_f.

During 2007 the seasonal N_f pattern of impala was obscured when N_f concentrations mostly fluctuated around 23 g N/kg DM (Figure 6.5) without increasing or decreasing much through the seasons. Their numbers were reduced to about a quarter of the total (from 45 to ~10) and the small herd probably concentrated on an area where they could maintain the same diet quality throughout the year. Seasonal movement of impala northwards during the years that they were observed, are illustrated in Figures 6.10 & 7.13. During 2007 they seemed to concentrate more in the dense thicket almost in the centre of the study area (Figure 6.10). If their numbers increase again it may force them to search wider for nutritious food items, like in previous years, which may become depleted by their higher numbers – this should result in a characteristic seasonal pattern again for the 2008/2009 season.

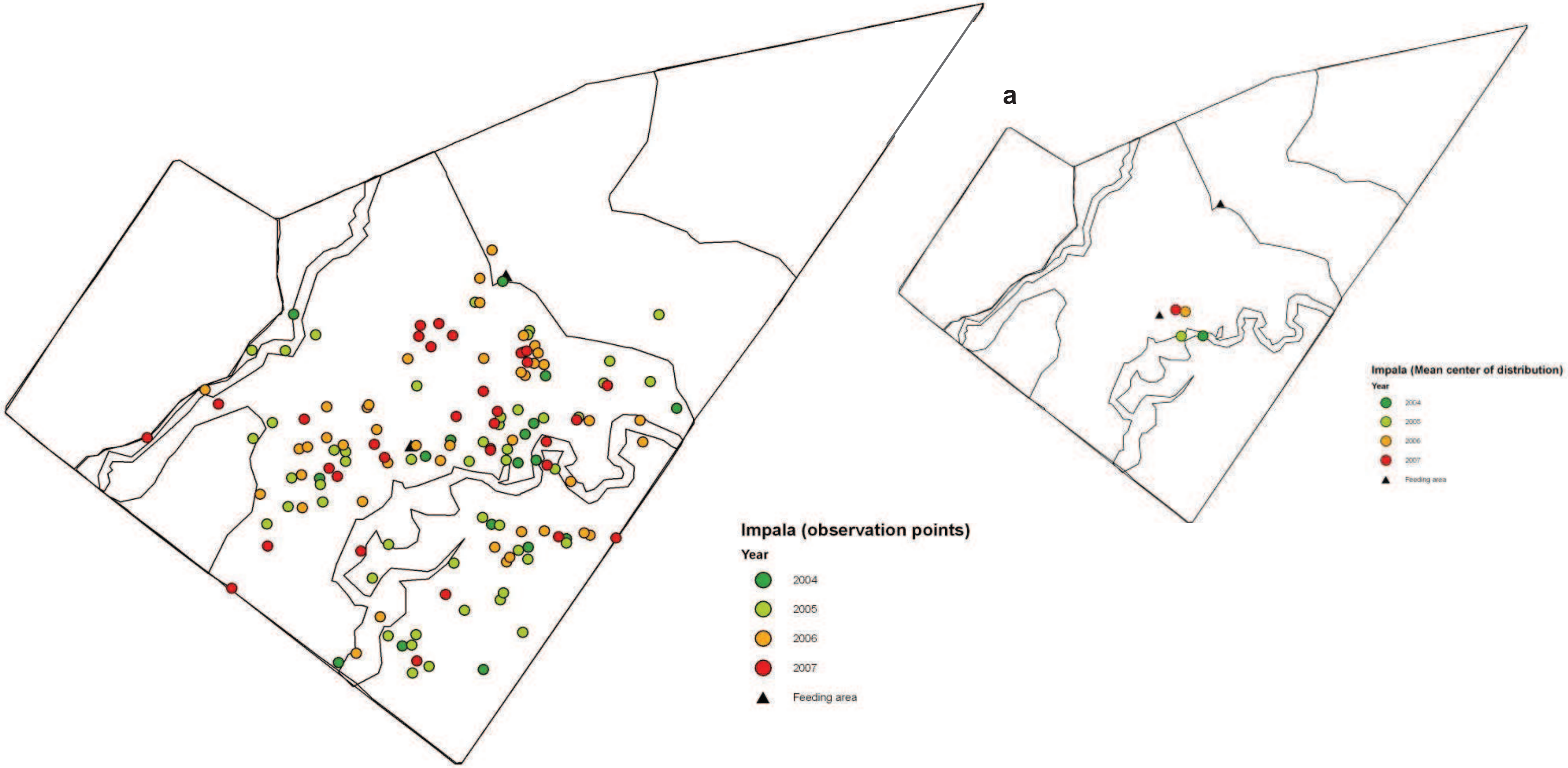


Figure 6.10 Global positioning system (GPS) locations where impalas were observed during the different years of study. Inset a) Mean centre of distribution if an oval or circle was drawn over the distribution points of each year.

Due to incomplete data for certain months when kudus were difficult to find, an accurate seasonal N_f pattern for this species during 2005/2006 was not possible (Figure 6.4). Other researchers seemed to have a similar problem in locating kudus or dung. Grant *et al.* (1995) mentioned the difficulty in collecting large numbers of faecal samples of browsers and Du Toit (1995b) indicated the difficulty of locating kudus in the dense riverine habitats. However, N_f concentrations of kudu in this study did follow a clear seasonal pattern in 2006/2007 (Figure 6.4): it peaked in October and November 2006, decreased sharply in April 2007 and continued to decrease until September whereafter it increased again in October 2007. Van der Waal *et al.* (2003) found that in the north-western part of the Limpopo Province the N_f of kudu also followed a distinctive seasonal pattern. It decreased from the cool-dry season (May and June) towards the dry-hot season (August and October), reaching a low during the dry-hot season and peaked in November and decreased slightly to concentrations higher than in the cool-dry season. This dry season pattern resembles that of kudu N_f in the Lowveld (Grant *et al.* 2000), which in turn corresponds with the calculated dietary nitrogen of kudu at the Nylsvley Nature Reserve as well (Owen-Smith and Cooper 1989). These seasonal N_f patterns from the savanna biome correspond to the pattern from this study, with the exception that the N_f peak was reached in October and decreased sharply in April in this study probably because of differences in the climate and leaf phenology of woody plants.

6.5.2 Faecal nitrogen of Giraffe

Minimum N_f concentrations for giraffes during the dry season were in close range if the two years of study are compared (Figure 6.3), namely 18.3 and 19 g N/kg DM, respectively (Table 6.1). Grant *et al.* (1995) recorded a N_f value of 20.3 g/kg for giraffe in Kruger National Park during the severe drought of 1992 – 1993, which was still higher than minimum values from this study under normal conditions. According to Dr CC Grant as quoted by Stoltz (1999), if the faecal protein level for browsers at the beginning of winter is at 9% (± 15 g/kg) supplementary feeding should be considered, while if the level is at 9% at the end of winter, it is still acceptable. The minimum N_f concentrations of giraffe in the study area (Table 6.1) were higher than this 15 g/kg critical N_f level and just above the critical level established for kudu (18 g/kg), which is also a specialist browser. During April and May of 2006 and 2008 some of the giraffe cows had small calves, which may still have been suckling. At that time their faecal protein was at 17 – 18% indicating that their nutritional status should have been sufficient for lactation (Table 6.2). No mortalities of young or adult giraffe were recorded during the study period, except for one juvenile that died due to infection after serious injury.

According to Grant *et al.* (1995), giraffe should only rarely experience a limitation in food availability and should not experience a limitation in food quality, because of essentially no browsing competition. However, Grant *et al.* (2000) concluded that giraffe underwent metabolic stress towards the end of the cool dry season. According to Theron (2006), the critical period of giraffe in the central Free State, when browse in any form is too scarce to sustain them, is towards the end of the dry season (August – October) and not the dry season as a whole. Kok and Opperman (1980) concluded that giraffes in the Willem Pretorius Game Park were subjected to suboptimal habitat conditions, because i) they were using a very high percentage of available browse plants; ii) they made regular use of forbs and grasses; and iii) they displayed osteophagial behaviour and licking of brackish soils. Kok and Opperman (1980) as well as Theron (2006) concluded that if giraffes showed osteophagia (chewing on bones) they likely had a mineral deficiency in their diet and probably had a high requirement for calcium and phosphate (Frandsen 1998, Skinner and Chimimba 2005). Results of Kok and Opperman (1980) indicated that two thirds of this osteophagia behavioral pattern occurred from May to September and was an indication of food scarcity during the critical period. Osteophagia was only once observed for giraffes in the study area, which should be a good sign in terms of deficiencies in their diet that included the supplied feed and salt licks.

The average range of percentage faecal protein for giraffe between the two and a half seasons in the study was almost similar to that of giraffes from Kenia (Table 6.2). This is noteworthy since feed was supplied to all animals in the study area in the form of 20 bags of lucerne pellets and 20 bales of lucerne hay (*Medicago sativa*) twice daily from around May to September annually (*vid.* Chapter 8). Giraffe in the study area made use of this supplied feed, which should have resulted in differences between the N_f concentration of the studied animals and those in Kenia.

Dörgeloh *et al.* (1998), as well as Van der Waal (2003) found that feed, in the form of lucerne hay and game cubes, significantly increased N_f concentrations. According to Robbins *et al.* (1987), protein availability was not significantly different from that of grasses and legumes for pelleted, concentrate-containing diets that were partly based on grasses, lucerne or other nitrogen-containing fiber. Results of Hatt *et al.* (2005) indicated that giraffes were unlikely to meet energy requirements on lucerne hay-only diets. They reported that: "in a feeding scenario where both lucerne hay and the concentrate component of the diet are fed *ad libitum*, the animals tended to exchange hay for browse when browse was added. Only the higher levels of browse supplementation led to a potentially beneficial increase in fibre intake". Thus, giraffes in the study area most probably supplemented their diet with other sources of browse and did not rely solely on the supplied feed.

Only shoots of deciduous woody species, leaf litter, fallen fruits and pods, small semi-evergreen shrubs (*vid* Chapter 5), three evergreen *Searsia lancea* trees, forbs and some dwarf karroid shrubs (Figure 8.17) are available to browse in the study area during the dry season. Theron (2006) reported that exotic plant species such as *Pinus* sp. (pine tree), *Eucalyptus* sp. (gum tree, "bloekom") and *Opuntia ficus-indica* (prickly pear) were seasonally utilised by giraffe in the central Free State. These plant species were also present in small numbers in the study area. Selection of other sources of browse and the elevated N_f levels associated with lucerne could explain similarities between faecal protein of the studied giraffes and those from Kenia.

6.5.3 Faecal nitrogen of Kudu

A very strong correlation ($r = 0.932$, $p < 0.001$) was found between N_f values of giraffe and kudu, both being browser species and their seasonal N_f patterns being largely similar (Figures 6.3 & 6.4). Minimum protein percentages of these two species in the winter are below levels normally required for maintenance of browsers (Table 6.2). The minimum N_f concentrations of kudu during both years of study were lower than the critical level established for kudu in the literature (Table 6.1). For approximately two to three months of the year, July to August/September, kudus appeared to be in poor physical condition (Figure 6.11), when they excreted nitrogen at concentrations (13 – 16 g N/kg DM – Figure 6.4) that are lower than known values for kudus in poor condition (18.1 g/kg). Van der Waal *et al.* (2003) concluded that dry, cool season faecal nitrogen concentrations lower than 18.5 g/kg and decreasing to values below 15.0 g/kg during the hot, dry season precipitated nutritional stress associated with visible condition loss and increased mortalities in kudu populations in the northwestern Limpopo Province. Owen-Smith and Cooper (1985), Owen-Smith (1990) and Grant *et al.* (1995) also found that kudus lost body reserves toward the end of the dry season caused by low nutrient assimilation rates, but the extent thereof could be limited by providing supplementary feeding. The loss of body reserves predisposes kudu to mortality agents such as cold weather spells, predation and disease (Owen-Smith 1990).

Kudus in the study area also experienced visible condition loss during the dry season. Their coats were scruffy and they appeared to have lost weight (Figure 6.11). Owen-Smith (1994) stated that kudus have a change in their hair coat during the dry season that made it appear thick and shaggy. In the case of the studied animals it was not only their winter coat that was observed, but they also appeared straggly and lean. In addition, they lost their usual fear of humans, mostly just waiting around during daytime in the vicinity of the feeding area for the feed to be delivered. Van der Waal *et al.* (2003) noted a greater difference in mean N_f between poor-condition and good-condition kudu

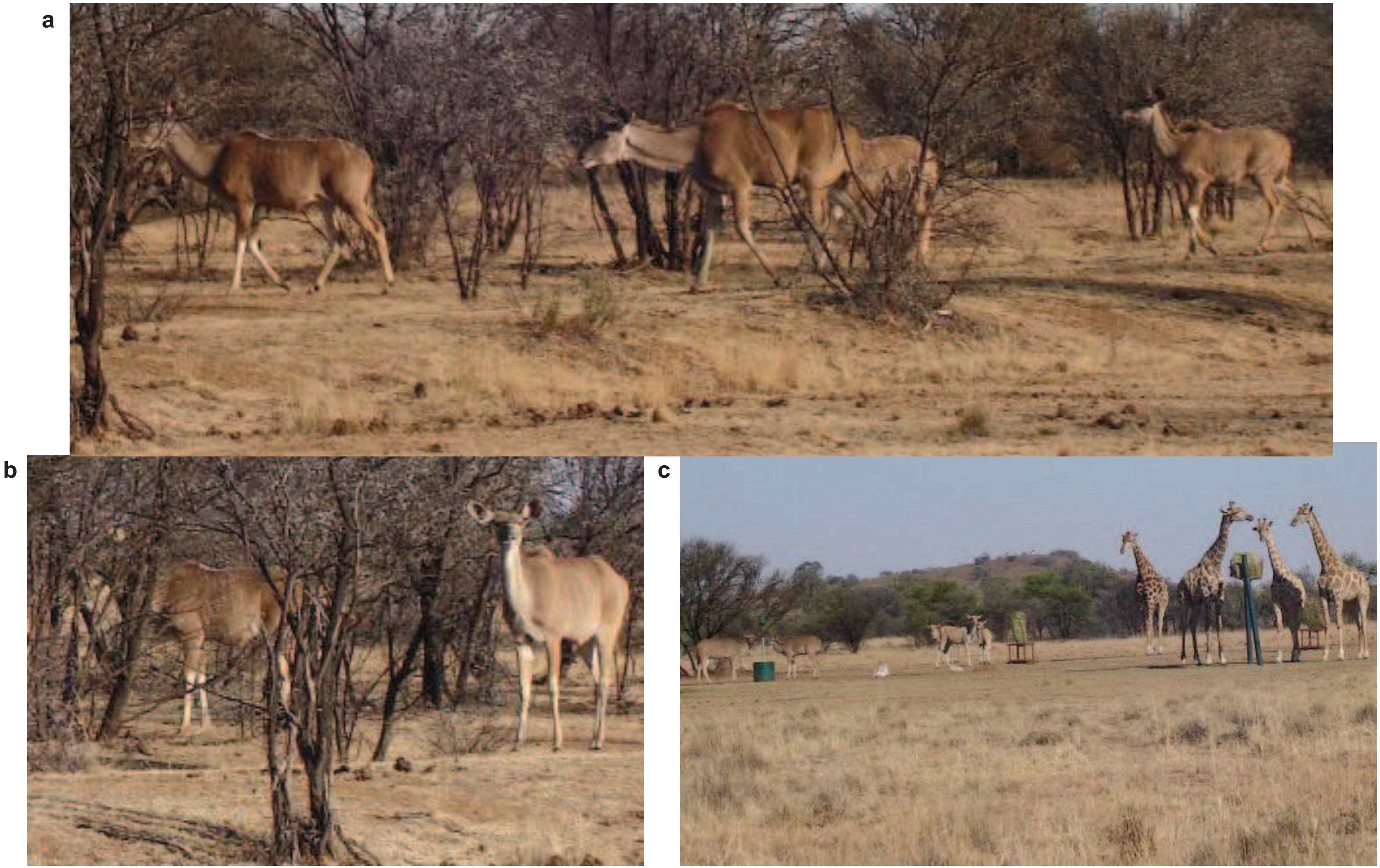


Figure 6.11 a) During the winter of 2006 kudus showed signs of condition loss. b) They stayed in vicinity of the feeding area, waiting for feed to be delivered. c) Kudu and giraffe at the feeding area during winter.

populations in the northwest of Limpopo Province during August and September compared to May and June. This suggests that the loss in condition and mortalities were closely related to nutritional constraints during the dry-hot season due to leaf fall of deciduous species and consumption of evergreen species. High kudu density can also result in some condition loss towards the end of the dry season as was reported for the Nylsvley Nature Reserve near Naboomspruit, though the extent of this was limited by the supplementary feeding provided (Owen-Smith and Cooper 1985, Owen-Smith 1994).

A difference was observed in minimum N_f concentrations for kudu (Figure 6.4) between 2006 (13.6 g/kg) and 2007 (17.2 g/kg). In 2006 feed was supplied twice daily and the kudus that were present in the study area made extensive use of the feed, staying close to the feeding area. Kudus usually moved freely between the southern and northern side (study area) of the private reserve, in their search of high quality browse, by means of the connecting tunnel underneath the Soutpan gravel road (Figure 3.2). At the beginning of 2007, the connecting tunnel was blocked for about three months in order to prevent the new Roan Antelope from settling in the southern side, which was home to the Sable Antelope. At this time the kudus were trapped in the southern side. During the lucerne shortage period in the winter of 2007 there was little or no feed supplied to game and kudus were mostly found in the dense riverine vegetation where shrubs were more abundant than in the northern side. When kudus are left to fend for themselves it seemed that they are able to find food of adequate nutrition, but given the opportunity they will readily rely on supplied feeding, as indicated in their N_f concentrations between the two winters.

6.5.4 Faecal nitrogen of Impala

The average range of impala faecal protein from winter to summer was 11 – 17% (Table 6.2), with a minimum of 10.5%. It gives a good comparison to reported protein percentages from the literature. Pietersen *et al.* (1993) reported that crude protein in the impala diet varied between 6.1% and 12.9% in the Timbavati Private Nature Reserve. The average N_f concentration of impala in the study area (Figure 6.5) was 22 g/kg during 2006 and 24 g/kg during 2007. N_f levels of impala in the northern Limpopo Province was reported by Theobald (2002) to average 18.23 g/kg, while Grant *et al.* (1995) indicated a 18.7 g/kg N_f concentration during a drought in the Kruger National Park. Botha and Stock (2005) reported that impala faecal protein fluctuated around 11.25% in the Hluhluwe-Umfolozi Park, central KwaZulu Natal and were significantly higher in spring, compared to the other seasons. The protein percentage of 11% in the study area (Table 6.2) is just higher than the 10% reported for impala in poor condition in the Kruger National Park (Grant *et al.* 1995) and than the yearly average of 9.38% of impala dung in the Timbavati area (Pietersen *et al.* 1993).

A big difference was observed in minimum N_f concentrations of impala between the two years (Table 6.1). The minimum N_f concentration of impala during 2006 (16.9 g/kg) was just above the critical level indicated by Grant *et al.* (1995) during drought conditions where impala started losing body condition. A large herd of more than 40 impala was present in the study area during 2006, but their numbers were drastically reduced to about 10 individuals through game capture for auctioning during 2007. This might have increased the quantity of food available for the remaining impala, or it may be that when impala did not receive feed during 2007 they were, just like kudu, better at finding their own nutritional food than relying on the feed supplied. According to Attwell and Bhika (1985), impala attempted to meet their nutritional requirements by seasonal selection for habitat, plant species and plant part, while seasonal changes in diet composition were generally interpreted as strategies to prevent seasonal declines in nutritional quality.

Grant *et al.* (1995) stated that being selective feeders, impala managed to obtain a nutritious diet adequate in quality and quantity almost throughout the year in the Kruger National Park, provided that succulent shrub, forb and herb leaves, as well as shoots were available. Similar trends were reported by Meissner *et al.* (1996). Higher levels of faecal nitrogen may be due to the shift in the feeding strategy of a mixed feeder, changing its diet to include more browse food plants than grasses during the winter months (Mbatha and Ward 2006). This trend, where N_f values increase in winter months, was also observed for impala in the study area (Figure 6.5). Impala optimize their diets for quality forage irrespective of plant composition (Grant *et al.* 1995, Meissner *et al.* 1996, Sponheimer *et al.* 2003). Further, impalas are prolific breeders and residential, so their numbers should not decline in adverse conditions (Meissner *et al.* 1996, Sponheimer *et al.* 2003).

6.5.5 Faecal nitrogen of Eland

The minimum N_f concentrations of the available data for eland in the study area were in close range between the two years, namely 16 and 17 g/kg (Table 6.1). Wrench *et al.* (1997) concluded that a N_f concentration of less than 14 g/kg would indicate a N deficiency in grazers. Both the above-mentioned N_f concentrations for eland are higher than the values given in the literature for grazers and browsers, 14 g/kg and 16 g/kg, respectively, as well as for cattle, 12 g/kg (Table 6.1). Eland have frequently been compared to cattle with which they have only a superficial similarity. Compared to cattle, eland seem to be less efficient in the utilization of energy. On average they would require 20 – 30% more metabolisable energy than cattle and in view of the similarity of the efficiency with which these animals use the digestible energy for metabolic purposes, eland would require a corresponding greater food intake (Hofmann 1973).

The average seasonal protein range of eland (11 – 20%) was very similar to that of impala (11 – 17%), likely as a result of both species being mixed feeders (Table 6.2). Buys (1990) reported that crude protein concentration of eland dung in the SA Lombard Nature Reserve, Bloemhof fluctuated between 8.06% and 11.53% – it started to increase in late winter when more browse and leaf litter have been taken and reached a peak in December when they selected more grass of high nutritive quality. The above-mentioned protein percentage of 11% and the seasonal pattern correspond to results of this study. An increase in eland N_f concentrations was observed between May and July 2007 (Figure 6.6) and this was also the case for impala (Figure 6.5).

In the Timbavati Private Nature Reserve crude protein in impala diet was higher during the wet season than during August and October, but lower than that of May to July when browse was selected and a flush of green grass was available after rain (Pietersen *et al.* 1993). Dunham (1982) related diet quality (measured in terms of crude protein and crude fiber) directly to the proportion of grass in the diet, being at a maximum in December – January and at a minimum in July – August in the Sengwa Wildlife Research Area, Zimbabwe. Results of this current study may also be explained by the mixed feeders' higher intake of browse in the winter months which leads to a higher nitrogen concentration being excreted (Figures 6.5 & 6.6), and/or by both eland and impala selecting for higher quality food items during the critical period. It seems that the two selective, mixed feeder species are better adapted to overcome the decline in nutritional quality and quantity during the critical period, compared to the pure browsers (Figure 6.2).

6.5.6 Interactions between woody plants and animals

There is an indication that the trend line of the average nitrogen values of the browsers (Figure 6.7) mostly follows the seasonal leaf phenology pattern of budding (rising N_f values) and shedding leaves (falling N_f values) of especially the trees, but not precisely. In the second year the N_f pattern corresponded to the leaf phenology pattern of trees, but in the first year it deviated from the pattern. According to McKillup (2006), correlation is used to examine whether two variables are significantly related and change together in a consistent way, with no expectation that the value of one variable can be predicted from the other. Giraffe N_f and kudu N_f values respectively correlate (Table 6.8) with median leaf phenology values of the four tree species (giraffe: $r = 0.687$, p =

<0.001; kudu: $r = 0.667$, $p = <0.001$) and with median leaf phenology of the three shrub species (giraffe: $r = 0.536$, $p = 0.001$; kudu: $r = 0.496$, $p = 0.001$). When trees started to shed leaves in April/May a decrease in N_f concentrations was observed (Figures 5.11 & 6.2), when the trees were leafless the N_f concentrations were mostly the lowest, and in October when all the trees had sprouted new leaves the N_f concentrations increased again.

Some of the high peaks in N_f concentration of giraffe and kudu dung (Figure 6.2) could be linked to higher rainfall totals in corresponding months (Figure 3.6). During these months, some of the woody plant species sprouted new leaves (Figures 5.1 – 5.6) which had a higher tannin content that was reflected in the higher N_f concentrations. The specific peak in faecal nitrogen of all four species in February 2006 (Figures 6.7 & 6.8) can be linked to trees sprouting abundant new leaves (Figure 5.11) which should contain more tannins as a protective measure against feeding. Owen-Smith and Cooper (1989) attributed a September peak in dietary nitrogen to the high N content of new leaves and flowers of early flushing species at Nylsvley Nature Reserve. It is known that N_f concentration is elevated whenever a diet contains tannins (Hobbs 1987, Cook *et al.* 1994, Wrench *et al.* 1997, Botha and Stock 2005). Under natural feeding conditions, however, kudu avoid forage high in phenol substances (Owen-Smith and Cooper 1985, Caughley and Sinclair 1994, Van Hoven 2010).

Some of the lower N_f values of giraffe in the study area (Figure 6.3) might be ascribed to their diet that included more woody components, like stems or bark, which are of poor quality and known to contain less nitrogen. Giraffe are known to feed on bark and stems of deciduous trees during winter (Kok and Opperman 1980). Hanley *et al.* (1992) reported that young stems contain few tannins. These stems are not yet so woody that it cannot be eaten and usually consists of the new season's growth. Consumption of browse is restricted to leaves, shoots, smaller branches and cambial layers of the larger branches (Van Soest 1994). A submaintenance diet could result either due to a slow intake rate of nutritionally adequate material or because of the ingestion of poor quality herbage (Owen-Smith 1979).

The trend line of the average nitrogen values of mixed feeders (Figure 6.8) only rises in accordance with the budding of leaves and then follows a different seasonal pattern. It is noteworthy that the protein percentages of the mixed feeders showed a higher correlation with the leaf carriage percentages of the *Lycium* species, compared to those of the trees (Table 6.8). The slight rise in N_f values in winter months, might explain the better correlations with the leaf phenology of shrubs that retained leaves longer than trees. The protein percentages of the browsers on the other hand had a higher correlation with the leaf carriage percentages of the trees than with that of the shrubs (Table

6.8). Leaf carriage of *Ziziphus mucronata* and *Asparagus laricinus*, two well known favourite food plants of browsing animals, showed an overall low correlation with the protein percentages of the game species ($r < 0.4$). The intake of feed during winter months should, however, play a role in concealing the correlation between woody plants and N_f values of the different game species.

Forward selection stepwise regression analysis (FSSR) was done to determine which dataset gave the best explanation of percentage variation in protein. FSSR indicated that *A. karroo* and *S. pyroides* played an important role in the percentage variation in protein of both browser species (Tables 6.9 & 6.10). *Lycium echinatum* and *Z. mucronata* correlated with protein in giraffe dung and could be used to predict protein values ($R^2_a = 68.1$). Median leaf phenology values of shrubs and trees, respectively, were also included in the kudu protein model ($R^2_a = 58.6$). In the case of eland (Table 6.11), *L. hirsutum*, *D. lycioides* and *Z. mucronata* correlated with the protein content in its dung, but protein in impala dung (Table 6.12) had no correlation with any of the plant data sets.

When comparing different vegetation units (VU) where dung was collected over 28 months in the study area, it appeared that habitat had no significant effect ($p = 0.923$; 0.491; 0.196) on three of the game species' N_f data (Table 6.7). Only in the case of giraffe did the N_f differ significantly ($p < 0.001$) between different vegetation units. This might be due to different food plants / items selected by giraffes in different VU, like supplied feed in the disturbed area, *Acacia karroo* in the open thickets and other tree and shrubs species that are more plentiful in the dense thicket and drainage line. Stapelberg *et al.* (2008a) also concluded that "habitat did not significantly affect N_f concentrations in the hot-wet or hot-dry seasons in the Kgalagadi Transfrontier Park, RSA." In the study area it was not possible to differentiate between seasons due to a lack of adequate samples available for analyses. This is a topic for further study.

6.5.7 Nitrogen concentration in leaves, fruits and seed pods

With regards to the leaves, a decrease in nitrogen (N) concentration in general has been indicated from immature- to yellow leaves for all the woody species (Table 6.3). Negi (1995) demonstrated that leaf nitrogen concentration showed a sharp rise from budding to mature leaves and a sharp decline till leaf senescence in some deciduous tree species. According to Owen-Smith (1994), crude protein levels in leaves dropped abruptly by 15 – 30% of their wet season concentrations at the onset of the dry season, followed by a further slow decline, while leaf protein levels were highest during new leaf flush. The greater nitrogen retranslocation efficiency of these tree species prior to leaf shedding allows a large proportion of absorbed nitrogen to be converted into plant biomass and less is recycled through litter fall (Negi 1995). It might be that nitrogen was already in the process of being translocated from mature leaves back into the plants before senescing commenced, when leaves were collected at the end of March in the study area. Consequently, not such a big difference was found between mature and yellow leaves in this study.

The biggest differences in crude protein content between the leaf phenophases were found for the *Lycium* species (Table 6.3). Dry, green leaves that were retained on trees (Figure 5.16), after black frost occurred during May (Table 3.3), had a higher crude protein content than mature leaves of *Acacia karroo* and *Ziziphus mucronata*. Classically tannins are believed to act through their protein-binding effects, either by making plant protein indigestible or through deactivating digestive enzymes (Owen-Smith 1993). Although it seems that a high crude protein content is present in leaves, it may not always be available for animals and may be excreted again in the bounded form. Regression analyses done by Holechek *et al.* (1982) between N_f percentage and digestibility vary between first growth and mature leaves, between leaf and stem components, from year to year and even between different varieties of the same herbage species.

Phenophases seem to play an important role in the feeding of animal species. It is known that unpalatable plant species that are usually rejected in the mature phenophase become highly acceptable when they have new leaves (Owen-Smith 1987). Kok and Opperman (1985) concluded that utilization peaks of the palatable plant species by giraffe in the Willem Pretorius Game Park occurred in successive months depending on their phenological development. Giraffe concentrated their feeding on tree species with the greatest quantity of new shoots and these shoots had higher protein and lower total fiber contents than mature shoots (Pellew 1984).

Crude protein contents of fruits and pods of trees in the study area were as follows: *Acacia karroo* 17.34%, *Diospyros lycioides* 7.12% and *Ziziphus mucronata* 3.85%. Meissner *et al.* (1999) also confirmed that pods from *Acacia* species had a high crude protein content. The pips of *Z. mucronata* fruits collected in the study area were extremely hard to ground up, so it may be possible that it could pass unharmed through the digestive system of the animals. During the grounding process of faecal samples large hard pieces were observed in the dung, appearing to be pieces of seeds, some of which did not pass through the 1 mm mesh screen but was added to the powdered dung. This confirms the fact that animals take fruits and pods to supplement their winter diet. The intake of fruits, pods and leaf litter by game species during winter months have been discussed in detail in the literature review.

6.6 CONCLUSIONS

In their unrestricted natural environment herbivore species have little need for supplied feeding as their free ranging habits enable them to search wider for more nutritious food. The study area is a small confined area where only deciduous species are available to browse, except for some small shrubs that retain leaves for longer periods. This necessitates some form of feeding, bearing in mind that availability of the supplied feed is also limited due to competition between giraffe, kudu, eland, impala and the grazers.

A positive correlation was found between percentage faecal protein and leaf phenology of the tree species. In general a decrease in crude protein content has been observed from immature leaves to yellow leaves for all the woody species. This also explained the drop in N_f concentration when leaf fall started. A seasonal pattern of N_f concentrations was observed for giraffe and kudu, with the highest concentrations during summer months and the lowest during winter. A seasonal pattern was also observed for impala and eland, with the highest N_f concentrations during summer months and the lowest during autumn and not during winter like in the case of the browsers. An increase in impala and eland N_f concentrations were observed between May and July 2007. These mixed feeders seem to select higher quality food items during the critical period and to include more browse in their diets that help them maintain sufficient nitrogen concentrations.

Minimum N_f concentrations for giraffes during the dry season were above critical levels for browsers in general. They seemed to be in good condition and were reproducing every year. The lucerne hay proved to be insufficient in sustaining kudu during the winter months, since the N_f concentrations dropped below critical levels where mortalities usually start occurring. However, without the supplied feed, the available browse may not be enough to sustain these animals through the winter period. It is suggested that the connecting tunnel in the study area should not be blocked in winter months to allow browsers and mixed feeders access to the shrubs present in a higher density on the river banks. These shrubs can be an important food source, along with the feed supplied, during the critical period.

Impala numbers were reduced to a quarter of the original number during 2007. This might have increased the quantity of food available in the veld for the remaining impala, leading to higher minimum N_f concentrations during the critical period of that specific year. It is known that bachelor herds are mostly forced out by territorial males to occupy poorer habitat and also that males tending to their territories and herding females during the rut lose some body condition because of reduced food intake and increased activity and that they may not be in the best condition that the habitat can support (Hanks *et al.* 1976, Mason 1976a, Van Rooyen 1993, Bednekoff and Ritter 1997). However, this should not have influenced the faecal nitrogen results, because as far as possible more than one herds' faeces were collected and pooled, meaning that the impact of the males in poorer condition with less nitrogen in their diet would have been incorporated in the mean of the group.

It is concluded that faecal nitrogen is a good indicator of the nutritional status of the studied game species. It can be used as a management tool in deciding the stocking density of animals, since nitrogen values can reach critical levels if food becomes limited. It offers the manager a useful tool to establish when supplementary feeding during the resource limited critical period of the season may be required.

CHAPTER 7
HABITAT USE BY GAME SPECIES, WITH EMPHASIS ON SMALL SEASONAL MOVEMENTS

7.1 INTRODUCTION

An animal's habitat is that area where it preferably occurs and where all its life necessities are fulfilled (Nel 2010). Habitat suitability, defined as the potential to support a species, is a measure of the presence of important environmental parameters, and relates to abiotic and biotic conditions (Barbour *et al.* 1987, Cox 1997). The distribution and habitat selection of many herbivores are determined, among other things, by forage availability, which is influenced by habitat structure (Barnes 1976, Johnson 1980, Dörgeloh 2001a, Gordon *et al.* 2004). Scogings *et al.* (1990) mentioned that: "maintenance of mixed ungulate populations in an area without detriment to either habitat or animals requires insight into habitat needs, habitat use and potential interspecific competition among animals of the area." According to Woolnough and Du Toit (2001): "A key question for large mammal assemblages in general is how shared resources are partitioned among coexisting species."

Many studies of herbivores in relation to their environments have been done, some of which will be referred to in the literature review. Studies range in complexity from qualitative descriptions of habitat use (e.g. Novellie 1990) to quantitative analyses made possible by computer methods such as detrended correspondence analysis (e.g. Scogings *et al.* 1990). Williamson (1990) stated that: "For conservation purposes it is sufficient to know what habitats are being used; for theoretical purposes it is interesting to know why habitats are used in a particular way." For the game farmer it is important to know what habitats are essential for survival and can aid in population increase. Therefore the objectives of this chapter were to:

i) identify preferred habitat types and areas used by different game species;
ii) determine if there were any local, small, seasonal movements to other habitats; and
iii) determine if interspecies competition for space and food existed, especially for browsers.

7.2 LITERATURE REVIEW

Herd sizes, preferred habitat, feeding preferences, active periods, territory- and/or home range sizes, social organisation and calving of game species, as reported in the literature, are summarised in Tables 7.1 & 7.2, followed by additional information and explanations. Browsers and mixed feeders will be discussed first, followed by the grazers in alphabetical order and lastly the ostrich.

Table 7.1 Herd sizes and habitat requirements from the literature of game species present in the study area.

Game species	Size of territory	Most active periods	Herd size	Preferred habitat	Type of feeder, diet and feeding height	Literature cited[1]
Giraffe (*Giraffa camelopardalis*)	Home range: 23 – 282 km^2 (1 km^2 = 100 ha)	Diurnal, will feed after dark	Loose herd structure, no consistency in size	Dry savannas ranging from scrub to woodland; bushy or open scrubby plains. Drink if water is available, not dependent	Concentrate selector, browses up to 5 m high, eats forbs, grazes occasionally. Includes fruit, seed pods, flowers, leaves, shoots.	Hofmann 1973, Kok and Opperman 1980, Wentzel 1990, Van den Berg 1999, Le Pendu *et al.* 2000, Theron 2006
Greater Kudu (*Tragelaphus strepsiceros*)	4 – 12 km^2 or 8 – 50 km^2 depending on space	Diurnal; night, early morning & late afternoon	6 – 8, rarely > 16	Savanna woodland, riparian woodland, thickets along drainage lines, hillslope base ecotones. Prefer water close by.	Concentrate selector, browses up to 2 m high. Eats leaves, shoots, fruits, seed pods, creepers, tubers, forbs.	Hofmann 1973, Grunow 1980, Owen-Smith 1979, 1984b, 1985, Owen-Smith and Cooper 1987, Du Toit 1990b, 1995b
Eland (*Tragelaphus oryx*)	Home range: 757 km^2 in Kenya. 120 km^2 was too small in eastern Transvaal	Morning & late afternoon; feed all day in cool periods; rest on hot dry days and feed at night	25 – 60, or up to 200. In summer large mixed herds, disperse in autumn	Open savanna country, semi-arid shrubland, semi-desert, montane grassland, floodplain, various woodland types, highly versatile in habitat selection. Shade is essential. Drink if water available, but not dependent.	Highly selective, intermediate, mixed feeder – eats up to 2 m high, mostly browses in winter and grazes in summer. Includes fruits, pods, seeds, herbs and tubers. Can satisfy moisture requirements from their food.	Hofmann 1973, Underwood 1978, Grunow 1980, Jankowitz 1982, Hillman 1988, Buys 1990, Watson and Owen-Smith 2000, Bothma *et al.* 2010
Impala (*Aepyceros melampus*)	5 – 8 ha, or up to 50 ha Home range: 80 – 120 ha	Diurnal, some nocturnal activity. Rest midday.	6 – 20, or 50 – 120 in the wet season	Ecotone (edge) species, woodland, grassland-ecotones, foothill-ecotones, light open associations. Cover, shade and water are essential.	Mixed feeder, browses up to 1.5 m high, grazes on low to medium height grasses. Forbs, fruits, seed pods, leaves and fine twigs are taken.	Hofmann 1973, Mason 1976a, Monro 1980, Pettifer and Stumpf 1981, Murray 1982, Owen-Smith and Cooper 1987, Matson *et al.* 2006, 2007, Oliver *et al.* 2006
Common or Grey Duiker (*Sylvicapra grimmia*)	Home range: 0.12 – 0.27 km^2 or 1.9 – 3.8 ha	Mainly diurnal, early morning & late afternoon, extending into the hours of darkness.	Solitary or in pairs, or female with young	Savanna and woodland with ample underbrush, fynbos, on the fringing scrub of agricultural lands and of forested areas. Presence of bushes important for shelter, shade, food. Water independent.	Concentrate selector, browse up to 1 m high. Leaves, twigs, flowers, fruit and seeds constitute their main food. They nibble bark, eat tubers, roots, young birds, mice, lizards and mopane worms.	Wilson and Clarke 1962, Wilson 1966, Hofmann 1973, Allen-Rowlandson 1986, Kigozi 2003, Lunt *et al.* 2006, Prins *et al.* 2006, Bothma *et al.* 2010
Blue Wildebeest (*Connochaetes taurinus*)	30 m in diameter around bulls or a harem herd.	Diurnal, early morning & late afternoon, moonlit nights	15 – 30 or >1000 in East Africa	Bush savanna, light- or closed woodland, river banks, but they will also utilize open grassland, floodplain grassland and slopes.	Grazer, prefers short green lawn-like grassland, rarely eats grass more than 100 – 150 mm high. Site selectors, selecting	Talbot and Talbot 1963, Bell 1971, Berry 1981, Attwell 1982, De Wet 1988, Wentzel 1990, Ben-Shahar 1991,

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Table 7.1 Continued

	Home range ♀: about 2.5 km^2	move to water in heat of day		Shade and drinking water (±4.4 litres/day) are essential.	grass patches rather than plant parts.	Dekker *et al.* 1996, Ego *et al.* 2003, Furstenburg 2007a
Game species	**Territory size**	**Active period**	**Herd size**	**Preferred habitat**	**Type of feeder , diet**	**Literature cited**[1]
Bontebok (*Damaliscus pygargus*)	0.04 – 0.28 km^2, or 0.1 – 0.40 km^2	Diurnal, morning & late afternoon	Up to 9	Coastal plains, renosterveld, riparian *Acacia* associations. Areas of short grass, with shelter, and drinking water.	Grazer, prefers short grass <25 cm and some forbs. Patch-selective feeding.	David 1973, Langley and Giliomee 1974, Furstenburg 2006b, Bothma *et al.* 2010
Buffalo (African Savanna Buffalo, or Cape Buffalo) (*Syncerus caffer*)	Home ranges: 41 – 120 km^2, up to 1 500 km^2	Early morning, late afternoon and at night.	20 or 50 – 350, > 1 500 for large herd aggregations	Variety of woodland types, woody riverbanks, vleis, grasslands. Water, shade and shelter for low night temperatures are essential.	Grass and roughage feeder, takes grasses of intermediate height, prefers grass from 200 mm up to 750 mm high.	Conybeare 1980, Wentzel 1990, Funston *et al.* 1994, Hunter 1996, Perrin and Brereton-Stiles 1999, Winterbach 2000, Macandza 2003
Burchell's or Plains Zebra (*Equus burchelli*)	Home range: 30 km^2 up to 600 km^2 depending on food availability, varies between years	Diurnal, active during most of the day. Will also feed after dark and on moonlit nights	Rarely more than 9, bachelor groups**:** 2 – 15, large herds composed of several families	Grassland, floodplain grassland, open areas of woodland, open scrub with a crown cover of trees and shrubs of less than 5%. Very water dependent – cannot utilise optimum grazing conditions if water is not available.	Unselective, bulk grazer and roughage feeder taking grasses of intermediate to tall height of about 100 – 150 mm from ground level but will also select shorter grass if given the choice. Very adaptable, successful grazer.	Turner and Watson 1965, Klingel 1969, Hofmann 1973, Smuts 1976, Grunow 1980, Wentzel 1990, Ben-Shahar 1991, Bodenstein *et al.* 2000, Neuhaus and Ruckstuhl 2002, Okello *et al.* 2002, Fischhoff *et al.* 2007a, 2007b
Gemsbok (*Oryx gazella*)	4 – 16 km^2, up to 26 km^2, Home range ♀: 52 – 212 km^2	Diurnal, with some activity on moonlit nights.	2 – 30, or up to 300. Large herds in wet season brake up into smaller herds in dry season when food is less abundant.	Open bush savanna, dry open grassland, light open woodland, but also penetrate into savanna woodland, short grass areas around brackish pans consisting of dry, semi-desert shrubs. Use shade and fresh water where available. Require 2.5 – 4 litres water/day, can obtain from food	Grazer, selective grass and roughage feeder of short (<5 cm), intermediate and tall vegetation. When grass is insufficient they eat browse, ephemeral plants, seed pods. Dig for succulent roots, rhizomes and bulbs when drinking water is unavailable.	Eloff 1959, Taylor 1968, Hofmann 1973, Dieckmann 1980, Dreyer 1987, Williamson and Williamson 1988, Knight 1991, 1995, Anonymous 1992b, Møller *et al.* 1996, Furstenburg 2007b, Ruckstuhl and Neuhaus 2009, Bothma *et al.* 2010
Red Hartebeest (*Alcelaphus buselaphus*)	0.10 – 0.30 km^2	Diurnal, active in early morning & late afternoon, rests in open in mid-day.	Up to 20, or large herds of >300 after summer rains	Plains antelope. Open country on grassland of various types like floodplain grassland and vleis, semi-desert bush savanna, open woodland. Water dependent, can obtain from food.	Selective grazer, also browses, prefers medium grasslands. Migrate between long grasslands in dry season and short, well drained pastures during rains, home ranges incorporate both. Patch-selective feeder.	Van Zyl 1965, Kok and Opperman 1975, Novellie 1990, Anonymous 1993a, Kilian 1993, Murray and Brown 1993, Ego *et al.* 2003, Bothma *et al.* 2010

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Table 7.1 Continued

Game species	Territory size	Active period	Herd size	Preferred habitat	Type of feeder, diet	Literature cited[1]
Red Lechwe (*Kobus leche*)	Small, cluster territories: 0.5 – 6 ha, 15 – 20 males per lek	Mostly diurnal, can become nocturnal due to hunting. Actively use water to moderate heat stress for mid-day activity.	9 – 15, or 33 – 56, or up to 5 000.	Specialized habitat requirement, occur on shallowly inundated floodplains fringing swamps and rivers on the ecotone of high standing beds of *Phragmites mauritianus, Cyperus papyrus* and semi-aquatic grasses; and on fringes of dry land. Rarely >2 km from water, but only drinks in hot, dry season, up to 3x /day.	Grazer of semi-aquatic grass, inundated grass, aquatic weed in deep water of up to 0.5 m, sedges, herbs like *Sida alba* and *Aeschynomene fluitans*. Grasses of ecotone between terrestrial areas and swamp provide most important food supply, also includes dry land grasses of medium to tall height.	Rees 1978, Williamson 1979, 1990, 1993, 1994, Furstenburg 2005a, Bothma *et al*. 2010
Roan Antelope (*Hippotragus equinus*)	Home ranges: 15 – 25 km^2, 60 – 120 km^2 Bull defends an area around herd of 300 – 500 m (intolerance zone) from other males.	Diurnal, but late risers especially on cool mornings when grass is soaked in dew, with at least one feeding peak at night.	5 – 12 up to 25, temporary aggregations of up to 80	Open savanna, open grassland, prefer floodplains during summer months. Tolerant of open, scattered bush growth up to 1.5 m high. Changes in habitat, like increase in woody vegetation or reduction of grass cover, produced by drought, bush encroachment or over-grazing render it less suitable. Usually found <5 km of water.	Grazer, feeds on medium to tall grass, highly selective for grass species. Delicate feeder, utilising higher part of grasses up to 80 cm above ground with green shoots being taken from 20 mm, well adapted to grass of 1.5 m height. Prefers areas that support grazing of low quality, patch selective feeder.	Joubert 1970, Poché 1974, Allsopp 1979, Martin 1983, Harrington 1996, Dörgeloh 1998, 2001b, Dörgeloh *et al.* 1998, Heitköning and Owen-Smith 1998, Perrin and Taolo 1999, Knoop and Owen-Smith 2006, Bothma *et al*. 2010
Southern or Common Reedbuck (*Redunca arundinum*)	0.73 km^2 for males to 1.23 km^2 for females. Home range: 0.05 – 0.35 km^2, in KwaZulu-Natal up to 1 km^2	Early morning & late evening. Nocturnal when plentiful water and food are available. From August to October active at all hours.	Singly, in pairs or family parties of 2-3 although 15-20 may be together from May to August	Vleis with central, wet drainage area, grassland next to streams, rivers, drainage lines or areas of permanent water. Tall grass, reed beds, herbaceous cover, preferably with some woody elements, and water is essential. Extensive areas of broken veld are of paramount importance: it provides escape from danger and adequate cover by means of boulder outcrops, gullies, etc.	Almost exclusively a grazer, prefers green grass near water, although they also eat forbs and may browse extensively in winter to compensate for cold temperatures that usually trigger mortality (especially without adequate plant cover). Patch-selective feeder	Ferrar and Kerr 1971, Jungius 1971, Venter 1979, Howard 1984, 1986a, Anonymous 1991, Bothma *et al*. 2010

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Table 7.1 Continued

Game species	Territory size	Active period	Herd size	Preferred habitat	Type of feeder, diet	Literature cited[1]
Springbok (*Antidorcas marsupialis*)	0.10 – 0.73 km^2	Early morning & late afternoon, some activity at midday and after dark depending on climate, hot days forage at night.	>9 – 102, or 476 up to thousands, aggregates during summer rainy seasons	Plains antelope with wide habitat tolerance, from 750 mm rainfall to deserts. Grasslands, savannas with short-growing grasses associated with dry pans. Will drink where water is available, but can satisfy thirst from food. They are cold-stressed animals and move to higher ground at night.	Intermediate mixed feeder, shifts from grasses in hot, wet season to leaves and shoots of karroid shrubs and some large woody species in cold, dry season. They stand on hind legs to forage on tall shrubs. Where water is unavailable they browse succulent karroid vegetation or dig for succulent roots.	Bigalke 1972, David 1978, Liversidge 1970, Mason 1976b, Davies *et al.* 1986, Fairall *et al.* 1990, Milton *et al.* 1992, Hofmann *et al.* 1995, Skinner *et al.* 1996, Bednekoff and Ritter 1997, Cain III *et al.* 2004, Mbatha and Ward 2006, Stapelberg 2007, Stapelberg *et al.* 2008b
Tsessebe (*Damaliscus lunatus*)	2 – 4 km^2	Diurnal animals	small herds, <4, <8, 3 – 31 animals, large herds occasionally of up to 60 animals	Ecotonal species on fringes of grassland forming an abrupt transition with woodland. Floodplains, hydromorphic- and broad drainage line grasslands. Water, shade and shelter are important. Often take to the open when disturbed.	Almost exclusively a grazer, favours green grass leaves and specific species. Prefer shorter grass, higher grass density, grasses high in protein and sodium. In drier areas they prefer grass up to 0.6 m tall. Bite selectors, selecting plant parts.	Child *et al.* 1972, Joubert 1972, Garstang 1982, Martin 1983, De Wet 1988, Dunham *et al.* 2004, Dörgeloh 2006, Furstenburg 2006c, Bothma *et al.* 2010
Waterbuck (*Kobus ellipsiprymnus*)	4 – 146 ha, or can be 1.2 – 2.8 km in diameter Home range ♀: 6.5 – 7 km^2	Early morning & late afternoon and also one feeding peak around midnight.	6 – 12, but occasionally up to 30, increase in group size in summer and herds fragment during winter.	Associated with water, near a river, open areas in reed beds, floodplains, valleys, vleis, riparian bush, e.g. next to drainage lines, areas with tall grass, woodland, rocky hills. Habitat preference is determined by grass quality, especially *Panicum maximum*.	Roughage feeder, medium and short grass, selects most abundant species available. Favours hydrophytic plants like *Hemarthria altissima*, *Setaria*, *Cyperus*, *Phragmites* and *Typha* spp. Ability to wade in deep water provides uncompetitive feeding niche.	Spinage 1969, Taylor *et al.* 1969, Herbert 1972, Hofmann 1973, Melton 1978, Tomlinson 1980a, 1981, Wentzel 1990, Anonymous 1993b, Bothma *et al.* 2010
Ostrich (*Struthio camelus*)	4 – 19 km^2 Namib Desert average home range: 84.3 km^2, smaller in mesic habitats	Diurnal and active by moonlight. Heat-tolerant and able to be active at mid-day.	2 – 5, or >30 birds that leave and rejoin at random	Open woodland, open, short-grass plains, arid savannas, semi-desert, largely independent of water, can metabolize it from food, but drink freely if available, normally within 24 km radius from water.	Highly selective. Green grasses and small succulent plants swallowed whole with roots. Eats herbs, leaves, flowers, seed-heads of grass, pods (*Acacia*, *Aloe*), locusts, small mammals. Feeds from 0 to 2 m.	Grunow 1980, Bertram 1980, 1992, Brown 1992, Williams *et al.* 1993, Dean 1997, Aganga *et al.* 2003, Furstenburg 2005b, Hockey *et al.* 2005, Brand and Gouws 2006, Olivier and Burger 2010

[1] **The following references were cited for all game species, except ostrich: Estes (1997), Frandsen (1998), Skinner and Chimimba (2005).**

Table 7.2 Social organization and reproduction of game species from the literature.

Game species	Social organisation	Gestation period	Calving peak	Calf/lamb movements	Literature cited[1]
Giraffe (*Giraffa camelopardalis*)	Non-territorial, gregarious. Loose, open herds of females and young, bachelors and mixed sexes. Some solitary bulls. Social bonds not strong.	457 days; or 550 – 650 days	Throughout the year, depends on rainfall	Calf lies out isolated for first 1 – 3 weeks, before joining herd.	Van den Berg 1999, Le Pendu *et al.* 2000, Caister *et al.* 2003
Greater Kudu (*Tragelaphus strepsiceros*)	Non-territorial, gregarious, sedentary. Solitary males, bachelor-, female- and breeding herds.	215 – 270 days	January to February	Calf is hidden for 2 – 3 weeks	Simpson 1968, Underwood 1978, Fabricius 1994, Du Toit 1995b
Eland (*Tragelaphus oryx*)	Non-territorial, gregarious, nomadic. Mixed- (breeding and non-breeding animals), unisexual- and calf herds. Matrilineal, age, size hierarchy	260 – 279 days	August to December	Calf may lie out for up to 2 weeks	Underwood 1981, Buys and Dott 1991, Rowe-Rowe 1994, Cransac and Aulagnier 1996
Impala (*Aepyceros melampus*)	Seasonally or perennially territorial, gregarious, sedentary. Bachelor-, female herds and breeding herds consisting of females with one adult male, as well as mixed herds and solitary animals.	194 – 200 days	November to January. Short-day, seasonal breeders	Left hidden for 1 – 2 days, but can follow the mother 24 hours after birth to herd.	Mason 1976a, Pettifer and Stumpf 1981, Murray 1982, Oliver *et al.* 2006, Matson *et al.* 2007
Common or Grey Duiker (*Sylvicapra grimmia*)	Territorial, monogamous, shy, inconspicuous. Solitary or male and female pair. Lambs mature very rapidly, at 6 months close to adult size.	191 days, or 250 days	No seasonal peak, perennial breeder	Lambs lie out for several weeks	Lunt *et al.* 2006, Rovero and Marshall 2004
Blue Wildebeest (*Connochaetes taurinus*)	Territorial, highly gregarious in mobile aggregations or dispersed in sedentary herds. Known for mass migrations. Territorial males, female- and bachelor groups.	250 days	November to January, some in May	Runs in 3 – 6 min., follows anything, mother stays close for imprinting.	Attwell 1982, Whyte 1985, Furstenburg 2007a, Bothma *et al.* 2010
Bontebok (*Damaliscus pygargus*)	Territorial, gregarious, sedentary dispersed on fenced range. Territorial males, female- and bachelor groups. Hierarchy in female herds of up to nine adult females and their young.	230 – 254 days	September to December, short-day breeders	No hiding or nursery groups, follow the mother in 15 min. ♀♀ calve in herds.	David 1973, Novellie 1986, Furstenburg 2006b, Bothma *et al.* 2010
Buffalo (African Savanna or Cape Buffalo) (*Syncerus caffer*)	Non-territorial, highly gregarious. Large mixed herds with male dominance hierarchy and bachelor herds. Smaller stable herds are part of a larger group that aggregates and disperses. Linear dominance hierarchy exists between cows to which are attached a number of bulls ranked according to age and dominance.	340 days	December to February, up to April	Too feeble to follow mother and is a slow runner, group defense of calf or hiding for several weeks if herd moves off to graze or drink.	Sinclair 1977, Mloszewski 1983, Funston 1992, Funston *et al.* 1994, Prins 1996, Ryan *et al.* 2006
Burchell's or Plains Zebra	Non-territorial, gregarious, nomadic, mass migrations occur. Stable 1-male harems or	360 – 390 days	Born at any time, peaks	Follows mother and herd within a few	Klingel 1969, Smuts 1976, Neuhaus and Ruckstuhl 2002,

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Table 7.2 Continued

(*Equus burchelli*)	family groups, bachelor herds, solitary males. Dominant stallion keeps family together and protects them. Bachelor rank based on age.		from October to March, depends on rain for food	minutes. Mother-foal bond is very close.	Fischhoff *et al.* 2007a, Bothma *et al.* 2010
Game species	**Social organisation**	**Gestation**	**Calving peak**	**Calf/lamb movements**	**Literature cited**[1]
Gemsbok (*Oryx gazella*)	Territorial, gregarious, nomadic. Mixed herds with male dominance hierarchy, nursery herds, some solitary males. No bachelor herds. Territorial alpha male courts and mates, are comparatively tolerant to other males.	264 days	Born any time of the year, can peak in September, depends on rain	First 3 - 4 weeks of life it lies hidden in a curled-up position, horns grow rapidly to 20 – 30 mm.	Anonymous 1992b, Møller *et al.* 1996, Furstenburg 2007b, Ruckstuhl and Neuhaus 2009
Red Hartebeest (*Alcelaphus buselaphus*)	Territorial, gregarious. Stable harem groups, female herds, bachelor herds and some solitary males. Members of herd lie scattered, not in a compact group. During temporary absence of territorial bull, leadership may be taken over by an adult female.	240 days	Most calves are born September to November, no other time. Short-day breeders	Hiding phase lasts about 2 weeks, but calf can already follow its mother within 45 minutes of birth.	Skinner *et al.* 1973, Kok 1975, Anonymous 1993a, Bothma *et al.* 2010
Red Lechwe (*Kobus leche*)	Both conventional territories and temporary lek systems during breeding peak. Highly gregarious, populations either mobile aggregated or sedentary dispersed. Loose herd associations: adult female-; adult male-; juvenile-; female/juvenile-; mixed sex/age-; and mixed male bachelor groups that also include juvenile females before the rut.	225 days	January to March, or June to October for different areas and depending on water levels	Hide for first 2 – 3 weeks in cover of tall grass on islands in a swamp or other dry ground. After weaning, calves may form independent crèches.	De Vos and Dowsett 1966, Lent 1969, Schuster 1976, Williamson 1979, 1993, 1994, Furstenburg 2005a
Roan Antelope (*Hippotragus equinus*)	Gregarious, mostly sedentary / dispersed in small herds, aggregates seasonally. Breeding herds each with a dominant bull, bachelor groups, solitary bulls. In some areas bulls have activity zones rather than territories and defend a harem of females throughout the year. Inside activity zones a herd occupies a home range while food and water is plentiful, moving to another when deficient. Hierarchy exists among females and juveniles, with one dominant female that takes the lead in herd movements.	276 – 287 days	Aseasonal breeders, mostly reproduce every 10 months, birth peaks January to March, or October to December, or in the winter.	Mother rejoins herd after birth, leaving calf in concealment for 6 weeks. By the age of 2 months they move with herd and form crèches, when alarmed they stay together, following leadership of a single female.	Joubert 1970, Allsopp 1979, Martin 1983, Dörgeloh 1998, Heitköning and Owen-Smith 1998
Southern or Common Reedbuck	Territorial, monogamous pairs. Solitary or family parties of 2 – 3. They rest and feed	225 days	Born any time of year, peaks	The lamb hides itself until 3 – 4 months	Howard 1986a, 1986b, Anonymous 1991

Continued on next page...

Table 7.2 Continued

(*Redunca arundinum*)	several meters apart, never close together. In winter adult females associate with adult males in family groups. Males become solitary towards summer.		from December to May	old, when lamb and female rejoin the male.	
Game species	**Social organisation**	**Gestation**	**Calving peak**	**Calf/lamb movements**	**Literature cited**[1]
Springbok (*Antidorcas marsupialis*)	Territorial, highly gregarious, mass migrations known as “trekbokken”. Solitary territorial males, female-, bachelor- (2 – 50 animals), mixed- (7 – 182 animals with non-territorial males associating on periphery), breeding- and harem herds consisting of an adult male, several females and juveniles (10 animals mean).	168 – 175 days	Prolific breeder, no restricted season, usually born in summer in summer rainfall areas	Hides for 1 – 2 days. At 2 weeks old it nibbles on plants, 3 – 4 weeks running strongly with herd. Ewes can give birth to 2 lambs/year	Bigalke 1972, David 1978, Fairall *et al.* 1990, Jackson *et al.* 1993, Skinner *et al.* 1996, Bednekoff and Ritter 1997, Cain III *et al.* 2004, Stapelberg *et al.* 2008b
Tsessebe (*Damaliscus lunatus*)	Territorial, gregarious. Territorial males, harems, breeding- (2 – 21 animals) and bachelor herds (3 – 31 animals). Each harem remains permanently associated with a territorial male. Single-male breeding system.	235 – 270 days	Peak October to November, may occur August to January	Females do not hide young, while she forages they form nursery herds of 2 – 5 which bed down in slight depressions.	Garstang 1982, Joubert 1972, Martin 1983, Furstenburg 2006c, Bothma *et al.* 2010
Waterbuck (*Kobus ellipsiprymnus*)	Territorial males, nursing- and bachelor herds. Bachelors tolerated on territories and close to females. Rank hierarchy based on seniority in bachelor herds, also dominance status within age classes. Serious fighting is common. Territorial bull accepts up to 3 "satellite bulls", assist to keep out other males and "understudy" the owner. Some calves associate with female groups others wander alone or form floating spinster groups. Mostly sedentary.	280 days	Calving mostly in December and July with peaks in October and February/March	Calf finds its own hiding place, 3 – 4 weeks old it follows mother. Weaned calves of both sexes are treated aggressively by females. Twins and triplets are common.	Tomlinson 1980a, 1980b, 1981, Melton 1983, Anonymous 1993b, Bothma *et al.* 2010
Ostrich (*Struthio camelus*)	Territorial male owns a nest, ratio of 1 male: 3 females; non-territorial adult males who sometimes mate; 'major' females mated with territorial male in monogamous bond; 'minor' females which wander widely, groups of immatures (40 – 100 birds). In moister parts sedentary for years, but in arid areas nomadic.	Incubation starts 16 days after first egg is laid for 39 – 53 days.	Spring-summer peak. Total number of eggs: 12 – 26, with clutch of major female: 8 – 14.	Hatched chick cannot walk well for 24 h, leaves nest after 3 days if able to run for 10 m. Form crèches under care of any >2 adults.	Bertram 1992, Brown 1992, Dean 1997, Furstenburg 2005b, Hockey *et al.* 2005, Olivier and Burger 2010

[1] **The following references were cited for all game species, except ostrich: Estes (1997), Frandsen (1998), Skinner and Chimimba (2005).**

7.2.1 Browser- and mixed feeder game species

7.2.1.1 GIRAFFE (*Giraffa camelopardalis*)

Giraffes appear to have a loose herd structure and there is apparently no consistency in the ratio of males to females in a herd, or in the size of herds (Owen-Smith 1988, Estes 1997, Van den Berg 1999, Skinner and Chimimba 2005). They form groups averaging between 3 and 17 animals with 35 being the maximum (Owen-Smith 1988) and 5.7 being the mean (Bothma *et al.* 2010). Bulls are mainly solitary and wander from herd to herd (Frandsen 1998, Le Pendu *et al.* 2000, Skinner and Chimimba 2005), or associate in loose all-male groups (Owen-Smith 1988). Skinner and Chimimba (2005) stated that: "Leadership of a herd tends to be arbitrary and it is impossible to tell which adult fills this role".

Giraffes occur in a wide variety of dry savanna associations, provided their particular range of food plants is available to sustain them through the seasons (Skinner and Chimimba 2005). They do not occur in forests and are not associated with open plains (Estes 1997, Frandsen 1998, Skinner and Chimimba 2005). Males usually prefer denser wooded habitats and females the more open habitats. Within particular habitats, the sexes feed at different heights with males feeding higher (up to 5.8 m) in the canopy (Du Toit 1990a, Ginnet and Demment 1999, Caister *et al.* 2003) than the 2 – 3 m of females, (Grunow 1980).

Giraffes browse on a wide range of food plants though they prefer new protein-rich shoots in the upper canopy (Owen-Smith 1988, Skinner and Chimimba 2005), but also graze occasionally on fresh sprouting palatable grasses (Frandsen 1998, Skinner and Chimimba 2005, Theron 2006). They select food with 14 – 19% protein content year round (Bothma *et al.* 2010). In the Kruger National Park, plant species utilized with the highest frequency were *Acacia nigrescens*, *A. tortilis* and *Dichrostachys cinerea* (Wentzel 1990). According to Owen-Smith (1988), important food genera during the wet season included *Acacia*, *Capparis*, *Combretum*, *Kigelia*, *Securinega* and *Ziziphus* and during the dry season *Albizia*, *Balanites*, *Boscia*, *Colophospermum*, *Diospyros*, *Euclea*, *Grewia* and *Melia*. Their food varies with the time of year (*vid.* Chapter 6). They select leaves of deciduous trees and shrubs in the wet season, *Acacia* spp. are preferred, while in the hot dry months when leaf mass is drastically reduced, they turn to evergreens or semi-deciduous species. They drink regularly when water is available, but can survive independently of surface water for long periods if adequate green foliage is available on trees (Owen-Smith 1988). Giraffes are partial to salt licks and have a high requirement for calcium and phosphate. They search for mineralized soil by walking over an area with the head lowered towards the ground. They lick the soil up with the tongue or may take mouthfuls and are also known to chew on bones, hooves and drying skin (Kok and Opperman 1980, Frandsen 1998, Skinner and Chimimba 2005, Theron 2006, Bothma *et al.* 2010).

7.2.1.2 GREATER KUDU (*Tragelaphus strepsiceros*)

Greater Kudu is a savanna woodland species and does not occur in desert, forest or open grassland areas (also see Table 7.1). They do, however, occur in clearings in woodland (Frandsen 1998, Skinner and Chimimba 2005). Woody plant density and percentage canopy cover probably also serve as cover for protection (Dörgeloh 2001a), since they are sensitive to cold and excessively cold spells can lead to severe mortalities (Bothma *et al.* 2010). They are best suited to areas of bushveld offering a mixture of *Acacia* species, broadleaved deciduous trees and evergreens, and especially if forbs are abundant (Owen-Smith 1985). In the Kruger National Park males have a preference for riparian woodland and thickets along drainage lines, while female herds utilised a variety of habitats (Du Toit 1995b), but during the critical period kudus specifically selected the richer hill slope base ecotone habitat (Owen-Smith 1979). Simpson (1968) showed that in Zimbabwe their preferred habitat throughout the year was riverine *Acacia* thickets. They are partial to areas of broken, rocky terrain where they have a cover of woodland and a nearby water supply (Skinner and Chimimba 2005). The availability of water supply is not an essential habitat requirement in years of normal rainfall, as they can obtain their moisture requirements from their food (Du Toit 1995b).

In the Kruger National Park the plant species utilised with the highest frequency were *Acacia nigrescens*, *Securinega virosa* and *Combretum hereroense* (Wentzel 1990). Skinner and Chimimba (2005) stated that: "Kudu eat a greater variety of browse plants than any other of the subregion's bovids, to the extent that most species that are available are utilised to a greater or lesser degree". Owen-Smith (1979) and Owen-Smith and Cooper (1985, 1987) reported that during the course of a 12 hour day, up to 26 woody species and 36 forb species were eaten by a kudu (also *vid.* Chapter 6). Leaves and shoots are preferred, but they also eat seed pods of *Acacia* trees, leaves of *Aloe* spp., fruits, forbs, creepers, tubers and many plants generally avoided by other browsing species or known to be poisonous (Owen-Smith 1985, 1994, Estes 1997). During the dry season they expand their diet to include evergreen and unpalatable deciduous species, but this alone is inadequate to satisfy their daily energy requirements, even though they extend their feeding duration (Owen-Smith 1994). Kudu exhibit marked sexual size dimorphism where the larger males feed on a higher level (Du Toit 1990a, 1995b) and on thicker shoots than females (Wilson and Kerley 2003).

They have a midday activity spell, particularly in the early growing season when forage is scarce. In other seasons they rest midday in thickets. Daily foraging activity is depressed when temperatures exceed 36°C (Skinner and Chimimba 2005). Mostly in September, they shed their winter pelage and are notoriously prone to mortality should cool damp weather conditions occur in early summer, since they may have inadequate body reserves to meet their energy requirements. By six years of age males show obvious signs of loss of physical condition in the dry season, August/September (Skinner and Chimimba 2005). They are a shy and retiring species and remain constantly on the alert, are cautious and hesitant in their progress when traversing open areas or when approaching water to drink. If disturbed they immediately run for the nearest cover without stopping to observe the cause. In woodland they are, however, less cautious and stand long enough to assess the situation (Skinner and Chimimba 2005).

Greater kudus are gregarious, but the common average group size seems to be four females (Underwood 1978, Owen-Smith 1985, Fabricius 1994, Du Toit 1995b, De Garine-Wichatitsky *et al.* 2004). Simpson (1968) and Underwood (1978) found two peaks in herd size, the first in November to January just before the females were due to calve and the second in June just before the mating season. Owen-Smith (1984a) recorded a peak in solitary males in the Kruger National Park in March just before the rut. Outside the rut, adult males may remain solitary or join up to form small bachelor herds of 2 – 5, occasionally up to 16 (Du Toit 1995b, Estes 1997, Skinner and Chimimba 2005). At the time of the rut an adult male may accompany a herd of females and their offspring from April to June (Owen-Smith 1985, Du Toit 1995b, Frandsen 1998, Skinner and Chimimba 2005). While several males may be seen together with a female group during the breeding season, usually only one of these is a fully mature bull (Owen-Smith 1985). Breeding bulls are not territorial but are spread out as a result of the spacing between home range centers of different female social units (Skinner and Chimimba 2005).

7.2.1.3 ELAND (*Tragelaphus oryx*)

Eland are highly versatile in habitat selection, occurring in the Nama Karoo and Succulent Karoo Biomes, the Grassland and Savanna Biomes (see Table 7.1), also penetrating into the Fynbos Biome and even in montane forests at altitudes of up to 4 600 m (Estes 1997, Skinner and Chimimba 2005). In mountainous habitat they are known to move up and down the mountains (Skinner and Chimimba 2005). They avoid dense forests and deserts (Estes 1997). Shade-seeking is an important behavioural characteristic for thermoregulation as eland are not prone to orientate their bodies according to the angle of the sun, as some other bovid species do (Skinner and Chimimba 2005).

A small percentage of grass is usually included in their mixed feeder diet, even in winter months when they include more browse (Skinner and Chimimba 2005). During the dry months eland are assiduous in their search for green foliage, but they also eat the dry fallen leaves of their normal food plants (also *vid.* Chapter 6). Eland use their horns effectively to gain access to higher foliage of shrubs and trees by breaking branches. There are distinct seasonal changes in the percentages of some of the main food plants utilized (Grunow 1980, Estes 1997, Skinner and Chimimba 2005). They occur in a wide variety of habitats and where they are highly nomadic it will enable them to utilize sparsely distributed shrub and woodland during the dry season (Buys and Dott 1991).

Rowe-Rowe (1994) described the unique social organization of eland as follows: During summer they form large mixed herds of up to 200, comprising non-breeding and breeding males and females. Breeding females are served only by dominant males. In autumn the large herds disperse in numerous small groups of 4 – 10 animals of any age or sex. They are widely dispersed in winter. Just after the calves are born in spring, small groups begin joining together again to form large herds that gradually increase in size (Rowe-Rowe 1994). Underwood (1981) recorded a similar social organization in the Loskop Dam Nature Reserve and suggested that the total population of approximately 80 animals formed one diffuse social unit. It is not unusual for young to outnumber adults and there may even be herds composed entirely of calves and juveniles. Conversely, unisexual or bisexual small groups consisting of adults only are also common. This variability reveals the open, fluid nature of eland society (Underwood 1981, Hillman 1988, Estes 1997).

Considerable home-range overlap has been observed in Kenya, but became less in the dry season (Hillman 1988). Underwood (1978), in a study of eland in a 120 km^2 fenced area (Loskop Dam Nature Reserve), considered the area to be too small for the purpose of home-range measurements and experienced adult females breaking out of the area. No territoriality, in the sense that eland defend an area, has been described. Their hierarchy appears to be based on matrilineal genealogy, age and size, with older larger males dominating younger smaller ones (Cransac and Aulagnier 1996, Skinner and Chimimba 2005).

Newly born calves have a tendency to follow any moving object larger than themselves, but soon learn to follow their mothers. Small groups of calves temporarily become associated with a single female and can be observed as strung out in single file in decreasing order of size behind her. A female only suckles her own calf (Anonymous 1992a, Skinner and Chimimba 2005). While the calf is still very young the female will take it to a suitable hiding place where it stays when she goes to feed. After weaning, the calves may join up in a nursery herd (Anonymous 1992a, Cransac and Aulagnier 1996, Estes 1997, Skinner and Chimimba 2005).

7.2.1.4 IMPALA (*Aepyceros melampus melampus*)

Impala is an ecotone (edge) species and can thrive in areas where natural vegetation has degenerated due to overgrazing or bush encroachment, like along reserve roads and tracks (Pettifer and Stumpf 1981, Estes 1997, Skinner and Chimimba 2005, Matson *et al.* 2006). They have some preference for *Acacia* woodland throughout most of the year (also see Table 7.1), but it usually becomes pronounced during the dry months from April to September (Monro 1980). In contrast to the common impala, the black-faced impala (*A. melampus petersi*) prefers dense riparian thickets next to open savanas in arid regions (Bothma *et al*. 2010).

Impala generally avoid open grassland and floodplains, but occur on the ecotone between these areas and woodland. However, they will graze in open grassland with a flush of fresh green grass, preferring grassland of low to medium height (Grunow 1980, Estes 1997, Skinner and Chimimba 2005, Matson *et al.* 2007) and a herbaceous cover of 26% – 75% (Wentzel 1990). Some separation occurs as males prefer denser habitats that females usually avoid – this is also the case for eland and giraffe (Murray 1982, Estes 1997). In Zimbabwe they moved from mopane woodland in the wet season to riverine habitat in the dry season (Dunham 1982, Murray 1982). In the Jack Scott Nature Reserve, Krugersdorp they frequented the ecotone between the *Protea caffra* tree veld and grassland (Mason 1976a). They are obligate drinkers and where water is freely available they drink daily (Matson *et al.* 2006), usually not venturing more than 2 km from water (Bothma *et al.* 2010). This dependence on water increases during the dry season due to the physiological need to eliminate nitrogenous waste imposed by their high crude protein intake (Fairall and Klein 1984).

Grass has been found to constitute 90% of their diet in the wet season, declining to 65% in the dry season (Van Rooyen 1992, Meissner *et al.* 1996, Skinner and Chimimba 2005). Owen-Smith and Cooper (1987) described impala as preferential grazers and woody plants only occupied 15% of their feeding time. They are patch-selective grazers (Bothma *et al*. 2010) that prefer green grass and sometimes move to riverine areas during the dry season in search thereof (Estes 1997, Frandsen 1998, Skinner and Chimimba 2005). They can change their diet in an area according to season and can also adapt to different habitats by being mainly a grazer in one and a browser in another (Estes

1997). Browse is eaten while green but dry leaves are picked up from the ground and still remain an important part of their mixed feeder diet, particularly in the dry season, even when an abundant supply of green grass is available (Estes 1997, Skinner and Chimimba 2005). Fine twigs and leaves of *Acacia* spp. are common items in their diet, while the seedpods are also sought-after (Owen-Smith and Cooper 1987, Skinner and Chimimba 2005). There is evidence of sex-based dietary differences (Wronski 2002), for example in the Kruger National Park males grazed 14% more than females (Sponheimer *et al.* 2003) and it is known that males (both territorial and in bachelor herds) usually have a suboptimal diet due to the habitat they use or time spend on other activities (*vid.* Chapter 6, General Discussion).

Murray (1982) demonstrated that the overall dispersion of females and juveniles were discontinuous in the Sengwa Wildlife Research Institute, Zimbabwe and referred to it as a clan system. Females and juveniles from the same cluster constituted one clan and clans consisted of 30 to 120 impala. These were not closed units and mixed-clan groups also occurred (Mason 1976a, Murray 1982, Estes 1997). According to Estes (1997), there is no sign of a rank order or regular leadership between females, even though the female herds can be very cohesive at times and herd activities are closely synchronized. Single females or a female with a lamb are also common during breeding times (Matson *et al.* 2007).

Breeding herds consist of juvenile and adult females and juvenile males, and at times also include several males. Nursery herds consisting solely of juveniles have been recorded, but are temporary. Bachelor herds occupy areas away from breeding herds. They are less cohesive than breeding herds and adults leave during the rut to establish and hold territories for a few months at a time and return after the rut (Mason 1976a, Pettifer and Stumpf 1981, Estes 1997, Skinner and Chimimba 2005, Oliver *et al.* 2006). There is a relationship between the size of the territory and population density, location, habitat quality, individual prowess and seasons (Estes 1997, Skinner and Chimimba 2005). Herds are usually not territorial, but move around a watering point. Territories of 2 – 10 ha are only formed during late summer and autumn (Bothma *et al.* 2010).

The whole of the lamb crop is born within a restricted period of a few weeks (Frandsen 1998), usually between November and January. There have been reports of occasional births out of season (Pettifer and Stumpf 1981, Skinner and Chimimba 2005, Oliver *et al.* 2006). Juvenile females grow up in the breeding herds and remain with them throughout their lives. Large nursery herds, up to 108 animals, were observed in the Loskop Dam Nature Reserve (Pettifer and Stumpf 1981).

7.2.1.5 COMMON DUIKER (*Sylvicapra grimmia*)

Common grey duikers are shy and inconspicuous species (Rovero and Marshall 2004, Lunt *et al.* 2006). They usually avoid koppies, areas that are too open under the canopy and open short grassland (also see Table 7.1). When they are observed in grassland they are probably seeking low-growing forbs and other browse plants growing there. They are found on the fringes of forested areas, but avoid forests themselves. They occur widely from *Acacia* woodland and scrub, to fynbos and on the fringing scrub of agricultural lands, as well as in cultivated lands where crops can provide shelter (Skinner and Chimimba 2005).

Duikers are predominantly browsers in savanna ecosystems, but are opportunistic frugivores that are fond of eating fruits (Wilson 1966, Lunt *et al.* 2006). Bothma *et al*. (2010) describe them as patch-selective feeders. In Zambia, leaves of 45 species of plants are known to be eaten, fruits and seeds of 33 species and the flowers of 15 species (Wilson 1966). Kigozi (2003) found that only two of the 19 species identified from duiker faecal material in the Eastern Cape Province were monocotyledons (grasses) and had a combined annual percentage of 2% in their diet. Duikers stand on their hind legs, steadying themselves on the branches with the forelegs to reach the fruits and twigs of shrubs. About 400 g of mushrooms were found in one stomach (Hofmann 1973) and they have been recorded to feed on chicory and other crops as well (Kigozi 2003). Duiker occasionally consumes animal matter such as eggs, small rodents or birds (Roosendaal 2008).

Home ranges of common duiker males and females appear to be equal in size. Male home ranges partially overlapped the ranges of at least two females (Estes 1997, Lunt *et al.* 2006). Lunt *et al.* (2006) estimated the density of duikers in the Dambari field station near Bulawayo, Zimbabwe as 9.68 duikers / km^2. Skinner and Chimimba (2005) described their characteristic behaviour when approached as “springing up almost under one's feet and bounding off with characteristic plunging jumps before disappearing into the nearest cover”.

Grazer game species

7.2.2.1 BLUE WILDEBEEST (*Connochaetes taurinus taurinus*)

The preferred habitat of blue wildebeest (also see Table 7.1) in northern KwaZulu Natal is open woodland dominated by *Acacia nigrescens* (Skinner and Chimimba 2005). At the Messina Experimental Farm, 20 km west of Musina, Limpopo Province they preferred the *Colophospermum mopane* low closed woodland in the dry, hot season and the *Kirkia acuminata* short closed woodland in the wet season (Dekker *et al.* 1996). In the Kruger National Park, they preferred the plains and higher slopes (De Wet 1988). They are associated with gentle north-facing slopes with no rockiness (Bothma *et al*. 2010). They have a wide distribution in savanna shrubveld and mixed- and sweet grassland over a wide range of rainfall conditions (Grunow 1980). Blue wildebeest are in general not more than 100 m from the nearest shade (Bothma *et al*. 2010). Black wildebeest (*C. gnou*), and not blue wildebeest, is the more common species in the Free State province and these two species hybridize readily (Skinner and Chimimba 2005, Bothma *et al*. 2010).

Blue wildebeest prefer feeding on short green lawn-like grassland that is leafy and nutritious (Estes 1997, Frandsen 1998, Ego *et al.* 2003, Skinner and Chimimba 2005, Furstenburg 2007a), where the herbaceous cover is 25% or less (Wentzel 1990). They are particularly partial to fresh sprouting grass on burnt areas or fresh grass sprouting after rain (Talbot and Talbot 1963, Grunow 1980, Wentzel 1990, Frandsen 1998, Skinner and Chimimba 2005). Ben-Shahar (1991) showed that the wildebeest diet alternated with seasons, showing high preferences during the winter for grasses that were rejected during summer. Ego *et al.* (2003) recorded a browse component of 1.9% in the wet season and 3.8% in the dry season in Kenya, while Bothma *et al*. (2010) reported up to 13% browse and forbs in their diet. According to Bell (1971) and Ego *et al.* (2003), blue wildebeest do not seem to be capable of selecting for grass leaves in tall grass vegetation types. Instead, they maximise their intake of grass leaves by migration or association with less selective ungulates in the grazing succession, like zebra or even gemsbok.

Blue wildebeest can occur in large mixed groups of mostly 15 – 30 in size, smaller bachelor herds, or alone (Berry 1981, Attwell 1982, Estes 1997, Skinner and Chimimba 2005). Breeding herds in the Umfolozi Game Reserve and the corridor connecting it to Hluhluwe Game Reserve (The Complex) are not a cohesive unit, but considerable fluidity exists, while in East Africa they have a fixed membership over at least 5 months following the calving season (Attwell 1982). Territories in the Kruger National Park are set and maintained all year round by bulls in the migratory subpopulation (Whyte 1985). In the Kgalagadi Transfrontier Park, territories are maintained as long as environmental conditions are favourable (Skinner and Chimimba 2005). Attwell (1982) observed that the territorial drive tended to wane at the end of the dry season. Bulls lose condition in times of drought and abandon territories as waterholes dry up, when they join bachelor groups (Skinner and Chimimba 2005). Verlinden (1998) showed that they tend to go back to the same wet season range.

Bachelor groups are loose associations of adult and young males that occupy areas on fringes of the populations' home range on the least desirable parts of the habitat (Estes 1997, Skinner and Chimimba 2005). A great majority of bulls are inactive during the rut, remain in bachelor herds or alone, with continuing interchange of bulls in these herds as previously inactive bulls become active and active bulls retire from attendance of their harem herds. Active bulls defend an area of up to 30 m in diameter around themselves or their harem herd, with a density of up to 270 bulls / km^2. The size of this zone depends on the density of the population and is spatial and moveable, it can range between 0.5 and 1.5 ha in total (Talbot and Talbot 1963, Estes 1997, Skinner and Chimimba 2005, Bothma *et al*. 2010). According to Attwell (1982), bachelor herds were small in the Umfolozi Game Reserve and the corridor connecting it to Hluhluwe Game Reserve (The Complex) and never attained sizes recorded in East Africa. If adaptation to open habitats favours group formation, the relatively small herd sizes in The Complex may be an adaptation to woodland.

In the Kgalagadi Transfrontier Park births were synchronised within a three week period and occurred in December, January and February. There seem to be an inherent rhythm in their breeding activities that may be influenced by prevailing climatic conditions (Skinner and Chimimba 2005). Females do not seek isolation during parturition, but congregate on calving grounds (Estes 1997).

7.2.2.2 BONTEBOK (*Damaliscus pygargus pygargus*)

The bontebok was an extremely endangered subspecies, its numbers fell to less than 100 individuals before conservation measures in the first half of the century enabled it to recover (Fabricius *et al.* 1989). Their IUCN conservation status is "vulnerable to extinction", because their total population size is < 3 500 animals (Bothma *et al.* 2010). Bontebok usually occur in the Fynbos biome (also see Table 7.1) in a narrow section of coastal plains at an altitude of 60 – 200 m above sea level, in a section of renosterveld (Skinner and Chimimba 2005, Furstenburg 2006b). In the Bontebok National Park they find their preferred grass species in a sandy alluvial plain with stony ridges and gravel terraces associated with shrubs 300 – 700 mm high that provide shelter (David 1973, Bothma *et al*. 2010). In riparian *Acacia* associations, more substantial cover in the form of trees is present on the banks of rivers or streams (Skinner and Chimimba 2005). Langley and Giliomee (1974) found that burnt areas and firebreaks were favourite feeding areas in the Cape Peninsula National Park, Western Cape as well as areas where *Stenotaphrum secundatum* (coastal buffalo grass) was well established. They also feed on *Oxalis hirta*.

The social behaviour of the bontebok is similar to that of blesbok (Bothma *et al*. 2010). Bachelor herds have no hierarchy or aggression between members and may consist of a large number of males, including young- and old, decrepit animals, as well as deposed territorial males and some young females (David 1973, Estes 1997, Frandsen 1998). According to Skinner and Chimimba (2005), territorial males might be so overwhelmed by the numbers of bachelor herds that they couldn't chase all the males out of the territory. Usually the bachelor herd gives way to the territorial male without encounter. According to David (1973), territorial density in the Bontebok National Park was 1.5 males/km^2, with an average spacing of 300 m between males. Females' home ranges included 2 – 3 territories, but a herd might also remain in a single territory for over a year (Estes 1997). Bothma *et al*. (2010) reported the range of a herd to vary between 350 – 600 ha and the territories from 4 to 30 ha. Furstenburg (2006a) calculated optimal habitat in the Bontebok National Park to be 10 ha/animal for feeding and 600 ha for movement.

Differences between bontebok and blesbok: Bontebok have a deep purplish colour contrasting with the pure white on the belly, legs and buttocks and rust brown of the back, together with the white facial blaze which extends unbroken from the top of the head to the tip of the snout (rhinarium). In comparison, the blesbok is much more drab and the coat is uniformly brown with only the underparts being offwhite (Frandsen 1998, Skinner and Chimimba 2005). Bontebok also differ in behaviour and social structure (Fabricius *et al.* 1989). Blesbok are the more common species occurring in the Free State (Frandsen 1998, Skinner and Chimimba 2005). The hybridization of blesbok and bontebok is a serious concern in areas where they are kept together (Fabricius *et al.* 1989, Skinner and Chimimba 2005). Hybrids have been widely translocated within southern Africa and can destroy the genetic integrity of the bontebok, thereby threatening its extinction (Fabricius *et al.* 1989, Furstenburg 2006b, Du Toit *et al.* 2010).

7.2.2.3 BUFFALO (*Syncerus caffer caffer*)

De Wet (1988) concluded that African Savanna Buffalo (or Cape Buffalo) preferred veld conditions with optimal grass species composition in the Kruger National Park (also see Table 7.1). They readily feed on old grass and are less partial than some other herbivore species to fresh, sprouting, young grass on recently burnt areas. They avoid areas where the grass has been trampled or overgrazed (Estes 1997, Skinner and Chimimba 2005). Perrin and Brereton-Stiles (1999), as well as Macandza (2003) indicated that buffalo selected for grass species offering a higher percentage of green leaves (*Panicum maximum*, *P. coloratum*, *C. ciliaris*, *Heteropogon contortus*, and *Digitaria eriantha*) and avoided grass species high in secondary plant compounds. Buffaloes are gregarious grazers and because of their large size can process taller grasses than most other members of the grazer guild, potentially playing a facilitative role for species limited to shorter grass resources (Senft *et al.* 1987, Perrin and Brereton-Stiles 1999, Jolles 2007).

Macandza *et al.* (2004) showed that buffalo adjusted their grass species selection and feeding localities through the critical period in relation to seasonally changing forage quantity and quality. Sinclair (1977) found that the distribution and movement of buffalo functioned to maximise utilisation of the optimum habitat at the height of food scarcity. According to Funston *et al.* (1994), there is a danger that the habitat will be irreparably damaged when the movement of buffalo is restricted, as happens in game reserves, if numbers are not controlled. Also, the provision of widely spread waterholes may allow buffaloes to utilise areas which would not have been available in hot dry months, thus reducing large mammal concentrations along normally depleted riverine areas and providing a management tool for dispersion of the herds (Funston *et al.* 1994).

In the Serengeti, large herds are subject to seasonal migration, moving to permanently watered areas during the dry season and moving out with onset of the rains (Sinclair 1977). Buffaloes at the back of a large aggregated herd are mostly in worse condition and as a result separate more easily from the herd (Estes 1997). In Sabi Sand Game Reserve, buffalo also showed seasonal variation in habitat selection due to water availability (Funston 1992). Macandza (2003) reported most feeding sites to be located in bottomlands in July, but with the progress of the dry season buffalo increased the utilisation of midslopes and uplands. According to Winterbach (2000), the most crucial vegetation types for buffalo in the Willem Pretorius Game Reserve are the woody riverbank and wetland grasslands. Buffalo in the Sabi Sand Game Park had favoured grazing areas and routes between resource patches but they did not show a fixed pattern of range utilisation (Funston 1992). Suitable grasses are found in a variety of woodland types, including *Acacia*, *Baikiaea*, *Brachystegia*, *Colophospermum* and in the open vleis that occur in association with some of these woodland types. They may temporarily use open grasslands for a time after sunset or before sunrise, but they require shade during the hotter parts of the day (Skinner and Chimimba 2005).

African Savanna Buffalo herds have clearly defined home ranges that show little overlap with those of neighboring herds. These home ranges vary in size seasonally to include areas where food or water becomes plentiful (Funston *et al.* 1994, Skinner and Chimimba 2005, Ryan *et al.* 2006). Buffaloes remain in vicinity of water in the dry season and move extensively from it during the rains (Sinclair 1977, Prins 1996). Buffaloes living in wetter areas have smaller home ranges than those in drier areas. In the Sengwa Wildlife Research area, Zimbabwe, home range sizes were 250 km^2 (Conybeare 1980), while on the Botswana/Zimbabwe border it was between 920 km^2 and 1 455 km^2 (Hunter 1996). In the Sabi Sand Game Reserve, Mpumalanga, buffalo had a home range of about 41 km^2 in the moist hot summer, while in the cool dry winter the herd used almost the entire home range of about 120 km^2 (Funston *et al.* 1994). Groups of old males of about 5 – 10 bulls may also form and remain sedentary in a small area of about 3 – 4 km^2 for a few years (Estes 1997).

7.2.2.4 BURCHELL’S ZEBRA (*Equus burchelli*)

Bothma *et al.* (2010) stated that: “despite being regarded as a distinct species *E. quagga* (plains zebra) by Skinner and Chimimba (2005), they are generally still accepted as subspecies of *E. burchellii* by most world taxonomic authorities such as Grubb (2005)”. Burchell’s zebras do not occur in forest or dune desert and avoid areas of dense woodland except in transit. Fischhoff *et al.* (2007b) concluded that zebras preferred grassland areas in the Sweetwaters Reserve, Kenya, but changed to woodland at night in order to try and avoid lions that hunted more in the grassland at night.

They are natural migrants and undertake daily and seasonal migrations to areas where better grazing conditions, or newly burned areas and water-supplies are available. They seldom move more than 8 km from water (Skinner and Chimimba 2005, Fischhoff *et al.* 2007a, Bothma *et al.* 2010). The local small-scale movements cannot attain the scope of those in Namibia or the Serengeti in East Africa, where they exceed 200 km during their well-known mass migrations (Skinner and Chimimba 2005). The mother-foal bond is very close and the mare will drive off any other zebras that approach too closely and defend the foal against predators. If the group is disturbed, the mare and foal take the lead position, protected by those behind and by the stallion at the rear (Skinner and Chimimba 2005).

They will occasionally browse and feed on herbs (Frandsen 1998, Okello *et al.* 2002, Skinner and Chimimba 2005, Fischhoff *et al.* 2007a). Zebras selected recently burnt areas in the Kruger National Park (Smuts 1972). They are equipped to deal with both long, tough stems and the early stages of a flush, which makes them the pioneers that leads the way into areas of long grass and prepare it for wildebeest, gazelles and other associated antelopes (Estes 1997).

Zebra and blue wildebeest are often classified as bulk and roughage grazers of a similar body weight, but they differ in their digestive system, buccal anatomy and incisor structure (Ben-Shahar 1991). Zebras consume more than twice the kg dry matter per day than wildebeests do (Bothma *et al.* 2010). These two ungulates normally graze in association with each other and usually occur in large numbers on reserves. They may therefore have a profound effect on the composition of vegetation (Ben-Shahar 1991, Bodenstein *et al.* 2000). There is an overlap in the grass species selected by zebra and wildebeest (Owaga 1975, Bodenstein *et al.* 2000) and Ben-Shahar (1991) found that they shared 19 of the 24 plant species consumed by both in the Sabi Sand Game Reserve. According to Ben-Shahar (1991), there was a certain degree of separation in their diets which was evident from seasonal patterns of species selected by wildebeest and through the hierarchy in the preferred species of zebra. According to Bodenstein *et al.* (2000), zebra will select shorter grass if given the choice, although they are regarded as tall grass feeders. The bite size of a zebra is bigger compared to the blue wildebeest and therefore the zebra can take bigger portions of grass at a time.

Fibre digestion is less effective in hindgut fermenters such as the zebra (Illius and Gordon 1992, Bodenstein *et al.* 2000, Fischhoff *et al.* 2007b). According to Bodenstein (2000), the zebra’s more rapid throughflow of food and its higher forage intake can be an advantage which outweighs its lower digestive efficiency, particularly on poor quality forage. As long as zebra can increase its intake of forage, provided that the total volume of food is not limiting, it will be able to compensate for its lower digestive efficiency (Ben-Shahar 1991, Bodenstein 2000). They eat mineralised soil to compensate for deficiencies (Frandsen 1998), like giraffe.

7.2.2.5 GEMSBOK / ORYX (*Oryx gazella*)

Gemsbok frequented open and dense habitats in Etosha National Park (also see Table 7.1), with females tending to be more associated with denser habitats than males (Møller *et al.* 1996). In Namibia they utilize a diversity of plant communities, such as those of the extensive dune fields, sand plains, mountains and the succulent steppe (Skinner and Chimimba 2005). In the Kgalagadi Transfrontier Park they showed a preference for sand dune country with a sparse cover of vegetation and short annual grasses (Eloff 1959, Knight 1991). When water became restricted due to a severe drought in Etosha National Park, some fatal body attacks by gemsbok were observed with dominant males and females mostly winning the fights (Walther 1980, Møller *et al.* 1996).

Gemsbok prefer green grass, but also eat dry grass. Their teeth, short face and narrow gape are specifically adapted for close cropping of coarse desert grasses (Estes 1997). They often have grazing peaks at night when dew on grasses can supplement their moisture intake (Bothma *et al.* 2010). In the Kgalagadi Transfrontier Park their summer diet consisted of 89% grass, 7% browse and 4% dicotyledons, while in winter it consisted of 76% grass, 16% browse and 8% dicotyledons (Knight 1991). Browsing was also reported by Dieckmann (1980) Estes (1997) and Bothma *et al.* (2010). Pods of *Acacia* trees are readily eaten by gemsbok (Bothma *et al.* 2010).

Field (1975) noted that buffalo, eland and gemsbok grazed within the grass/herb layer during the early growth period. He also noted that annual and drought tolerant grasses formed the main diet of gemsbok, while buffalo and cattle fed on bulky perennial grasses. Knight (1991) found a diet overlap also between blue wildebeest and gemsbok and it was greatest during the wet-hot period when food was abundant. When food became scarcer and of poorer quality, greater partitioning between the two species became evident and occurred at the habitat, time of day, plant species and plant-part levels.

7.2.2.6 RED HARTEBEEST (*Alcelaphus buselaphus*)

Red hartebeest graze selectively on leafy perennial grasses (Estes 1997, Ego *et al.* 2003) and specialize on tall grass (Novellie 1990, Murray and Brown 1993). According to Murray (1993), "they digest fibre more efficiently, but have a smaller appetite, than other grazing ruminants". Van Zyl (1965) and Kok and Opperman (1975) recorded 44% and 40% browse in their diet respectively. Bothma *et al.* (2010) reported a browse component of between 25 and 44%. Kilian (1993) found browse to contribute significantly to their diet in the limiting, critical period (Sept/Oct), but in other seasons they were overwhelmingly grazers. Ego *et al.* (2003) calculated a browse component of 1.2% during the wet season in a private game ranch in Kenya and 3.4% in the dry season. They found a dietary overlap with blue wildebeest of 77% – 86% between wet and dry seasons. They are the first antelope to lose body condition when veld deteriorates (Bothma *et al.* 2010).

According to Skinner and Chimimba (2005), the social organisation of naturally occurring red hartebeest has not been studied in detail. Kok (1975) found that males herded females and were territorial, actively defending their territories. He found that harem herds were stable for up to three years in the Free State and consisted of females with their offspring, a dominant bull and young bulls. Solitary males were not uncommon in Botswana (Skinner and Chimimba 2005) but were rare in the Free State (Kok 1975).

Expectant females isolate, accompanied by one or more previous offspring (Estes 1997). The female leaves the newborn calf hidden (also see Table 7.2) while she grazes nearby or temporarily joins the harem herd (Kok 1975, Anonymous 1993a). A calf lies motionless if approached during the first few days of its life, with its head lowered to the ground (Kok 1975). When the calf is strong enough to follow the mother she leads it back to the harem herd. As the calves grow up they form calf groups in the harem herd (Skinner and Chimimba 2005).

7.2.2.7 RED LECHWE (*Kobus leche*)

Red Lechwe are associated with swamps and specifically adapted for this habitat type, therefore most of the information available on lechwe is for swamp, marshy habitat types. The floodplain in the Linyanti Swamp, Botswana is seldom more than a kilometer wide and red lechwe occur there in densities of 7 – 12/km^2 (Williamson 1994). Williamson (1990) identified 52 plant species eaten by lechwe of which 54% were grasses, 25% sedges and semi-aquatic plants, and 21% dicotyledons, although less than 0.2% of time was spent feeding on dicotyledons. The most intensively grazed species in the Linyanti Swamp, Botswana were *Eragrostis inamoena*, *E. lappula*, *Cynodon dactylon*, *Panicum repens* and *Setaria anceps*. Burning of the floodplain created a short sward of green, vigorously growing grass that attracted large numbers of lechwe (Williamson 1990). Rees (1978) listed *Brachiaria* spp., *C. dactylon*, *Digitaria* spp., *Diplachne fusca*, *Echinochloa holubii*, *Eragrostis* spp., *Leersia* spp., *Panicum coloratum*, *P. repens*, *Setaria sphacelata*, *Sporobolus natalensis* and *Vossia cuspidata* as some of the grasses utilized by lechwe in the Lochinvar National Park, Zambia. Introduced lechwe in South Africa adapted well to sweet tall grass environments next to rivers and wetlands. Common grass species included are *P. repens*, *Eragrostis lappula* and *Cymbopogon excavatus* (Furstenburg 2005a).

They usually have a classic lek mating system, namely a cluster of small territories, from 0.5 – 6 ha in size, with a density of 70 – 90/km^2 (Table 7.2). There are 15 – 20 territorial males per lek in the Linyanti Swamp in Botswana (Williamson 1979, 1994) and 50 – 175 Kafue lechwe males (*K. leche kafuensis*) in the Lochinvar National Park, Zambia (Schuster 1976). Lechwes have minimal sexual segregation during the breeding season and maximum segregation outside it (Estes 1997, Furstenburg 2005a). De Vos and Dowsett (1966) described it as a resource defense territoriality among adult males. A number of these males, along with females and young, occupy a mating ground of 0.04 km^2 in which territorial males tend to situate themselves in the centre, but not necessarily equal distances from each other. On the fringe of this mating ground other males establish themselves in small herds. This territorial behaviour may occur from a few days to several months (2 weeks – 20 months in Linyanti Swamp), depending on water levels in the swamps (Williamson 1994).

Territorial males remain on the same piece of ground (diameter 50 – 100 m) of about 2 – 6 ha in the swamp during occupancy of the mating ground, even if the females move elsewhere (Williamson 1994, Skinner and Chimimba 2005). Territorial males permit sexually inactive males into their territory (Frandsen 1998), but other adult males usually avoid territorial areas during the day (Williamson 1993) while spending the night next to the water in a territory (Williamson 1994). Changes between territorial ownership can be from 2 days to over a year (Williamson 1994). In small, resident populations, like in wildlife reserves, the conventional arrangement of female and bachelor herds kept segregated by territorial males can also be seen (Estes 1997). Differences in territory size and duration of territory tenancy may be linked to ecology via density. Higher densities result in more competition and increased energy expenditure per unit area of defense (Williamson 1994).

Lechwe are water-loving animals. They are not fast on land, but swim strongly (Williamson 1990, Frandsen 1998, Furstenburg 2005a, Skinner and Chimimba 2005, Bothma *et al.* 2010). They actively use water to moderate heat stress, resulting that they are often active when animals in drier conditions would be resting (Williamson 1990, 1993, Estes 1997, Frandsen 1998). Resting sites are usually on termitaria or near water with good visibility (Williamson 1990). Rising water levels may act as the proximate cue for initiation of mating. This enables lechwes to produce calves at times of optimum forage seven months later when the flood waters recede and the advent of the rains produces a lush growth of grass (Skinner and Chimimba 2005).

Lechwe and waterbuck are in direct competition and may cross-breed where they are confined in small areas (Furstenburg 2005a). Lechwe are intolerable to overgrazed grassland and cannot co-exist with short grass feeders. They are shy of humans and will usually move away. Lechwe cannot stand high density game species and will show a decline in production if they are subjected to it (Furstenburg 2005a).

7.2.2.8 ROAN ANTELOPE (*Hippotragus equinus*)

Roan antelopes were regarded as endangered in the South African Red Data Book (Smithers 1986), because of habitat loss and –fragmentation (Martin 1983, Perrin and Taolo 1999). The Antelope Specialist Group classified roan as "Lower Risk (conservation dependent)" in the IUCN Red Data Book (ASG 1998). Currently its conservation status is "vulnerable to extinction" (Bothma *et al.* 2010). These antelopes reach their highest abundance in moist savannas (1 000 – 1 200 mm annual rainfall), where soils are mainly infertile and support grazing of low quality (Martin 1983, Heitköning and Owen-Smith 1998). Areas of short grass or thick woodland with a closed canopy are usually avoided (Allsopp 1979, Martin 1983, Heitköning and Owen-Smith 1998, Skinner and Chimimba 2005).

They are predominantly grazers that feed on medium to long grass (also see Table 7.1). Consequently it is important to monitor herbivores that keep grass cover short, like white rhino, red hartebeest, black- and blue wildebeest, as well as zebra (Harrington 1996, Perrin and Taolo 1999). Roan are extremely sensitive to the presence of other herbivores, especially around a waterhole (Bothma *et al.* 2010). Roan are not close croppers, such as zebra or wildebeest (Martin 1983, Skinner and Chimimba 2005, Knoop and Owen-Smith 2006). Roan's habitat selection of floodplains and 'vleis' with tall grass cover isolates them to some extend from grazing competition from short-grass grazers (Knoop and Owen-Smith 2006). The availability of grass species plays an important role in food selection. A few grass species make up the bulk of their diet and their preferences of grass species change between different seasons and vary between their different distribution areas. Sprouting grass in newly burnt areas is sometimes attractive to roan, but they prefer taller grass stands (Dörgeloh 1998, Perrin and Taolo 1999, Skinner and Chimimba 2005).

Roan, like sable antelopes, select perennial grasses that grow in leached soils of poor nutrient status which support a low herbivore biomass (Estes 1997, Heitköning and Owen-Smith 1998). Wilson (1975) stated that roan remained in better body condition than sables in the Limpopo Province because they switched to browse during critical periods, including leaves of *Acacia* spp., *Searsia lancea*, *S. pyroides* and *Olea africana***.** Poché (1974), Dörgeloh *et al.* (1998), Frandsen (1998), Skinner and Chimimba (2005) also indicated browsing as part of roan's diet in winter. In Namibia 19 woody species, including karroid shrubs were incorporated in the diet, with some of the trees being *Acacia karroo*, *S. lancea*, *S. pyroides* and *Ziziphus mucronata* (Martin 1983). Different dry and wet season home ranges are used to compensate for areas that cannot sustain roan during dry seasons (Estes 1997, Perrin and Taolo 1999). In Weenen Nature Reserve, KwaZulu Natal roan showed a preference for low-lying medium to open bushveld in the dry season and for upland tall grassveld in the wet season (Perrin and Taolo 1999). They often associate with hartebeest and waterbuck (Poché 1974).

Depending on the situation, roan may or may not exhibit territorial behaviour, probably determined by the degree of aridity (Martin 1983), where they have an activity zone rather than a territory and defend a harem of females throughout the year (Joubert 1970). All members of the herd vigorously horn bushes and grass, thrusting and twisting to strip leaves and debark stems, or just gently rub their faces against it to serve as visual and scent markers that indicate their possession of the area (Skinner and Chimimba 2005). Individual members of roan herds space themselves 5 – 10 m apart, giving the herd the appearance of a loose structure (Estes 1997, Skinner and Chimimba 2005).

The female leaves the herd before the calf is born and seeks cover for her and concealment for the calf (Allsopp 1979, Dörgeloh 1998, Heitköning and Owen-Smith 1998, Skinner and Chimimba 2005). After it is born she remains nearby for a few days, thereafter rejoins the herd, leaving the calf in concealment. She suckles the calf in the morning and evening (Allsopp 1979, Estes 1997, Skinner and Chimimba 2005). If she is the dominant female, the whole herd may follow her to near where the calf is concealed. The association between a female and her female calf may persist for a long time, but a bull calf is driven from the herd by the dominant bull resulting in an increase in mortality rate (Skinner and Chimimba 2005).

7.2.2.9 SOUTHERN REEDBUCK (*Redunca arundinum*)

Southern reedbuck (or Common Reedbuck) prefer wetlands and drainage lines (O'Connor and Krüger 2003), with tall grass up to 2 m high, reeds or herbaceous cover (Bothma *et al.* 2010). Extensive areas of broken veld are of paramount importance to reedbuck: it provides adequate cover by means of boulder outcrops, gullies and ledges that support rank vegetation, and generally broken physiography which allows escape from danger by disappearing over a ridge, around a hillside or over its top, etc. (Howard 1986b). They avoid flat open veld and vacate areas where bush encroachment and clean burning have occurred (Howard 1984, Estes 1997, Skinner and Chimimba 2005). They tend to use fixed trails leading to water (Skinner and Chimimba 2005). Reedbuck are almost exclusively grazers, although they also eat forbs and may browse extensively in winter (Anonymous 1991, Estes 1997, Frandsen 1998, Skinner and Chimimba 2005).

Reedbuck is not a gregarious species and usually forms family parties of 2 – 3. A female is often accompanied by two successive offspring (Table 7.2). Daughters mature and leave the territory after two years, up to a year earlier than sons, which are tolerated almost to maturity by their fathers (Estes 1997). Reedbuck in KwaZulu-Natal are not as territorial as those in the Kruger National Park: at St Lucia a social hierarchy is evident whereby dominant males compete to serve females in oestrus, while in the highland regions males display evidence of territoriality only during the rut, with dominant males occupying territories closest to the food source (Venter 1979, Howard 1984, 1986a, 1986b). In the Kruger Park a pair occupies a territory and move about independently, but maintains contact through numerous olfactory and visual signals as well as whistling (Jungius 1971). Normally they rest in the cover of tall grass or reed beds several meters apart, with the individuals orientating themselves in different directions (Skinner and Chimimba 2005). They are not agile animals and use concealment as a first means of defense (Howard 1984).

7.2.2.10 SPRINGBOK (*Antidorcas marsupialis*)

Springbok is typically a plains antelope of arid regions and open grassland (Table 7.1). They have a wide habitat tolerance and occur from the Highveld (2 000 m) to sea level. They are usually absent from mountainous areas, rocky hills, and thick woodland (Estes 1997, Cain III *et al.* 2004, Skinner and Chimimba 2005). They do not appear to require shade to the same extend as other species (Skinner and Chimimba 2005). Factors that influence their choice of habitat are the availability of food as well as the height and density of vegetation, which affect visibility (Cain III *et al.* 2004, Skinner and Chimimba 2005). According to Milton *et al*. (1992), springbok use pans as display sites for various social interactions and favour the plants that remain green for longer in pans than in surrounding karroid shrubland and grassland areas. They shift between pans in the wet season and areas with shorter vegetation (burnt areas, heavily grazed areas) in the dry season, depending on local vegetation condition (Verlinden 1998).

Bigalke (1972) found six species of karroid shrubs, and also *Searsia ciliata*, *Acacia tortilis* and *Ziziphus mucronata* to be important food plants in the winter diet. In Botswana, leaves of the following species were recorded in the stomach contents: *Acacia erioloba*, *Boscia albitrunca*, *Rhigozum trichotomum*, *Salsola* spp., *Grewia* spp., leaves and pods of *Acacia mellifera*, the fruit and leaves of *Z. mucronata*, green and dry leaves of *Colophospermum mopane* and the fruits of *Solanum* spp. (Skinner and Chimimba 2005). In comparison, Davies *et al.* (1986), Fairall *et al.* (1990) and Cain III *et al.* (2004) indicated that karroid shrubs were preferred by springbok, but that a greater proportion of grass was utilised. Stapelberg *et al.* (2008b) concluded that springbok favoured grass and herbs overall more than shrubs and trees. They are patch-selective grazers, subjecting small areas to intense grazing pressure, so their habitat consists of a mosaic of grazed and ungrazed patches (Novellie 1990).

In contrast to herds migrating to better pastures, territorial males, especially in smaller fenced reserves, are more sedentary in nature and remain permanently on their territories throughout the year where they tend to the maintenance thereof (David 1978, Jackson *et al.* 1993, Cain III *et al.* 2004). These solitary, dominant males do not appear to respond in the same way to the availability of food or water as the others, but will leave the territory when there is no more food to eat (Jackson *et al.* 1993, Skinner *et al.* 1996). Male mortality is attributed to poor nutritional condition and predation due to their solitary nature (Bednekoff and Ritter 1997). Territories are generally in open areas and contain resources that attract females, since only territorial males mate (David 1978, Cain III *et al.* 2004, Skinner and Chimimba 2005). Along the Nossob riverbed in the Kalahari Gemsbok National Park RSA, the distance between rams varied from 0.4 – 2.9 km depending on the season and whether the rams were rutting (Skinner *et al.* 1996). According to Frandsen (1998), springbok associate loosely with hartebeest, black wildebeest, blesbok, gemsbok and ostriches, while Estes (1997) listed associations with blue wildebeest, red hartebeest and zebra and Stapelberg *et al.* (2008b) indicated blue wildebeest and gemsbok associations.

7.2.2.11 TSESSEBE (*Damaliscus lunatus*)

Tsessebes are one of the rare antelope in South Africa and their numbers have declined considerably, with bush encroachment being a primary cause (Dunham *et al.* 2004, Skinner and Chimimba 2005, Dörgeloh 2006). Under the IUCN Red Data Book, tsessebes were classified as "Lower Risk (conservation dependent)" by the Antelope Specialist Group (ASG 1998). Currently their conservation status is “Endangered”. Dunham and Robertson (2001), as well as Dunham *et al.* (2004) demonstrated a strong relationship between the survival of tsessebe and accumulated surplus or deficit in rainfall over a long period. Rainfall in the late dry season appears to be critical, affecting the animals' condition, survival rate, late stage of pregnancy and early stage of lactation (Martin 1983).

During the rains they move away from floodplains used extensively in the dry season, into neighbouring woody vegetation to use palatable grasses and seasonally available water supplies (Dunham *et al.* 2004, Skinner and Chimimba 2005). Tsessebes are usually found within 1 km of water (Martin 1983), but they are averse to using artificial water points unless it resembles natural pools (Skinner and Chimimba 2005, Bothma *et al.* 2010). De Wet (1988) concluded that tsessebe in the Kruger National Park was limited to areas where optimal grass species composition existed (also see Table 7.1). Tsessebes have a preference for grasses up to 0.6 m tall but also frequent grass up to 3 m tall (Furstenburg 2006c, Bothma *et al.* 2010). They make heavier use of burnt than unburnt areas (Martin 1983, Dunham *et al.* 2004, Skinner and Chimimba 2005, Dörgeloh 2006). They are selective low impact feeders (Furstenburg 2006c). Their habitat corresponds to a certain degree to that of buffalo, eland, zebra, roan, sable, reedbuck and waterbuck (Furstenburg 2006c). There is a possibility of hybridization with bontebok and blesbok, since all three species fall in the genus *Damaliscus* (Skinner and Chimimba 2005, Du Toit *et al.* 2010).

Tsessebes are semi-migrators that will move if environmental conditions change and water dries up. The territory is permanent, not seasonal. The harem will stay on it with the dominant male and not move through different territories in the territorial network. If the harem herd becomes too large, they will split up into new family herds. Around the nucleus of the territory, some bare, trampled patches are created where they regularly lie down (Furstenburg 2006c). Sub-adult males will form bachelor groups that move around on peripheral areas of territories until they reach sexuality. Old, non-reproducing males do not associate with bachelor herds, but remain solitary or rather associate with zebra, waterbuck and blue wildebeest (Frandsen 1998, Furstenburg 2006c).

7.2.2.12 WATERBUCK (*Kobus ellipsiprymnus*)

Waterbuck are associated with water (Anonymous 1993b, Estes 1997) due to their inherent dependence on open surface water and water-associated habitat (Smit *et al.* 2007)**.** Taylor *et al.* (1969) found that they had unusually high water requirements. They drink several times per day and are always within 1.8 km from water (Bothma *et al.* 2010). Burnt areas are also utilized by all social groups of waterbuck when available (Tomlinson 1981). While mainly grazers, they may very occasionally add to their diet browse plants such as *Acacia tortilis* and fruits such as marula (*Sclerocarya birrea*) (Tomlinson 1980a, Anonymous 1993b, Skinner and Chimimba 2005)**.** Herbert (1972), Tomlinson (1980a) and Skinner and Chimimba (2005) found that waterbuck selected different plant species at different times of the year, which may be attributed to changes in percentage moisture, crude protein and crude fibre of the various species. Melton (1978) found that nutritious food represented a limited resource during winter in the Umfolozi Game Reserve, KwaZulu-Natal and that waterbuck were out-competed for this by nyala and impala.

Melton (1983) indicated a mean density of 2.6 animals/km^2 in the Umfolozi Game Reserve, while Tomlinson (1981) calculated the overall density to be 4.8 animals/km^2 in Zimbabwe. According to Estes (1997): "The sizes of home ranges and territories depend on the quality of the habitat and on population density, as well as on individual age and fitness: area decreases with increasing density and age". The home ranges occupied by the nursery herds may overlap with the territories of several males (Tomlinson 1981, Estes 1997, Skinner and Chimimba 2005). Young females remain with their mothers in the nursery herds after weaning, but young males join bachelor herds one or two months after weaning (Estes 1997).

Bachelor males at Lake McIlwaine in Zimbabwe avoided areas occupied by territorial males during the rainy season. In the dry season, when the only green food could be found in territories, they were forced to feed there, but were obliged to carry out a series of submissive displays to avoid conflict (Tomlinson 1981). Some males tolerate bachelors and "satellite bulls" as long as they behave themselves (see Table 7.2), but not all territorial males are so tolerant (Estes 1997). Serious fighting is commoner among waterbuck than some of the other ungulates and can lead to death of the combatants (Estes 1997, Skinner and Chimimba 2005). Aspects of the expressive behaviour of waterbuck during interactions between neighbouring territorial bulls; between territorial bulls and challenging males; between territorial bulls and subservient bachelor males; in bachelor groups; between females; and during courtship are summarized by Tomlinson (1980b).

7.2.2.13 OSTRICH (*Struthio camelus australis*)

Five subspecies of ostrich are recognised, but the one that occurs in southern Africa is *Struthio camelus australis* (Brown 1992, Furstenburg 2005b, Olivier and Burger 2010). They occur at densities of 1 / 5 – 20 km^2. Ostriches usually avoid tall grass more than 1 m high, dense woodland (Brown 1992, Olivier and Burger 2010) and stony or rocky hills (Hockey *et al.* 2005). In the Namib Desert they move up to 18.5 km daily in search of food (Hockey *et al.* 2005). They walk about completely exposed in the heat of day, seldom seeking shade, unlike many antelopes (Brown 1992). Wild ostriches are shy, alert and will flee with the slightest disturbance (Olivier and Burger 2010).

Ostriches are mostly highly selective vegetarians. They prefer dicotyledonous plants, but eat all parts of both herbs and grasses (Bertram 1980, Brown 1992, Williams *et al.* 1993, Aganga *et al.* 2003) and usually strip off the leaves from larger woody plants (Aganga *et al.* 2003, Hockey *et al.* 2005). Olivier and Burger (2010) classified ostriches as mixed feeders due to grass and forbs forming 80% of their diet and browse and fruit 20%. They are high impact animals that can cause damage to vegetation and the veld, thus their numbers need to be regulated (Furstenburg 2005b). They avoid plants with high concentrations of phenolic substances, high salt contents and many species toxic to domestic livestock (Hockey *et al.* 2005, Furstenburg 2005b, Brand and Gouws 2006). Ostriches differ from ungulates in that they eat silica-rich plants that are not utilised by ungulates (Aganga *et al.* 2003, Furstenburg 2005b). They usually ingest stones or grit that act as gastroliths to grind food in the gizzard (Brown 1992, Aganga *et al.* 2003, Hockey *et al.* 2005, Brand and Gouws 2006). Their digestive system is that of a simple stomached (monogastric) herbivore that can digest fibre and is hind gut fermented, like the zebra, horse and donkey (Aganga *et al.* 2003, Brand and Gouws 2006). The ostrich has no crop or gallbladder (Brand and Gouws 2006).

According to Furstenburg (2005b) and Hockey *et al.* (2005), the territorial male mates with up to 4 females and may occupy the same territory for successive years, while home ranges of females are undefended and overlap several male territories. Several nest scrapes of 2 – 3 m across are dug by the male within its territory. The first female to accept and lay in the scrape is the major female who guards and incubates the eggs (Table 7.2). Eggs are also laid in the nest by up to 5 minor females for 2 – 30 days afterwards (Bertram 1992, Hockey *et al.* 2005, Olivier and Burger 2010). The major female recognises her own eggs and moves eggs laid by minor females to the nest perimeter, so they are not incubated, leaving a total of about 20 eggs in most cases. Males and females cooperate in rearing the chicks, but the male defends the hatchlings and teaches them to feed (Hockey *et al.* 2005).

7.2.3 Habitat separation and local movements in general

Habitat features and requirements of herbivores may change with time and space. Main determinants of local movements are forage availability, forage quality in terms of mineral nutrition, water availability (Ben-Shahar and Coe 1992) and certain landscape types and features such as topography, soil types, vegetation composition and structure (Ben-Shahar 1995). Seasonal migration of animals may be attributed to climatic conditions, the seasonal phenological development of forage and fire (Dörgeloh 1998). Rainfall is a central climatic factor governing herbivore population dynamics in African savannas (Owen-Smith 1990, Ogutu and Owen-Smith 2006, Ogutu *et al.* 2008).

Ungulates respond to cumulative past rainfall and seasonal fluctuations in rainfall (Ogutu and Owen-Smith 2006, Owen-Smith and Mills 2006). Herbivore biomass is governed by net annual aboveground primary production (i.e. annual food supply), which in turn is governed by annual rainfall (Du Toit 1995a). Ogutu *et al.* (2008) concluded that animal abundance correlated with accumulated monthly rainfall for zebra; late wet season rainfall for giraffe, red hartebeest, impala and warthog; and annual rainfall for waterbuck in the Masai-Mara National Reserve, Kenya. Small-scale seasonal movements are found where feeding specialisations determine the species involved, while rainfall seasonality determines the direction of movements (Ogutu *et al.* 2008).

Dekker *et al.* (1996) suggested that the pattern of ungulate separation was specific to a study area. However, effects of restricted animal movement due to the size of the study area, absence of predators and limited types of habitat to select apply to most game ranches. These factors do not nullify spatial separation. Preferences for plant communities, seasonal variations in these preferences and selection for specific environmental parameters contributed to the spatial and temporal separation of ungulates on the Messina Experimental Farm. Diet selectivity and use of different feeding levels will also further contribute to ecological separation (Dekker *et al*. 1996).

Feeding competition in the dry season can be seen as leading to resource partitioning by ungulates, since availability of food also determines the seasonal choice of habitat for an animal. Some examples from the literature are as follows. Dekker *et al.* (1996) concluded that the highest degree of spatial separation of ungulates in the Messina Experimental Farm, Limpopo Province occurred in the dry, hot season (August – November) and coincided with the period in which resources were limited. Brooks (1982) reported that animals tended to vacate the open grassland ridges as winter approached and moved down to the more densely wooded valley and riverine areas. Koekemoer (2001) found the greatest habitat overlap in the Eastern Cape subtropical thicket between kudu and impala in winter, which might have been due to limiting resources. Impala diet in autumn and winter was similar to kudu diet, probably because impala consumed more browse than graze in winter. According to Underwood (1978), because of their smaller body mass, kudu should be more selective than eland in accepting or rejecting individual food items and selection of higher quality habitats might be an extension of this process. Du Toit (1995b) concluded that the riverine/watercourse habitat was a lean season food reserve in Kruger Park, because of simultaneous increase in use of this habitat in the late dry season by giraffe, kudu and impala.

Schoener (1982) interpreted resource partitioning as the consequence of strong directional selection, resulting from interspecific competition that produced in each species adaptations most suited for the resources used relatively exclusively by that species. Theoretically, competitive interactions among herbivores are predicted to be most severe between species that have the same feeding style and similar body weights (Jarman 1974); when body weights are different, it is predicted that species may partition resources by size and quality in such a way that each species has exclusive resources (Du Toit 1995a, Prins 2006). According to Woolnough and Du Toit (2001): "The smallest sized classes in an ungulate guild have to feed on the highest quality food available. Although larger species also prefer high-quality food, their daily intake requirements force them to accept more abundant food of lower quality, which they can tolerate". According to Sinclair and Norton-Griffiths (1979), interspecific competition was the dominant structuring process in the Serengeti ungulate community of northern Tanzania and southern Kenia, producing separation and coexistence of herbivores.

Knowledge of habitat preferences and other ecological requirements of herbivores is basic to any management programme. It is also a prerequisite for understanding the abundance and distribution of game species and to be able to judge which species may be introduced in a certain area (Grunow 1980). Spatial distribution of abiotic and biotic resources should therefore be regularly recorded to monitor the efficacy of management actions (Fabricius and Coetzee 1992). According to Coughenour (1991): “Failure to consider the spatial components of herbivory in calculations of carrying capacity and assessments of ecosystem persistence can contribute to overgrazing, failed economic development efforts and declines of wildlife populations”.

7.3 PROCEDURE

Nine fixed routes covering the entire study area have been traveled by vehicle every fortnight from September 2004 to December 2007 and the following data of all species encountered was recorded: i) The game species, ii) number/herd size (males and females if possible), iii) vegetation unit, iv) date and time, v) general activity (running, standing, resting) and vi) the climate conditions at that time. The Global Positioning System (GPS) coordinates where the animal was first spotted from the road (Figure 7.1a) were also noted along with the direction and an estimate of the distance from the road to where the animal(s) was standing at that specific time. It was established that more game species were observed early in the mornings than at dusk, probably because of the greater visibility of animals at that time. It is known that animals mostly feed early in the morning and at dusk and remain inactive during the hottest parts of the day (Estes 1997). Consequently, it was decided that the best time to do the survey would be during the first three to four hours after sunrise, when animals were more visible during feeding or while heating themselves after cold winter nights. This approach was also followed by Scogings *et al.* (1990).

The twelve calendar months were divided into seasons with regard to the average daily temperatures and total rainfall per month (Figure 3.6). The following seasons were recognized:

Summer:	Nov – Feb	Wet, hot season
Autumn:	March – May	Wet, cool season
Winter:	Jun – Aug	Dry, cool season
Spring:	Sep – Oct	Dry, hot season

Scogings *et al.* (1990) defined the dry season in the Krugersdorp-area as May to September and the wet season as October to April. Dekker *et al.* (1996) identified the dry, hot season in the Messina-area as August to November, with the wet season ranging from November to March.

7.3.1 Data analysis and mapping

All the spatial analyses and mapping, including the conversion of the coordinates, were done with ArcGIS 9.3.1. A Geographic Information System (GIS) is defined as "an organised collection of computer hardware, software, geographic data and personnel designed to effectively capture, store, update, manipulate, analyze and display all forms of geographically referenced information" (Perrin and Taolo 1999). Fabricius and Coetzee (1992), as well as Perrin and Taolo (1999) indicated that data organisation in a GIS could be either based on a grid-cell approach (the raster system, suitable for modelling purposes) or on vectors and points (the polygon system, suitable for mapping purposes). The polygon system was used in this study and although grids were used for the frequency data it was still in vector format.

Global Positioning System (GPS) coordinates were noted from the road together with the direction and estimated distance to all observed animals. The spatial and attribute data were stored in Windows EXCEL (Microsoft Corporation 2002). The GPS point for a specific animal or herd (geographic coordinates) was converted into x (longitude) and y (latitude) values (cartesian coordinates in meter) by means of the following calculation: Degrees + Minutes / 60 + Seconds / 3600 with a negative sign allocated to the latitude values for being in the southern hemisphere. The x and y values were converted to the specific point where the animal was standing, by means of Pythagoras' formula. The Gauss conformal projection with 27°E as central meridian was used for all analyses and maps.

Each species was classified by herd size and graduated symbols were used to provide a visual presentation of herd size. Map legends were standardised for all the species. Differentiation was made by means of selection between the different seasons, indicating the game species' position in the wet, hot- (summer) and dry, cool seasons (winter) on one vegetation map and the dry, hot- (spring) and wet, cool seasons (autumn) on another map. A lighter colour was used for summer and spring than for winter and autumn. The two feeding areas next to the waterholes was also indicated.

In order to indicate the number of times that a specific game species was observed in an area, frequency maps were created for each species. Grids of 150 x 150 m were layered on the vegetation map (Figure 8.1). Two layers were used, namely observation points and the reference grid, and a spatial join was established between them in order to represent the frequency of observations per grid block. A dark colour was used to indicate the highest number of observations in that specific grid block, with a gradient decreasing in darkness through to white indicating no observation of a specific game species in a grid block. Since this study's focus is on browsing animals, the frequency of observations of giraffe, kudu, impala and eland was indicated for the combined summers and the combined winters of the study period, while for all the other game species the total number of observations per grid block from August 2004 to December 2007 was indicated on one frequency map per species. For buffalo (9 sightings), steenbok (2 sightings) and tsessebe (26 sightings) the total number of observations was not sufficient enough to indicate territorial or seasonal patterns and consequently no figures are being presented.

To determine if small local movements occurred, directional, geographical distribution was indicated for browser- and mixed feeder game species. Two separate distribution figures were created per species, one for the calendar years and one for combined seasons (i.e. all the summers of the three years of study, all the winters, etc.) representing distribution patterns as standard deviational ellipses in different colours. This indicated the core area that the animal frequented in a specific year or season.

Correspondence Analysis from the CANOCO 4.5 software (Ter Braak and Smilauer 2002) was used for ordination (Gauch 1982, Ter Braak 1986, 1987). Ordination was applied to the herd sizes, including solitary animals or pairs, of all game species as observed in each grid block (Figure 8.1). Buffalo and steenbok were excluded, due to very low number of sightings in the study area.

7.4 RESULTS AND DISCUSSION

The general discussion of this chapter includes a brief overview of the vegetation types (Figure 7.1a). A detailed vegetation description is given in Chapter 4. Total frequency of observations of all species present in the vegetation units during the study period is presented in Figure 7.1b.

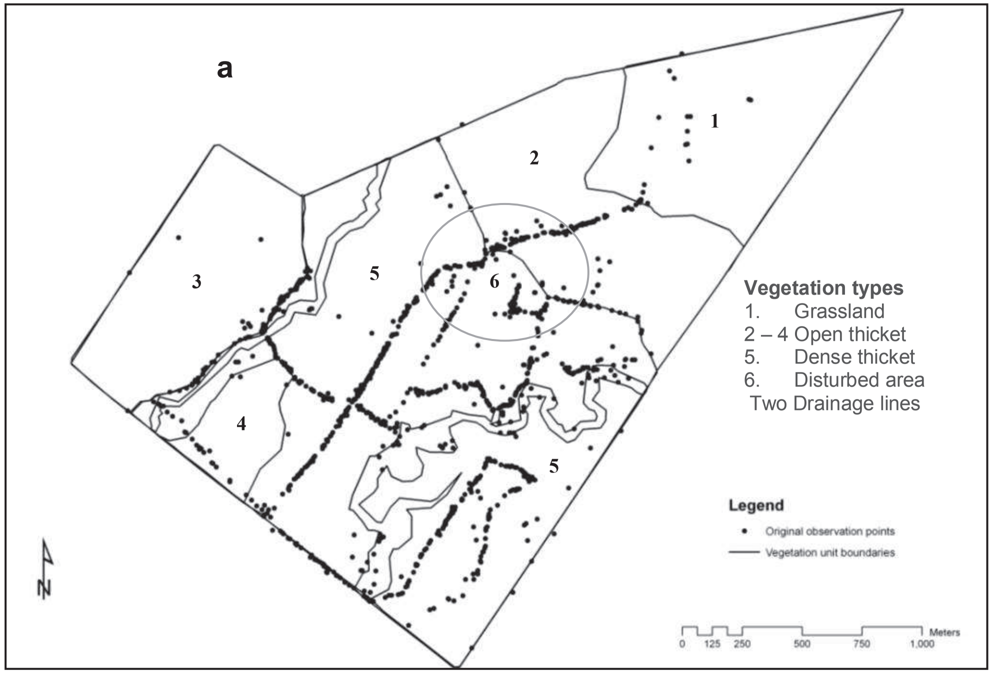
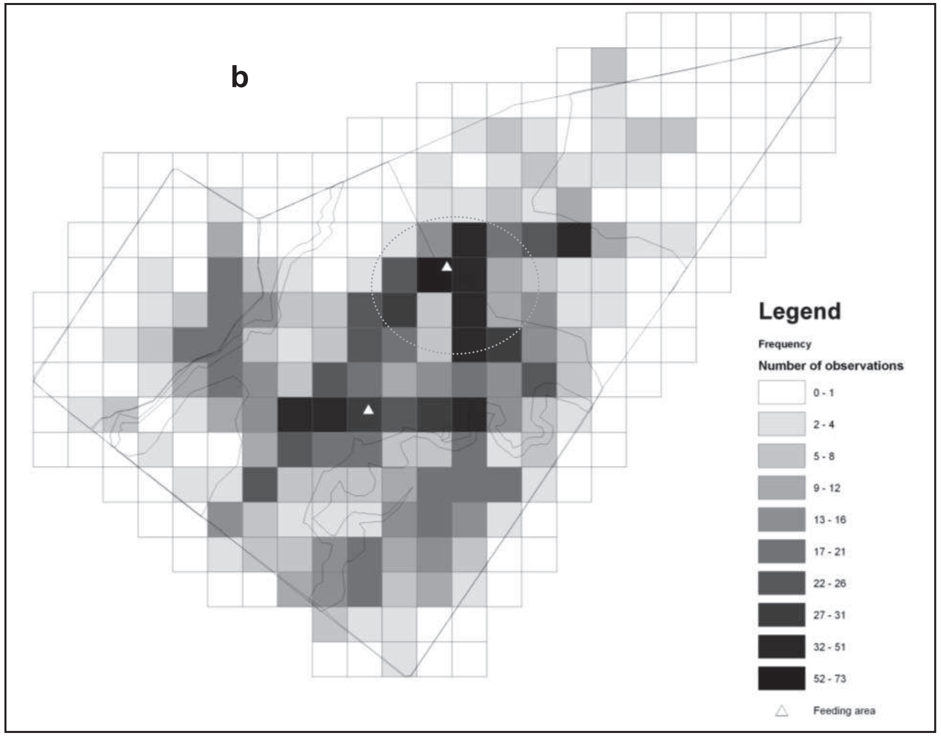


Figure 7.1 a) Original GPS positions on the roads where animals were spotted, before converting it to their actual positions in the veld.
b) Frequency of observations (actual positions) per 150 m^2 grid block of all the game species during the study period.



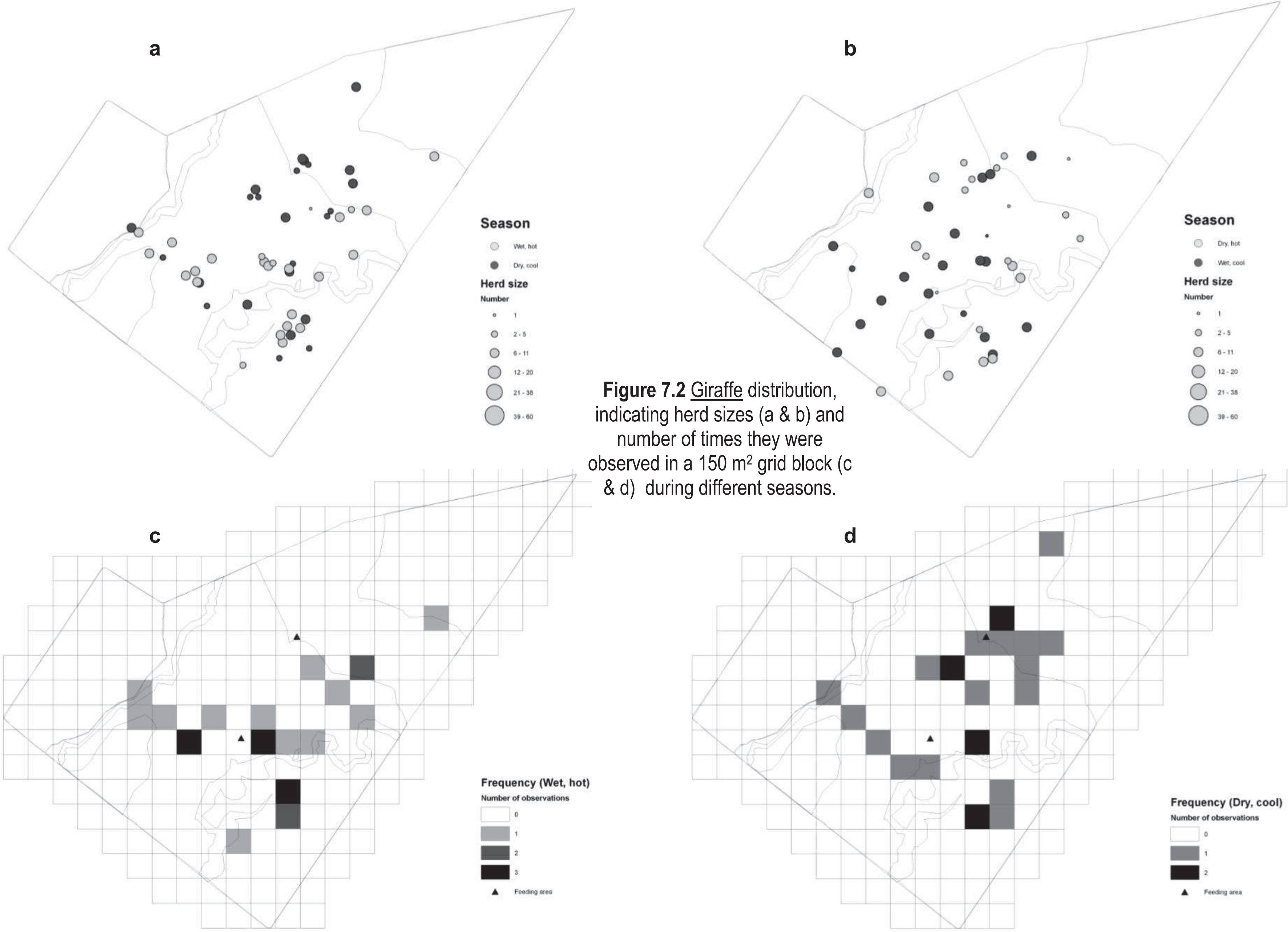


Figure 7.2 Giraffe distribution, indicating herd sizes (a & b) and number of times they were observed in a 150 m^2 grid block (c & d) during different seasons.

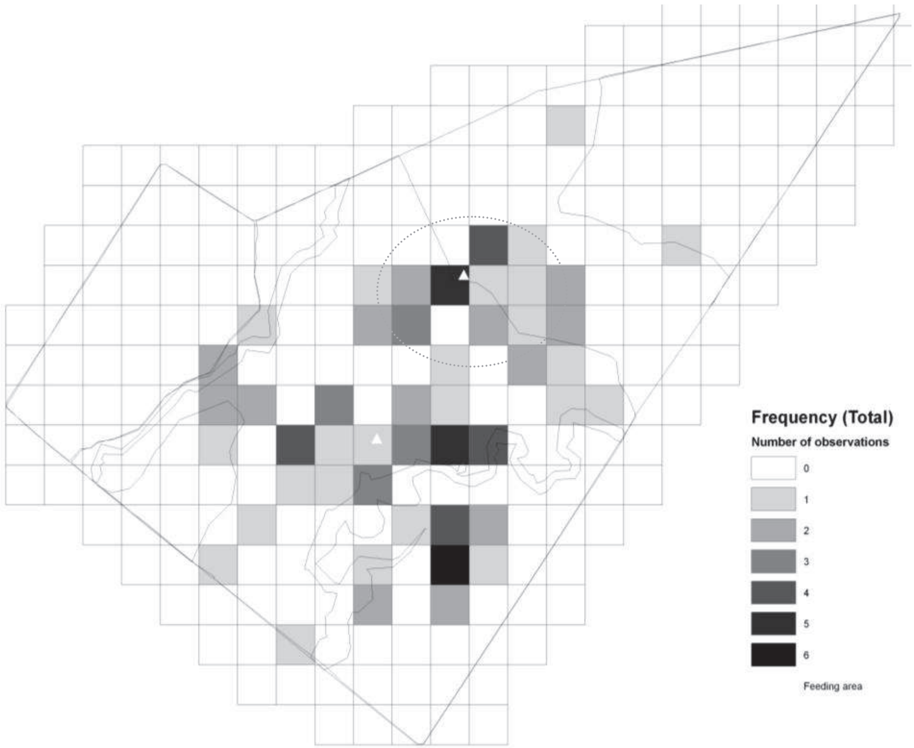


Figure 7.3 Total number of times giraffes were observed (frequency) from August 2004 to December 2007 in each 150 m^2 reference grid block.

Figure 7.4 Directional, geographical distribution of giraffe between different calendar years for the period of study.

Species that did not historically occur in the Free State are bontebok, giraffe, impala, Burchell's zebra, red lechwe, tsessebe and waterbuck (Skinner and Chimimba 2005). It is often stated that blue wildebeest did not occur in the Free State, but historical evidence suggests that they did (Skinner and Chimimba 2005). Chapter 2 includes a discussion on historically absent game species in the Free State. The complete scientific names with species authorities of the following 18 species are listed in Table 3.1 (Chapter 3).

7.4.1 Browsers and mixed feeders

7.4.1.1 GIRAFFE

The herd size of giraffe (*Giraffa camelopardalis*) in the study area ranged from 5 – 8 animals (Figure 7.2 a & b) but were usually limited to six individuals (2 – 3 males and 3 – 4 females) by means of auctioning the excess animals. They had one to two calves each year. The herd mostly moved together as a unit and where a bull was observed on its own, it was not too far away from the rest of the herd. According to the literature, males usually prefer denser wooded habitats and females the more open habitats (Du Toit 1990a, Ginnet and Demment 1999, Caister *et al.* 2003). This was not observed in the study area probably because there are no large differences in the denseness of the vegetation in their chosen habitat. The giraffes were only present on the northern side of the Soutpan road that divides the private reserve in two, and never moved through the connecting tunnel to the southern side of the private reserve (*vid*. Chapter 3, Figure 3.2).

The habitat types selected were dense thicket and drainage lines, with the open thicket next to the main feeding area also being used (Figure 7.3). Giraffes are browsers and thus did not use areas where trees were scarce like the other open thickets and grassland, or areas where trees were too dense to move through. These preferred habitat areas and avoided areas correspond to the literature (Kok and Opperman 1980, Estes 1997, Frandsen 1998, Skinner and Chimimba 2005). Since they are not territorial (Table 7.2) they moved through a large part of the study area on a daily basis in search of acceptable browse plants located in different localities. This is probably to avoid the build-up of tannins in trees located in the same area in response to a warning mechanism from trees that are being browsed and as part of chemical defence (*vid*. Chapter 8, 'Effect of browsing on woody plants').

A small difference was observed in habitat selected (Figure 7.2 c & d) in the wet, hot season (summers) compared to the dry, cool season (winters). In the wet, hot season they frequented the area surrounding the bigger drainage line. In the dry, cool season they concentrated in areas more to the north to be in the vicinity of the disturbed area where the main feeding area is located (Figure 7.14a). At the end of the dry, hot season (spring) and the beginning of the wet, cool season (autumn) they frequented the disturbed area (Figure 7.2b). During the critical period (July/August – middle October) when trees were mostly leafless, they relied increasingly on supplied feed (*vid*. Chapters 5 & 8), which would explain the higher frequency of observations in vicinity of the feeding areas.

In larger areas with a bigger choice of vegetation units, like the Willem Pretorius Game Reserve in the central Free State, Kok and Opperman (1980) reported a definite correlation between availability of food in different vegetation units and the seasonal movement pattern of giraffes. Giraffes occurred on the plains in the wet season for a period of eight months and moved to the rocky hills (koppies) for four months of the dry season. They made use of other food reserves in the dry season that are usually neglected, like evergreen species growing mostly on koppies, while in the wet season they moved to the plains where winter deciduous species, like *Acacia karroo* having full leaf carriage in the summer, are abundant (Kok and Opperman 1980). A considerable increase in herd size in the wet season was reported by Kok and Opperman (1980) as well as by Le Pendu *et al.* (2000), probably because more individuals can be sustained by the abundance of leaves present on deciduous plants in the wet summer season. None of this was found in the study area, because of the small size of the private reserve and lack of vegetation units where evergreen plants are usually found. Also, no big change in selected areas was observed between different calendar years in the study area (Figure 7.4). Giraffes were introduced into the study area in 2004. During 2004 and 2005, they were still observed in the same general area, while during 2006 and 2007 they were using an increasingly larger area within their preferred habitat type.

7.4.1.2 GREATER KUDU

Herd sizes of the Greater Kudu (*Tragelaphus strepsiceros*) ranged between 2 and 7, while a group of 11 and some solitary males were also occasionally observed (Figure 7.5 a & b). Females were usually seen in herds, sometimes accompanied by one or two males, with a bachelor herd of 4 males also noted. According to the manager, 30 kudu in total was initially present in the private reserve, of which 16 were auctioned during 2007. They are shy animals that usually hide in the dense thickets and it proved difficult to determine their exact numbers in the study area. It is known that they are also active at night (Table 7.1), which made it even more difficult to observe them during the day.

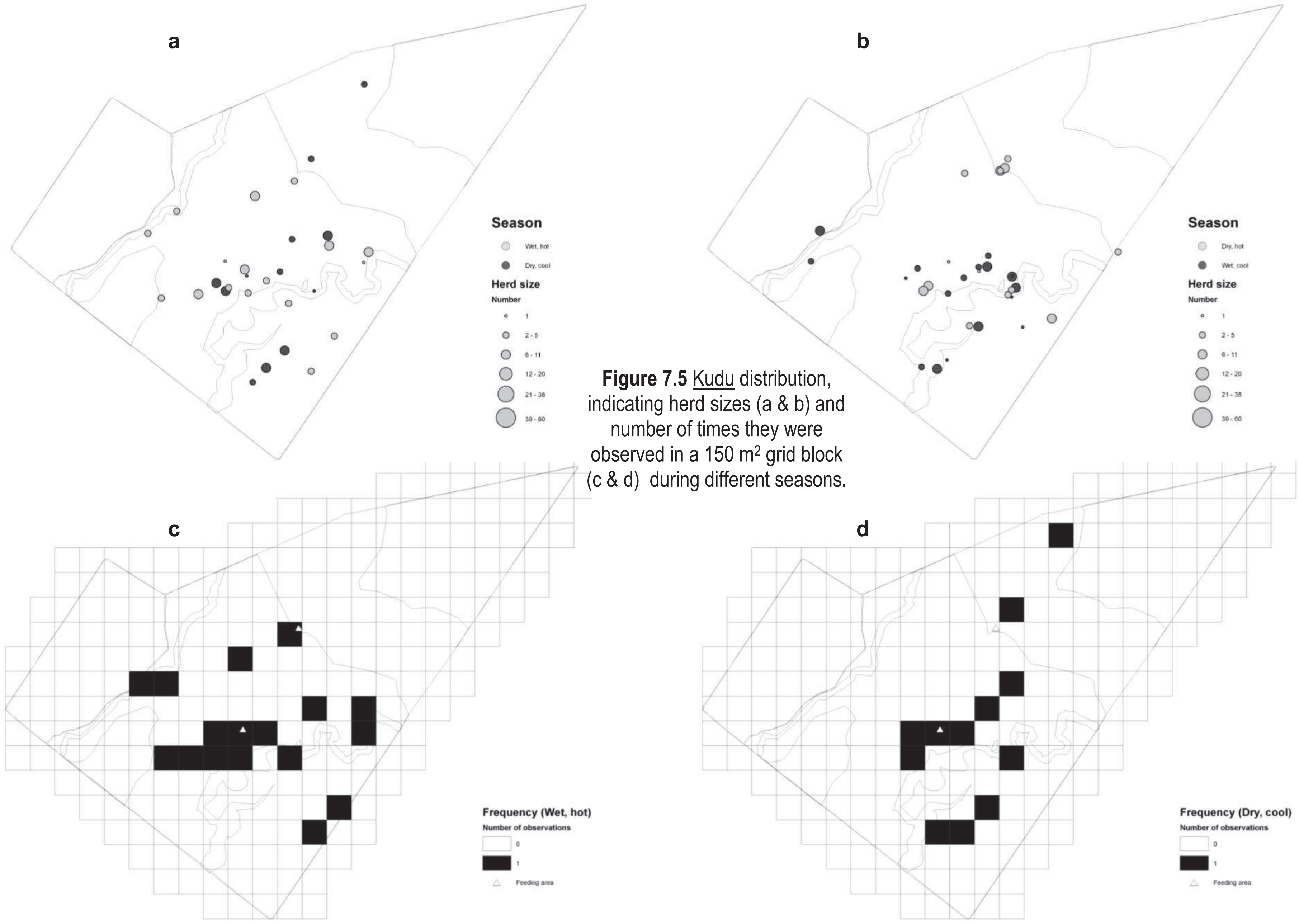


Figure 7.5 Kudu distribution, indicating herd sizes (a & b) and number of times they were observed in a 150 m^2 grid block (c & d) during different seasons.

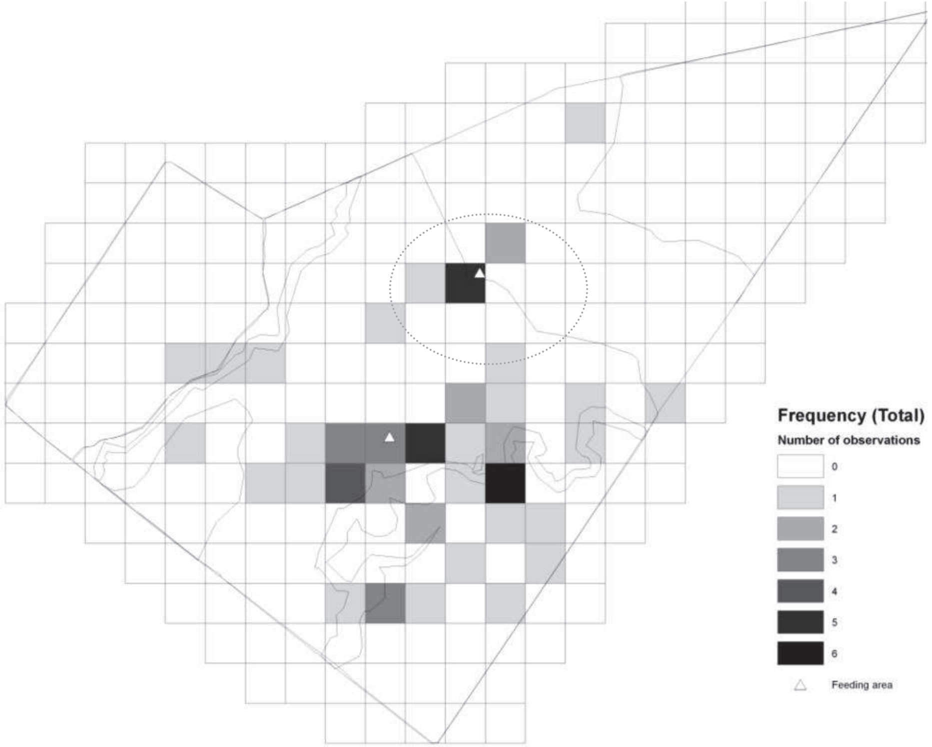


Figure 7.6 Total frequency of observations of kudu from August 2004 to December 2007 in each 150 m^2 reference grid block.

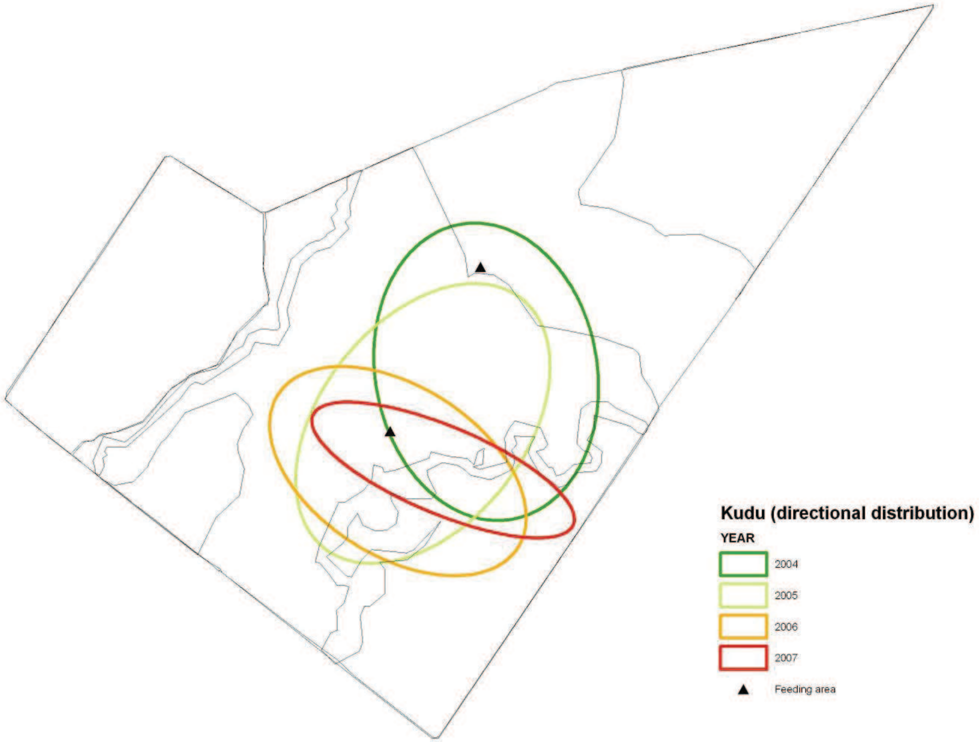


Figure 7.7 Directional, geographical distribution of kudu between the different calendar years for the period of study.

Their preferred habitat proved to be the dense riverine thicket in and around the drainage lines, especially the bigger drainage line in the study area (Figure 7.6). Since they are not confined by territorial boundaries (Table 7.2) they moved through the connecting tunnel underneath the Soutpan road, whenever the conditions became unfavourable in the study area, to make use of food reserves in the southern side of the private reserve (Figures 3.1 & 3.3). The vegetation closer to the river is much denser than in the northern part (study area) of the private reserve, but the dense, steep river bank itself is not accessible to the animals. Different authors reported that kudu preferred riverine thickets, but might move to hills or other areas where evergreen plant species are present in search of food in the critical period (Simpson 1968, Owen-Smith 1979, 1985, Du Toit 1995b, Estes 1997, Skinner and Chimimba 2005, Smit *et al.* 2007).

The only difference observed in habitat used in the study area between the wet, hot season (summers) and the dry, cool season (Figure 7.5 c & d) was that they were also found in the smaller drainage line and at the feeding area in the dry, cool season (winters). Figure 7.14b clearly indicates their northwards distribution in the dry, cool- and dry, hot seasons to include the main feeding area in their habitat. In the dry, hot season (spring) they were more frequently found in the disturbed area around the main feeding area (Figure 7.5b). The beginning of spring is the most critical period for kudu, when most of the semi-deciduous shrubs have also shed their leaves and the deciduous trees have not started sprouting new leaves yet (*vid*. Chapter 5 and Figures 5.5 to 5.10).

The data available for kudu observations is not complete, since they were difficult to find in the study area. However, the annual, directional, geographical distribution of kudus in the study area (Figure 7.7) indicated that they used the main feeding area more during 2004 and 2005, than in the other two years. In 2007, when feed supply was limited due to a drought, they were more concentrated in a small area around the dense thicket.

7.4.1.3 ELAND

Eland (*Tragelaphus oryx*) were observed as small mixed groups of up to six individuals and as a large group of between 20 and 33 individuals of both sexes (Figure 7.8 a & b). Some single males were also observed from time to time. Eland are not territorial (Table 7.2) and made use of both the northern and southern sides of the private reserve (Figure 3.1), but appeared to prefer the southern part more. This may be as a result of less interspecies competition for space and food, especially browse in the southern side. A small herd was, however, resident in the study area. They were mostly found in an open grassland type habitat surrounded by woody plants and inside the neighbouring basin of the big drainage line. According to Skinner and Chimimba (2005), eland populations were relatively sedentary in some areas, while in others they exhibited extensive movements. These movements relate to seasonal availability of food following rains or may be attributed to climate such as high winds or in seeking shade or shelter from rain (Verlinden 1998, Skinner and Chimimba 2005).

The large herd's chosen habitat in the study area, being mixed feeders, was grassland, open thickets where tree density was very low, open areas inside the dense thicket and also close to the superficial border or ecotone of the dense and open thickets (Figure 7.9). The study area should definitely provide enough shelter and shade in the form of trees to fulfil in their needs, with the exception of the grassland. This thermoregulatory behaviour of shade-seeking (Skinner and Chimimba 2005) might explain why they were not so frequently observed far out in the open grassland. During the dry, cool season (winters, Figure 7.8a) and the dry, hot season (spring, Figure 7.8b) a smaller herd was frequently observed in close vicinity of the main feeding area. During the wet, hot season (summers) a large, combined eland herd, consisting of all the smaller herds, was frequenting the open thickets and grassland areas (Figure 7.8a)**.** Figure 7.14c also illustrates this seasonal movement through the different vegetation units. Underwood (1981), Hillman (1988) and Rowe-Rowe (1994) described eland society as forming small groups in autumn and winter and congregating into large herds in summer months. Underwood (1981) suggested that the entire population of about 80 eland in Loskop Dam Nature Reserve was one diffuse social unit. In the study area the total herd of more than 30 animals was also observed to form part of a single unit that fragments into smaller groups that rejoin seasonally.

Eland are highly versatile in habitat selection (Table 7.1), but are known to select grassland and various woodland types (Buys and Dott 1991, Estes 1997, Skinner and Chimimba 2005), as was also observed in the study area. Scogings *et al.* (1990) found that eland and giraffe show a large random use of habitats in the Jack Scott Nature Reserve. Eland's big range in habitat selection in the study area is also clear in their annual, directional, geographical distribution (Figure 7.10). In 2004 they frequented the dense thicket and drainage line, in 2005 they selected the open thicket and disturbed area, in 2006 they were again in the dense thicket and drainage line and in 2007 they selected the northern part of the drainage line, the open thicket and grassland. This might be due to competition from other animals using the same areas in the absence of eland that forced them to shift to available spaces when they return at a later stage due to their nomadic nature.

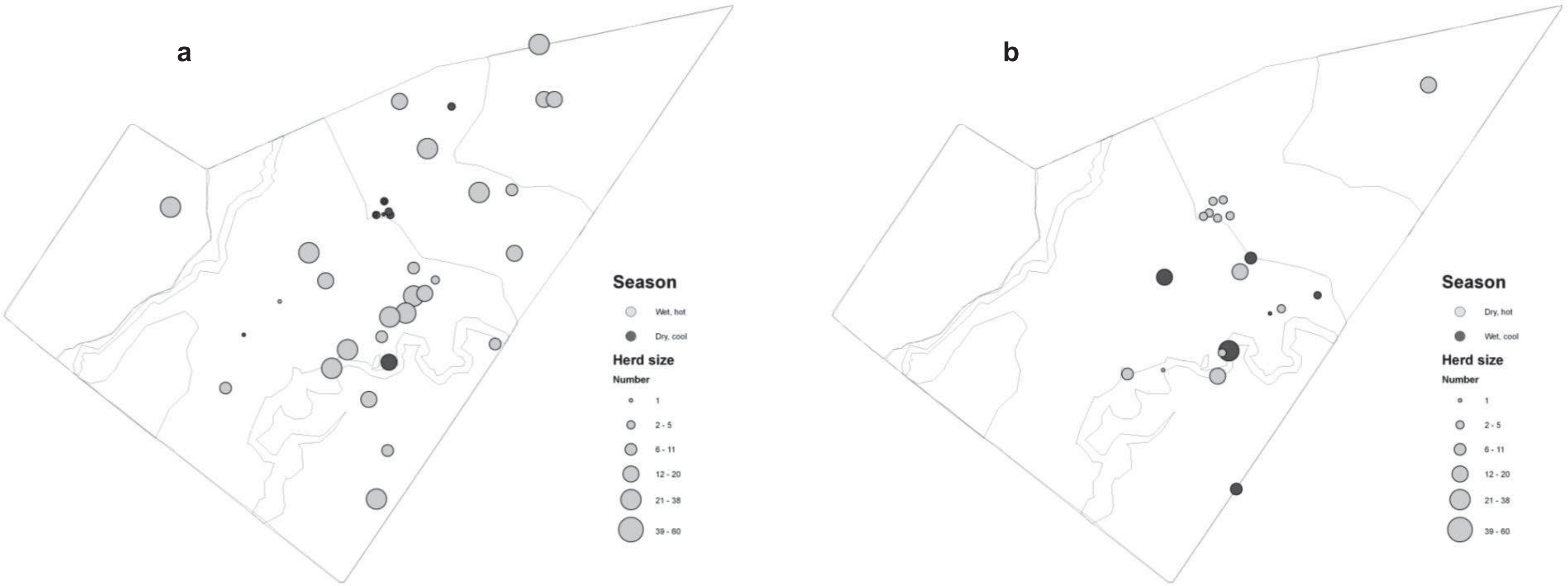


Figure 7.8 Eland distribution, indicating herd sizes in different seasons (a & b). Due to eland being nomadic and frequenting the southern part of the nature reserve, frequency of observations in 150 m^2 grid blocks had insufficient data and was not indicated.

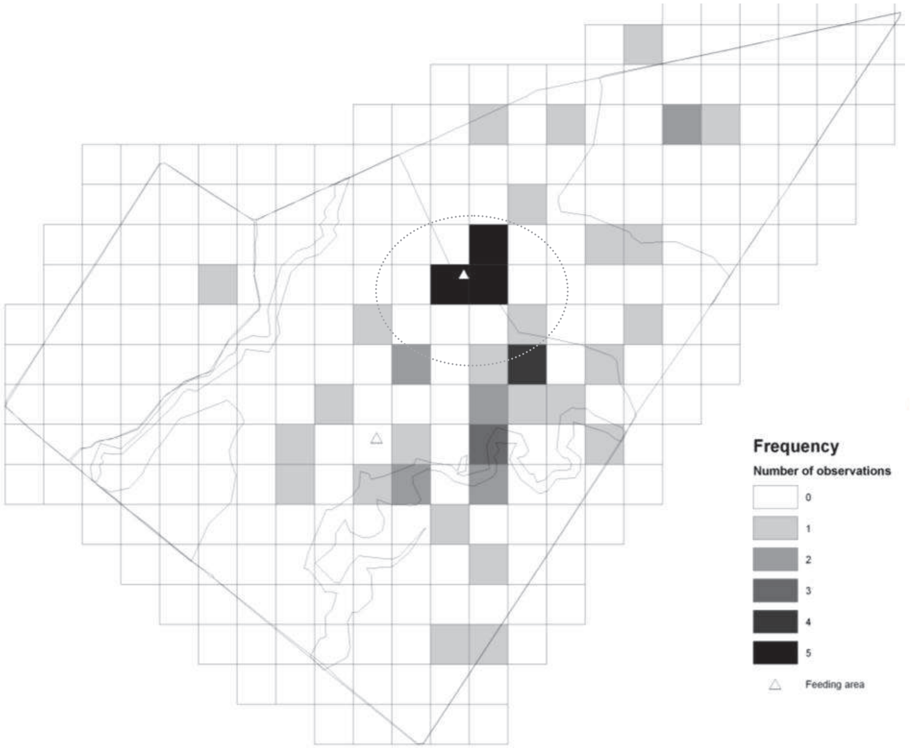


Figure 7.9 Total frequency of observations of eland from August 2004 to December 2007 in each 150 m^2 reference grid block.

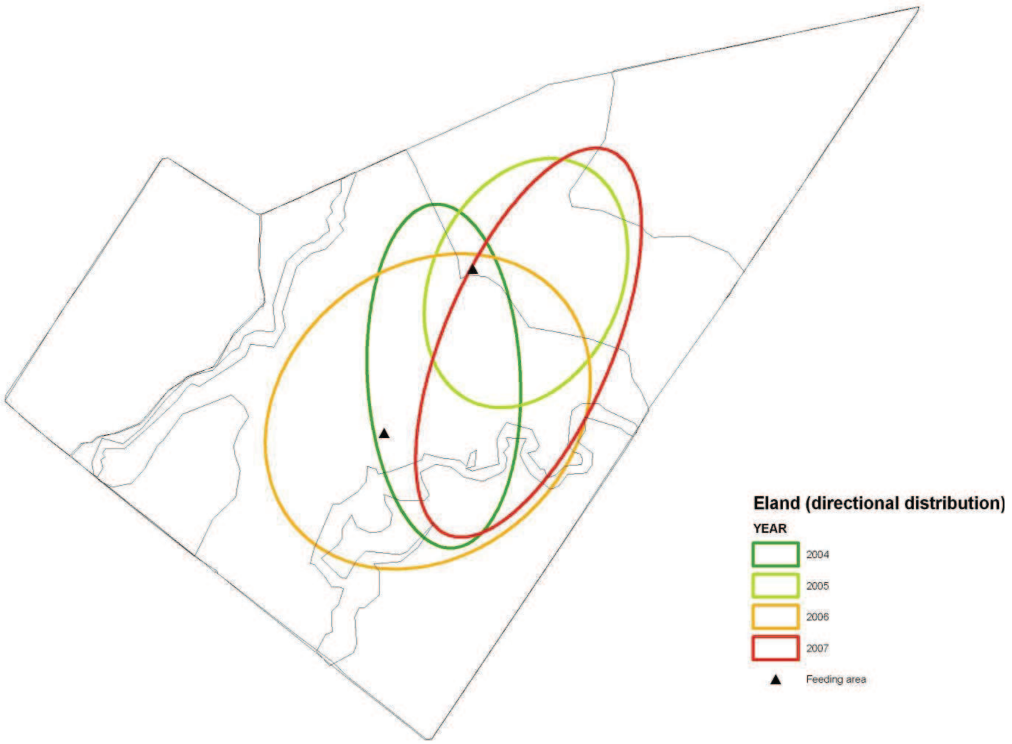


Figure 7.10 Directional, geographical distribution of eland between the different calendar years for the period of study.

7.4.1.4 IMPALA

Large variation in herd sizes of impala (*Aepyceros melampus melampus*) was observed (Figure 7.11 a & b). A big mixed herd of between 30 and 45 individuals was present, as well as female herds of up to 11 or 20 animals, bachelor herds of 2 – 8 males, solitary males and smaller mixed herds of 3 – 7 individuals of which one or two were males. In the dry, cool season of 2007, their numbers were reduced to about 10 individuals by means of game capture and auctioning. It is uncertain whether all the impalas used both the northern and southern sides of the private reserve during the time of study, since impala were always present in the study area. It is also not certain whether the big group of more than 40 individuals remained as a cohesive unit or if they dispersed into smaller groups from time to time, since they were difficult to count in their dense habitat. These animals were highly strung and fled at the first sound of a person or vehicle approaching, probably because they were one of the main hunting species on the private reserve.

The complicated social structure of impalas consisting of various combinations of males and/or females and juveniles is well known (Mason 1976a, Pettifer and Stumpf 1981, Estes 1997, Skinner and Chimimba 2005, Oliver *et al.* 2006, Matson *et al.* 2007). Some examples of their social structure are listed in Table 7.2**.** Murray (1982) indicated the overall dispersion of females to be discontinuous and referred to it as an open clan system. Impalas are seasonally or perennially territorial, but still sedentary (Estes 1997, Skinner and Chimimba 2005).

Impalas in the study area selected the denser thicket areas and the drainage lines as habitat (Figure 7.12). They also remained in close vicinity of the southern waterhole (next to the feeding area), located close to the big drainage line. It is known that where water is freely available they drink daily, since they are obligate drinkers (Fairall and Klein 1984, Matson *et al.* 2006). Only small differences in selected habitat were noted between different seasons (Figure 7.14d). In the wet, hot season (summers) they were more on the north-western side of the drainage line (Figure 7.11c), while in the dry, cool season (winters) they were more frequently observed in the south-eastern side of the drainage line (Figure 7.11d), and also closer to the main feeding area. Sometimes during the dry, cool season the water dried up in the southern waterhole that the impalas were frequenting, this might be a reason why they were observed closer to the other waterhole located at the main feeding area. However, they remained in the denser areas of the thickets and did not use the open thickets that characterise the disturbed area. In the dry, hot- (spring) and wet, cool seasons (autumn) they were more frequently observed north of the drainage line, next to the open thicket (Figure 7.11b) in areas where a higher density of grasses are present which form part of their diet as mixed feeders.

Mason (1976a), as well as Pettifer and Stumpf (1981) reported that seasonal movements of impala correlated to water and food availability and quality. According to Pettifer and Stumpf (1981): "If water and food is sufficient to sustain the herd, no seasonal movement would take place except where social organisation and territorial behaviour of males influence the distribution of impala herds". In some regions, impalas have separate wet and dry season ranges (Mason 1976a, Murray 1982, Meissner *et al.* 1996) and in other regions they have a year round preference for one habitat only, especially where evergreen grass species (impala becomes almost 100% grazer) and a permanent water supply are available (Anderson 1972, Attwell and Bhika 1985, Smith and Cain III 2008). Impala have some preference for *Acacia* woodland throughout most of the year, but it usually becomes pronounced during the dry winter months from April to September (Monro 1980).

Impala used a rather large home range in the study area (Figure 7.12). Figure 7.11 a & b indicates that certain herds were repeatedly found on the same spot (or area) regardless of seasons. Matson *et al.* (2007) stated that "large home ranges of black-faced impalas (*A. melampus petersi*) may reflect the wide dispersion and low quality of resources in their semi-arid environment and the patchy occurrence of suitable microhabitats among a matrix of unsuitable microhabitats". This also seems to be the case in the study area where certain preferred microhabitats are patchily distributed, therefore explaining the wide dispersion of impalas. A slight northwards distribution of impalas during the four different calendar years is evident from Figure 7.13. During 2007 when their numbers were reduced, they occupied a smaller core area, but still used the same vegetation types than in other years. Their habitat overlaps with that of giraffe and kudu in and around the big drainage line (Figure 7.15). Eland, the other mixed feeder, mostly avoid overlapping habitats with impala, because they also use the open thickets and grassland that is ignored by impala.

7.4.1.5 COMMON DUIKER

Most of the 67 sightings of common grey duiker (*Sylvicapra grimmia*) during the study period occurred in the vicinity of the two dry drainage lines (Figure 7.16a). Some individuals were always found in the same area, since they are territorial, and sometimes even under the same bush in the bigger dry drainage line. Solitary individuals were mostly observed in the study area, but there were also some observations of a male and female pair (Figure 7.16b) mostly during September, November and December.

Figure 7.11 Impala distribution, indicating herd sizes (a & b) and number of times they were observed in a 150 m^2 grid block (c & d) during different seasons.

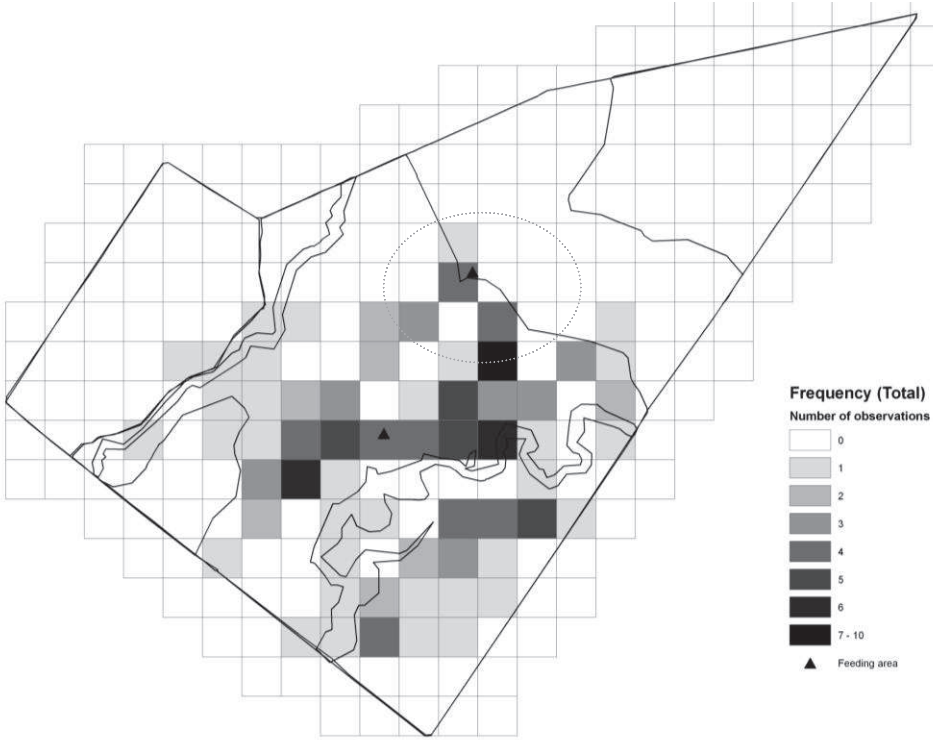


Figure 7.12 Total frequency of observations of <u>impala</u> from August 2004 to December 2007 in each 150 m^2 reference grid block.

Figure 7.13 Directional, geographical distribution of <u>Impala</u> between the different calendar years for the period of study.

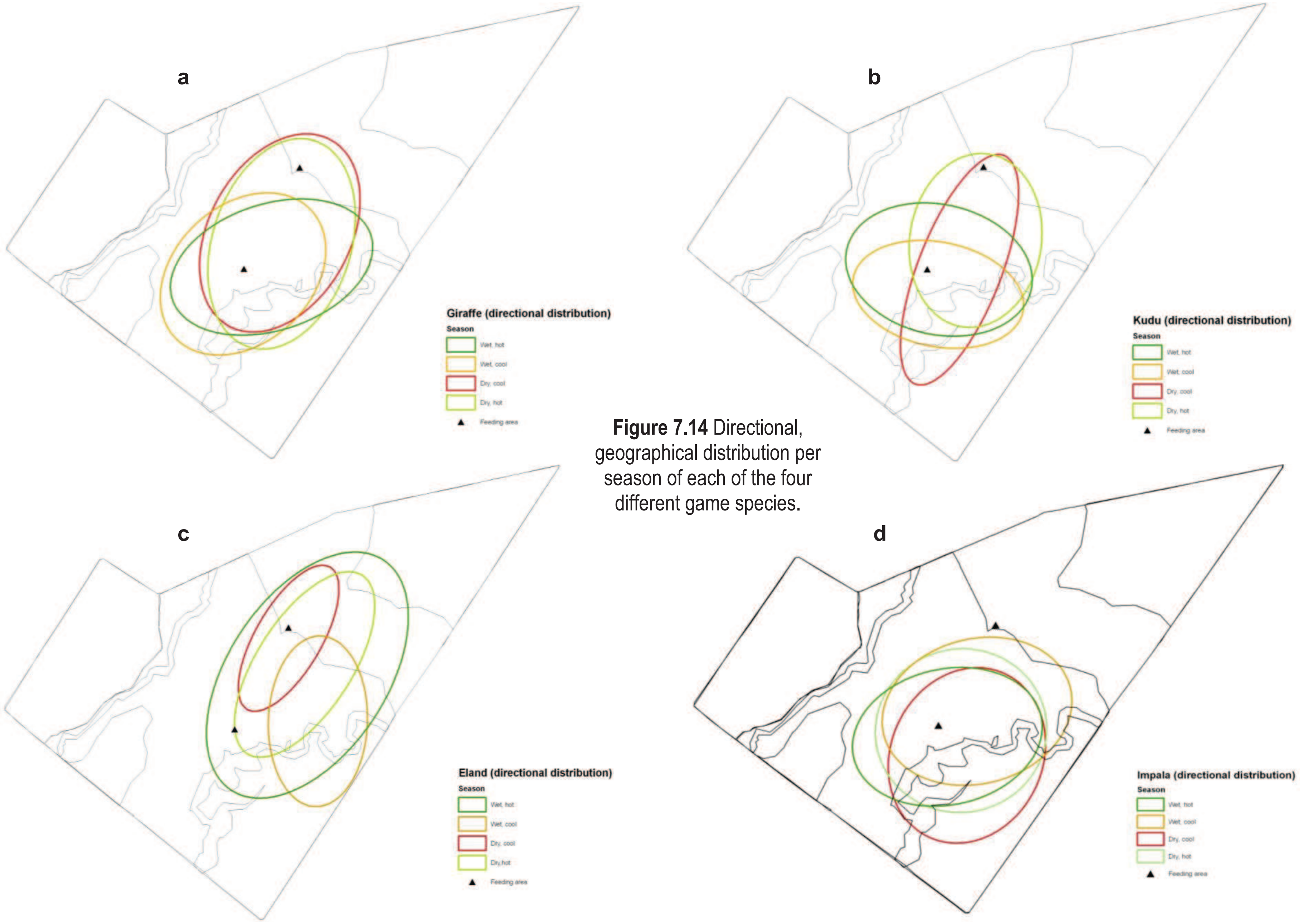


Figure 7.14 Directional, geographical distribution per season of each of the four different game species.

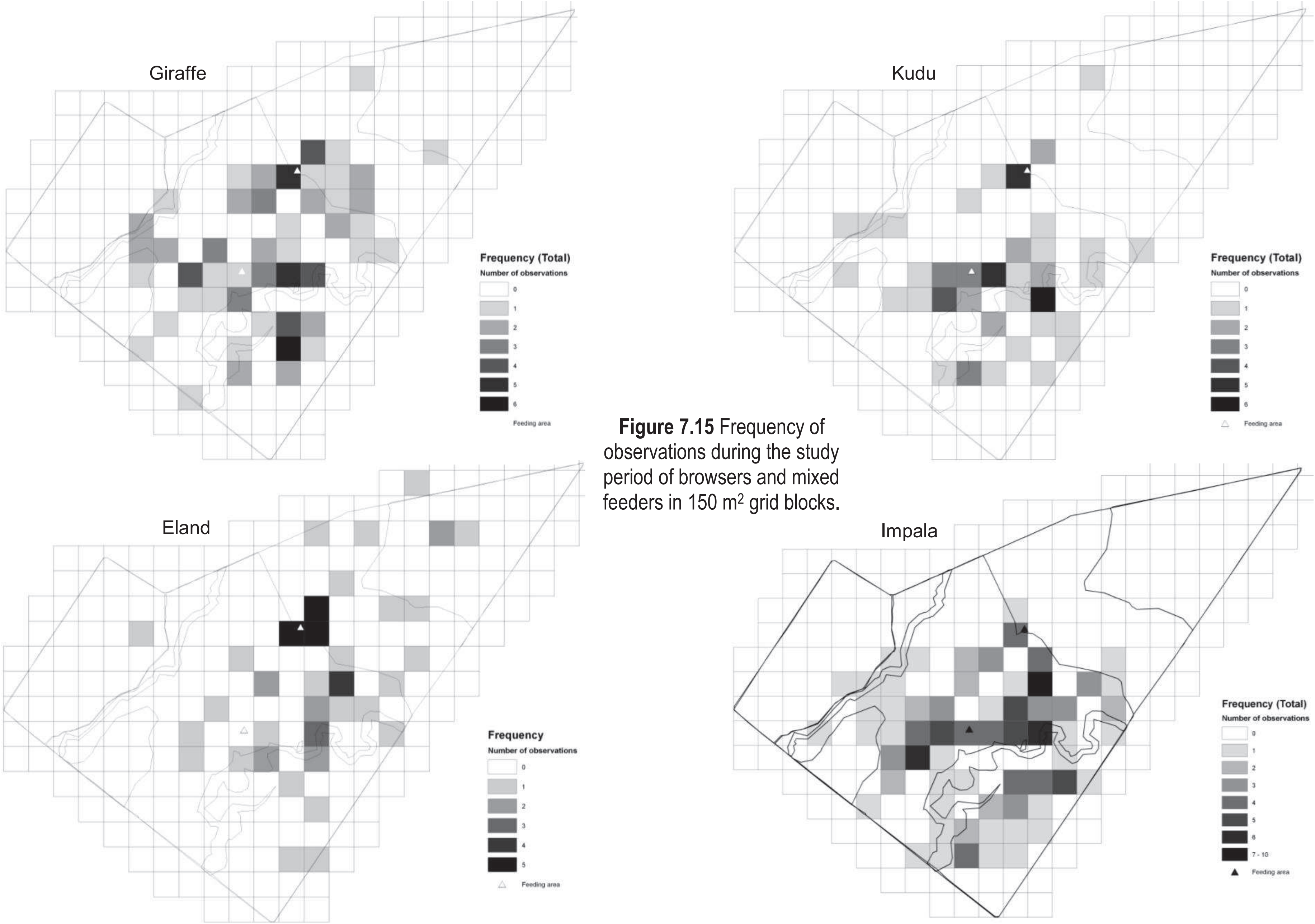


Figure 7.15 Frequency of observations during the study period of browsers and mixed feeders in 150 m^2 grid blocks.

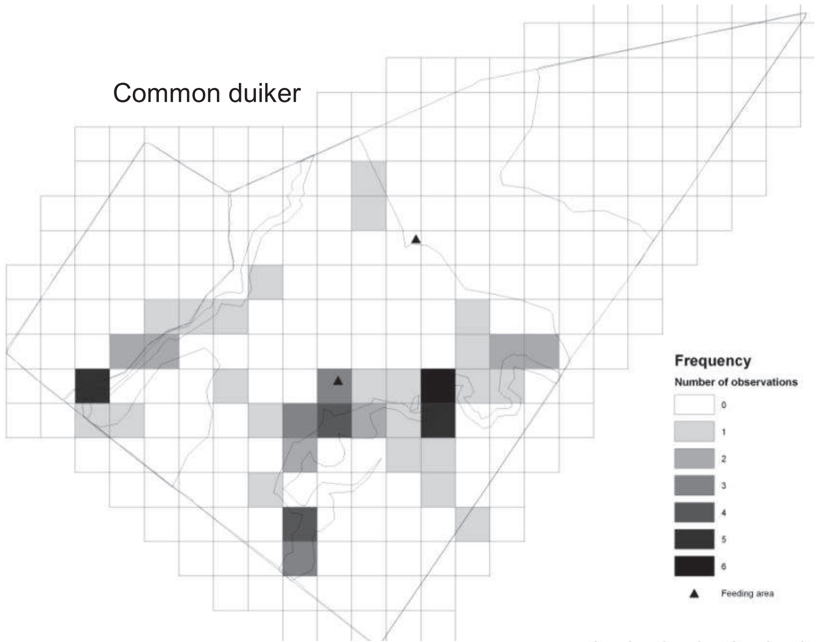
Duikers are predominantly browsers in savanna ecosystems, but are also opportunistic frugivores with a wide variety of food items, including fruits (Wilson 1966, Lunt *et al.* 2006, Codron *et al.* 2007a). A clear indication of the feeding type that duikers fall into is given under the heading 'Differentiating between browsers, grazers and mixed feeders' in Chapter 6. According to Codron *et al.* (2007a), duiker diets varied between 5% and 30% grass from the dry to the wet season in the Kruger National Park. Gagnon and Chew (2000) also found a 12% grass diet in this species. The duiker is a shy, small species that is not easily seen (Lunt *et al.* 2006), mostly only when scared from its hiding place under a bush (Table 7.2). This is also the reason why the duiker was not included in detail in this study like the other browsers and mixed feeders.

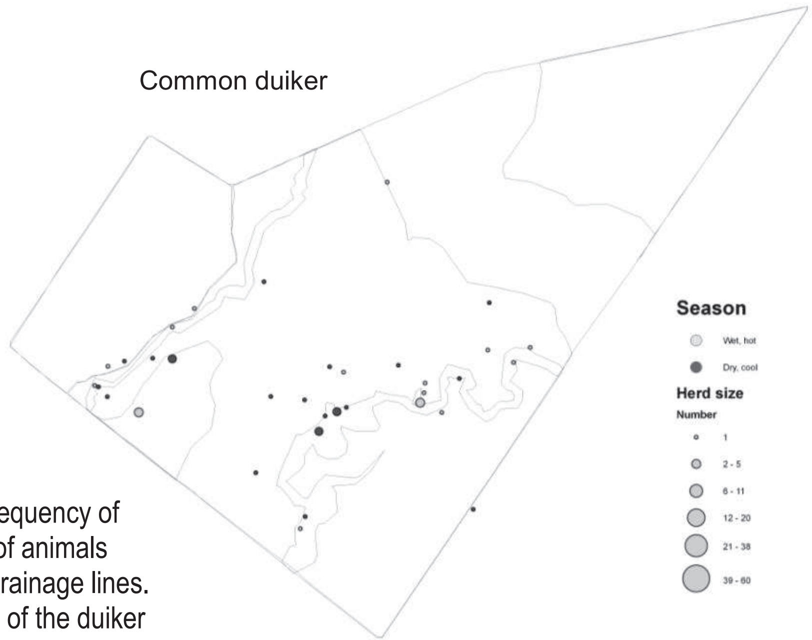
7.4.2 Grazers

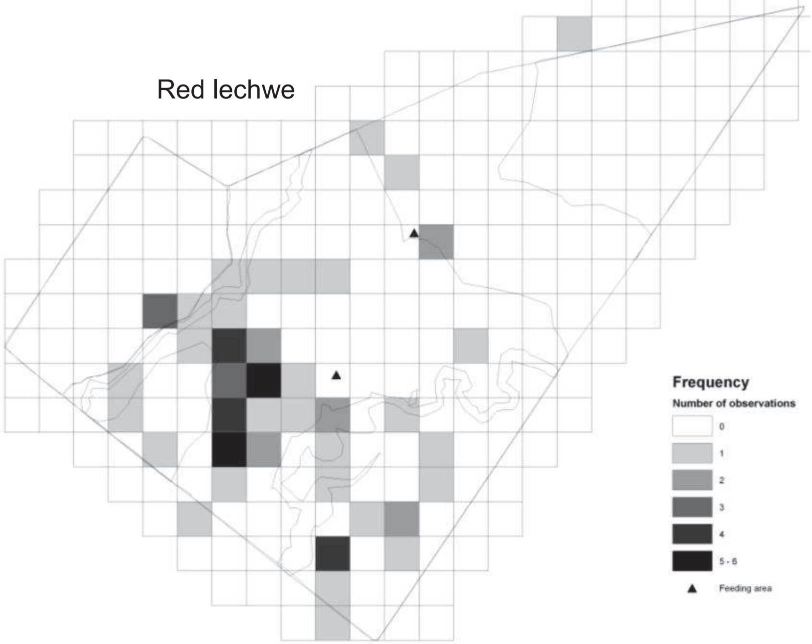
7.4.2.1 ANIMALS FREQUENTING THE DRAINAGE LINES

Red lechwe (*Kobus leche*) occurred as a group of 7 – 11 females, sometimes accompanied by one or two males; bachelor herds of 3 – 5 males; one female and one male as a pair; a mixed group of about 16 individuals; and as solitary males. They have specialised habitat requirements and prefer inundated floodplains and river ecotones (Table 7.1). In the study area (Figure 7.16) they were mostly found in ecotonal areas, the vicinity of the two waterholes and in areas where rainwater collects, namely in the drainage lines and in the remains of round waterholes/cribs of an old cattle enclosure located between the two drainage lines. There were only 68 sightings for the period of study in the northern side (study area), for the rest of the time they were south of the Soutpan road that divides the private reserve in two. In the southern side they frequented the large wetland dam and surrounding riverine thicket next to the owner's house (Figure 3.1), as well as the wetter drainage line close to the Modder River.

A small number of Southern Reedbuck (*Redunca arundinum*) was present in the study area and less than 10 individuals were observed. They were mostly hiding in tall grass during the day and only seen when disturbed, thus there were only 25 sightings in the study period. Reedbuck were usually in pairs of a male and a female; or single; and only rarely two males and a female; or two females and a male were seen together. They were usually found close to the two drainage lines (Figure 7.16) and inside the drainage lines in the wetland areas (indicated by large basins of the drainage lines on the map). They also occurred in the open thicket areas, in tall grass patches.


Common duiker


Common duiker


Red lechwe

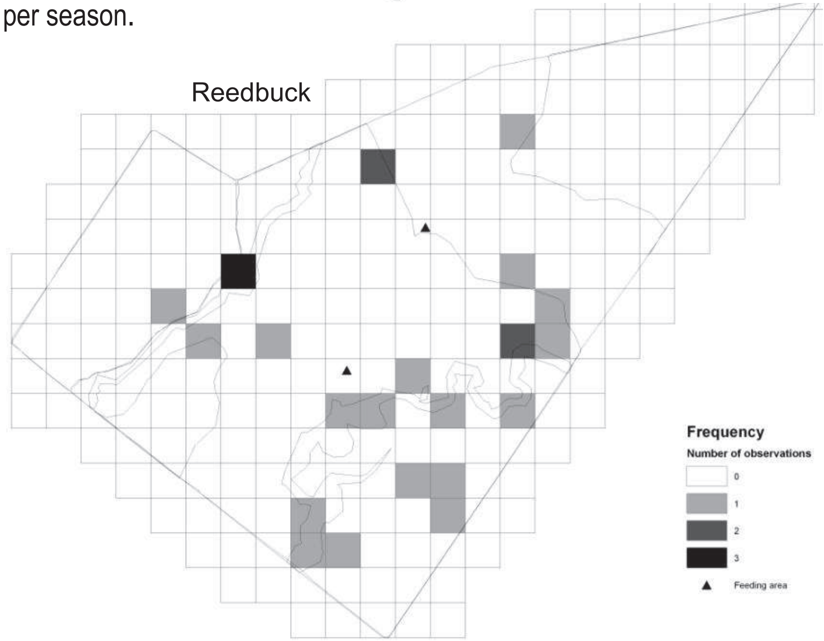
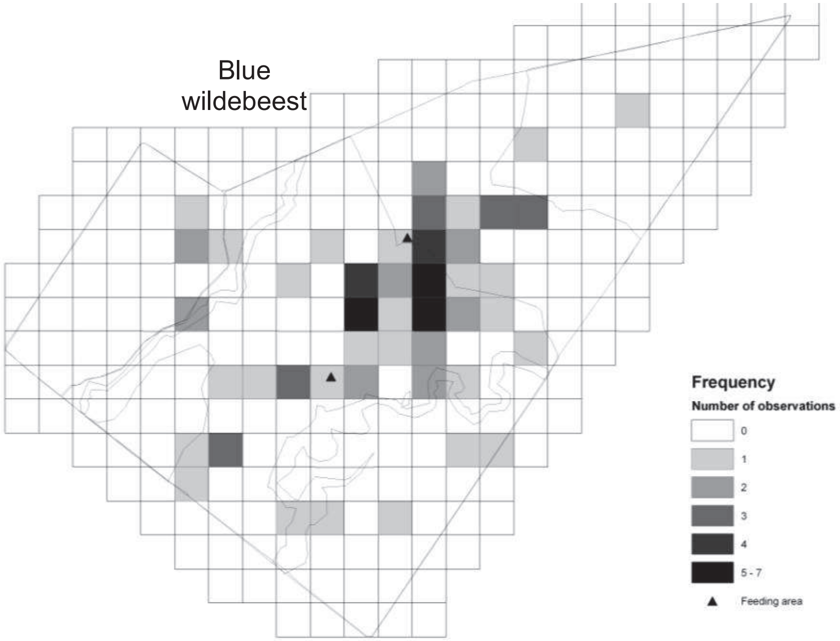
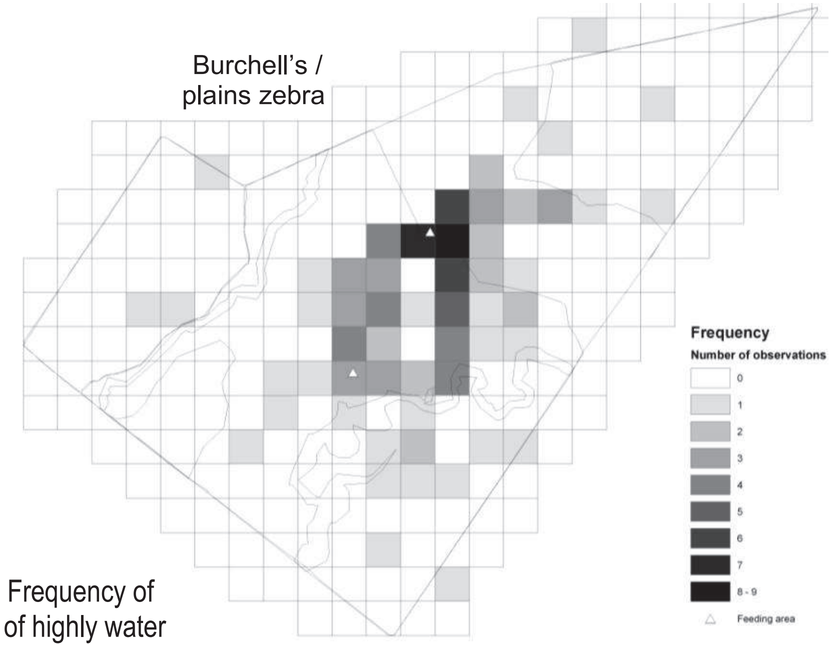
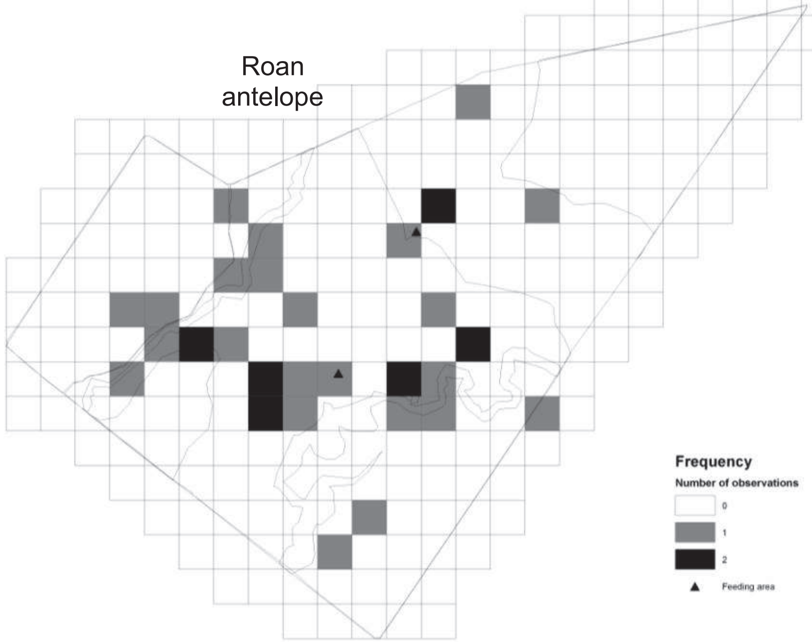

Reedbuck

Figure 7.16 Frequency of observations of animals concentrating in drainage lines. Specific locations of the duiker are indicated per season.







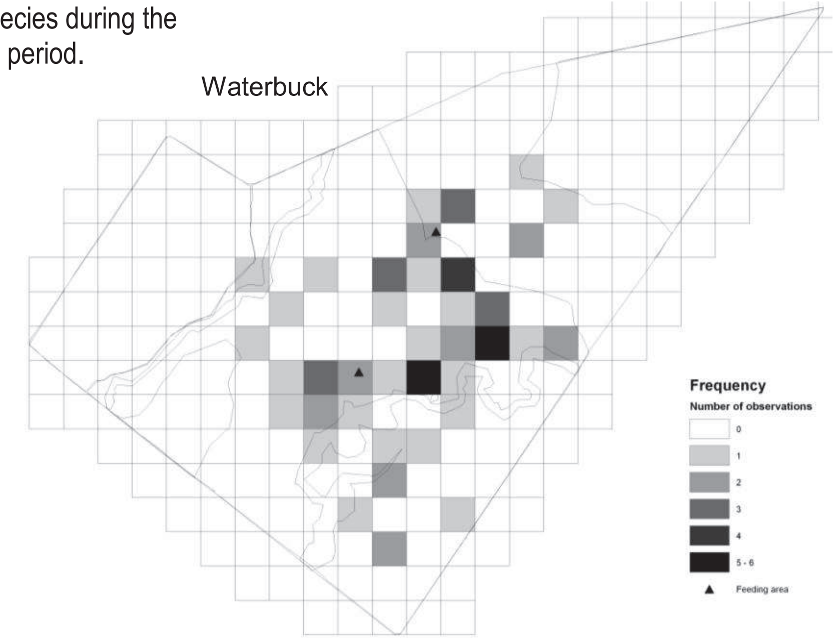


Figure 7.17 Frequency of observations of highly water dependent species during the study period.

7.4.2.2 HIGHLY WATER DEPENDENT SPECIES

Blue wildebeest (*Connochaetes taurinus*) were usually found together as one herd of between 10 and 17. Some bulls were solitary from time to time. Their numbers were reduced annually by means of hunting or live capture until 2007 when all the wildebeest, except for two escapees, were caught and auctioned. The herd was mostly found (Figure 7.17) in the dense thicket between, and also including, the two waterholes. They further frequented the northern open thicket between the grassland and main waterhole, but were less frequently in the other two open thickets (Figure 7.1a). Their preferred habitat is close to the main waterhole, because of their dependence on surface water (Estes 1997, Frandsen 1998, Skinner and Chimimba 2005) and also for the presence of trees to provide shelter (Table 7.1), while for feeding purposes they used the open thicket area next to it where grasses have a higher dominance. Blue wildebeest are known for their long distance migrations to seek better grazing (Brooks 1982, Verlinden 1998) and also for their seasonal movements during the dry season, mostly to short-grass areas on sandy river banks, when other areas are heavily overgrazed (Estes 1997, Skinner and Chimimba 2005). No obvious differences were observed in habitat selected between different seasons in the study area, except that they concentrated more in the open thicket and grassland in the dry, hot season than in other seasons.

The disagreement over the common and scientific names of Burchell's zebra (*Equus burchelli*), also known as Plains zebra (*E. quagga*) is commented on in the literature review. Their numbers were maintained as a family group of about 10 individuals with one dominant male. There were also one male and a female that formed their own separate group and always accompanied the giraffes. Two observations were made of a large herd of about 20 animals during the time of study that must have consisted of the combined resident herd and the herd from the southern side of the private reserve that was looking for greener pastures. Zebras are known to be nomadic, non-territorial (Table 7.2) and for migration (Brooks 1982). In the Kruger National Park, Smuts (1976) showed that parts of the zebra population had significant local movements and full-scale migrations. These movements take place between winter and summer grazing areas provided that their water requirements are met. The resident family in the study area was mostly found in vicinity of the two waterholes, disturbed area, open thicket and grassland, associating with the blue wildebeest (Figure 7.17). Smit *et al.* (2007) also found wildebeest and zebra to occur in higher densities close to waterholes. Zebras are often found in close association with blue wildebeest (Ben-Shahar 1991, Estes 1997, Frandsen 1998, Bodenstein *et al.* 2000) and other species, their acute sense of sight, smell and hearing being of benefit to the group as a whole (Skinner and Chimimba 2005). In the wet, hot season (summer), the zebras had a wider distribution in the study area and were more frequently found in the open thickets and grassland, while in the dry, cool season (winter) they focussed more on the main feeding area. The zebra pair frequented the preferred habitat of the giraffes, namely the denser thicket and big drainage line and was mostly on the move with giraffes in their daily search for acceptable browsing (moving to areas where the chemical defence mechanism of trees does not prevent browsing on plants in the same location, *vid*. Chapter 8).

Roan antelope (*Hippotragus equinus*) was introduced in the study area in 2006, consisting of four females and two males. They formed one herd for the first few months, where-after one male became solitary (Table 7.2) and permanently moved to the southern side of the private reserve (Figure 3.1), out of the study area. The other (dominant) male were mostly seen with the females in the study area, but were also solitary from time to time. One female disappeared in 2007, but three calves were observed in November with the remaining three females. The roans frequented the two waterholes and drainage lines (Figure 7.17) and were also found in the same area than lechwe, where the cattle enclosure ruins are found (Figure 7.16). Smit *et al.* (2007) listed roan as being water dependent and positively associated with artificial waterholes. At first, roan in the study area were mostly found in the open thicket next to the small drainage line, but then moved to open areas inside the dense thicket next to the bigger drainage line, closer to the waterhole. The open thicket to the west of the smaller drainage line was at that time occupied by large herds of red hartebeest, bontebok, gemsbok, springbuck and ostriches. Roan feed on medium to long grass (Table 7.1). Thus, herbivores that keep grass cover short, like red hartebeest, blue wildebeest and zebra (Harrington 1996, Perrin and Taolo 1999) may cause changes in habitat that render it less suitable for roan (Martin 1983, Harrington 1996, Skinner and Chimimba 2005). This might be the reason why they moved to the other drainage line, into the denser vegetation that has less grazing pressure. Herds are usually stable units and remain in particular areas, known as activity zones, for long periods, even years (Joubert 1970, Frandsen 1998, Skinner and Chimimba 2005).

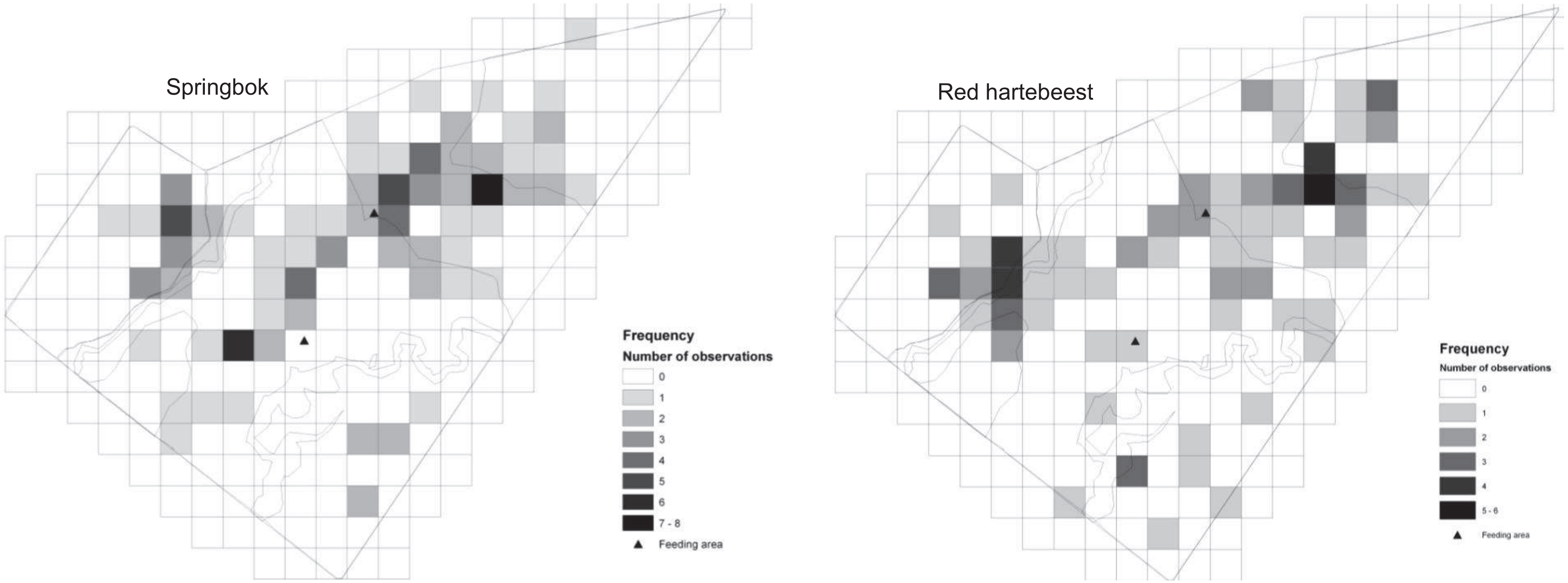
Waterbuck (*Kobus ellipsiprymnus*) occurred as mixed groups of 1 – 5 males together with 7 – 13 females in any number grouping between the sexes, but with females in majority. Other social groupings included: seven males and three females; or 3 – 5 males in bachelor groups and solitary males. The largest mixed herd observed in the study area consisted of about 16 individuals. Most of the time in the wet, hot season, waterbuck were in the northern side of the private reserve and in the dry, cool season they were south of the Soutpan road (Figure 3.1). They were usually found in the drainage line and dense, riparian thicket close to the Modder River in the southern side of the private reserve. In the study area (Figure 7.17), they frequented the dense thickets, drainage lines, waterhole area, disturbed area and open thicket close to the waterhole.

Waterbuck are mostly dispersed in the wet season, when females with calves tend to prefer woodland, and move to open grassland near water during the dry season (Tomlinson 1980a, 1981, Estes 1997, Skinner and Chimimba 2005). Females prefer to have some cover within reach (Estes 1997). Waterbuck are known to be associated with water near a river or drainage lines (Tomlinson 1981, Melton 1987, Wentzel 1990, Anonymous 1993b, Estes 1997, Skinner and Chimimba 2005). Smit *et al.* (2007) found that waterbuck were very strongly associated with rivers up to 3 km in the Kruger National Park, but exhibited no consistent distribution pattern around waterholes.

7.4.2.3 PLAINS ANTELOPES

Springbuck (*Antidorcas marsupialis*) occurred as smaller groups of 2 – 15 and up to 25, as a big herd of about 70 animals and as solitary males. They usually flee quickly when approached on foot or by vehicle by running through long grass into the dense thickets, making it impossible to determine the sex of animals in herds, especially the large herd. Possible social groupings of springbuck are listed in Table 7.2. In 2007, their numbers were reduced drastically in the study area, but being prolific breeders (Fairall *et al.* 1990, Skinner *et al.* 1996, Estes 1997, Cain III *et al.* 2004, Skinner and Chimimba 2005), their numbers increased again to about 40 at the end of that year. They were mostly found in the grassland and open thicket areas (Figure 7.18). In the dry, cool season they were more often found in the dense thicket in between the two large open thickets, possibly for shelter against cold temperatures, since they are cold-stressed animals (Skinner and Chimimba 2005). They will drink where water is available, but are not dependent on it (Skinner and Chimimba 2005, Stapelberg 2007). They are known for mass migrations in suitable areas (Bigalke 1972, Estes 1997, Cain III *et al.* 2004, Skinner and Chimimba 2005, Stapelberg *et al.* 2008b), but only small local movements were observed in the study area. Springbuck are considered to be intermediate feeders that shift from grasses in wet, hot seasons to shrubs and karroid shrubs in dry, cold seasons (Fairall *et al.* 1990, Cain III *et al.* 2004) with the tendency to become concentrate selectors when forage is optimal (Skinner and Chimimba 2005, Stapelberg *et al.* 2008b). However, most authors list karroid shrubs (Liversidge 1970, Bigalke 1972, Davies *et al* 1986, Fairall *et al.* 1990, Cain III *et al.* 2004) to be of higher preference than leaves from large woody species. Therefore, for this study the springbuck was not included in the mixed feeder group that concentrate their feeding on grass and leaves of trees and shrubs.

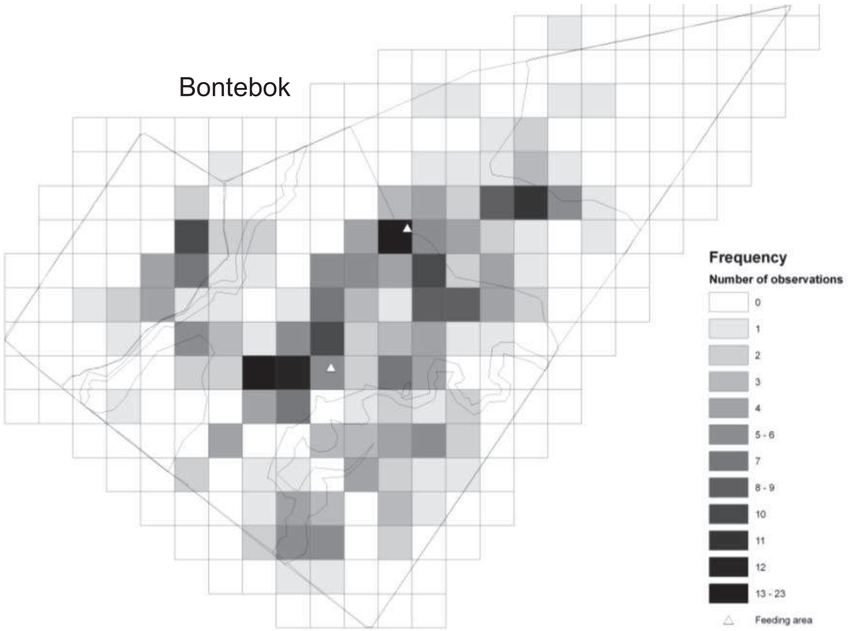
Red hartebeest (*Alcelaphus buselaphus*) were mostly observed together as a harem herd of 8 – 13 animals, but their numbers were normally kept on 10. There were also some solitary males. In 2007 their numbers were reduced to four animals. Their preferred habitat was the grassland and the three

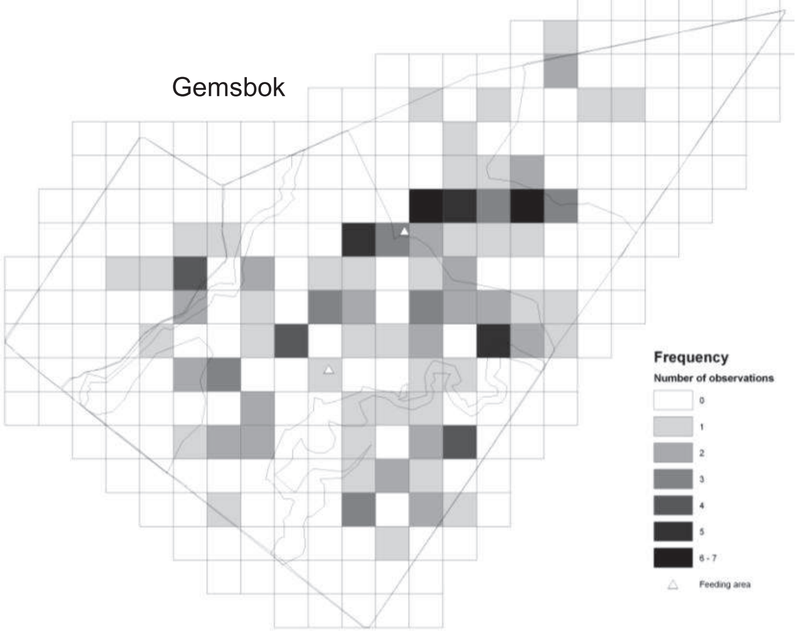


Springbok

Red hartebeest

Figure 7.18 Frequency of observations in 150 m^2 grid blocks during the study period of plains antelopes present in the open thickets and grassland.


Bontebok


Gemsbok

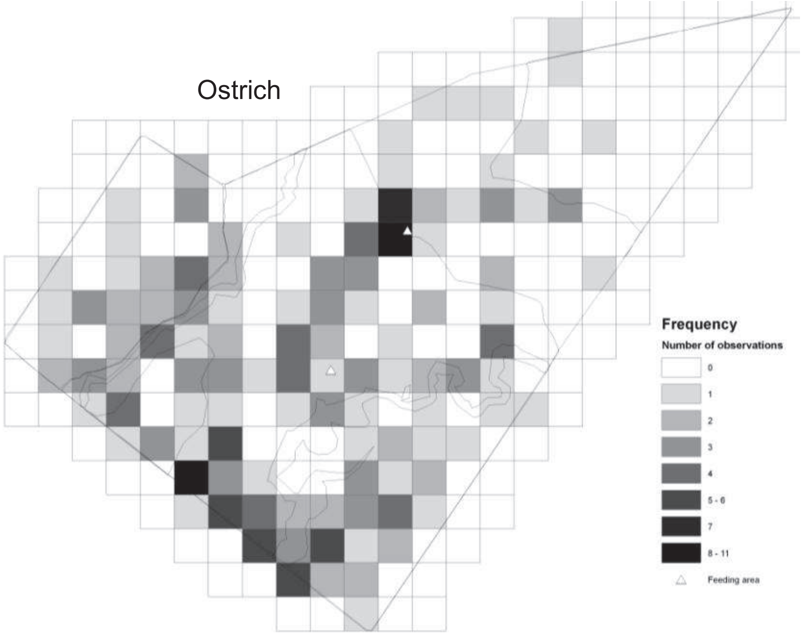

Ostrich

Figure 7.19 Frequency of observations in 150 m^2 grid blocks of species observed all over the study area in all the vegetation types.

open thickets (Figure 7.18). In order to reach the two open thickets on opposite sides of the small drainage line (Figure 7.1a), they crossed the drainage line frequently. They were also observed at the waterholes. According to the literature they are dependent on surface water (Skinner and Chimimba 2005), but can also obtain moisture from their food if necessary (Anonymous 1993a). Red hartebeest are more often found on the edge of open woodland and tall bush grassland than far out on the plains (Estes 1997), as was the case in this study area as well. They avoid the more closed types of woodland, except in transit (Skinner and Chimimba 2005). No obvious differences were observed in the study area in habitat selected between different seasons. Verlinden (1998) also stated that they were mostly sedentary. In open plains red hartebeest may migrate between long grasslands in the dry season and short (10 cm or more), well drained pastures during the rains (Anonymous 1993a, Estes 1997). Their home ranges usually incorporate abovementioned pastures for all seasons (Estes 1997). This might explain their movement between different open thickets in the study area.

7.4.2.4 SPECIES PRESENT IN ALL VEGETATION TYPES

Bontebok (*Damaliscus pygargus pygargus*) occurred as small, mostly sedentary groups of 4 to 9 animals and as solitary territorial males. During the wet, hot season (summers) they were present in larger groups of up to 11 that included juveniles, but in the dry, cool season (winters) these groups were smaller in size. One reason might be that the juveniles are cast out of the herd and they search wider for food resources. Also, the hunting season coincides with the wet, cool- and dry, cool seasons, reducing the numbers of larger herds. The total number of bontebok in the study area was 25 – 30. Bontebok seems to be the dominant species in the study area, since they were widely dispersed and recorded in all vegetation types. They have a preference for short grass (Frandsen 1998, Skinner and Chimimba 2005) and preferred the more open areas inside dense thickets. They maintain fixed territories and specific groups of bontebok were mostly found in the same locality during the study period. Eight areas were identified as possible territories indicated by the higher frequency of observations of bontebok in those grid blocks (Figure 7.19). Some areas with lower frequency of observations (indicated by a lighter colour) in-between these eight areas might be used in transit by animals moving to waterholes and/or female- and bachelor herds moving between territorial areas. It is known that drinking water is essential (David 1973, Frandsen 1998, Skinner and Chimimba 2005). It is highly possible that the territory next to the main feeding area and waterhole might belong to the dominant male in the territorial network, since it is prime habitat for bontebok: dominated by short grass, include shelter, drinking water and supplementary feed.

Tsessebe (*Damaliscus lunatus*) herds were located in the southern side of the private reserve, but one animal was always observed with a herd of bontebok in the study area on the northern side of the Soutpan road. In 2007 there were two tsessebe accompanying this bontebok herd. The single animal frequented the area close to the main feeding area and was sometimes observed solitary (without the bontebok herd) next to the big drainage line, in proximity of the connecting tunnel between the two sides of the private reserve underneath the Soutpan road (Figure 3.1). No figure for tsessebe is included in the results, because the movements of a single animal cannot be viewed as representative of the habitat preferences of the herd/s. Their preferred habitat is usually ecotonal areas and drainage line grasslands (Child *et al.* 1972, Martin 1983, Dunham *et al.* 2004, Skinner and Chimimba 2005, Dörgeloh 2006). De Wet (1988) concluded that tsessebe in the Kruger National Park were limited to areas where optimal grass species composition existed, but no significant preference was observed with regard to grass height (Table 7.1), while Dörgeloh (2006) concluded that they preferred shorter grass. If this individual in the study area should prefer shorter grass, it might explain its association with bontebok that also have a preference for short grass. Both these species belong to the genus *Damaliscus*, which might also be another reason why they associate together. It is known that animals of a similar genus can cross-breed (*vid.* Chapter 9) and can associate with each other if they occur in a similar area (Estes 1997, Skinner and Chimimba 2005).

Gemsbok (*Oryx gazella*) occurred as one large herd of about 20 individuals and as solitary males. During the winter (dry, cool season) they split into at least two smaller groups consisting of 6 – 10 individuals and combined again into one large group containing all the individuals during summer (wet, hot season). Dieckmann (1980), Anonymous (1992b) and Skinner and Chimimba (2005) also found that they usually occurred in large herds in the wet season, which broke up into smaller herds in the dry season when food was less abundant. In the study area their total number ranged between 20 and 32 during the time of study and numbers were also regulated by means of hunting and live capture. These gemsbok were shy and fled into the cover of trees or into the deep basin of the large drainage line at first sight. They had a higher frequency of occurrence (Figure 7.19) in the disturbed area around the main feeding area, open thickets and in open areas in the dense thickets. In the wet, hot season they were more frequently observed in the open thicket areas and grassland than in other seasons. They were observed in most of the study area and in all the vegetation types. They are known for large territories and especially large female home ranges. In the Kgalagadi Transfrontier Park, territories are maintained for three years and averaged 26 km^2, while female home ranges averaged 1 430 km^2 (Knight 1991). In the Central Kalahari Game Reserve female home ranges were 52 – 212 km^2, while five males had annual ranges of 10 – 16 km^2 (Williamson and

Williamson 1988). Where shade is available, gemsbok may congregate under trees during the hotter parts of the day (Ruckstuhl and Neuhaus 2009).

The disease-free African savanna (or Cape) buffalo (*Syncerus caffer*) in the study area were mostly found together in one herd of approximately 25 animals. During 2005 all the buffalo were caught and auctioned. Buffalo were reintroduced in 2007, with a total herd size of 20. In the study area, only 9 sightings in total were made of the two successive buffalo herds and they were widely dispersed, not giving a clear indication of a specific preferred habitat, therefore no figure is included. The buffalo were known for moving between the two sides of the private nature reserve, but they were mostly found on the southern side of the Soutpan road that divides the nature reserve in two (Figure 3.1), possibly to be closer to the Modder River. It is well-known that the buffalo is a riverine species and they have a preference for areas in close proximity to water (Winterbach and Bothma 1998, Skinner and Chimimba 2005). Most of the private reserve could be considered suitable habitat for buffalo, since the largest part consists of riverine thicket. It is possible that they may even use the grassland and more open areas during their night grazing in the warm season (Sinclair 1977, Funston 1992, Skinner and Chimimba 2005). It is known that buffaloes usually prefer shelter in the form of trees during the warm periods of the day, but that the highest quality food is usually available in open grassland (Winterbach and Bothma 1998, Skinner and Chimimba 2005). Funston *et al.* (1994) indicated that buffalo in the Sabi Sand Game Reserve did not select the open grassland communities, but rather preferred the savanna and thicket communities. Winterbach and Bothma (1998) found that in the Willem Pretorius Game Reserve, buffalo moved toward the riverine habitat during the dry, cool season, resulting in a reduced home range. Further, buffalo will intensively utilise *Panicum* species, especially *P. maximum* where it is available (Funston *et al.* 1994, Macandza *et al.* 2004, Ryan *et al.* 2006) and it is usually associated with riverine vegetation or growing in shade of woody plants. Smit *et al.* (2007) indicated that buffalo are very water dependent and utilized rivers and waterholes in the Kruger National Park.

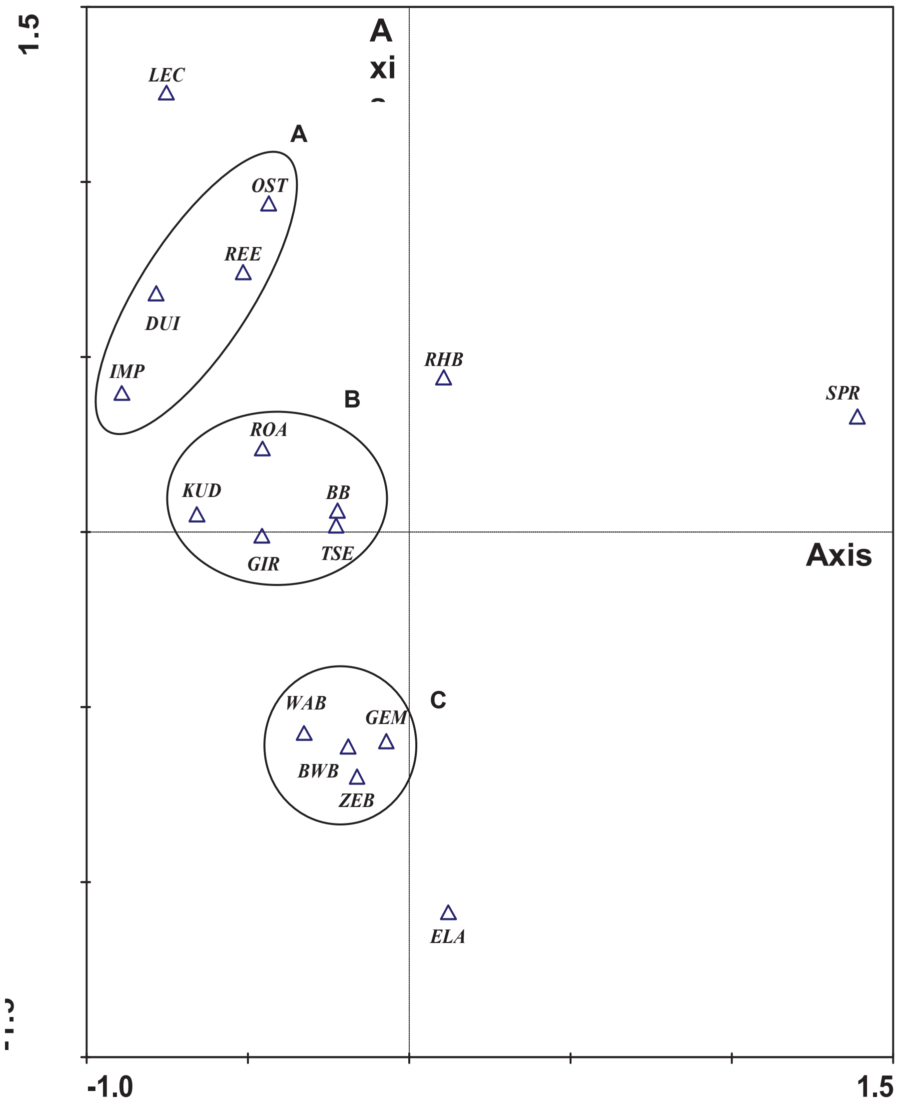
Ostriches (*Struthio camelus*) were observed solitary or in groups of 2 – 7, or occasionally in larger groups of 9 – 14. Immatures of roughly the same age grouped together for a season or longer. Ostriches numbered approximately 80 in total in the private reserve, until in 2007 when 40 were removed. Ostriches moved freely through the connecting tunnel between the two sides of the private reserve (Figure 3.1). They were observed in all the vegetation units in the study area (Figure 7.19) and almost all the grid blocks, even if they were just running through it when disturbed, to reach cover. They usually avoid tall grass higher than 1 m and very dense woodland (Brown 1992). They covered large distances per day and the same group were seen in the western part of the study area early in the morning and later in the most eastern part. Since they were all over the study area, no obvious differences could be found between areas frequented in different seasons. These large, flightless birds were included because they compete with game for space and food (Table 7.1).

7.4.3 General discussion

Game species are usually grouped as high or low density animals in accordance with their herd size (Table 9.1). Low density animals include duikers and reedbuck. Intermediate density species are bontebok, giraffe, kudu, roan, tsessebe, waterbuck and ostrich, while the following are some intermediate to high density species: eland, impala, red hartebeest, red lechwe, springbok and zebra. Blue wildebeest, buffalo and gemsbok are high density species (Smit 2002, 2007).

In the study area, high density species like Burchell's zebra, blue wildebeest, red hartebeest and tsessebe occur in smaller herds due to stocking densities. CA-ordination provides a summary of herd sizes of species observed per grid block (Figure 7.20). This is, however, not a representation of the total number of each species present. Ordination grouped species along Axis 1 from the least number (1) to the largest number (71) in herd sizes and along Axis 2 from animals occurring solitary or in a small herd, to animals occurring mostly in large herds and not solitary. Springbok, grouped at the far right, had the biggest range in herd sizes (1 – 71, mostly 60) and were the dominant species in terms of numbers. Duiker, at the far left side of Axis 1, were observed solitary or occasionally in pairs. Red hartebeest, in the centre, were mostly in a stable herd of 10 animals.

Lechwe, grouped in the top left corner along Axis 2 (Figure 7.20), had low herd sizes of 1 – 12, mostly being < 5 in total. All the animals in Group A were from time to time observed solitary or in pairs (reedbuck herds: 1 – 3), whereas impala were, besides being solitary or in small groups, also in herds that ranged between 10 and 40 individuals and ostriches were in groups of 5 – 10. The animals of Group B usually occurred in stable herds of 6 – 8 individuals, excluding tsessebe that closely associated with bontebok. Blue wildebeest and zebra (Group C) were mostly seen in herds of 10 – 13 animals, while waterbuck herds ranged from 10 – 15 and gemsbok from 10 – 22. Eland, in the opposite corner than lechwe, had herd sizes of 10 – 33 animals between different seasons, mostly being 20 in total. For the most part, these ordination results correspond to herd sizes as mentioned in the literature (Table 7.1). Species that usually aggregate to form large groups in summer months are already grouped together (Group C excluding WAB, Figure 7.20). Lechwe, red hartebeest, eland, impala and tsessebe are not grouped together in this setup, but can also form large aggregations if there is enough space and numbers.



	Axis 1	Axis 2	Axis 3	Axis 4
Eigen-values	0.532	0.350	0.288	0.246
Cumulative % variance:				
of species data	19.1	31.6	41.9	50.8

Figure 7.20 Correspondence analysis (CA) based on herd size of each game species as observed during the study period. This is specific to the study area and depends on the size of the area and the management of animal numbers. Legend: BB = bontebok; BWB = blue wildebeest; DUI = common duiker; ELA = eland; GEM = gemsbok; GIR = giraffe; IMP = impala; KUD = kudu; LEC = red lechwe; OST = ostrich; REE = southern reedbuck; RHB = red hartebeest; ROA = roan; SPR = springbok; TSE = tsessebe; WAB = waterbuck; ZEB = Burchell's zebra.

There are several factors that determine the habitat that animals occupy, for example water, food, shade, shelter, space, competition, vegetation units, plant species composition and physical structure, terrain, preferences, combined with aspects of herbivore sociability and gregariousness (Joubert 2010). The vegetation structure can also change seasonally, like when deciduous trees and shrubs shed their leaves in the dry season, or after a fire (Joubert 2010). According to Funston *et al.* (1994), the pattern of habitat use does not necessarily include the best available habitat, as judged by a single criterion of the main factors that determine habitat selection (preferred food species, water, shade, shelter for cold temperatures and cover for predators), but rather proved to be the most suitable overall. The suitability of the habitat is reflected in the way in which the animal populations react to their habitat (Joubert 2010). According to Melton (1987), a species' habitat is the sum of the environments in which it occurs. Habitat is therefore a concept of distribution as opposed to niche, which describes the role of a species within a community. Brooks (1982) described a home range as an area with a certain productivity that meets the energy requirements of the individual, or group that occupies it.

7.4.3.1 WATERHOLES AND THE PIOSPHERE EFFECT

Water is mostly one of the main determinants of the habitat that animals prefer. Two waterholes in the form of earth dams are available for game and the feeding areas are located next to it (Figure 7.1). The southern waterhole normally dried up during the cool, dry season. The main waterhole also dried up occasionally when the pump broke that supplies water to it from a cement dam connected to a wind pump. However, a water trough around the cement dam always contained water and was located about 50 m from the main waterhole.

The only game species present in the study area that is water índependent is the common duiker, all other species are dependent or will drink if water is available, while gemsbok, springbok and ostrich can get water from food in their natural habitat if surface water is unavailable (Table 7.1). Zebra, wildebeest, buffalo and impala are obligate drinkers (Brooks 1982, Matson *et al.* 2006)**.** Furstenburg (2006a) and Du Toit (2010b) summarised the water requirements of each species in a table. Smit *et al.* (2007) found that giraffes and kudus in Kruger National Park are more likely to be found closer to rivers than further and appear neutral to waterholes. This might be due to the riparian habitat that they prefer. Smit *et al.* (2007) concluded that eland in Kruger Park have a consistent positive association with artificial waterholes, but distribution is indifferent to rivers, while impala is the opposite and do not occur in high densities close to waterholes.

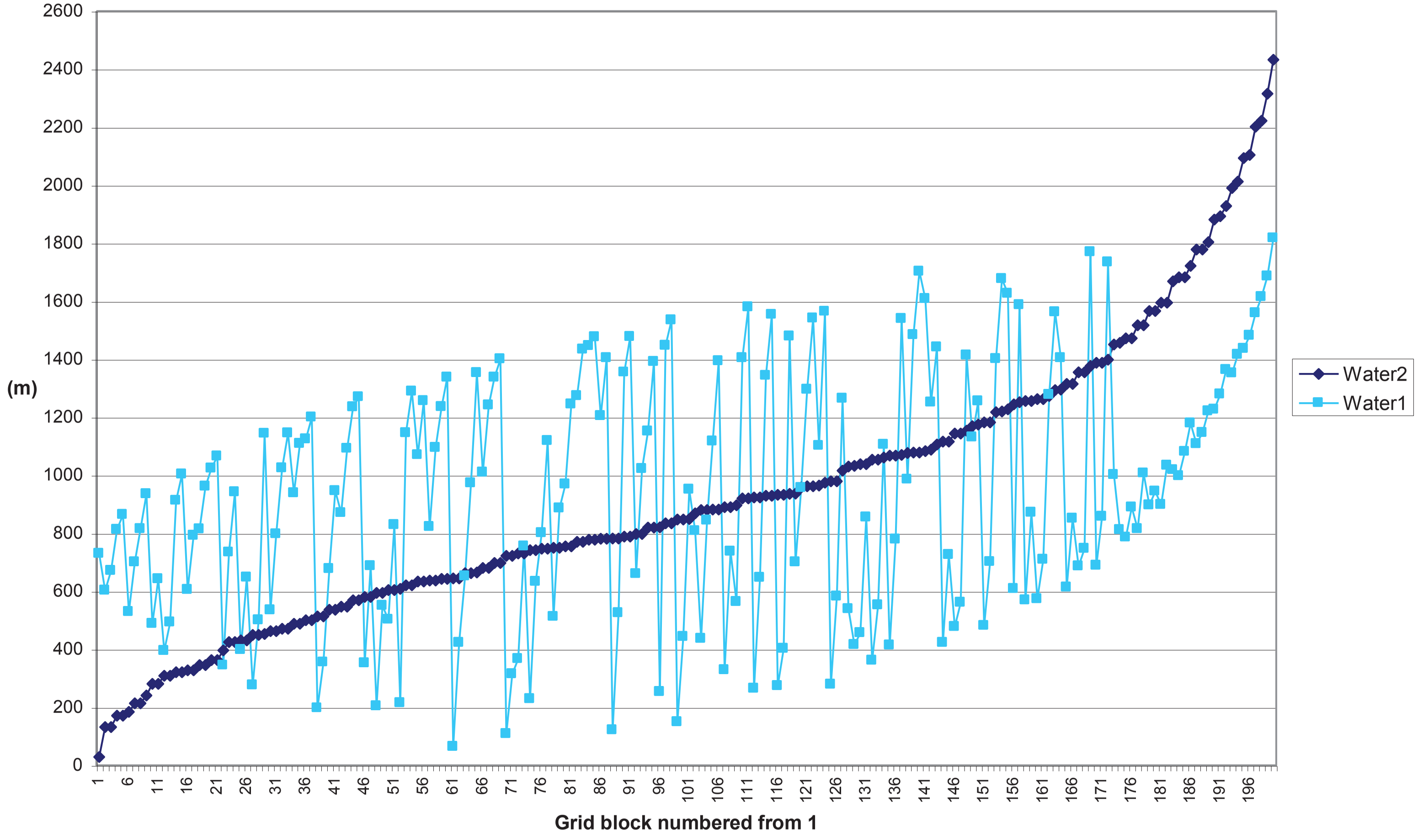


Figure 7.21 Distance (m) of the centre of each grid block from the two waterholes. Grid blocks were arranged from the one containing the southern waterhole (water 2) to the furthest block from it. Distances from the main waterhole (water 1) are also indicated in relation to the southern one. The table on the next page indicates the original block numbers as given by the Geographic Information System (GIS).

Table of Figure 7.21 listing the original GIS grid block numbers on the graph starting from no. 1 at the southern water point to the furthest block from it, no. 200.

Block Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Original GIS no	177	201	178	176	153	202	200	154	152	225	179	226	203	175	129	224	155	199	130	151	128	227	223	131	249

Block Number	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Original GIS no	180	250	204	127	248	156	174	105	198	106	150	104	251	228	247	132	222	107	126	103	273	181	274	205	272

Block Number	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Original GIS no	157	252	173	81	197	82	246	108	149	80	275	229	271	133	102	221	83	125	79	276	253	297	182	298	206

Block Number	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Original GIS no	270	109	296	158	245	84	172	57	101	78	196	58	299	230	148	56	295	134	220	59	277	124	55	300	254

Block Number	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125
Original GIS no	269	294	321	183	244	60	322	207	320	171	33	323	231	195	34	301	278	147	319	293	219	35	268	123	324

Block Number	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Original GIS no	255	243	345	302	346	208	325	279	292	347	232	170	317	194	10	146	267	218	348	256	326	303	242	316	291

Block Number	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175
Original GIS no	349	280	266	169	193	327	217	372	257	350	304	315	241	290	373	281	351	328	192	374	305	216	282	352	375

Block Number	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Original GIS no	329	398	306	376	353	399	330	377	400	354	331	401	378	355	402	379	356	403	380	427	404	428	405	429	430

Figure 7.21 presents distances of each grid block (Figure 8.1) from the waterholes, starting at the grid block where the southern waterhole is located. The sharp tip of the grassland in the north-east and the open thicket in the western corner are the furthest away from any waterhole, between 1 and 2.5 km. Red lechwe and roan antelope will mostly occur less than 2 km or 5 km, respectively, from water (Martin 1983, Williamson 1990, Frandsen 1998, Skinner and Chimimba 2005), while the water dependent species (Table 7.1) prefer to have water close-by: impala not more than 2.2 km, zebra 7.2 km, blue wildebeest 7.4 km and buffalo 7.8 km (Van Rooyen 2010). Thus the distances from waterholes in the study area are within reach of even the least mobile, water dependent species (Figure 7.22). If the southern waterhole dries up in the winter, the furthest distance from the other waterhole is less than 2 km (Figure 7.21). Grossman *et al.* (1999) describes a 'natural', multi-species system in a savanna region, where a watering point supplies a radial area of at least 15 km, as indicated on Figure 7.22. As distance from the watering point increases, the density of non-mobile water dependent species decreases, followed by the mobile water dependent species. This is usually accompanied by a change in vegetation structure due to a change in grazing pressure.

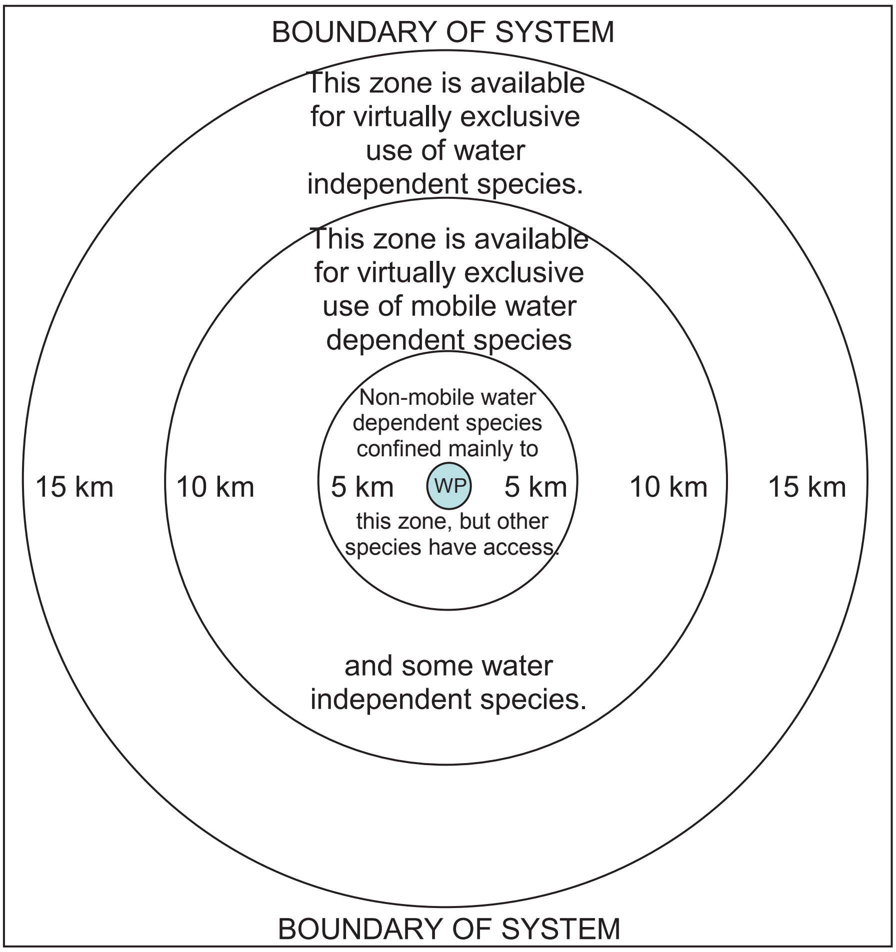


Figure 7.22 Diagrammatic illustration of distribution of game species in a theoretical system with a permanent water point situated in the centre (after Grossman *et al*. 1999).

Smit *et al.* (2007) stated that: "To increase grazing heterogeneity, habitat diversity and system resilience waterholes should be spaced far enough apart to ensure adequate areas of low or seasonal use". Owen-Smith (1996) proposed a simplistic geometric model, suggesting spacing watering points at least three times the potential daily distance animals will travel for water, with 4 – 5 km being the assumed distance medium sized ungulates will travel between grazing and water resources. The furthest distance in the study area is 3.5 km from north to south and if the watering point should be moved it will still be within range of all the animals. Scogings *et al.* (1990) reported that areas without permanent water were selected by blesbok, springbok, zebra, gemsbok and eland in the Jack Scott Nature Reserve, but that the furthest distance from water was < 4 km. In the Kruger National Park, the water provision programme brought most of the park within less than 10 km of permanent water, stopping attempts of blue wildebeest and zebra to migrate in winter in search of water and food resources (Smit *et al.* 2007).

Watering points usually lead to the development of a gradient of utilisation pressure which is greatest near the watering point and decreases as a function of distance, of up to 200 m (Child *et al.* 1971, Graetz and Ludwig 1978, Thrash *et al.* 1993, Van Rooyen *et al.* 1994, Brits *et al.* 2000, 2002, Van Rooyen 2010). Brits *et al.* (2002) concluded that in Kruger Park, an overall low tree and shrub density was found close to water and it increased with distance from water. A high vegetation density was only reached at 2.8 km from watering points and still increased with distance, while the sacrifice area around the watering point was 0.25 km. Large numbers of animals, including elephants, are present (Brits *et al.* 2002) that influence the vegetation in these piospheres. Lange (1969) used the word ‘piosphere’ to describe the area of rangeland which surrounds a permanent watering point and defined it as "an ecological system of interactions between a watering point, its surrounding vegetation and the grazing animal".

In the study area, with the absence of elephants, no increase in tree density except for a change in vegetation units was observed with distance from waterholes, but shrub density increased, especially *Asparagus laricinus*. The piosphere effect was not studied in detail in this study and vegetation density data is only available from the woody plant density of grid blocks that surround the two waterholes (Figure 8.3). With regards to visual observations of the surrounding area, the main waterhole located in the disturbed area (Figure 7.1a) was the worst off. The grass layer was trampled to dust in an area of about 100 m around it and was in a short, pioneer state for about 500 m from the waterhole, with a network of foot paths traversing the open thicket area to the north. Further detailed study is needed on this aspect in the study area.

Nsinamwa *et al.* (2005) concluded that grass species diversity was low close to watering points in Botswana and increased with distance, while diversity of forb species was high close to watering points and drastically decreased with distance from it. Soil acidity (pH), organic carbon, macro- and micro-elements decreased with distance from watering points in communal grazing areas in Botswana. Janse van Rensburg and Bosch (1990) also determined a gradient from heavily-grazed and trampled plots close to watering points to ungrazed plots some distance away. Owen-Smith (1996) and Smit *et al.* (2007) suggested that a spacing of 12 – 15 km between watering points should lead to development of the full grazing gradient spectrum, ranging from highly utilised to rarely utilised. The disturbed heavily grazed areas near watering points will be favoured by species that prefer short grass and grazing lawns, while selective grazers, such as roan antelope, need virtually ungrazed tall grass that are expected further away from waterholes. A variety of other species will occur along the disturbance continuum radiating from the waterhole (Smit *et al.* 2007). This is, however, not possible in this study area because of its size, the distance between borders from east to west is 2.8 km, while from the northern to the most southern corner is 3.7 km. Trollope (1990) reckoned that the opening and closing of watering points could play an important role in application of a rotational resting program. Therefore drinking troughs are preferred to permanent waterholes as they are more manageable and can easily be moved.

7.4.3.2 VEGETATION TYPES AND HABITATS USED

Another one of the main factors that determines the habitat that animals occupy is the vegetation types available (Gordon *et al.* 2004). The vegetation types in the study area are limited, unlike large nature reserves and game parks where a multitude of different vegetation types and habitats are available. The vegetation of the two dry drainage lines in the study area represents riparian vegetation (as it is found next to the Modder River on the southern side of the private reserve) and a dense thicket formed in between the drainage lines (Figure 7.1a). To the north of the study area, a grassland is present and the ecotone between the grassland and dense thicket formed an open thicket with a low density of trees. On the western and south-eastern sides of the small drainage line are also open thickets. A disturbed area, consisting of short grass and large trees, is present next to the main waterhole, where remains of walls, a row of *Eucalyptus* trees and an old cement water-tank can be found.

The density of woody plants differs between vegetation types (Table 8.1), with a decrease in density from the drainage lines to the dense thicket, while the open thickets have low densities of trees and shrubs (mostly *Acacia karroo* and *Asparagus laricinus*) and the grassland has an absence of trees. Some plant species are characteristic of the drainage lines (*vid*. Chapter 4), while large parts of the disturbed area contain a distinguishing ‘carpet’ of the creeper grass *Cynodon transvaalensis*. Dekker and Smit (1996) concluded that "different vegetation types represent habitats of varying quality in terms of benefits such as food and costs such as predators. Large mammalian herbivores display varying degrees of habitat selectivity and thus exhibit a heterogeneous distribution, which coincides with the distribution of vegetation types. The relative preference of ungulates for plant communities is generally a linear function of the relative abundance or nutritional quality of the preferred plants in the communities." Furstenburg (2006a) summarised the type of vegetation, type of veld (sweet or sour) and topography preferred by different game species, while Van Rooyen (2010) illustrated the habitat overlap and ecological separation of herbivores between grassland, open and dense savanna in a figure.

Browsers and mixed feeders in the study area are supposed to largely use the same area, namely where browse is available. Some overlap in total habitat used was observed on the frequency maps (Figure 7.15) between eland, giraffe and kudu in the vicinity of the centre of the big drainage line and at the feeding area, although eland seemed to occur more north-east in the drainage line than the browsers did. In the open thickets and grassland little to no overlap was found between eland and the browser species, or the impalas (Figure 7.15 & Table 7.3). The giraffes were mostly found in the dense thicket between the two drainage lines with some overlap of the kudu’s habitat, especially in the dry, cool season, but the kudus usually concentrated more in the drainage line itself (Figure 7.15 & Table 7.3). Dekker and Smit (1996) also found that plant community preferences of giraffe and kudu (both being browsers) in the Messina Experimental Farm mostly did not coincide, except for a short period in the dry, hot season (Aug – Nov).

Impala remained in the denser areas of the thickets in the study area and did not use the open thickets, therefore establishing its own space and mostly avoiding areas frequented by the other three species. The common duikers were mostly found in the drainage lines (Figure 7.16) at specific locations, in their smaller territories. Giraffe, kudu, eland and impala were using large areas of the study area, since they are not territorial, with only impala being seasonally territorial. These species were thus not staying in small confined locations for a long time like the duikers. Therefore these five browser- and mixed feeder species reduce competition between them in the long run by means of spacing themselves and by not all being in the same local area for a long period of time.

The grazers were grouped regarding their dominant habitats used (Figures 9.16 – 9.19), into animals frequenting the drainage lines (Red lechwe, Reedbuck); highly water dependent species (Blue wildebeest, Burchell's zebra, Roan antelope, Waterbuck); plains antelopes (Springbuck, Red hartebeest); and animals present in all vegetation types (Bontebok, Gemsbok, Buffalo, Ostriches). Table 7.3 gives a summary of these vegetation units that were preferred by each animal species. A solitary tsessebe, later followed by another one from the southern side of the private reserve, joined a herd of bontebok and were most of the time in the disturbed area or the big drainage line, not giving a clear indication of what habitat tsessebes in general should prefer in the study area. Buffalo frequented the big drainage line and dense thicket during the day, but it is known that they feed at night in grasslands and open areas (Sinclair 1977, Funston 1992, Skinner and Chimimba 2005). It was assumed that they would also do so in the study area and their dung was found in these areas, thus they were grouped with the species that occur in all vegetation types.

The main focus of this study is on the browser- and mixed feeder game species and not on the grazers. They were mostly included to determine competition with the studied species for available habitat and food. Therefore not too much detail will be included on the grazers and how they divide the available area into preferred habitats between each other. However, it is known that a grazing succession exists where animals reduce competition and promote interaction by preferring to graze at different grass heights, namely short-, medium- or tall grasses (*vid*. Table 7.1). De Wet (1988) gave an example of grazing succession in Kruger Park from the heavier animals (bulk, roughage feeders that prepared the area by reducing grass height) to the lighter ones, namely buffalo, zebra, blue wildebeest, impala. Grazer species can use the same small area and further reduce competition by separating into feeding niches. They can be unselective feeders, or highly selective feeders that select plant species or plant parts (*vid*. Table 7.1). Amongst others, plant selection by herbivores is determined by the animal's response to sugars, salts, amino acids and other nutrients in plants, and its response to secondary metabolites. They often select plants or plant parts with a low level of secondary chemical substances (Van Hoven 2010).

7.4.3.3 COMPETITION FOR SPACE AND FOOD RESOURCES

Viewed in general, the space available in the study area was well used by all game species during some time or other (Figure 7.1b) with little open, unused areas. Only small local patches inside the dense thicket and drainage line were not used extensively by game because of accessibility. The grassland in the north-east of the reserve (inside the sharp tip of the boundary fences – Figure 7.1a) may appear from Figure 7.1b as if it was not used, but it is possible that the animals heard the vehicle approaching and fled before they were observed there. The view of the grassland is obscured by trees in all directions, even if you approach it on foot. No road traverses the grassland, except the road next to the border fences and visibility is mostly obscured by tall Smuts Finger grasses (*Digitaria eriantha*). When walking through the grassland, however, some dung of springbok, red hartebeest, bontebok, gemsbok and ostrich were observed inside the sharp tip of the grassland and signs of grazing were also visible.

Generally the smaller the area being used for game, the more intensively it must be managed (Pietersen *et al.* 1993). The size of the private reserve leads to competition for space between different species, regardless of whether they browse or graze. If a large herd of eland or gemsbok, for example, occupies an area, the space will become limited for any other animal. Competition for prime habitat proved to be high, especially in the dense thicket and big drainage line where most of the woody plants and game species occurred (Table 7.3), with a high game species density closer to the main feeding area as well. According to Prins *et al.* (2006): "Related species living together are thought to show specialisation or niche differentiation to avoid competition. Niche differentiation may result from habitat segregation, morphological adaptations (e.g. of the gut to feed on browse or grass), or behavioural adaptation (e.g. specialised dietary adaptations). Morphological separation could be advantageous if it diminishes competition with other species." Schoener (1982) and Sinclair and Norton-Griffiths (1979) indicated that interspecific competition produced separation, structuring of communities and coexistence of herbivores. Ecological separation becomes important where the animals are in confined areas and habitat of a species is not optimum or habitat changes has occurred (Nel 2010).

The drainage line (watercourse) habitat was found to be a lean season food reserve in this study. This was also reported by Du Toit (1995b) in the Kruger Park. The drainage lines, and specifically the bank of the Modder River on the southern side of the Soutpan road (Figure 3.1), have a higher percentage of shrubs that retain leaves for longer periods in the critical period in contrast to the deciduous trees (*vid.* Chapter 5). Most of the kudu and eland became sedentary in areas closer to the river on the southern side of the private reserve in winter months, probably for this reason. All the tree species in the study area are deciduous, with the exception of three large *Searsia lancea* trees. There are no vegetation units where evergreen species are present that the animals can move to when trees are leafless as in regions referred to above, so the browsing animals have to rely on shrubs to help sustain them through the critical period. Lucerne bales and -pellets were also supplied next to the waterholes for most of the dry season (*vid* Chapter 8).

Table 7.3 Vegetation units where each game species were observed are indicated: the darker the colour, the higher the animal's preference for that vegetation unit, whereas white indicates no observations during the time of study. The observations of browsers and mixed feeders were differentiated between the wet and dry seasons.

Game species	Grassland	Open thicket north	Open thicket west	Open thicket small	Dense thicket	Drainage lines	Disturbed area
Eland (Wet season)	▨	▨	░		■	░	
Giraffe (Wet season)					■	▨	
Impala (Wet season)					■	■	▨
Kudu (Wet season)					▨	■	
Eland (Dry season)	░	░				▨	■
Giraffe (Dry season)					▨	▨	■
Impala (Dry season)					■	■	░
Kudu (Dry season)						■	▨
Blue Wildebeest		▨	░		░		■
Bontebok	░	▨	▨	░	■	▨	■
Buffalo (African/Cape)	░	▨				▨	▨
Burchell's Zebra		▨	░		▨		■
Common Duiker					▨	■	
Gemsbok	░	■	░	░	▨	▨	▨
Ostrich	▨	▨	▨	▨	▨	▨	▨
Red Hartebeest	■	■	■		░		
Red Lechwe				░	▨	■	
Roan Antelope		░	▨	░	■	▨	■
Southern Reedbuck		░			▨	■	
Springbok	■	■	▨		░		
Waterbuck		▨			■	▨	■

In the wet season, when food is abundant and new growth is high in crude protein and digestibility and contains less fibre (Ego *et al.* 2003), the grazers and mixed feeders mostly feed on grass. In the dry season when abundance of quality grass declines below sub-minimum levels of crude protein, some grazers switch to browse due to the superior nutritive quality thereof (Perrin and Brereton-Stiles 1999). The following grazers may include a small percentage of browse in their winter diet: African savanna buffalo (Perrin and Brereton-Stiles 1999, Ryan *et al.* 2006, Codron *et al.* 2007a); blue wildebeest (Owaga 1975, Ego *et al.* 2003, Codron *et al.* 2007a); gemsbok (Dieckmann 1980, Knight 1991, Estes 1997); Burchell's zebra (Frandsen 1998, Okello *et al.* 2002, Skinner and Chimimba 2005, Fischhoff *et al.* 2007a); red hartebeest (Van Zyl 1965, Kok and Opperman 1975, Kilian 1993); roan antelope (Wilson 1975, Martin 1983, Poché 1974, Dörgeloh *et al.* 1998, Frandsen 1998, Skinner and Chimimba 2005); southern reedbuck (Anonymous 1991, Estes 1997, Frandsen 1998, Skinner and Chimimba 2005); springbok (Bigalke 1972, Skinner and Chimimba 2005, Stapelberg *et al.* 2008b); waterbuck (Tomlinson 1980a, Anonymous 1993b, Van Essen *et al.* 2002, Skinner and Chimimba 2005); and ostriches that usually strip off leaves from large woody plants (Aganga *et al.* 2003, Hockey *et al.* 2005). Thus, in the critical period of the dry season when browse is already scarce, the possibility exists that some grazers may increase the pressure on this resource and then enter into direct feeding competition with browsers and mixed feeders.

7.4.3.4 SEASONAL MOVEMENTS

Small, seasonal movements / shifts occurred in the study area leading to changes in habitat used by browsers and mixed feeders. In the wet, hot season (summers) when food is abundant, giraffe frequented the area surrounding the bigger drainage line, while in the dry, cool season (winters) they concentrated more in the disturbed area in vicinity of the main feeding area (Figure 7.14a). Kudu included the smaller drainage line and the main feeding area in the dry, cool season to their usual big drainage line habitat (Figure 7.14b). Eland were frequently observed in open thickets and grassland in the wet, hot season and in close vicinity of the main feeding area in the dry, cool season (Figure 7.14c). Impala were more on the north-western side of the drainage line in the wet, hot season (Figure 7.14d), while in the dry, cool season they were more frequently observed in the south-eastern side of the drainage line (Figure 7.11 c & d). Thus as can be expected, the drainage lines are a very important food resource for these species, not only in the critical period, but also in summer, while the main feeding area increases in importance in winter due to feed supplied.

Some of the grazers are known for mass migrations in search of better quality food or water during winter months, like African buffalo (Sinclair 1977, Du Toit 1995a), blue wildebeest (Bell 1971, Ego *et al.* 2003), Burchell's zebra (Du Toit 1995a, Skinner and Chimimba 2005), red hartebeest (Anonymous 1993a, Du Toit 1995a, Estes 1997) and springbok (Bigalke 1972, Estes 1997, Cain III *et al.* 2004). Seasonal movements of the grazer species in this small fenced private reserve were only indicated in general and not studied in detail, but it seems that overall there were no obvious differences between their summer and winter habitats. This is probably because of the small size of the private reserve and most species being territorial and remaining in their territorial network area. The only big differences observed were gemsbok, zebra, hartebeest, springbok and waterbuck that frequented the grassland more in the wet, hot seasons and moved to denser thickets in the dry, cool seasons. Waterbuck were also more in the southern side of the private reserve, in the riparian vegetation of the Modder River in the dry, cool seasons probably due to the shelter it provides.

Patchy distribution of game species was found in this study. Some areas were seasonally or permanently vacant, mostly due to accessibility, while in other areas there were always animals present. No large predators roam freely and weather elements being mostly the same for the study area could also not play a role in patchy distribution. The only factors that can play a role are space available and resource quality, followed by social structure which has been discussed separately for each species. Large home ranges or territories may exclude other animals of the same species from an area, leaving it vacant for some time while the owner and/or female herds have moved to another area of the territory, or large home range.

Wildlife often show a clumped distribution in patchy landscapes as a result of factors such as predation, disease, population genetics, weather elements and resource quality. Resource quality includes the quality and availability of forage, shelter and cover (Schamberger and O'Neil 1986). According to Fabricius (1994): "Fine-scaled within-patch richness is determined by the quality and quantity of resource components (food and shelter) within a habitat patch. Coarse-scaled resource richness at the home range level depends on the spatial arrangement of habitat patches, i.e. how closely spaced patches are within an animal's home range. The relation between animal density and resource quality is also scale dependent. At a fine resolution, forager group size varies according to within-patch richness. At a coarse resolution, an animal's home range is determined by spatial arrangement of resource patches within the home range. A forager should expand its home range until all its resource requirements can be met within the smallest possible area. Landscapes with densely packed habitat patches may contain many small home ranges, whereas landscapes with sparsely distributed habitat patches may contain few large home ranges. As habitat patches become very sparsely distributed, the animals show a net energy loss in moving between patches to forage."

7.5 CONCLUSIONS

Interspecies competition for habitat resulted in animals spacing themselves through the study area to have maximum food resources combined with minimum competition in the small restricted space available. Grazers competed for prime habitat in the grassland and open thickets, also entering into the dense thicket due to lack of space. There they competed for habitat with browsers and mixed feeders that need the presence of trees for food. The browsing species had large home ranges and spaced themselves in order to reduce interspecies competition for browse. The area with the highest use was that between the big drainage line and the disturbed area around the main waterhole.

The percentage of semi-deciduous shrubs in the study area is too low to sustain the current number of browsers and mixed feeders if the grazers also start browsing on it during the critical period (July/August to middle October). Feed is supplied during this period due to a management choice, in order to help maintain the animal‘s body condition when the quality and quantity of browse and grass decline. The supply of feed is the main factor in causing small, local movements by attracting animals to the feeding areas in the dry season, whereas they are dispersed through the dense thicket and drainage lines during the wet season. This is especially true for giraffe and impala.

In the dry season, when the demand on the scarce browse resource became very high in the study area, kudu and eland occasionally moved through the connecting tunnel to reach the riparian vegetation in the southern side of the private reserve. A higher density of trees and shrubs are present in the vicinity of the river that serves as an essential food reserve during the limiting, critical period, while competition for this browse resource is also less in the southern side. Although numbers of all species were regulated and monitored regularly, kudu and eland moved approximately 3 – 4 km south due to a too high browsing pressure in the study area in the critical period.

This study is essential in providing information on habitats used by certain introduced game species and shared with other species, as well as their local movements and food resources. It further provides insight on specific vegetation types that animals have adapted to in a certain degree due to a lack of space and preferred habitat. The placement of waterholes, choice to supply feed, choice of animal species and regulating their numbers are important to make the game ranch sustainable.

CHAPTER 8

BROWSE AND GRASS PRODUCTION, CARRYING CAPACITY AND FEED SUPPLIED

8.1 INTRODUCTION

Availability of forage that can support different species is considered to be the most important factor influencing habitat selection by large herbivores (Abule *et al.* 2007, Smit 2006). Knowledge of the composition of vegetation and what is available to grazing and browsing animals, combined with knowledge of their diet preferences is of basic importance in the management of vegetation and the development of efficient systems of animal production (Barnes 1976). According to Bond and Loffell (2001): "Conservation of biodiversity requires a better understanding of the interplay between charismatic large vertebrates and the plants they feed on."

The presence of large woody plants in the study area may have influenced the decision to introduce browsing game species in the area. The quantity and quality of food available for the stocked game species are fundamental requirements for the success of any game ranch. All the trees in the study area are, however, winter deciduous and the shrubs are semi-deciduous. Consequently, browse becomes scarce in winter months and it is of utmost importance to determine the availability of food for browsing animals during this critical period. The objectives of this study were to:

i) determine browse and grass phytomass production;
ii) calculate browsing and grazing capacity; and
iii) provide guidelines regarding the most appropriate time to supply feed.

8.2 LITERATURE REVIEW

8.2.1 Browsing and browse availability

Indigenous browse is the main source of forage (leaves and twigs) for several species of wild ungulates in Africa (Topps 1997). Some browse species offer a high dry matter yield, biological nitrogen fixation (leguminous trees), improved soil fertility and better performance due to improved nitrogen supply in the diet of browsing animals (Aremu and Onadeko 2008). Four major environmental variables are thought to influence savanna structure, regulate woody cover and thus play a role in browse production, namely herbivory, fire, water- and nutrient availability (Skarpe 1990, Chirara *et al.* 1998, Smit 2004, Augustine and McNaughton 2004, Sankaran *et al.* 2008). Fire and herbivory act partly by influencing availability of, and competition for water and nutrients (Skarpe 1990). At above 650 mm mean annual precipitation, Sankaran *et al.* (2008) found that water availability supported a closed woody canopy in such a way that fire and herbivory were needed for substantial proportions of both grasses and trees to persist in mesic savannas.

According to Scotcher (1979), the choice of food plants by herbivores will depend, amongst other factors, on the choice and acceptability of plant species available. Results of food studies can therefore only realistically be interpreted by comparing the species in the diet with some quantitative value of the availability of the species in the habitat. Owen-Smith and Cooper (1987) concluded that "among the favoured species of the browsing ungulates there was no relation between the acceptability of a plant and its relative abundance along the foraging pathway. However, plants growing in monospecific clumps, e.g. *Grewia flavescens*, *Dichrostachys cinerea*, and *D. lycioides* appeared relatively less acceptable on a per plant basis than on a site basis." The determination of browse availability is further influenced by height distribution of browse material, phenology of the plant species, whether they are evergreen, early- or late winter deciduous and the seasonal presence of flowers, fruits and seed pods with a high nutrient content (Smit 2006). Scotcher (1979) indicated that this was probably one of the most difficult parameters to measure as availability of food is governed by a host of factors, like age, growth form, proximity to water, soil conditions, rainfall, the feeding behaviour of the animal itself and position of plants in relation to others. Tree-on-tree competition, that determines the position of trees in relation to each other, is often species specific. In several woody species a significant positive correlation exists between size of the tree and distance to its nearest neighbour of the same species (Smit *et al.* 1999, Smit 2001).

Two variables are important in influencing consumption of leaf tissue by herbivores, namely nutritional value and accessibility (Gowda 1997). According to Owen-Smith and Cooper (1985), habitat carrying capacity for a specialist browser like the kudu is limited by two factors: “(i) most of the foliage produced by woody plants is out of reach in the higher levels of tree canopies and though much of this potential food material falls to the ground during the dry season, it becomes too dispersed to be ingested efficiently by an ungulate as large as the kudu; (ii) the evergreen species providing browse during the dry season form only a very minor vegetation component in most savanna regions." This is also applicable to giraffe feeding.

According to Topps (1997), browse has a medium to high value of crude protein and the protein in browse is less subject to seasonal changes than in grasses. Enhanced nutritional value of foliage may lead to higher preference of the plant by browsers (Cooper and Owen-Smith 1985). Gowda (1997) found that increasing concentrations of nitrogen in leaves were related to a reduction in concentrations of secondary substances (like tannins). Twigs and foliage of woody plants, the edible parts, are normally restricted to tips of branches. It is difficult to define, especially in the case of twigs, what portion of the plant is edible. According to Owen-Smith (1979): "Large herbivores generally consume only a small fraction of the vegetation components that they could eat. Thus assessments of food availability by direct measurements on the vegetation could be a poor reflection of food availability as experienced by the animals." Further, larger animals feed at the same level as smaller animals, in addition to feeding at heights that is not available to small animals. Thus, production and utilization are more difficult to measure than in the case of herbaceous plants (Barnes 1976, Smit 2006).

On average, impala browse at a height of up to 1.5 m, eland and kudu up to 2 m and giraffe up to 5 m (Table 7.1). Milewski and Madden (2006) determined the collective browsing heights of giraffe, eland and impala feeding on thorny plants to range from near-ground to a maximum of 5.2 m. Abule *et al.* (2007) calculated 60% of the browse to occur above a height of 1.5 m in their study area, while Dekker and Smit (1996), Smit (2001), as well as Van Essen *et al.* (2002) also indicated that the majority of leaves were carried above 2 m and therefore out of reach of most browsing ungulates. According to Grant *et al*. (1995), giraffe should only rarely experience a limitation in food availability, because of little to no competition at their browsing height and should not experience a limitation in food quality. Giraffe numbers could even increase where bush encroachment is a feature of veld deterioration. Hofmann (1973) stressed the fact that giraffe move slowly through their habitat as long as food is sufficiently available, i.e. they browse the vegetation intensively.

According to Milewski and Madden (2006): "Browse handling techniques of browsers were recorded as either i) strip, when tongue, lips, or inside of mouth was used to rip leaves off a section of a branch; ii) pull, where a branch was pinioned between palate and lower teeth and tugged entirely free from a plant; or iii) nibble, when the lips cropped leaves from branches without the distinctive head movements associated with pulls or strips." When browse becomes scarce, leaf litter, as well as other sources of food are included in the winter diet of browsing animals. Animals may also break branches with their horns to reach higher browse material. These aspects are discussed in more detail in the literature reviews of Chapters 5 and 6.

Results of browse production in different areas are rather limited and differ due to variation in soil, terrain, season, climate, vegetation units and management to list only a few. Rutherford (1982) reported a production of 1 100 kg/ha in *Burkeya africana – Ochna pulchra* savanna. Scholes (1987) indicated a yield of 801 kg/ha for *Colophospermum mopane* veld, Walker (1980) found a yield of

600 – 2 100 kg/ha in *C. mopane* veld in Zimbabwe, while Smit (2002) reported a production ranging between 1 500 kg/ha and 1 700 kg/ha in different growing seasons for mopane veld in the Limpopo Province and Dekker and Smit (1996) indicated 1 224 – 2 672 kg/ha for mopane veld in Limpopo Province. Abule *et. al.* (2007) calculated peak biomass produced across different rangeland sites in Ethiopia to be 196 – 3 311 kg/ha. Van Essen *et al.* (2002) worked in south-western Kenya and determined browse production to differ between different communities in the Kiloriti plain from 52 – 8 042 kg/ha, with a range of 56 – 1 452 kg/ha below a 2 m browsing height.

8.2.2 Effect of browsing on woody plants

Larger browsers often remove shoot ends while feeding and hence have a pruning effect (Du Toit *et al.* 1990, Augustine and McNaughton 2004). Du Toit *et al.* (1990) proposed that severe browsing of *Acacia* trees not only stimulated shoot production, but also induced a physiological response that increased palatability, leading to a feedback loop of further browsing. Stuart-Hill and Tainton (1988) concluded that mature trees in the Eastern Cape thornveld were rejuvenated by defoliation, while immature trees were harmed by the same level of defoliation. Medium trees (1.4 – 1.8 m tall) were producing progressively more browse than low trees below 1.2 m. Skarpe (1990) found the leaf area of shrubs to be significantly higher with heavy browsing than with no or moderate browsing. Gowda (1997) indicated that pruned *Acacia tortilis* trees produced significantly more shoot biomass than unpruned ones, but significantly more biomass was allocated to twigs and long spines without a significant increase in leaf production. In general, this may reduce feeding efficiency through smaller bite sizes (evenly distributed leaves) and/or bigger distances between bites (clustered leaves). The plant's response to browsing by creating structural defense mechanisms and by making use of chemical substances, especially tannins, to deter browsing is dealt with in Chapter 6.

The energy cost of browsing may be influenced by a reduction in accessibility due to increased spinescence (Gowda 1997). Milewski *et al.* (1991) showed that spinescence (spine length and density) in *Acacia seyal* and *Acacia xanthophloea* increased with increasing density of giraffe. Sankaran *et al.* (2008) found a clear negative relationship between woody cover and biomass of browsers and mixed feeders. It could arise directly as result of browsing induced mortality of woody seedlings, or indirectly when browsing suppresses growth and maintains woody vegetation within the flame zone rendering it more susceptible to fire induced mortality (Smit 2004, Sankaran *et al.* 2008). Vavra *et al.* (2007) indicated similar trends. Augustine and McNaughton (2004) also concluded that browsers had significant effects on species composition of the shrub community in central Kenya, especially when shrubs lacked thorn defenses.

Milton (1987) found that *Acacia karroo* sustained heavy losses of its soft green shoots to browsers where it was the first species to sprout in spring. *Acacia karroo* would be most sensitive to defoliation in October when rapid extension of shoots occurs. Shoots produced in late summer in response to damage during the growing season, remain leafier in winter. In this way browsing may increase browse availability for browsers, but repeated damage reduces regrowth in the following season. At low browser densities none of the *Acacia* trees were browsed at a constant rate throughout the year. Stuart-Hill and Tainton (1988) also confirmed that frequent intense browsing might reduce vigour and have a depressing effect on growth in the long-term.

When leaves of a tree are damaged, a chemical activator, ethylene, is released through stems and twigs which stimulates tannin production in leaves. This reaction can also spread to other plants in the area, before they are damaged as a preventative measure, by means of chemicals released in the air (Van Hoven 2010). According to Van Hoven (2010), studies on kudus indicated that concentrated tannin levels in leaves of *Acacia caffra* increased with 94% within 15 minutes after feeding commenced. Kudus adapted to this by browsing only for a short while on a specific tree before moving on to the next tree. Smit (2006) described a case of *Acacia nigrescens* leaves that displayed a 70% increase in tannin concentration 2 minutes after disturbance, followed by a delayed response 30 to 100 minutes after the disturbance. Giraffes were forced to select plants with a lower tannin content. Baldwin and Schultz (1983) and Van Hoven (1984) also described cases where browsing have resulted in increased chemical defense from the plants.

Negative impacts of browsers and mixed feeders (specifically the elephant) have been reported in some ecosystems (Owen-Smith 1985, Pietersen *et al.* 1993, Bond and Loffell 2001, Birkett 2002, Augustine and McNaughton 2004, Bezuidenhout 2005, Sankaran *et al.* 2008), but in others no damage were recorded (Kok and Opperman 1980, Owen-Smith and Cooper 1985, Du Toit 1990a, Van Rooyen 1992, Dörgeloh 2001a, Watson and Owen-Smith 2002, Matson *et al.* 2006). Increases in woody cover in different ecosystems have been attributed to both overgrazing (Stuart-Hill and Tainton 1989, Chirara *et al.* 1998, Skarpe 1990, Vavra *et al.* 2007) and relief from grazing (Lenzi-Grillini *et al.* 1996). Additionally, herbivory can act as an agent in the spread and establishment of non-native invasive plants that can exert a considerable impact on structure and composition of native plant communities (Vavra *et al.* 2007).

According to Bezuidenhout (2005): “The crude protein and moisture content of leaves seem to be the deciding factor when giraffe select food". They specifically select flushing shoots that have a high protein content. This explains why they tend to defoliate everything in a selected small proportion of a reserve rather than browsing over a wide area. When stocking rate is correct and the browsing impact is acceptable, animals help maintain biodiversity. Generally, dominant preferable trees may eventually be wiped out at densities of 1.23 giraffe/km^2 (Bezuidenhout 2005).

Three of the game species included in this study can have a major impact on the veld. The results of Bond and Loffell (2001) indicated major long-term browsing impacts of giraffe on some *Acacia* species in the Ithala Game Reserve, Kwa-Zulu Natal. They found that *Acacia davyi* has almost disappeared from areas of high giraffe density and *A. caffra* might suffer a similar fate. *Acacia karroo* showed high mortality in heavily browsed areas of Ithala, but some trees still produced foliage on heavily browsed branches. They predicted heavy mortality of these trees should the population experience drought, disease or other stress in coming years. They suspected that the available browse resource was too small relative to giraffe numbers, with few alternative feeding areas available to spread the browse load. Birkett (2002) found that giraffe browsing, at a density of 1.9 giraffes/km^2, along with low rainfall of <600 mm per year reduced tree growth in Kenya. Growth retardation was height specific and giraffe impact was greatest at 3 – 5 m in the *Acacia* woodland. At increased densities in small confined areas kudus could also exert a more severe impact on woody plant growth and recruitment than they do naturally (Owen-Smith 1985). According to Pietersen *et al.* (1993), impalas exert a major impact on the veld of most game farms and nature reserves in terms of biomass and sheer numbers and play a central role in overgrazing and veld deterioration.

Contrary to common believe that bush encroachment and tree thickening are detrimental to grazers only, it may also be detrimental to browsers (Smit 2004). According to Smit (2001), trees in low density stands display a better distribution of browse and have leaves in younger phenological states over an extended period compared to high densities. Abule *et al.* (2007) also found a variation in leaf DM for similar species across rangelands with the same ecological conditions and attributed it to differences between vegetation types.

8.2.3 Bush encroachment and the effect of grasses in preventing it

A savanna is characterized by having a continuous, well-developed grass layer and an open, discontinuous layer of shrubs and/or trees (Knoop and Walker 1985). Bush encroachment, the thickening-up of trees and shrubs beyond a critical density, in grassland and savanna has been reported from many arid and semi-arid parts of the world. Skarpe (1990) provided a list of references on bush encroachment, including Walker *et al.* (1981), Van Vegten (1983) and Tolsma *et al.* (1987a, 1987b) for southern Africa. The fire regime, lack of browsing, elimination of mega herbivores like elephant, climatic change, droughts, human disturbance and overgrazing by livestock have been identified as contributing to bush encroachment (Skarpe 1990, Smit 2001, 2005, Van Rooyen 2010). Van Rooyen (2010) held the view that the competitive interaction between trees and grass is strongly assymetrical, with the trees having a much greater effect on the grasses than the reverse.

Stuart-Hill and Tainton (1989), Chirara *et al.* (1998), as well as Smit (2004, 2005) found that an increase in cover of woody species occurred particularly in heavily-grazed areas where grass competitiveness was reduced. Competition from grasses for water and space can prevent germination and establishment of woody plant seedlings by being sufficiently dense (Knoop and Walker 1985, Chirara *et al.* 1998, Smit *et al.* 1999, Van Rooyen 2010). The opposite is also true, intense grass defoliation under controlled conditions during the wet season in particular have resulted in increased availability of soil water and created conditions favourable for woody seedling establishment (Walter 1971, Walker and Noi-Meir 1982, Chirara *et al.* 1998). Ludwig *et al.* (2004) suggested that competition for water resources between trees and grasses, may lead to lower grass sward productivity in the presence of trees. Stuart-Hill and Tainton (1988) concluded that grass production within a radius of 9 m from *Acacia karroo* trees was negatively related to tree height. Tree thinning will have an effect on the long-term stability as influenced by the state of plant succession, e.g. predominance of climax grasses that are mainly perennials, as opposed to the predominance of pioneer grasses that are mainly annuals (Smit 2003). Smit (2001) concluded that *Colophospermum mopane* trees from low density plots in the Limpopo Province increased in growth mainly horizontally, rather than in mean tree height after thinning. Large trees may provide increased stability in a structured savanna, as it may suppress the development of woody seedlings under their canopies or in their close proximity, since tree-on-tree competition are often species specific or related to shade tolerance of seedlings (Smit 2004).

According to Skarpe (1990): "A net increase in shrubs can either be the result of a uniform increase, with unchanged relative species abundances, or the sum of different species increasing, decreasing or remaining unchanged". Skarpe (1990) indicated that there were areas in Botswana known for bush encroachment of about 50 – 70% increase in canopy cover of shrubs under heavy grazing. Van

Vegten (1983) also recorded large areas with 50 – 70% shrub cover and some with 100% cover in Botswana.

8.2.4 Interaction between woody- and herbaceous plants

Trees in savannas have been referred to as 'islands of fertility' (Belsky *et al.* 1989), because elevated soil nutrients are found beneath their crowns (Smit 2003), together with decreased solar radiation, reduced evapotranspiration and reduced soil temperatures (Treydte *et al.* 2007). Soil enrichment under tree canopies usually occurs with regard to percentage total nitrogen, organic carbon and various exchangeable cations like calcium, potassium, magnesium and sodium (Smit *et al.* 1999, Smit 2004). Treydte *et al.* (2007) found that grass leaf nitrogen and phosphorous contents were higher beneath tree canopies than in open grassland. Stuart-Hill *et al.* (1987) demonstrated a consistent pattern of grass production around isolated *Acacia karroo* trees with higher yields under the canopy. In savannas where soil fertility is low and nutrients limit plant production, a grass patch of high nutrient content created by large trees is likely to be an important food resource for grazers (Treydte *et al.* 2007). Smit and Swart (1994), Smit *et al.* (1999), as well as Treydte *et al.* (2007) concluded that higher fiber contents in grass leaves under canopies might also result from a high abundance of the shade-loving *Panicum maximum* in the sub-canopy habitat. Van Rooyen (2010) stated that research had shown little evidence for niche separation of trees and grasses in depth of their rooting and suggested that savannas were an unstable mixture that persisted because of disturbances such as fire, herbivory and fluctuating rainfall.

In open grasslands without trees, grasses face high solar radiation and soil temperatures and lower water and nutrient availability in the soil than grasses beneath single-standing trees (Ludwig *et al.* 2004, Treydte *et al.* 2007). According to Treydte *et al.* (2007), single standing trees of medium to low density usually have a positive effect on sub-canopy vegetation productivity due to decreased light intensity. Older and larger trees have been found to enhance sub-canopy soil nutrients more than younger ones (Ludwig *et al.* 2004). Fixing of atmospheric nitrogen by leguminous species, like *A. karroo*, might further enhance the already elevated soil nutrient level provided by non-leguminous trees species in the neighbourhood (Belsky *et al.* 1989, Danso *et al.* 1992, Binkley *et al.* 2000, Vitousek *et al.* 2002, Treydte *et al.* 2007).

In dry savannas where water is a limiting factor, the 'hydraulic lift' effect of a tree (Ludwig *et al.* 2003), together with shading, can lead to increased water availability for grasses and might improve growing conditions for grasses relatively more than in humid savannas (Stuart-Hill *et al.* 1987, Treydte *et al.* 2007). Treydte *et al.* (2007) concluded that trees were important in maintaining pasture quality in dry and nutrient poor savannas with high inter-annual fluctuations in rainfall and that the influence might become more important if climate change reduced rainfall. Walter (1971), as well as Walker and Noy-Meir (1982) discussed a model involving a two-layered soil-water system in which grasses were superior competitors for water in the topsoil and woody plants had exclusive access to a lower (subsoil) water supply. However, Knoop and Walker (1985) found that grasses also have access to subsoil water.

Themeda triandra is not known for growing under tree canopies (Smit 2004). The common name of *Ehrharta erecta* is Shade Ehrharta because of its association with areas of shade. This is also the case for *Eragrostis biflora* and it is echoed in its common name (Shade Eragrostis) as well (Van Oudtshoorn 1999). Some other common, widespread species that usually grow in shade are *Andropogon appendiculatus*, *Brachiaria brizantha*, *B. deflexa*, *Bromus catharticus*, *Coelachyrum yemenicum*, *Melica decumbens*, *M. racemosa*, *Panicum deustum*, *P. maximum*, *Setaria verticillata* and *Sporobolus fimbriatus*. A few examples of species with a narrow distribution area that can also grow under trees are *Andropogon gayanus*, *Briza maxima*, *Digitaria velutina*, *Dinebra retroflexa*, *Ehrharta longiflora*, *Enteropogon macrostachyus*, *Lagurus ovatus* and *Setaria megaphylla* (Van Oudtshoorn 1999).

8.2.5 Supplementary feed

Owen-Smith and Novellie (1982), as well as Owen-Smith and Cooper (1989) suggested that for large ruminant browsers, energy rather than protein is the most likely limiting nutrient during critical times of the year. Crude protein content of browse is relatively high, but the extent of its degradability in the rumen may be low due to presence of interfering substances like tannins. Thus, the yield of microbial protein may be less than that needed for maintenance of the animal (Topps 1997).

According to Topps (1997), digestible organic matter in roughage and forages has an energy value close to 19.5 MJ/kg. "For ruminant livestock, digestible energy may be converted to metabolisable energy by multiplying by 0.82, since combined losses in urine and methane are 18% of digestible energy for many feeds.” Robbins (1993) listed values of this coefficient for wild ruminants given either deciduous or evergreen browse. Values ranged from 0.76 to 0.83 with a mean of 0.79 which was used, along with 19.5 MJ/kg to derive the metabolisable values.

According to Roosendaal (2008): "Balanced concentrates or antelope cubes can initially be mixed with chopped hay and when eaten readily, be fed separately at 1 – 1.5% of body weight together with roughage fed *ad libitum*". Concentrates should not exceed 40% of natural feed intake and should be introduced gradually over a 2 – 3 week period, since acidosis can be a serious problem in game. Non-protein nitrogen should not be used as a protein source for non-ruminants. Game species that are under nutritional, social or environmental stress can easily succumb to parasite infestation (Roosendaal 2008).

8.2.6 Grazing and the effect of grazers on vegetation

Many commonly used techniques of veld condition assessment involves grouping of species into categories according to their response to grazing. Those species that are characteristic of a well-managed range are termed 'decreasers', while those that are promoted by over- or undergrazing are termed 'increasers' (Janse van Rensburg and Bosch 1990, Novellie 1990, Smit 2006). Several other classifications have been used, like the one discussed by Janse van Rensburg and Bosch (1990), or grouping of species into pioneer, subclimax and climax classes. Pioneer and subclimax grass species increase with underutilization or overgrazing, while palatable, climax grasses, like *Themeda triandra*, *Panicum coloratum*, *Digitaria argyrograpta* and *D. eriantha*, are abundant in good veld, but decrease in number when the veld is overgrazed (Van Oudtshoorn 1999).

According to Trollope (1990): "Botanical composition of the grass sward is a good indicator of the inherent ability of the veld to produce forage for grazing ungulates". Species composition of herbaceous plants is important, as species vary significantly in their acceptability to grazing herbivores (Smit 2004). There is a tendency for abundant herbaceous species to predominate in the grazer diet, e.g. *Themeda triandra*, provided these species are reasonably palatable and acceptable (Grunow 1980). Quantity is mostly more limiting than quality in semi-arid, sweetveld areas (Smit 2006) like the study area. Veld dominated by vegetation in a climax state has a higher grazing capacity than veld dominated by low yielding pioneer species like *Aristida congesta* (Trollope 1990, Smit 2006). In the Free State region, in the 1980's it was determined that grazing capacity of climax veld was 7 ha/large stock unit (LSU); 12 ha/LSU in subclimax veld and 18 ha/LSU in pioneer veld (Fourie and Fouché 1985). Fourie *et al.* (1985) calculated grazing capacities according to rainfall for most of the central Free State. The specific region where this study area is located, between Bloemfontein and Brandfort, was estimated to have a grazing capacity of 7 – 10 ha/LSU.

The standing crop of grass is a good indicator of the physiognomic structure of the grass sward, because it describes volume and density of plants at ground level. In the Kruger National Park, the standing crop of grass is closely related to habitat preferences of certain game species that prefer tall or short grassland (Trollope 1990). Novellie (1990) indicated that grass species that were promoted by heavy grazing were short and procumbent, while grasses adapted to lenient defoliation tended to be tall and stemmy in the Mountain Zebra National Park, Eastern Cape. The tall grass grazers favoured communities dominated by taller decreaser species, while short grass grazers were not strongly associated with decreasers. According to Novellie (1990), a high veld condition score may be indicative of a high forage value for tall grass grazers, but not for short grass grazers. The habitat should ideally represent a mosaic consisting of heavily utilized to underutilized patches as part of a natural grazing system, because of the differences in habitat preferences of wild herbivores (Novellie 1990, Van Rooyen 2010).

Blesbok and springbuck are patch selective grazers that subject small areas to intense grazing pressure, creating grazing lawns of short grass (Novellie 1990) that are more productive and nutritive than tall sparser grass growing on the lightly grazed periphery (McNaughton 1984, Smit 2004). McNaughton (1984) proposed that individual grazers benefit by feeding in a herd because of the greater forage yield per bite from grazing lawns compared with lightly grazed vegetation. Decreaser grasses are poorly adapted to frequent heavy defoliation and thus do not persist in grazing lawns. The foraging requirements of short grass grazers are consequently met by increaser grasses that predominate in these grazing lawns. Therefore, veld dominated by increaser grasses is not inferior to veld dominated by decreasers, so patch-selective grazing can be an important agent of plant community diversity (Novellie 1990). According to Gordon *et al.* (2004), at landscape scale heavy grazing may lead to increasing dominance of grazing-tolerant or unpreferred plant species that may reduce diversity, but at local scales it may increase diversity through provision of new germination niches by trampling or improved nutrient cycling.

According to Grunow (1980), grass and browse species can be grouped into four classes, namely

i) preferred food species: the degree that the species is taken in greater proportion than its representation in the community, due to its palatability;
ii) principal species: a species making a large contribution to the diet and animal nutrition, even though it may be less palatable than the preferred species;
iii) intermediate species: are taken under fairly high grazing pressure; and
iv) non-forage species: are either not taken at all or taken only when grazing or browsing pressure become very high.

Acceptability of grass species to grazers may be limited by a high fiber content and presence of chemical substances like volatile oils. Acceptability may also change with the age of the plant with young plants being acceptable, but mature plants not (Smit 2006). Productivity of large herbivores depends on biomass and species composition of grazing available, as well as on the nutritive composition and digestibility of species at any particular time. Animals generally cannot compensate for low quality forage by increasing intake (Skarpe and Bergström 1986).

Bulk grazers are defined as large roughage eaters which do not exercise a high degree of selection. Concentrate grazers are generally smaller, grazing animals (< 200 kg) that exercise some form of extreme species or area selective grazing (Trollope 1990, Roosendaal 2008). A grazing succession takes place where different classes of animals utilise a pasture and involves heavyweight, bulk feeding animals preceding lightweight, selective feeding animals by preparing the pasture for use by the animals that follow (Trollope 1990). In the Kruger National Park, the preference of use of an area shifted in the grazing succession from buffalo, to Burchell's zebra, waterbuck, blue wildebeest, impala and then warthog (Van Rooyen 2010). The movement of animals into an area, or the order of grazing succession, is also related to their different tolerances to long and short grass (Table 7.1). In sweetveld areas with a low rainfall the veld is more sensitive to selective grazing by concentrate grazers. Therefore, and in order to achieve relatively uniform utilisation of all forage types, the metabolic mass of concentrate grazers should not be permitted to exceed that of bulk grazers. A stocking rate of 1 animal unit (AU) bulk grazers : 0.5 AU concentrate grazers is recommended for sweetveld areas to prevent it from being overgrazed (Owen-Smith 1999). The definitions of sweetveld and sourveld are given in Chapter 4.

Where two grazers occupy the same space and the first grazes grass which is too short for the second to graze, then the first species is the dominant one by interference competition (Melton 1987). However in the case of springbok and blue wildebeest, competition is avoided through niche separation (Stapelberg 2007). Blue wildebeest is a bulk, high level grazer that seems to precede the springbok as selective low-level grazers. Blue wildebeest have wide muzzles that are suited for grazing relatively close to the ground, while springbok have narrow muzzles suited for selective feeding. Gemsbok were in closer proximity to springbok than blue wildebeest, but few similarities were found between preferred plant species selected by these first mentioned antelope (Stapelberg *et al.* 2008a). The different feeding heights of grazers in the study area and a general description of their diet are summarized in the literature review of Chapter 7.

An overestimation of grazing capacity is the one management factor that has the highest impact on veld condition and animal production (Fourie and Fouché 1985, Fourie *et al.* 1985). Grazing pressure due to an increase in animal numbers in semi-arid savannas is widely known to cause changes in soil nutrients, vegetation structure, production, composition, productivity and is one of the main causes of vegetation and soil degradation by means of trampling, reduced water-infiltration and soil-erosion (Fourie *et al.* 1985, Nsinamwa *et al.* 2005, Van Rooyen 2010). Overgrazing is well known in livestock areas, but is also a problem in game reserves (Janecke *et al.* 2005). There are quite a number of articles on grazing, overgrazing and related topics, but since the main aim is to focus on browsing it will not be included or dealt with in detail in this study.

8.2.7 Carrying capacity in general

Browsing and grazing capacity combined form the ecological carrying capacity of the ranch for herbivores. Browsing capacity is a measure of the areas' potential to carry a specific number of browsers in a good reproductive and productive condition over a prolonged time, without the natural resources deteriorating (Van Rooyen 2010). The factors that determine availability of browse and difficulties in determining browse capacity are discussed under the heading 'Browsing and browse availability' (8.2.1).

Van Rooyen (2010) defined grazing capacity as "relating only to the grazeable vegetation," where the "productivity potential is expressed as the area of grazing land that is required to maintain a specified animal unit in a good physical condition over an extended number of years without deterioration of the grazing or the soil". Booysen (1967), Danckwerts (1982) and Fourie *et al.* (1985) also defined grazing capacity in a similar way. However, if the productivity changes over time, then grazing capacity will also change – thus grazing capacity is an instantaneous parameter and is expressed per length of the grazing season and not over an extended period. Soil erosion or changes in the botanical composition that reduce the potential of the vegetation to produce animal products is not permitted by the definition of grazing capacity (Danckwerts 1982).

Grazing capacity is determined in part by veld condition (Trollope 1990) and the availability of nutritious fodder. For impala and eland which are intermediate feeders, this implies availability of grass and browse (Meissner *et al.* 1996). Actual consumption is limited by palatability of the plant material, grazing preferences of the animals and losses due to trampling and environmental factors.

Even when the animals are able to consume a high percentage of available dry matter, their intake should be limited to a predetermined level to avoid overgrazing (Smit 2002, 2006).

Carrying capacity is primarily a function of the grazing and browsing capacity of the veld, thus a principle factor in such calculations is food and food intake (Trollope 1990). The difference between the stocking rate and grazing capacity is that stocking rate is a production decision, while grazing capacity is a habitat characteristic that is primarily a function of vegetation condition (Van Rooyen 2010). Stocking rate/density refers to the number of animals that feeds on a specific surface area without necessarily considering the carrying capacity and reflects a managerial decision of the number of animals they want to put on the veld (Fourie *et al.* 1985, Smit 2006, Van Rooyen 2010).

Types and condition of the different available habitats as well as management objectives, like trophy hunting, venison production, sport hunting or game viewing, determine the stocking density of the ranch (Trollope 1990). Trollope (1990) used the following definition for ecological carrying capacity (ECC): "The maximum population of animals that an area can support without deterioration to the habitat." For venison production he recommended a stocking rate equivalent to 50% of the ECC to have the increase in the population at a maximum. For trophy hunting he recommended 50% below the ECC so that environmental conditions are optimal for animal performance, while for sport hunting and viewing the stocking rate should be higher than the maximum rate of increase (50% of ECC) in order to maximise animal numbers. A possible solution for higher stocking rates is to base the number of breeding stock of game on the mean annual rainfall. It will provide a viable strategy for coping with drought periods (Trollope 1990). Van Rooyen (2010) also discussed similar principles.

Fabricius (1994) stated that "a common criticism of the carrying capacity concept is that it depicts a static quantity, and does not take into account seasonal fluctuations in resource availability. The term carrying capacity is uninformative and confusing when dealing with wildlife in a dynamic and patchy environment". Failure to consider the spatial components of herbivory in calculations of carrying capacity and assessments of ecosystem persistence can contribute to overgrazing, failed economic development efforts and declines in wildlife populations (Dekker *et al.* 1996). Larger species are able to feed in a wider range of habitats due to their wider feeding tolerances, while smaller species are more evenly spread through the ecosystem, are habitat specialists and their populations are clumped in suitable habitat types (Du Toit 1995a).

Neither the approach of comparing each species to standard livestock units (Mentis and Duke 1976), nor the livestock unit equivalents of wild ungulates (Meissner 1982) allow for ecological separation (Dekker *et al.* 1996, Van Rooyen 2010). According to Dekker *et al.* (1996), quantifying the overlap in ungulate resource use and incorporating such indices in the conversions to livestock units will contribute to more feasible calculations of stocking rates for game ranches. In an attempt to find a system more suitable to multi-species systems, Dekker (1996) described a grazer unit and a browser unit as defined elsewhere in this chapter (pages 243, 246).

8.3 PROCEDURE

8.3.1 Determination of browse phytomass production

Leaf dry mass (DM) or phytomass at peak biomass was estimated for the woody vegetation in each of the eight vegetation units in the study area by using a quantitative technique for describing woody plants (Smit 1989a, 1989b), incorporated into the BECVOL-model (Biomass Estimates from Canopy VOLume) (Smit 1994, 1996). Estimates of the leaf DM is based on the relation between the spatial volume of a tree and its true leaf DM. The BECVOL-model uses different regression equations, obtained from harvested trees, to estimate leaf DM for microphyllous and broad leaved woody species (Smit and Swart 1994, Dekker and Smit 1996, Smit 2001).

A grid index overlay on the vegetation map of the study area was created with the Geographic Information System (GIS). Department of Geography, UFS supplied longitude and latitude values for the centroid of each grid block (Figure 8.1) in order to reach that specific point with the aid of a GPS. Two transects (50 m x 2.5 m each) were placed at approximately 90° angle originating from the centroid of each 150 x 150 m grid block, in order to fit a 100 m transect into the block in such a way to provide a good representation of the woody vegetation of that block. Dekker and Smit (1996), Van Essen *et al.* (2002) and Abule *et al.* (2007) used a total survey area of 200 m^2 per belt transect and adapted the survey area to the terrain, while 250 m^2 was used for this study.

Three height- and four width measurements (Figure 8.2) were taken of all rooted, living woody plants within each transect. The height of the tree was assumed to be the height of the main tree crown, ignoring any small stems protruding from the crown. Maximum canopy diameter was calculated as the mean of two measurements (D_1 and D_2) taken perpendicular to each other in a horizontal plane. The same procedure was applied to the estimate of the base diameter measurements (E_1 and E_2 – Figure 8.2). Measurements were taken by means of a 2.5 m aluminium

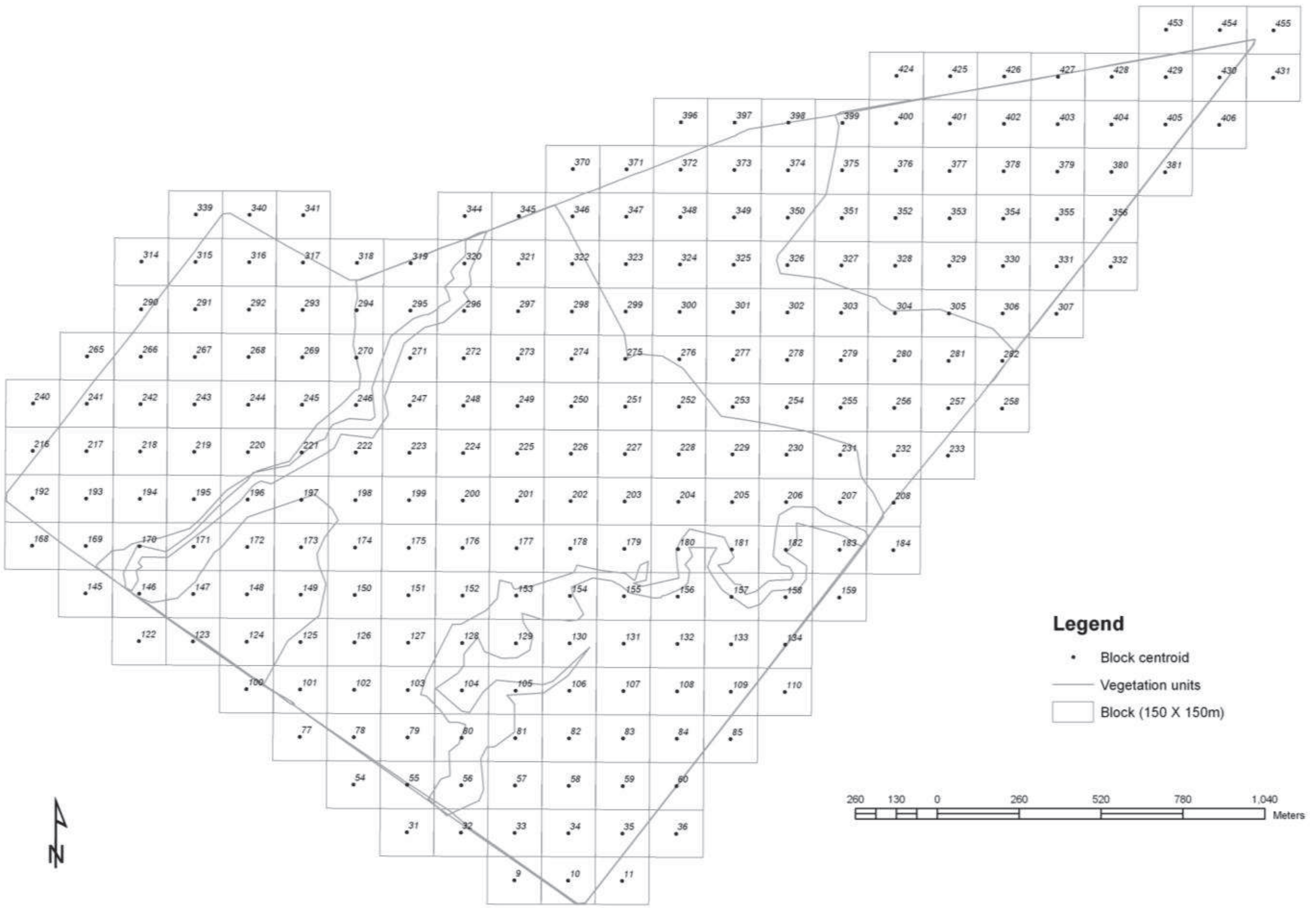
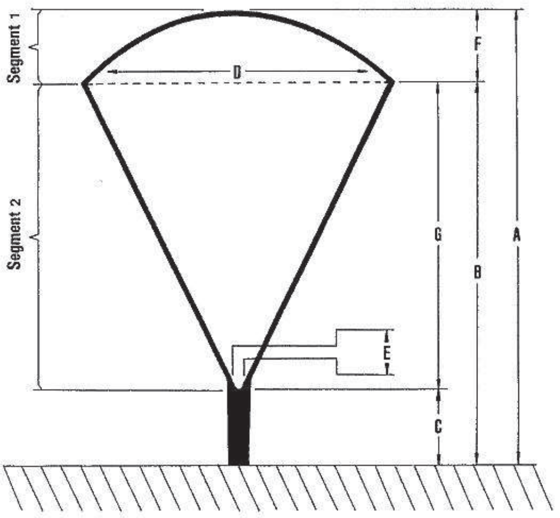


Figure 8.1 Raster of grid blocks as an overlay on the vegetation map of the study area, compiled by Department of Geography, UFS. The centroid of each block and the block number as used for woody plant surveys are indicated.

rod with 10 cm divisions indicated on it. In the case of a tree being too large (>5 m) to measure with the aluminium rod, a dimension meter (Smit 1989c) was used. The dimensions of the tree were measured by moving a specific observation distance of 14 m or 34 m from the tree (depending on the size of the tree). The method is based on a visual overlap of two images, namely the tree to be estimated and a group of length scales located on a 35 mm slide (the 2.5 m rod was used for calibration).



A = Tree height
B = Height of maximum canopy diameter
C = Height of minimum canopy diameter
D = Maximum canopy diameter at height B
E = Base canopy diameter at height C
F = Difference between A and B
G = Difference between B and C

Figure 8.2 Different measurements taken for the BECVOL-model of each woody species as indicated on the ideal shape of a tree (from Smit 1989a).

The BECVOL-model (Smit 1989b) was applied to calculate leaf dry mass (DM) and tree density (individuals/ha) from the measurements of each woody species per 100 m transect in a grid block. It also calculated total leaf dry mass/ha for each grid block separately, as well as for all the grid blocks combined in a specific vegetation unit. In addition to total leaf DM/ha, the model further facilitates stratified estimates of the DM/ha below 1.5 m, 2.0 m and 5.0 m. A height of 0 – 1.5 m represents the mean browsing height of the impala, while below 2 m and below 5 m represent the mean browsing heights of kudu and giraffe, respectively (Dayton 1978, Grunow 1980, Du Toit 1990a, Estes 1997, Skinner and Chimimba 2005). These are mean browsing heights and not maximum browsing heights. It is known that large individuals are able to reach higher than these heights, while breaking of branches may enable some browsers to utilise browse at even higher stratums (Du Toit 1990a, 1995b, Smit 2001). Available browse was assumed to be those quantities below the specified mean browsing heights, following Dekker and Smit (1996), Smit (2001), Van Essen *et al.* (2002) and Abule *et al.* (2007). The number of evapotranspiration tree equivalents per hectare

(ETTE/ha) was also calculated from leaf volume estimates (Smit and Swart 1994, Smit 2003, Abule *et al.* 2007).

8.3.2 Calculation of browsing capacity

Dekker (1996) and Van Rooyen (2010) defined a browser unit (BU) as the metabolic equivalent of a kudu cow (100% browser) with a mean body mass of 140 kg. On average the daily DM requirement of a BU is 3.5 kg (2.5% of a kudu's body mass) (Owen-Smith 1999). The browser units that can be supported by the vegetation were calculated per vegetation unit by using the following formula: Surface area of the vegetation unit (ha) / browsing capacity (ha/BU) of that vegetation unit as determined by the browsing capacity formula. The total number of browser units that can be supported by the vegetation of the study area as a whole was also calculated by dividing the surface area of the study area with the browsing capacity of the study area.

Browsing capacity was calculated by using the following formula (Smit 2006):

$$y = d \div \left[\frac{(DM1 \times f1 \times p1) + (DM2 \times f2 \times p2) + (DM3 \times f3 \times p3) + ...(DMx \times fx \times px)}{r} \right]$$

where y = browsing capacity (ha / BU);

d = number of days in a year (365);

DM = leaf DM yield per ha of each species, as calculated by the BECVOL-model;

f = utilization factor of each plant species;

p = phenology of each plant species (leaf carriage percentages, *vid.* Chapter 5); and

r = daily leaf DM required per browser unit (3.5 kg per day).

The f-values used in abovementioned formula indicate an estimation of the percentage browse that can be utilized by the animals and were 40% for highly palatable plants, like *Acacia karroo* and *Asparagus laricinus*; 30% for *Diospyros lycioides*; 25% for *Lycium echinatum* and *L. hirsutum*; and 16% for the less palatable *Searsia pyroides*. Higher utilization factors than general (Smit 2006, 2007) were used to compensate for animals feeding on shoots, since the method only determines the leaf material available. An accurate approach was followed in the determination of browsing capacity, since the vegetation is dominated by deciduous woody species, by adjusting the calculated browse capacity value (at peak biomass) for the specific p-value (phenology / leaf carriage percentages) of each month of the year, as determined for the study area. Thus, the browse capacity value was corrected in relation to the actual seasonal fluctuation in leaf presence, as discussed by Smit (2002). Median values were determined between leaf carriage percentages (phenology) of the four tree species and of the three shrub species, respectively (*vid.* Chapter 5). An average phenology value was then calculated per month, between the median tree- and median shrub values, which was multiplied by the total browse production to indicate browse production per month. A further differentiation was made between browse capacity of a wet year (Jul 2005 – Jun 2006) and a dry year (Jul 2006 – Jun 2007) by means of incorporating the specific p-values in the formula above. This was done for each vegetation unit separately by means of grouping the grid blocks (Figure 8.1) into specific vegetation units. The number of browser units that can be supported by each height stratum (0 – 1.5 m, 0 – 2.0 m and 0 – 5.0 m) was calculated individually from the leaf mass available at these strata.

8.3.3 Determination of herbaceous dry matter production

Above ground dry matter (DM) production of herbaceous plants (phytomass) was determined from 2005 – 2007 at the end of each growing season, normally April or May, following Smit (2005). Each vegetation unit was randomly divided into line transects depending on the size of the unit. A harvesting (clipped quadrate) technique as used by Grunow *et al.* (1980), Catchpole and Wheeler (1992), Smit and Swart (1994), as well as Chirara *et al.* (1998) was applied to forty quadrates in each vegetation unit, divided into twenty quadrates each for sampling under tree canopies and between tree canopies, following Smit and Swart (1994). Grossman *et al.* (1980) demonstrated that species composition differed between these subhabitats. A metal quadrate of 0.5 m^2 was randomly thrown every 15 m along transects into the area being surveyed to eliminate the subjective choice of sample areas. The wetland was not sampled as a single vegetation unit, but rather included in the dry drainage line unit during sampling.

All the rooted grasses, dwarf karroid shrubs and forbs present in the quadrates were clipped to stubble height of roughly 1 – 3 cm using hand clippers, depending on whether the species was tufted or not. Stubble height represents the maximum quantity of plant material that can be removed by the grazer (Smit 2005). The different grass species were sorted in paper bags per vegetation unit, differentiating between the two subhabitats mentioned. Forbs and dwarf karroid shrubs were not sorted on a species basis, but treated as separate groups. Samples were dried to a constant mass in an oven at 70°C for 48 hours and weighed. The DM weight of each grass species and the grouped forbs and dwarf karroid shrubs were calculated per vegetation unit.

The Canopied Subhabitat Index (Smit 1989b) at a 2 m plant height (CSI-2), as calculated by the BECVOL-model per vegetation unit, was used to determine the area covered by tree canopies, since herbaceous species composition differs in shaded habitats, mostly due to higher nutrient levels. The uncovered area was calculated by subtracting the CSI-2 percentage from 100%. Grass production per utilization class (UC) where trees were present in a vegetation unit was calculated for each of the three years of study by the following formula: DM I = (DM UC-I of covered areas in the vegetation unit (kg/ha) x CSI-2 % cover for the vegetation unit) + (DM UC-I uncovered areas (kg/ha) x uncovered area %).

Grass production (kg DM/ha) was only determined at the end of each growing season in April. In order to obtain monthly production values to estimate the grazing capacity, the Putu 11-Simulation Model (Fouché 1984, 1992, Fouché *et al.* 1985) was used. This model functions by using the rainfall totals per month in order to estimate the grass production for that month (Fouche 1984).

8.3.4 Calculation of the grazing capacity

Herbaceous species were grouped into utilization classes, as described by Edwards (1969). The sum total of the herbaceous DM (kg) per total quadrate size in a vegetation unit was expressed as DM per hectare for each utilization class and the grazing capacity was determined from these grazing production values. The utilization factor, expressed as a decimal value, represents that part of the available herbaceous material that can be consumed by the animal (Smit 2006). The utilization factor used in this study for grasses with a low acceptability (utilization class I) was 0.20 (20%), 0.30 for intermediate acceptability in utilization class II and 0.40 for grasses with a high acceptability in utilization class III. Dwarf karroid shrubs and forbs were grouped into Utilization Class I (UC-I), due to most of the species identified being of a low acceptability to grazers.

Herbaceous DM per hectare values, adapted to include canopied areas, were used per UC to calculate the grazing capacity in each of the vegetation units. In order to calculate grazing capacity for the study area as a whole, the sum total of all the DM x f values was used in the formula below and not just that of the three utilization classes. Grazing capacity (ha/GU) per month was calculated from the Putu 11-Simulation Model values, but with an average value for the utilisation factor of each plant species. This was done in order to compare it with the monthly browsing capacity and feed values. The formula described by Moore *et al.* (1985) and Smit (2002) was used:

$$y = d \div \left[\frac{(DM\ I \times f1) + (DM\ II \times f2) + (DM\ III \times f3)}{r} \right]$$

where y = grazing capacity (ha/GU)

d = number of days in a year (365)

DM = total herbaceous DM production/ha, as calculated by the harvesting method for UC I, II & III separately

f = utilization factor for each utilization class

r = daily grass DM required per GU (4.5 kg per day)

Grazer units (GU) were calculated in the same manner as browser units. Dekker (1996) and Van Rooyen (2010) defined a grazer unit (GU) as the metabolic equivalent of a blue wildebeest (100% grazer) with a mean body mass of 180 kg. Daily DM requirement of a GU will be 4.5 kg (2.5% of a blue wildebeest's body mass) (Owen-Smith 1999).

8.3.5 Estimating quantities of feed supplied

The private reserve's manager provided information annually on the time period that feed was supplied to all animals, as well as the number of lucerne bales and bags of game pellets distributed at the various feeding areas. The private reserve baled its own lucerne from fields in the southern part of the property (Figure 3.1). In order to calculate the monthly weight of lucerne bales supplied, the average weight of one bale (28 kg) was multiplied with the number of bales fed per day in the study area and with the number of days in that specific month. Similar calculations were done for the number of 50 kg bags fed per day to derive an estimation of the weight of game pellets fed in that month. The calculations were done separately for two feeding heights of supplied feed, namely 1 m and 2.5 m. The sum total of all feed given per month was also calculated.

8.3.6 Statistical analyses

GenStat® (Payne *et al*. 2009) was used to do an Analysis of Variance (ANOVA) on the data and where significance occurred, means were separated using Fisher's Protected Least Significant Difference procedure at 5% level of significance (Snedecor and Cochran 1980, McKillup 2006, Fowler *et al.* 2006). Standard errors of means for ANOVA were calculated with SEM = S / √n where S is the standard deviation of the sample and n the number of data points per variable (Fowler *et al.* 2006).

ANOVA was applied to test for differences in browsing capacity (ha/BU) of each month separately between the wet and dry years of each vegetation unit. ANOVA was also applied to test for differences in browser units (BU) between the wet and dry years of each vegetation unit. Significance of differences between the wet and dry year browsing capacity values (ha/BU) and between the two years' browser units (BU), respectively, were tested for the study area as a whole.

Differences in grazing capacity (ha/GU) between different vegetation units over the three years of this study (2005 – 2007) were tested by applying ANOVA. The vegetation units were divided into uncanopied areas between trees and canopied areas under trees. ANOVA also tested for differences in grazing capacity (ha/GU) per vegetation unit between the three years. Significance of differences was lastly tested for grazer units between the vegetation units over the three years, but without the distinction of open- and canopied areas within those vegetation units.

Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) from the CANOCO 4.5 software (Ter Braak and Smilauer 2002) were used for ordination (Gauch 1982, Ter Braak 1986, 1987). CA-ordination was applied to dry leaf mass (kg/ha) of each woody species in a grid block at the different feeding heights of 1.5 m, 2 m and 5 m with a distinction between summer, early winter and late winter, also including plant densities (plants/ha). The distinction between seasons was made by using the average leaf carriage value (phenology, *vid.* Chapter 5) of that woody species at the height of the specific season and multiplying it with the leaf mass. CCA-ordination was applied for the summer- and the winter season, respectively, on the dry leaf mass of each woody species at the different feeding heights, with the number of times giraffe, kudu and impala were observed in that specific grid block superimposed on it.

8.4 RESULTS

8.4.1 Density of woody plants and browse production

The number of evapotranspiration tree equivalents per hectare (ETTE/ha) are presented in Table 8.1, where 1 ETTE equals the mean leaf volume of a single stemmed tree with a height of 1.5m = 500 cm^3 leaf volume (Smit 1989a). Density data of each woody species in the different vegetation units is also summarised in Table 8.1, while the density of each species, along with the total leaf mass per species in the study area as a whole are presented in Table 8.2. *Acacia karroo* and *Asparagus laricinus* have the highest density overall (Tables 8.1 & 8.2), while *Diospyros lycioides*, *Ziziphus mucronata* and *Lycium echinatum* were abundant in the big drainage line (Table 8.1). As expected, the total density of woody plants is lower when the grassland and other open areas of the study area are included (Table 8.2). Although *Lycium* species are present (Table 8.1), they do not contribute substantially to the browse production due to intensive browsing thereof and are thus listed as zero kg/ha (Table 8.2).

Densities of woody plants per grid block (Figure 8.1) are presented in Figure 8.3 in the four main wind directions from the grid block containing each of the two waterholes. In the northerly and easterly direction from waterhole 1, two vegetation units are crossed before the border fences are reached. In the other two directions (S, W) three and four vegetation units, respectively, are crossed. Moving away from waterhole 2 in a northerly-, southerly- and easterly direction result in the crossing of two vegetation units, while four vegetation units are crossed in a westerly direction. On average small plant density increases were recorded in two to three grid blocks when moving in any direction from each waterhole. Overall, no clear pattern was observed in woody plant density in relation to the waterholes.

Browse production in each vegetation unit is presented as stack bars giving the sum total of each height stratum as it adds up to the >5 m stratum (Figure 8.4), while browse production of each plant species in different height strata (each starting from ground level) is presented in Table 8.3. The dense thicket and drainage lines (Figure 4.1) had the highest browse production in the 0 – 1.5 m height stratum (Figure 8.4). In the >1.5 – 2 m height stratum the highest browse production was recorded in and around the small drainage line, while in the >2 – 5 m and the > 5 m height strata the highest browse production was recorded in the disturbed area, followed by the drainage lines.

The browse production data in Table 8.3 represent all available browse per woody species below the specified browsing heights, for example the 0 – 2 m stratum includes the browse available at the 0 – 1.5 m stratum, while the 0 – 5 m stratum includes the available browse of both of these smaller strata. *Acacia karroo* is by far the dominant species in terms of browse production in all the height strata of the different vegetation units, with the exception of the big drainage line (Table 8.3). *Searsia pyroides* and *Ziziphus mucronata* contributed an estimated browse production of 58 and 71 kg DM/ha respectively at the 0 – 5 m height stratum of the big drainage line. All the species, except *A. karroo*, have a low browse phytomass production in the open thickets and disturbed area. *Asparagus laricinus* has the highest browse production of the three shrub species. Very few of the shrub plants reach heights of more than 2 m (Table 8.3), since they are browsed to a height of approximately 1.5 m (Figures 5.17 & 5.18).

Table 8.1 Evapotranspiration tree equivalents (ETTE/ha) and density of woody plants (plants/ha) in each vegetation unit.

	Open thicket north	**Open thicket west**	**Open thicket small**	**Dense thicket**	**Disturbed area**	**Small drainage line**	**Big drainage line**
ETTE / ha	490	242	281	669	1,613	1,014	1,473
Plant / ha	177	276	560	980	628	898	2,348
Acacia / ha	70	166	273	356	245	369	428
Diospyros / ha	3	12	0	102	58	120	680
Searsia / ha	2	7	14	28	0	58	115
Ziziphus / ha	10	12	38	95	25	98	308
Asparagus / ha	90	74	235	383	268	240	468
L. echinatum / ha	0	0	0	0	0	0	320
L. hirsutum / ha	0	0	0	8	30	13	23

Acacia karroo; *Diospyros lycioides*; *Searsia pyroides*; *Ziziphus mucronata*; *Asparagus laricinus*; *Lycium echinatum; Lycium hirsutum*

Table 8.2 Total leaf mass (kg DM/ha) and density of species (plants/ha) in the study area.

	Leaf mass	**Density**
Acacia	103	238
Diospyros	6	104
Searsia	9	24
Ziziphus	23	69
Asparagus	12	233
L. echinatum	0	31
L. hirsutum	0	8

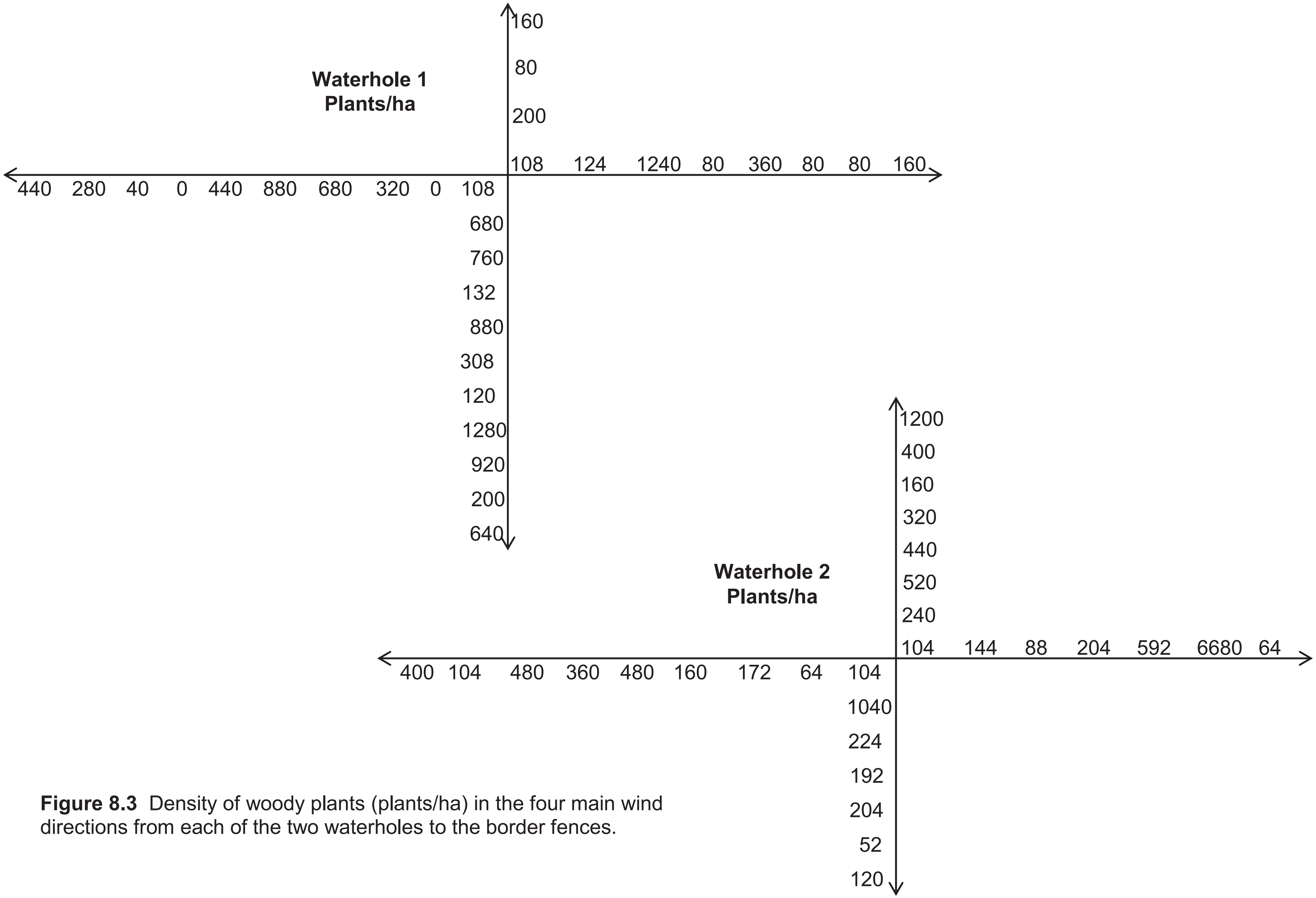


Figure 8.3 Density of woody plants (plants/ha) in the four main wind directions from each of the two waterholes to the border fences.

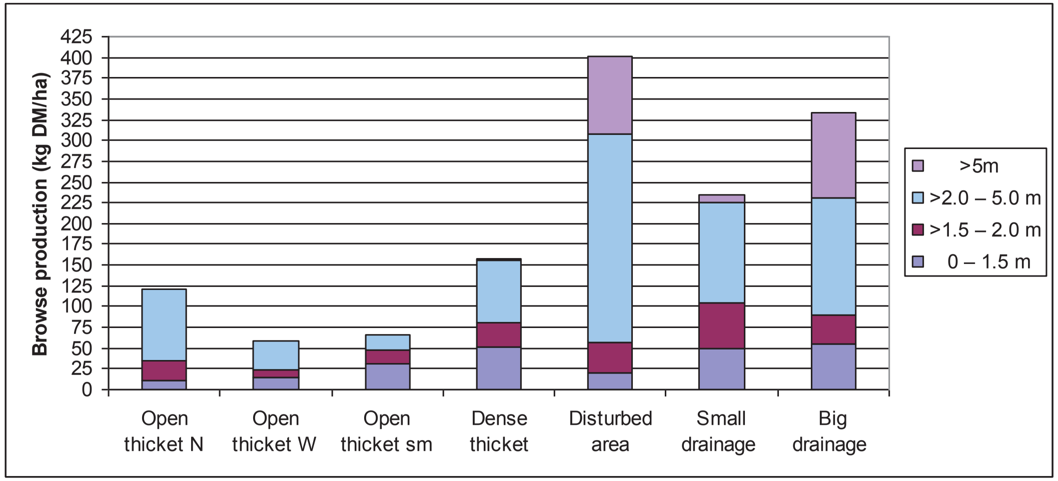


Figure 8.4 Browse production totals at four height strata between different vegetation units.

Table 8.3 Browse production at peak biomass (kg dry mass/ha) per species at different height strata in each vegetation unit.

	Open thicket north	Open thicket west	Open thicket small	Dense thicket	Disturbed area	Small drainage line	Big drainage line
Aca 0 - 1.5 m	7	9	18	19	14	26	9
Aca 0 - 2 m	29	17	34	39	48	53	21
Aca 0 - 5 m	112	52	52	102	294	113	52
Aca > 5 m	112	52	52	104	390	122	64
Dio 0 - 1.5 m	0	1	0	4	1	7	7
Dio 0 - 2 m	0	1	0	3	1	11	12
Dio 0 - 5 m	0	1	0	6	2	23	26
Dio > 5 m	0	1	0	6	2	23	26
Sea 0 - 1.5 m	0	0	0	2	0	6	8
Sea 0 - 2 m	0	1	1	3	0	20	24
Sea 0 - 5 m	0	1	1	5	0	47	58
Sea > 5 m	0	1	1	5	0	47	58
Ziz 0 - 1.5 m	0	1	2	5	0	4	9
Ziz 0 - 2 m	2	1	2	11	1	12	10
Ziz 0 - 5 m	5	1	2	19	5	35	71
Ziz > 5 m	5	1	2	19	5	35	162
Asp 0 - 1.5 m	4	3	11	24	5	8	18
Asp 0 - 2 m	4	3	11	24	5	8	18
Lech 0 - 1.5 m	0	0	0	0	0	0	4
Lech 0 - 2 m	0	0	0	0	0	0	4
Lhir 0 - 1.5 m	0	0	0	0	1	0	1
Lhir 0 - 2m	0	0	0	0	1	0	1

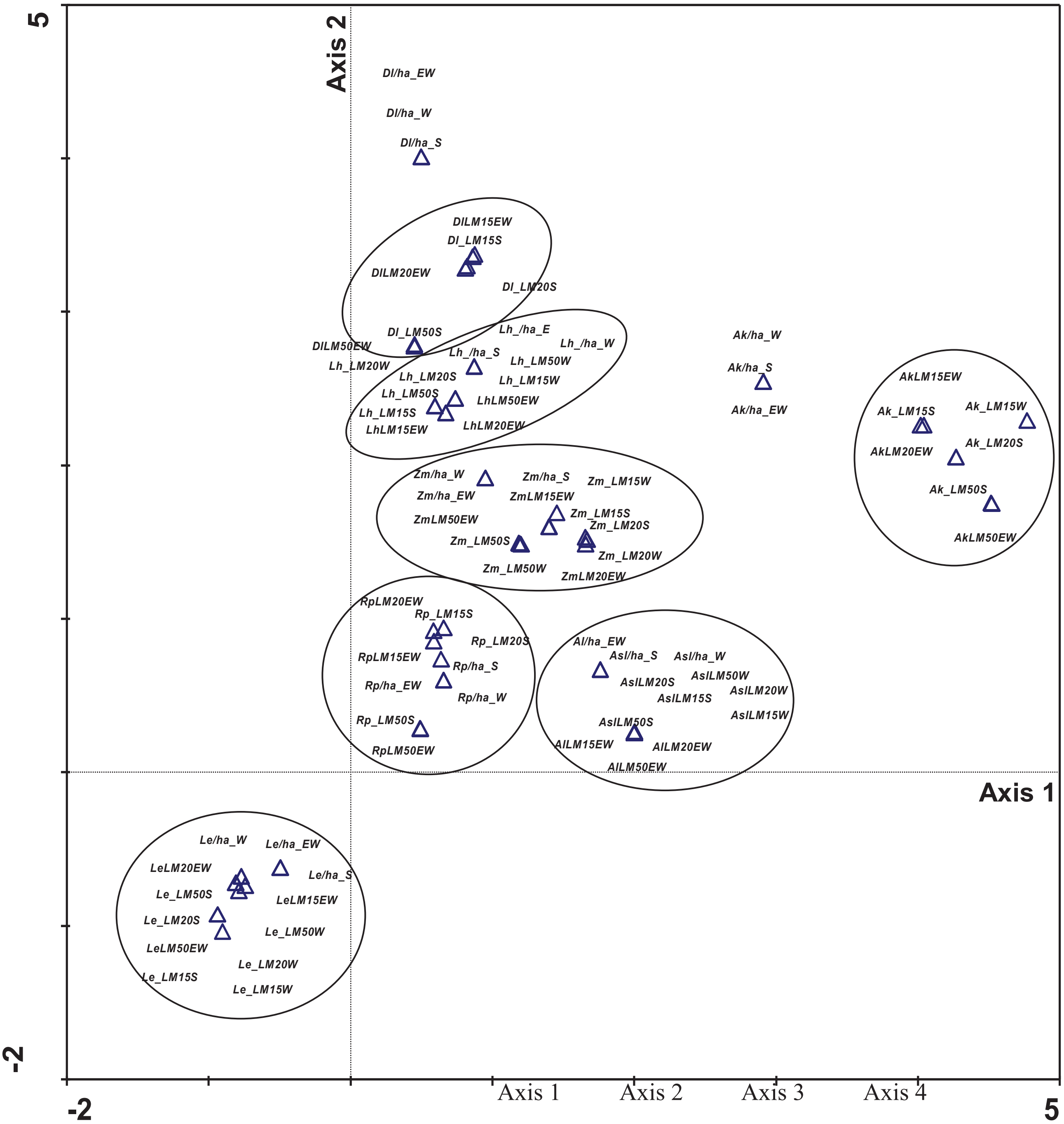
Aca= *Acacia karroo*; Dio= *Diospyros lycioides*; Sea= *Searsia pyroides*; Ziz= *Ziziphus mucronata*; Asp= *Asparagus laricinus*; Lech= *Lycium echinatum*; Lhir= *Lycium hirsutum*

CA-ordination (*vid.* page 53) results of the leaf production per woody species at different browsing heights in the summers (wet, hot seasons) and winters (dry, cool seasons) are presented in Figure 8.5. The plant species were mostly grouped together, regardless of the season. The plant densities (that are obviously similar between the different seasons per species) were grouped a distance away from the leaf mass data points of *Acacia karroo* and *Diospyros lycioides*, but closer to the leaf mass data points of the other plant species. The most dominant species, *A. karroo*, was grouped at the far right of the graph, while the scarce *Lycium echinatum* with the lowest leaf mass was grouped at the far left and the other species almost vertically in the same plane between these two extremities. Low Eigen-values were the result of a high number of zero values and similar values (low variation) in the dataset, but the associations or groupings are still meaningful.

CCA-ordination was also done for the two main seasons separately on the dry leaf mass (LM) data of woody species combined with the number of times that certain animal species were observed in similar grid blocks (*vid.* Chapter 7). No significant associations could be distinguished between the woody plants and the presence of animals in the summer season (Eigenvalues 0.055, 0.029 – graph not shown). In the dry cool season (Figure 8.6), a strong association is evident between giraffe observations and the 0 – 5 m browsing stratum LM of *Ziziphus mucronata* and with *Asparagus laricinus* plants per hectare. Kudu observations had the strongest association with *Lycium hirsutum* LM, while impala observations could be associated with some *Z. mucronata* values. Eland is not indicated because of too few observations. It is known that *Z. mucronata* is highly palatable and leaf litter is well used in the dry season by browsing animals (*vid.* 'Food sources of giraffe, kudu, impala and eland' in Chapter 6). The semi-deciduous shrubs, *A. laricinus* and *L. hirsutum*, are important lean season browse reserves in the study area (Figures 5.6 & 5.7). Although the leaf litter use of *Z. mucronata* and the semi-deciduous nature of the palatable shrubs can explain the presence of these animals in their vicinity, opposed to the deciduous species, the R- and Eigenvalues are very low.

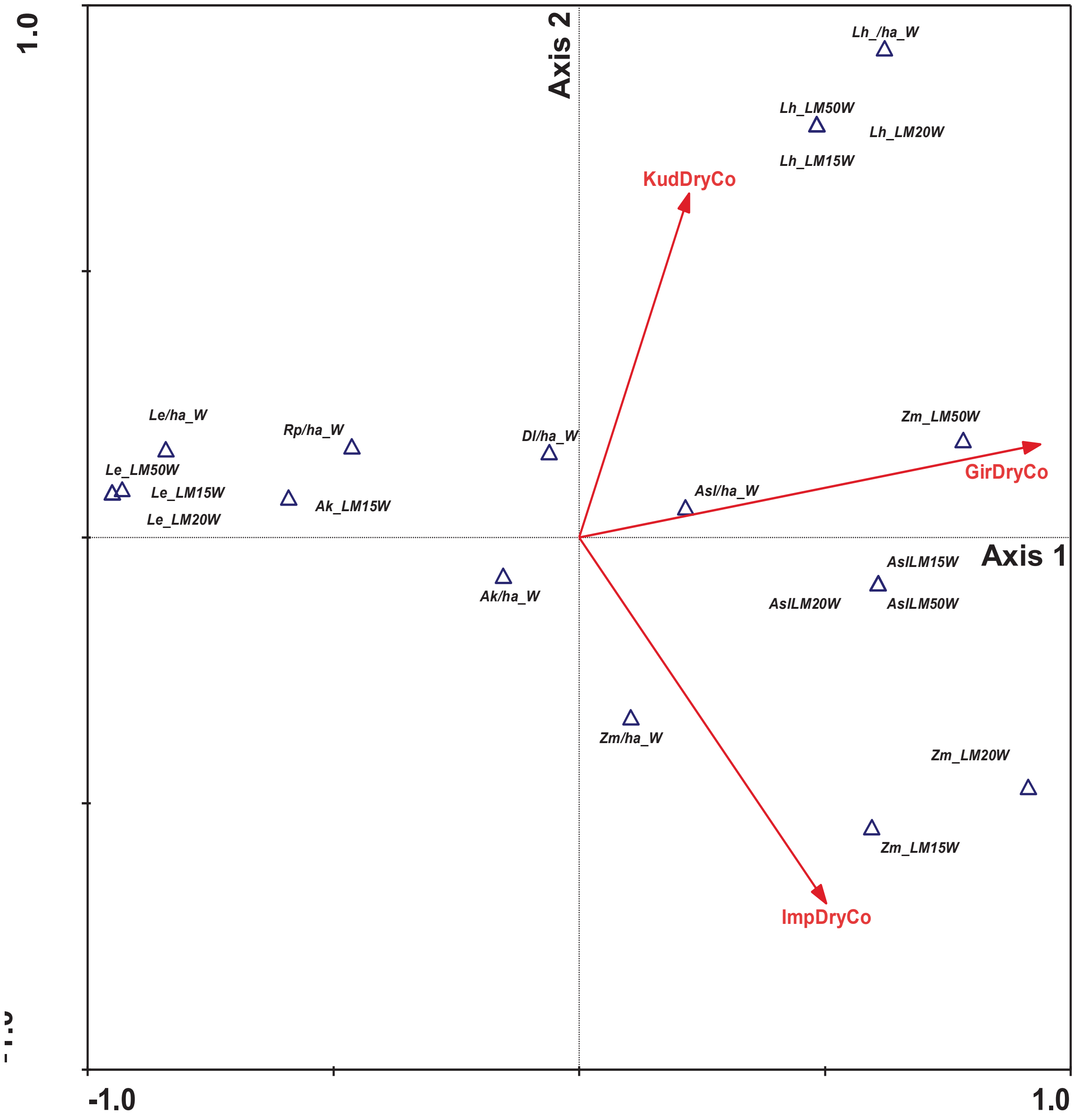
8.4.2 Browsing capacity and browser units

Significant differences ($p < 0.001$) in the browsing capacity based on leaf phenology of the 0 – 2 m height stratum of separate vegetation units (Figure 4.1) were evident for each month between the wet and dry years, indicated by the means followed by different alphabet letters in Table 8.4. The browsing capacity mean of the two large open thickets mostly differed significantly in all the months from that of the other vegetation units. Results of the western open thicket indicated a difference of 470 ha/BU in September between wet- and dry years and the other open thickets



	Axis 1	Axis 2	Axis 3	Axis 4
Eigen-values	0.373	0.156	0.103	0.061
Cumulative % variance:				
of species data	28.7	40.8	48.7	53.5

Figure 8.5 Correspondence analysis (CA) of densities and dry leaf mass (kg/ha) available per woody species at different browsing heights in the summers (S), early winters (EW) and late winters (W). Legend: LM = Leaf mass; 15 = 0 – 1.5 m height stratum; 20 = 0 – 2 m height; 50 = 0 – 5 m height; Ak = *Acacia karroo*; Asl = *Asparagus laricinus*; Dl = *Diospyros lycioides*; Le = *Lycium echinatum*; Lh = *L. hirsutum*; Rp = *Searsia pyroides*; Zm = *Ziziphus mucronata*.



	Axis 1	Axis 2	Axis 3	Axis 4
Eigen-values	0.010	0.004	0.002	0.360
Sp-environment correlation	0.227	0.171	0.128	0.0
Cumulative % variance:				
of species data	0.9	1.3	1.4	34.4
of species-climate relation	63.6	87.9	100	0.0

Figure 8.6 Canonical correspondence analysis (CCA) of the number of times an animal species were observed in a grid block, superimposed on dry leaf mass (kg/ha) available per tree species at different browsing heights in the dry, cool season, including plant densities. Legend (trees): LM = Leaf mass; 15 = 0 – 1.5 m height; 20 = 0 – 2 m; 50 = 0 – 5 m height; W = winter months; Ak = *Acacia karroo*; Asl = *Asparagus laricinus*; Dl = *Diospyros lycioides*; Le = *Lycium echinatum*; Lh = *L. hirsutum*; Rp = *Searsia pyroides*; Zm = *Ziziphus mucronata*; (animals): DryCo = dry cool seasons; Gir = giraffe; Imp = impala; Kud = kudu. Monte Carlo permutation test of significance of first canonical axis indicated an Eigenvalue of 0.010 (F-ratio 1.430, P-value 0.548) and of all canonical axes had a Trace of 0.016 (F-ratio 0.754, P-value 0.534).

differed approximately 200 ha/BU between the years (Figure 8.7). The remaining vegetation units had differences during September of 135 – 152 ha/BU between the two years. Significant differences were indicated between all vegetation units from November to January (Table 8.4). No significant differences (Table 8.4) were found in browsing capacity of July in the small open thicket, drainage lines and dense thicket between the two years. From November to March there were only mathematical differences of less than 5 ha/BU between the wet and dry years' browsing capacity in the vegetation units (Figure 8.7). This is confirmed by statistical analyses (Table 8.4).

The number of browser units (BU) per month that can be supported in each vegetation unit in the height stratum of <2 m, are too low to be meaningful for a game rancher (in general <2 BU per vegetation unit and ±6 between the disturbed area and dense thicket in summer) and are thus not presented in a figure. When woody plants have full leaf carriage in summer months, browsing capacity is at its highest, while during July, August and September when trees are leafless the browsing capacity is very low (Figure 8.7). No significant differences ($p = 0.85$, $n = 24$, SEM = 0.141) were found between numbers of BU that can be sustained during the wet and dry year in different vegetation units, mathematical differences were on average 0.07 BU.

The browsing capacity of the study area as a whole during a wet- and a dry year is presented in Figure 8.8, along with the true number of browser units (based on browse within reach of browsing animals) that the study area can support per month. No significant differences ($p = 0.83$, $n = 12$, SEM = 5.81) were found in the study area's browsing capacity between the wet and dry years in general. However, browsing capacity of the study area in August and September was found to be lower in the dry year (79 & 61 ha/BU) than in the extremely wet year (64 & 42 ha/BU). In summer the total browsing capacity of the study area was approximately 73 ha/BU and 80 ha/BU for a wet and dry year, respectively (Figure 8.8).

No significant differences ($p = 0.90$, $n = 12$, SEM = 10.31) were found in BU that can be supported by the study area as a whole between the wet and dry years. Available browse in the 0 – 2 m height stratum of the study area can sustain 6.6 – 7.3 BU in summer (Figure 8.8). In September the number of BU at the 0 – 2 m height stratum decreases to 1 BU and 0.8 BU in the two years, respectively. Numbers of BU at the end and at the height of each growing season for the different browsing strata are presented in Table 8.5. Browse at the 5 m height is only within reach of large giraffes and these values cannot be used to determine the numbers of smaller browsing animals that can be kept on the private reserve. The lower height strata are more suitable to determine the number of BU for the study area.

Table 8.4 Results of the ANOVA test for differences in 0 – 2 m monthly browsing capacity totals (ha/BU) between the wet and dry years (n = 2).

July	**Mean**		**August**	**Mean**
Open thicket west	914.2 a		Open thicket west	1707.0 a
Open thicket north	609.2 b		Open thicket north	1243.4 b
Disturbed area	428.9 bc		Disturbed area	882.0 c
Open thicket small	313.2 cd		Small drainage line	575.5 d
Small drainage line	246.6 d		Open thicket small	493.4 e
Big drainage line	174.4 d		Big drainage line	272.2 f
Dense thicket	147.1 d		Dense thicket	227.2 f
Summary statistics (Jul)			**Summary statistics (Aug)**	
SEM	54.20		SEM	21.13
p	<0.001		p	<0.001
L.S.D (5%)	181.2		L.S.D (5%)	70.7
CV%	18.9		CV%	3.9
September	**Mean**		**October**	**Mean**
Open thicket west	1277.1 a		Open thicket west	286.5 a
Open thicket north	879.5 ab		Open thicket north	177.9 b
Disturbed area	548.4 bc		Open thicket small	135.2 c
Open thicket small	479.2 bc		Big drainage line	116.1 cd
Small drainage line	377.0 c		Disturbed area	108.7 cde
Big drainage line	289.5 c		Dense thicket	93.6 de
Dense thicket	259.0 c		Small drainage line	81.2 e
Summary statistics (Sep)			**Summary statistics (Oct)**	
SEM	121.10		SEM	9.85
p	0.005		p	<0.001
L.S.D (5%)	404.9		L.S.D (5%)	32.9
CV%	29.2		CV%	9.8
November	**Mean**		**December**	**Mean**
Open thicket west	185.3 a		Open thicket west	161.8 a
Open thicket north	117.3 b		Open thicket north	102.4 b
Open thicket small	86.2 c		Open thicket small	74.9 c
Disturbed area	72.6 d		Disturbed area	64.2 d
Big drainage line	63.1 e		Big drainage line	52.7 e
Dense thicket	55.7 f		Dense thicket	47.1 f
Small drainage line	49.3 g		Small drainage line	41.9 f
Summary statistics (Nov)			**Summary statistics (Dec)**	
SEM	1.30		SEM	1.66
p	<0.001		p	<0.001
L.S.D (5%) = 4.4	CV = 2.0%		L.S.D (5%) = 5.6	CV = 3.0%

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Table 8.4 Continued

January	**Mean**		**February**	**Mean**
Open thicket west	145.3 a		Open thicket west	137.9 a
Open thicket north	92.1 b		Open thicket north	87.3 b
Open thicket small	67.8 c		Open thicket small	64.4 c
Disturbed area	57.9 d		Disturbed area	55.2 c
Big drainage line	46.5 e		Big drainage line	43.6 d
Dense thicket	42.2 f		Dense thicket	39.6 d
Small drainage line	36.7 g		Small drainage line	34.4 d
Summary statistics (Jan)			**Summary statistics (Feb)**	
SEM	0.90		SEM	3.36
p	<0.001		p	<0.001
L.S.D (5%)	3.1		L.S.D (5%)	11.2
CV%	1.9		CV%	7.2
March	**Mean**		**April**	**Mean**
Open thicket west	137.9 a		Open thicket west	139.6 a
Open thicket north	87.1 b		Open thicket north	88.2 b
Open thicket small	64.4 c		Open thicket small	66.0 c
Disturbed area	55.2 c		Disturbed area	55.9 cd
Big drainage line	43.6 d		Big drainage line	44.6 de
Dense thicket	39.6 d		Dense thicket	40.7 de
Small drainage line	34.4 d		Small drainage line	34.5 e
Summary statistics (Mar)			**Summary statistics (Apr)**	
SEM	3.41		SEM	4.74
p	<0.001		p	<0.001
L.S.D (5%)	11.4		L.S.D (5%)	15.8
CV%	7.3		CV%	10.0
May	**Mean**		**June**	**Mean**
Open thicket west	183.4 a		Open thicket west	381.4 a
Open thicket north	117.0 b		Open thicket north	249.4 b
Open thicket small	82.8 c		Disturbed area	165.4 c
Disturbed area	75.0 cd		Open thicket small	155.2 c
Big drainage line	53.1 de		Small drainage line	94.7 d
Dense thicket	48.2 e		Big drainage line	88.3 d
Small drainage line	45.4 e		Dense thicket	80.8 d
Summary statistics (May)			**Summary statistics (Jun)**	
SEM	7.49		SEM	9.99
p	<0.001		p	<0.001
L.S.D (5%)	25.0		L.S.D (5%)	33.4
CV%	12.3		CV%	8.1

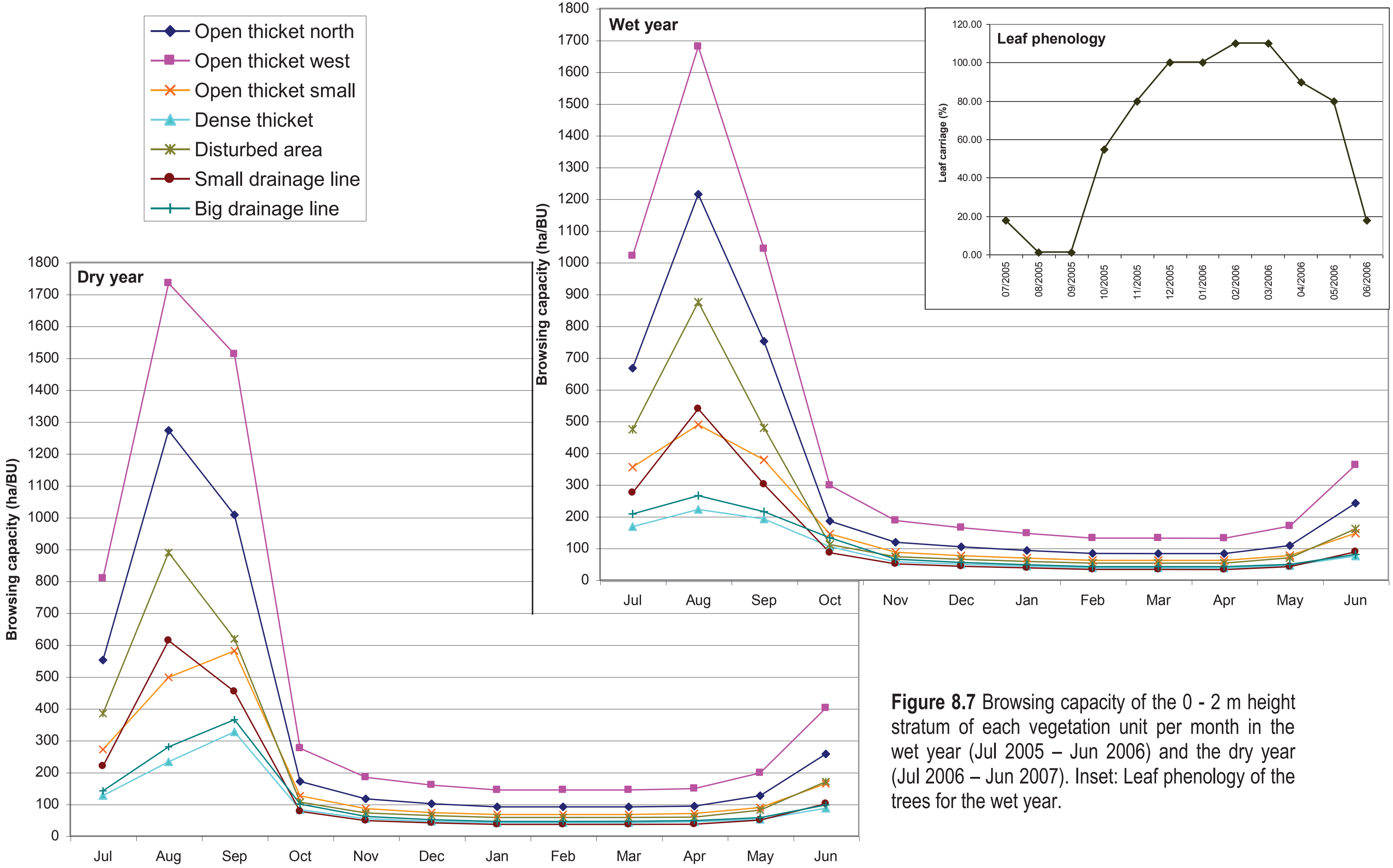

Figure 8.7 Browsing capacity of the 0 - 2 m height stratum of each vegetation unit per month in the wet year (Jul 2005 – Jun 2006) and the dry year (Jul 2006 – Jun 2007). Inset: Leaf phenology of the trees for the wet year.

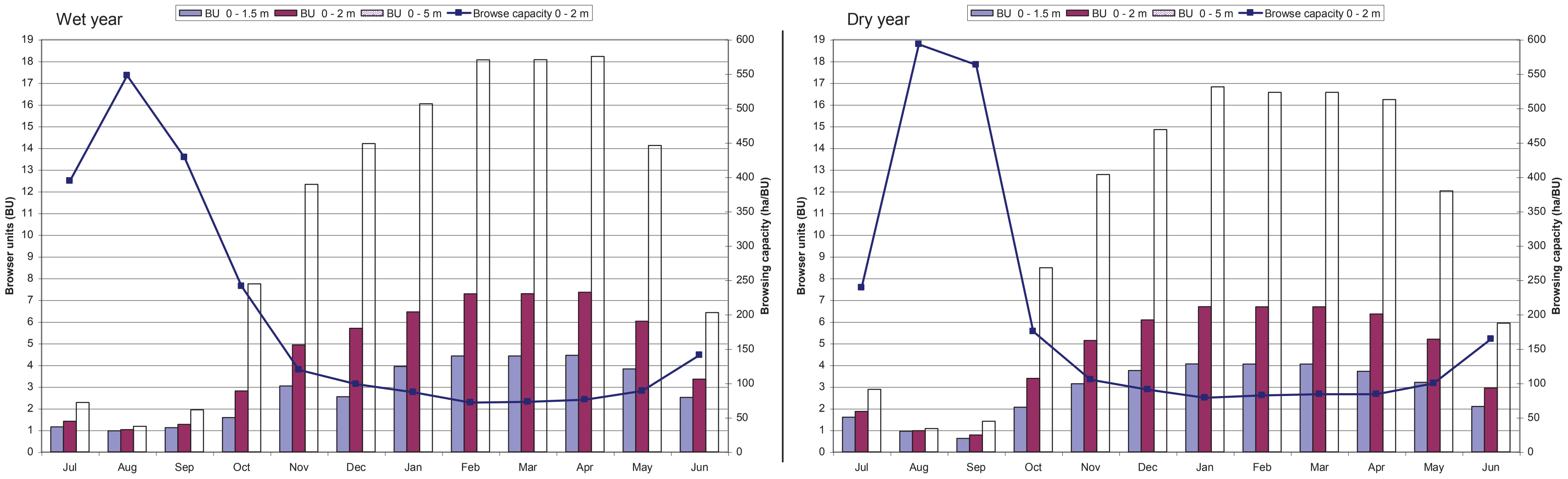

Figure 8.8 Monthly browsing capacity totals of the 0 – 2 m height stratum for the study area and monthly browser units that can be sustained at different height strata in the wet year (Jul 2005 - Jun 2006) and the dry year (Jul 2006 – Jun 2007). Giraffe can reach up to 5 m while browsing, kudu and eland up to 2 m and impala up to 1.5 m.

Table 8.5 Minimum and maximum browser units (BU) that the study area can sustain in a growing season and at each height stratum. The 0 – >5 m height stratum represents the grand total, although browse higher than 5 m is out of reach of all browser species in the study area.

	Sep 2004	Feb 2005	Aug 2005	Feb 2006	Aug 2006	Feb 2007	Aug 2007	Feb 2008
BU 0 - 1.5 m	0.85	3.72	0.97	4.42	0.95	4.05	0.65	4.04
BU 0 - 2 m	1.00	6.36	1.02	7.29	0.98	6.69	0.83	6.66
BU 0 - 5 m	1.63	16.24	1.18	18.06	1.08	16.57	1.52	16.52
BU >5 m	1.73	16.82	1.22	19.96	1.10	18.34	1.65	18.29

8.4.3 Grass production, grazing capacity and grazer units

Grass species harvested in each vegetation unit over the study period are listed in Table 8.6, as well as the utilization classes that they were grouped into. Species that were only recorded in the grassland and the adjacent northern open thicket were: *Barleria* sp., *Cymbopogon pospischilii*, *Digitaria eriantha* (Smuts Finger Grass), *Eragrostis superba*, *Heteropogon contortus*, *Panicum coloratum* and *Pogonarthria squarrosa*. Shade-loving species found under trees were: *Bromus catharticus*, *Eragrostis biflora*, *Melica decumbens*, *Panicum maximum*, *Setaria verticillata* and *Sporobolus fimbriatus*. *Echinochloa holubii*, *Eragrostis curvula* and *Setaria nigrirostris* were characteristic of the drainage lines (*vid.* Chapter 4).

Average grass dry mass production, between the three years of study, in each utilization class (UC) is presented in Figure 8.9, while the grass production separated into uncanopied and canopied areas per vegetation unit in each year of study is presented in Table 8.7. UC-I mostly contains pioneer species that increase with over-utilization (Table 8.6). The highest grass production in UC-I (Table 8.7) was recorded in 2005 in the dense thicket canopied areas, followed by all the other canopied areas, in 2006 in canopied drainage lines and the dense thicket and in 2007 in the canopied subhabitat of the dense thicket. An increase in dry mass in UC-I of approximately 100 kg/ha annually was observed in the canopied dense thicket. An annual increase in UC-II, mostly incorporating subclimax species like *Eragrostis* spp., occurred in the grassland and the uncanopied disturbed area.

UC-III contains the palatable herbaceous species and has the highest average grass production (Figure 8.9) in the dense thicket (1 127.3 kg/ha), followed by the open thickets (1 017.8 kg/ha) and grassland (795.4 kg/ha). The very large tufts of *E. curvula*, present only in the drainage lines, contributed the most dry mass to the uncanopied, open drainage line vegetation in UC-II namely 2 168.3 kg/ha, while tall *D. eriantha* (Smuts Finger Grass) plants contributed to the dry mass of the grassland and open thickets. The drainage line basins, however, only cover a small percentage (5.4%) of the study area. The highest average grass production in UC-I (Figure 8.9) was recorded in the canopied drainage lines (660.5 kg/ha) and dense thicket (579.0 kg/ha). During 2005, 2006 and 2007 total grass production for the study area was 1 075.3 kg/ha, 1 488.3 kg/ha and 1 218.6 kg/ha respectively. These actual values are close to the slightly higher estimated grass production for the area by the Putu 11-Simulation Model, namely 1 348 kg/ha, 1 545 kg/ha and 1 308 kg/ha for the three respective years.

Table 8.6 Species sampled between- and under trees in each vegetation unit and grouped into utilization classes (UC*), following Van Oudtshoorn (1999) and Van Rooyen (2010).

Grass species	UC	Grass species	UC
Grassland (including purple finger grassland)			
Aristida congesta	I	*Eragrostis superba*	II
Barleria species	I	Forbs	I
Cymbopogon pospischilii	I	*Heteropogon contortus*	II
Cynodon dactylon	II	*Panicum coloratum*	III
Digitaria argyrograpta	III	*Pogonarthria squarrosa*	I
Digitaria eriantha	III	*Setaria* species	II / III
Digitaria eriantha (Smuts Finger)	III	*Sporobolus fimbriatus*	III
Eragrostis chloromelas	II	*Themeda triandra*	III
Eragrostis lehmanniana	II	*Tragus koelerioides*	I
Eragrostis obtusa	I		
Open thicket			
Aristida congesta	I	*Eragrostis chloromelas*	II
Cymbopogon pospischilii	I	*Eragrostis obtusa*	I
Cynodon dactylon	II	Forbs	I
Digitaria argyrograpta	III	*Panicum coloratum*	III
Digitaria eriantha	III	*Sporobolus fimbriatus*	III
Digitaria eriantha (Smuts Finger)	III	*Themeda triandra*	III
Dwarf karroid shrubs	I		
Open thicket under trees			
Aristida congesta	I	*Eragrostis chloromelas*	II
Brachiaria eruciformis	II	Forbs	I
Bromus catharticus	III	*Heteropogon contortus*	II
Chloris virgata	I	*Melica decumbens*	I
Cynodon dactylon	II	*Panicum maximum ?*	III
Cynodon transvaalensis	III	*Setaria verticillata*	I
Digitaria argyrograpta	III	*Sporobolus fimbriatus*	III
Dwarf karroid shrubs	I	*Themeda triandra*	III
Eragrostis biflora	I		
Dense thicket			
Aristida adscensionis	I	*Eragrostis chloromelas*	II
Aristida congesta	I	*Eragrostis obtusa*	I
Chloris virgata	I	Forbs	I
Cynodon dactylon	II	*Panicum coloratum*	III
Cynodon transvaalensis	III	*Sporobolus fimbriatus*	III
Digitaria argyrograpta	III	*Sporobolus ioclados*	II
Digitaria eriantha	III	*Themeda triandra*	III
Dwarf karroid shrubs	I	*Tragus koelerioides*	I
Dense thicket under trees			
Cynodon dactylon	II	Forbs	I
Cynodon transvaalensis	III	*Melica decumbens*	I
Digitaria argyrograpta	III	*Panicum maximum ?*	III
Digitaria eriantha	III	*Setaria nigrirostris*	II
Dwarf karroid shrubs	I	*Setaria verticillata*	I
Eragrostis biflora	I	*Sporobolus fimbriatus*	III
Eragrostis chloromelas	II	*Themeda triandra*	III
Eragrostis obtusa	I		

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Table 8.6 Continued			
Grass species	**UC**	**Grass species**	**UC**
Disturbed area			
Cynodon dactylon	II	*Eragrostis lehmanniana*	II
Cynodon transvaalensis	III	*Sporobolus fimbriatus*	III
Disturbed area under trees			
Bromus catharticus	III	Forbs	I
Cynodon dactylon	II	*Melica decumbens*	I
Cynodon transvaalensis	III	*Setaria verticillata*	I
Eragrostis biflora	I	*Sporobolus fimbriatus*	III
Dry drainage lines			
Cynodon dactylon	II	*Panicum coloratum*	III
Echinochloa holubii (2006)	II	*Setaria nigrirostris*	II
Eragrostis curvula	II	*Sporobolus fimbriatus*	III
Eragrostis lehmanniana	II	*Themeda triandra*	III
Forbs	I		
Dry drainage lines under trees			
Bromus catharticus	III	*Melica decumbens*	I
Cynodon dactylon	II	*Panicum coloratum*	III
Cynodon transvaalensis	III	*Setaria nigrirostris*	II
Dwarf karroid shrubs	I	*Setaria verticillata*	I
Eragrostis curvula	II	*Sporobolus fimbriatus*	III
Forbs	I		

*Utilization class I	=	low acceptability / unacceptable
Utilization class II	=	medium acceptability
Utilization class III	=	highly palatable / acceptable

Forbs mostly consisted of *Chenopodium album* = UC I

Dwarf karroid shrubs mostly consisted of *Lycium horridum* species = UC I

There were no significant differences (p = 0.532, n = 9, SEM = 1.83) in grazing capacity between the three years. All the vegetation units have grazing capacities of less than 5 ha/GU in all three years (Figure 8.10), with exception of the disturbed area where up to 14.9 ha is needed per grazer unit. As a result of the high grass production in the drainage lines, a high grazing capacity of 2 – 3 ha/GU was recorded over the three years. During 2006, after above-normal rainfall conditions and flooding (Figure 3.7, Table 3.2), the grazing capacity reached a peak. Similarities in grazing capacities were observed between the three years in vegetation units that were in open areas between trees (uncanopied areas), including the grassland (Table 8.8), while the canopied areas of the disturbed area differed significantly from the other vegetation units. Grazing capacity means of the three calendar years followed by the same alphabet letter on Table 8.8 did not differ significantly between vegetation units.

Table 8.7 Grass production (kg DM/ha) in each utilization class (UC) per vegetation unit separated into open and canopied habitats for the three years of study. Grasses with a low acceptability were grouped in UC-I, an intermediate acceptability in UC-II and grasses with a high acceptability in UC-III.

	2005			2006			2007		
	UC-I	**UC-II**	**UC-III**	**UC-I**	**UC-II**	**UC-III**	**UC-I**	**UC-II**	**UC-III**
Grassland	74.14	98.99	804.21	103.43	206.85	960.41	92.06	227.34	621.56
Open thicket open	163.04	159.22	1001.76	48.88	112.02	1228.44	100.6	220.82	823.3
Open thicket canopied	396.42	89.2	457.36	158.98	59.68	619.6	253.06	11.02	265.8
Dense thicket open	86.3	150.42	1070.46	312.58	616.7	1180.98	50.18	511.36	1130.48
Dense thicket canopied	480.78	212.64	429.58	567.58	0	571.82	688.58	112.64	579.48
Disturbed area open	0	86.8	250.36	0	119	721.4	0	153.32	234.08
Disturbed area canopied	312.76	29.32	28.32	120.76	128.92	116.2	149.16	46.56	74.84
Drainage lines open	2.48	1595.86	412.92	26.7	2682.44	519.02	158.84	2226.62	945.7
Drainage lines canopied	456.48	79	125.38	1314.8	32.4	197.6	210.18	315.6	152.16

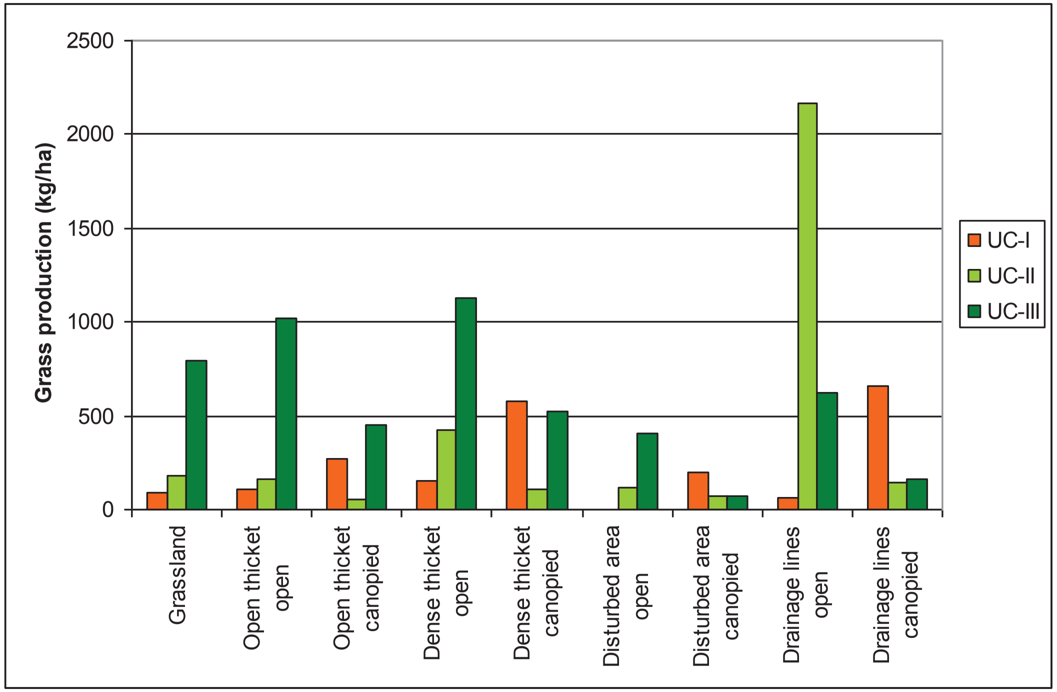

Figure 8.9 Average grass dry mass production (kg/ha) of the three years of study in each utilization class at the end of the growing season in different vegetation units.

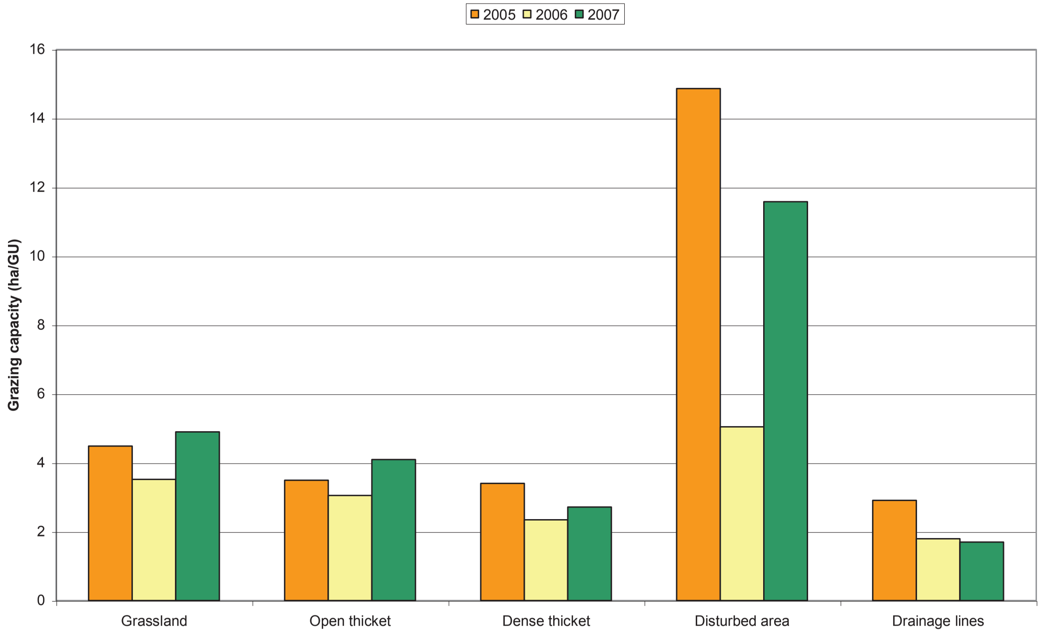

Figure 8.10 Grazing capacity at the end of the growing season of each of the three years of study in the different vegetation units.

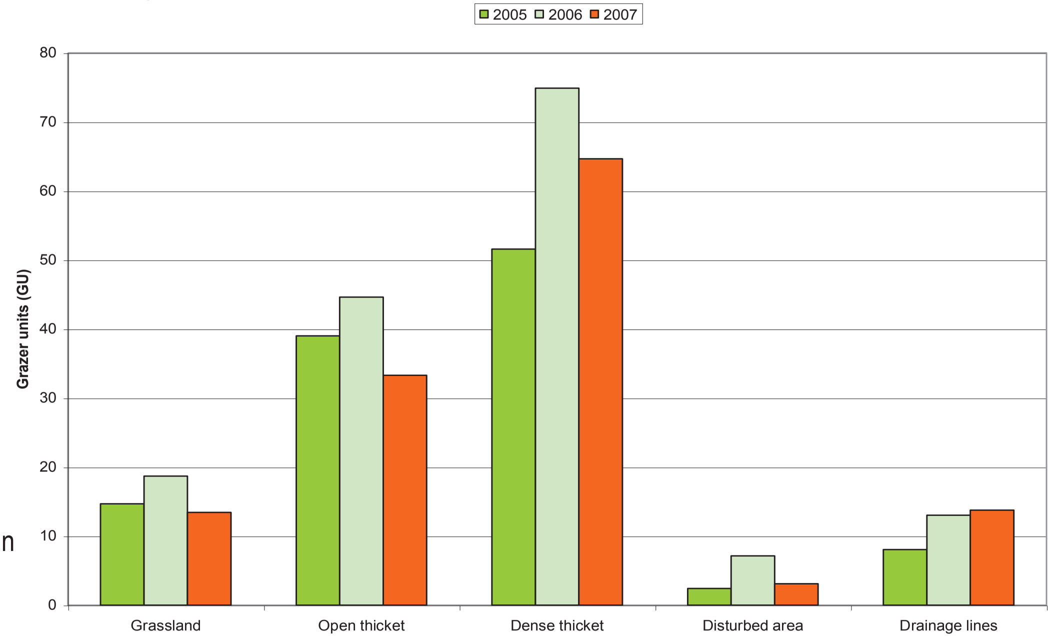

Figure 8.11 Grazer units that can be sustained in each vegetation unit in the three years of study.

Table 8.8 Results of the ANOVA test for differences in grazing capacity (ha/GU) between vegetation units over three calendar years (n = 3).

Vegetation unit open and canopied	**Mean**
Disturbed area canopied	19.1 a
Disturbed area uncanopied / open	9.9 b
Drainage lines canopied	7.6 bc
Open thicket canopied	7.2 bcd
Dense thicket canopied	4.6 cde
Grassland	4.3 cde
Open thicket uncanopied / open	3.5 de
Dense thicket uncanopied / open	2.8 e
Drainage lines uncanopied / open	1.9 e
Summary statistics	
SEM	1.333
p	<0.001
L.S.D (5%)	3.959
CV%	34.1

Table 8.9 Results of the ANOVA test for differences in grazer units without distinction between open- and canopied areas in vegetation units over three calendar years (n = 3).

Vegetation unit	**Mean**
Dense thicket	63.7 a
Open thicket	39.0 b
Grassland	15.6 c
Drainage lines	11.6 cd
Disturbed area	4.2 d
Summary statistics	
SEM	3.580
p	<0.001
L.S.D (5%)	11.29
CV%	23.1

The number of grazer units that each vegetation unit can sustain is presented in Figure 8.11. The dense- and open thickets can support the most grazer units of between 52 – 75 GU and 33 – 45 GU, respectively, between dry and wet years. The disturbed area can support only 2 – 7 GU between wet and drier years and the grassland 13 – 18 GU (Figure 8.11). Significant differences (Table 8.9) were found in grazer units between various vegetation units. The study area as a whole can carry 116 – 158 GU between wet and dry years (Figure 8.12), with a grazing capacity of 2.8 – 3.8 ha/GU.

Estimates of the monthly grazing- and browsing capacities over the three years of study are presented in Figure 8.13 for the sake of completeness. Estimates and averages had to be used, since specific values proved difficult to calculate per month due to differences in species' phenology values (leaf carriage percentages) and utilization factors. Clear seasonal patterns were observed in browsing and grazing capacities needed, with high values needed when food was scarce and lower values when food was in abundance.

8.4.4 Feed supplied

Two feeding areas were used (Figure 7.1b). At the one feeding area, only lucerne bales were supplied at ground level. At the main feeding area, feed was supplied in the form of lucerne bales and lucerne-based game pellets at two heights (Figure 8.14), 1 m and 2.5 m above the ground. The higher platform was for exclusive use of the giraffes, while all the other animals were sharing the lower feeding cages (Figure 6.11c) and the bales at ground level.

The quantities of food supplied are presented in Figure 8.14 and the total kg of feed supplied per month in Figure 8.15. Initially, eight bales per day were supplied at the 0 – 1 m feeding height and two at the 2.5 m feeding height (Figure 8.14). Then it was reduced to 4 bales at 1.5 m and 1 bale at the 2.5 m level. Four 50 kg bags of game pellets at the 1.5 m feeding height and 1 bag at the 2.5 m height were reduced to 1½ bags and ½ bag, respectively. The giraffes were privileged to be given feed during the winter of 2007, when the drought of the previous season resulted in a shortage of lucerne hay that is clearly visible on Figure 8.14.

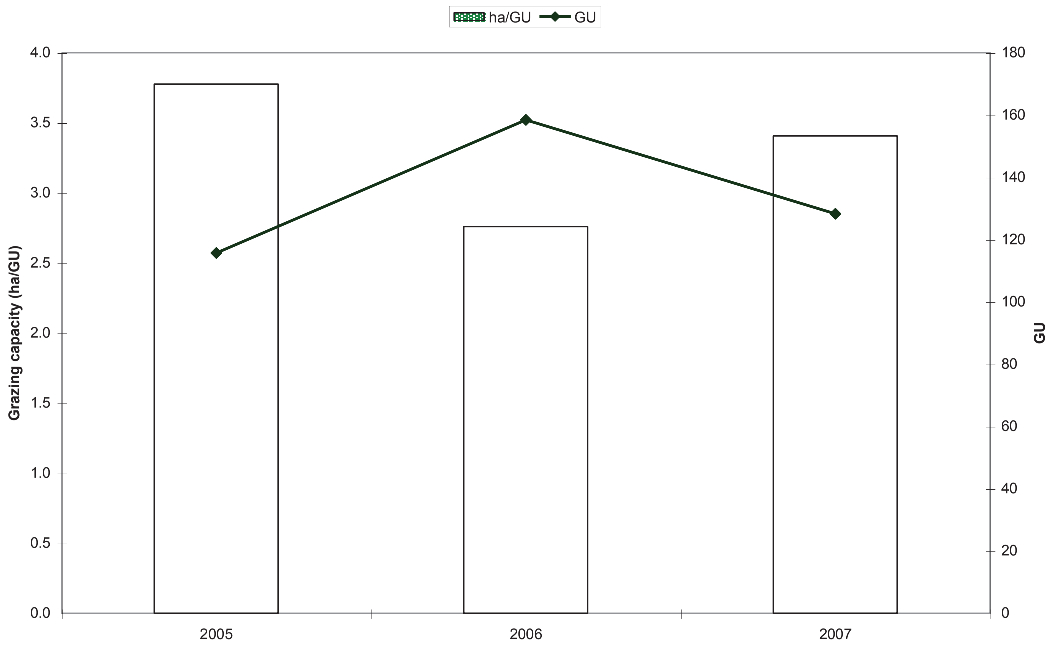

Fig 8.12 Grazing capacity and grazer units (GU) of each of the three years in the study area as a whole.

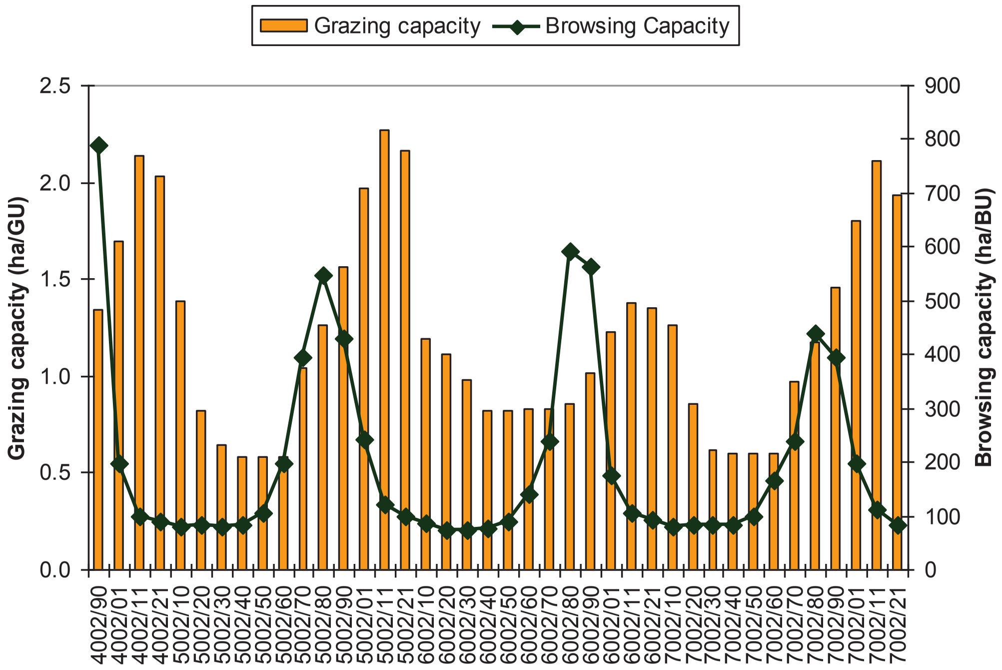

Fig 8.13 Browsing capacity (ha/BU) at the 0 – 2 m height stratum and estimates of the grazing capacity (grass production estimated by means of Putu-11 Simulation Model) over the study period in the study area as a whole.

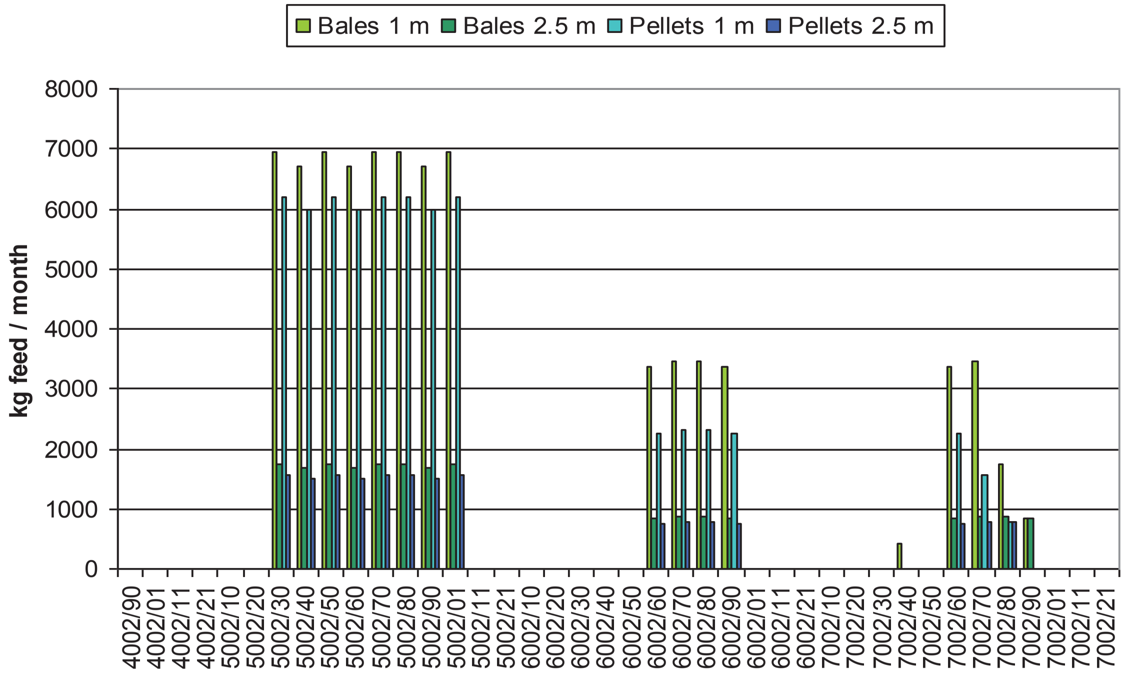

Fig 8.14 Quantities of feed supplied per month, in terms of lucerne bales and game pellets supplied at two different heights.

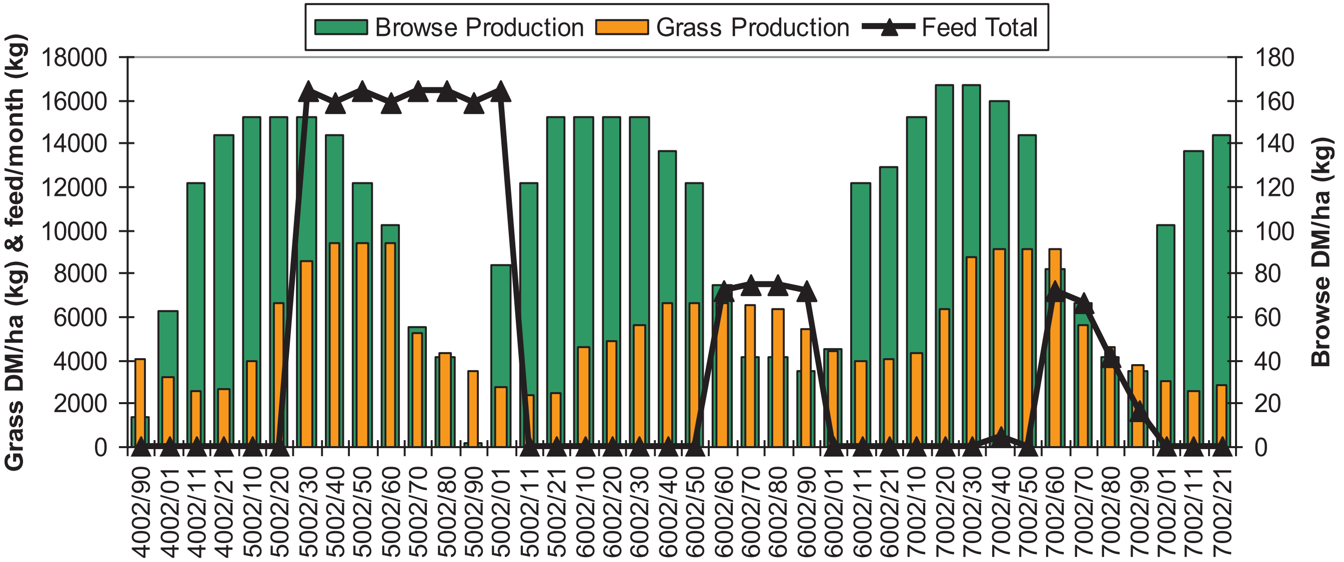

Fig 8.15 Estimated grass- and browse production totals (kg/ha), as well as total feed (kg) supplied per month.

8.5 DISCUSSION

8.5.1 Browse production and browsing capacity

At browsing heights of 0 – 2 m where most herbivores browse, with exception of giraffe that can reach up to 5 m heights, the drainage lines and dense thicket (Figure 4.1) produced the highest browse quantities (Figure 8.4, Table 8.3). The small open thicket and disturbed area contain more woody plants that carry leaves below 2 m height, compared to the other two open thickets. All the vegetation units have trees as tall as 5 m and higher, with the exception of open thickets. The disturbed area stands out in having trees as tall as 5 m and reasons for this might be that: i) due to the proximity of the waterhole in this area, permanent water seepage into the deeper soil layers can occur; ii) in order to escape intensive browsing pressure in this vegetation unit, trees grow taller; and iii) a possible reduction in competition for water from grasses may occur due to high grazing pressure, since all the browsing and grazing animals congregate at the waterhole. Table 8.6 indicates the lower grass species composition in the disturbed area.

Stuart-Hill and Tainton (1988), Dekker and Smit (1996), as well as Abule *et al.* (2007) reported that the available browse component of medium to large sized trees (>2 m tall) differed from that of smaller trees (0.8 – 1.2 m) in the Eastern Cape, Limpopo Province and Awash valley of Ethiopia, respectively. This was also observed in the study area (Table 8.3). Tall trees appeared to be less intensely defoliated than medium-sized trees in the Eastern Cape (Stuart-Hill and Tainton 1988) and this was also observed in the study area. The specific plant species and type of growth form play a very important role in browse production and differ between geographical regions. Consequently, it was not possible to compare the study area directly to the savanna areas. Published browse production data for the Free State Province proved very difficult to find, since very few studies on browse production were conducted in this province. It emphasizes the importance of this data.

The area of rangeland which surrounds a permanent watering point is called a piosphere (Lange 1969). Brits *et al.* (2002) concluded that overall tree and shrub density increased with distance from watering points in a large area like the Kruger National Park. The short distances between vegetation units and the small confined space occupied by the study area, resulted in no clear pattern of increase in woody plant densities in the piosphere with an increase in distance from the waterholes (Figure 8.3). Chapter 7 includes a detailed discussion on piospheres in the study area.

The criteria on which a specific year was classified as a wet or a dry year for browsing related calculations were based on a comparison of the monthly rainfall totals of the growing season, which is from December to March. Data presented in Figure 3.6 was used in the determination of a wet- and dry year and not the seasonal rainfall totals (Table 3.2). The biggest differences between wet and dry years in terms of the browsing capacity were observed from July to September (Figure 8.7). September is the month when deciduous woody species sprout new leaves after the winter (Figures 5.9 & 5.10). Abule *et al.* (2007) demonstrated similar differences in ranges between dry (17 – 25 ha/BU) and wet months (7 – 13 ha/BU) in diverse areas of Ethiopia. The seasonal pattern in browsing capacity in the current study area corresponded between the wet- and dry years and followed the inverse pattern of leaf phenology (Figures 8.7 & 5.11). A larger area (ha) is needed per browser unit (lower browsing capacity) when leaf carriage is low in July, August and September, and *vice versa*.

The number of browser units (BU) that can be sustained by the study area, as adjusted to the leaf carriage percentages per month in the wet and dry years, is presented in Figure 8.8. Barnes (1976) and Du Toit (1990a) stated that it is necessary to define the height to which a specific animal species can browse. In the 0 – 5 m and >5 m height strata (Table 8.5), most of the browse is out of reach of animals smaller than an adult giraffe bull. Therefore, if the study area is stocked with 16 – 20 BU (based on total browse production >5 m), there will not be sufficient browse available to sustain them. It is advised to stock less than 6.8 BU (the average 2 m height stratum maximum in Table 8.5) in order to compensate for drought periods when the vegetation can sustain less BU. In February 2005, for example the BU dropped to 6 (Table 8.5), while in February 2006, after flooding occurred, it increased to 7 BU. Stocking density and advised browser numbers are discussed in Chapter 9.

8.5.2 Grass production and grazing capacity

Grass production was highest in open areas between trees, or uncanopied areas (Table 8.7), notably that of the herbaceous species in Utilization Class III (UC-III). As can be expected, the surface areas of uncanopied habitats (± 84%) were much larger than canopied habitats (2 – 16%) in the riparian thicket vegetation of the study area. Shade-loving grass species that were present did not have large basal areas and were mostly grazed intensely. Bare patches were evident due to animal activity in shaded areas, especially in the canopied open thickets. Only in the canopied subhabitats of the disturbed area and the drainage line were the grass production of UC-III species less than 200 kg/ha (Table 8.7). Canopied drainage line subhabitats were mostly subjected to deep shade, partly due to the banks of the drainage lines. Consequently, more *Chenopodium album*, *Setaria verticillata* and *Melica decumbens*, that are adapted to deep shade, were abundant.

The grazing capacity range of all vegetation units, except the disturbed area, over the three year study period is 2 – 5 ha/GU (Figure 8.10). Danckwerts (1982) clearly stated that the grazing capacity of sweetveld in general was low. Relatively small variations in the grazing capacity between wet and drier years with differences of approximately 1 ha/GU were observed in all vegetation units (Figure 8.10), except in the disturbed area. Only during 2006 did the grazing capacity of the disturbed area improve to the 5 ha/GU level, being 15 and 12 ha/GU during 2005 and 2007, respectively. Compared to the other vegetation units, the disturbed area has a low species diversity (Table 8.6). The area is dominated by the creeper grass *Cynodon transvaalensis* with a low abundance of *C. dactylon*, *Eragrostis lehmanniana* and *Sporobolus fimbriatus*. This area is in close proximity to the waterhole and feeding area that are regularly visited by all game species, with the resulting high grazing pressure leading to the characteristic species composition.

The dense- and open thickets represent the larger vegetation units of the study area (Figure 4.1) and consequently contributed the most to the grazing capacity (Figure 8.11). On average the dense thicket can support 63 GU, the open thicket 39 GU, the grassland 16 GU, the drainage lines 12 GU and the disturbed area 4 GU. The entire study area can support an average between the three years of 134 GU (Figure 8.12) but if 2006 is ignored due to flooding conditions, the average is 122 GU. These grazer unit values will decrease in a dry year due to a lower grass production. Chapter 9 includes a discussion on stocking density and the proposed herbivore species mix for the study area.

Grass phenology depends on the rainfall pattern (Fourie *et al.* 1985, Skarpe and Bergström 1986). Skarpe and Bergström (1986) reported that the growing season of grasses in the Kalahari, Botswana usually extended from November to February when grasses were in a late stage of sprouting or just becoming fully developed and being in a stage of flowering in February. They also reported that the *in vitro* dry matter digestibility and nutrient content were correlated with grass phenology and increased after the spring flush in November, with the highest levels recorded in February and a sharp decrease following maturity and seed production in late March and April.

8.5.3 The need to supply feed

The browsing- and grazing capacity during different months of the study period have been estimated and presented in Figure 8.13. The seasonal leaf phenology pattern of the deciduous trees and semi-deciduous shrubs are clearly visible in the browsing capacity values. When trees are leafless, the hectares needed per browser unit will invariably increase. A rapid decline in browsing capacity is observed just before the woody plants start to bud in spring. Grazing capacity is rainfall dependent, but also follows a seasonal pattern, being lower during spring and early summer and increasing again during summer before it stabilises in winter. The low browsing- and grazing capacity during winter and early spring indicate the necessity to supply additional feed. Other factors that play a role in the necessity to supply feed is that the limited other food resources available in the critical period (*vid.* Chapter 6) are exposed to severe browsing (Figure 8.16) and pruning (Figures 8.17 & 5.17), while the small confined space of the private reserve prevents migration in search of other food resources. Quality of browse and grass resources also declines at the end of the growing season and as result herbivores will select other available food sources of lower quality when the quantity of their preferred foods declines.

Estimated browse and grass production (kg/ha) during the three years of study are presented in Figure 8.15, along with the total quantity of feed (kg) supplied per month. The months when feed should be supplied are clearly visible on the graph during times of low browse and grass availability. During 2005, too much feed was supplied over a too long time interval, while in 2007 lucerne became scarce due to drought conditions and less was given over a too short interval. It appears that during 2006 the correct quantity of feed was given over the correct time interval, based on the available grass and browse phytomass. The best time to supply feed would be from middle June/beginning of July to middle October after the spring rain, because good quality browse and grass become scarce during this period (Figure 8.15). A discussion on the quality of browse and feed during the critical period, when deciduous woody plants alone cannot support browsing animals, is given in Chapter 6.

The critical period, when woody plants cannot sustain browsers, is generally from July – September, but differs between years depending on the retention of dry leaves (Figure 5.11). The period of supplying feed is important, because starting too early leads to unnecessary financial losses and stopping too early may lead to animal losses, which also has financial implications. It is best to start feeding from June in order for animals to retain condition, but at a low ration and then increase feed towards the end of the critical period when very little browse is available. The trees should be observed to determine when to feed. Yellowing and brown leaves are still edible, while budding leaves are not always taken in great quantities due to its indigestibility (*vid.* Chapter 5). Dörgeloh *et al.* (1998) concluded that artificial feeding during winter is advantageous for the animals by increasing their nutritional status.

Figure 8.16 Evidence of severe browsing on different plant species, namely on a) *Chenopodium album* (exotic species) in spite of its strong foul smell, b) *Lycium hirsutum*, c) *Sphaeralcea bonariensis* (exotic species) and d) karroid shrubs.

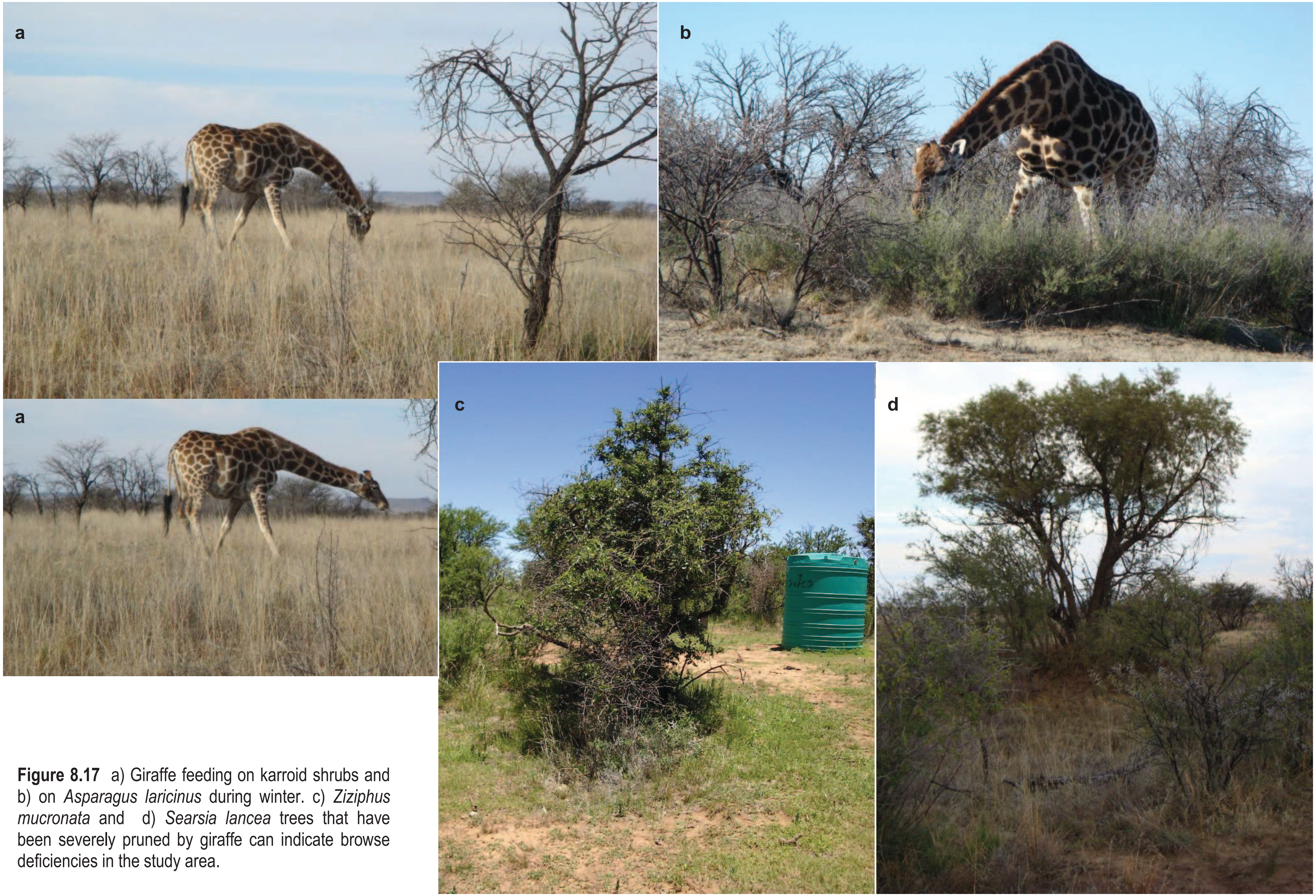

Figure 8.17 a) Giraffe feeding on karroid shrubs and b) on *Asparagus laricinus* during winter. c) *Ziziphus mucronata* and d) *Searsia lancea* trees that have been severely pruned by giraffe can indicate browse deficiencies in the study area.

The study area is small and, except for some shrubs that retain leaves for longer periods and a few *Searsia lancea* trees (Figure 8.17), only deciduous species are available to browse. Kudu and eland moved to the southern side of the private reserve during the late winter, probably due to too much competition for the limited browse resource in the study area (*vid.* Chapter 7). The dense drainage line in close proximity to the river represents a critical resource area in this particular environment that provides browse in times of shortages. In their natural environment, herbivores have normally little need for supplied feeding as their free ranging habits enable them to search for more nutritious food in critical resource areas, e.g. rivers and hills. Wild ungulates have increasingly been confined to small areas through game fences and this has necessitated some form of supplementary feeding (Roosendaal 2008). However, not all animals will have equal access to the supplied feed due to competition (between browsers and grazers) and differences in the dominance and status of individual animals within their herd structures.

8.6 CONCLUSIONS

Browsing capacity does not appear to change as much as expected between wet and dry years. Even flooding conditions in the study area resulted in an increase of only 1 – 3 BU between the three feeding height strata after woody plants sprouted excessive new shoots and leaves. Grazing capacity is, however, influenced more severely by rainfall totals. Numbers changed from 116 to 128 to 158 GU from dry to wet to extremely wet years. Veld degradation as a result of overgrazing or bush thickening will also play a role in the decrease of GU numbers that can be stocked between different years. Veld condition is not static and changes annually. It is thus essential to monitor it closely to prevent deterioration of the available grazing.

Browser units that can be sustained by the 0 – 2 m height stratum ranged from 0.96 – 6.75 BU between winter and summer, while at the 0 – 1.5 m stratum it ranged from 0.85 – 4.06 BU. The necessity to supply feed in the critical period, becomes evident when the true leaf carriage percentages of woody species are brought into calculation. From July to middle September, the deciduous trees are leafless and the semi-deciduous shrubs retain leaves until August/September. Consequently, the study area can support only 1 BU at the end of the critical period and therefore feed should be supplied to the other approximately 6 BU to make up the deficit. The time period and quantity of feed supplied should be determined from the presence of leaves on trees.

The drainage lines and dense thicket associated with them, contribute largely to the number of browser units that can be stocked in the study area. The higher density of trees in these areas, however, also results in a lower grazing capacity than in other environments where open grassland areas are dominant. The wetland in the big drainage line represents a critical resource area in the study area, where the highest density of semi-deciduous shrubs is present. Game ranches in the Free State that include koppies or rocky hills are characterized by the presence of other woody species that are mostly evergreen and not as palatable than the deciduous woody species associated with drainage lines, but these areas serve as critical resource areas in the dry season. These aspects should be kept in mind when carrying capacities of game ranches in other localities are determined.

CHAPTER 9

DETAILED MANAGEMENT PLAN FOR THE STUDY AREA, INCLUDING GENERAL GUIDELINES APPLICABLE TO ANY GAME RANCH IN THE PROVINCE

9.1 INTRODUCTION

The primary objective of any game ranch or conservation area should be to stimulate ecologically-sustainable economic activities based on wildlife. Du Toit (1995a) stated that: "wildlife conservation is an expensive business and the global experience has been that wildlife resources have to generate enough revenue for their own conservation or they will be lost." NAMC (2006) summarised the financial contribution of relevant subsectors in the wildlife sector, namely wildlife auctions, the hunting industry (recreational and trophy), taxidermy industry, meat/venison industry and the capturing/translocation industry, to be roughly R 4 696 million during 2005.

In order to ensure that a game ranch is economically and ecologically viable, there are certain aspects that have to be monitored and managed regularly in such a multi-species 'farming' system. These aspects include the management and monitoring of the vegetation and natural resources in such a way that it remains sustainable, the maintenance of infrastructure, managing animal numbers and species introduction so as not to exceed the carrying capacity necessary to maintain the type of activities presented by the game ranch, regulating hunting and live sales, supplying water and feed where necessary, complying to legal aspects, etc. To facilitate all of the above and more, a management plan for the specific activities, setup and needs of the game ranch needs to be compiled and strictly applied. With the correct management, enough income can be generated to ensure that the game ranch is successful and progressive.

The management suggestions and operational guidelines that are presented in this chapter have been tried and tested for a long time by ecologists in other areas concerned with wildlife and have been adapted to the central Free State conditions in this study. The objectives of this chapter are:

i) to provide a management plan specific to the study area; and
ii) to provide general suggestions and operational guidelines that could aid in sustainable game ranching and the prevention of resource degradation in other areas in the Free State province as well.

9.2 BACKGROUND AND HISTORY OF THE WnB PRIVATE NATURE RESERVE

Wag-'n-Bietjie Private Nature Reserve is located approximately 30 km north of Bloemfontein in the Brandfort district, Free State province. The Modder River forms the southern boundary. It falls in the summer rainfall region of South Africa with the highest rainfall occurring from December to

April. The geology (mostly alluvium and quaternary depositions), land type, topography and soil types (Figures 3.4 & 3.5) of the study area are discussed in Chapter 3.

The private reserve with a total size of 750 ha is divided into two parts by the gravel road to Soutpan (Figure 3.1) and a connecting tunnel underneath the road allows limited passage of game (Figure 3.2). This connecting tunnel is blocked periodically to keep newly introduced animals, especially the rare species, separate from other species in the opposite part of the private reserve until they are settled. The northern side of 437 ha was used as study area where riparian vegetation and grassland in a good condition (at the commencement of this study) occurred, while the smaller southern side housed less animal species and had more human disturbance (*vid.* Chapter 3).

Initially the private reserve was mainly used for grazing by Brahman cattle and only limited game ranching. During 1998 an ecological assessment of the northern part was executed to determine the potential for intensive game ranching and the area was restocked with game. A second ecological assessment was carried out in August 2000 in the southern part to include it as part of the functioning private reserve in the northern part (Schulze 2000). During 2004, when this current study commenced, the established Wag-‘n-Bietjie Private Nature Reserve was sold to the current owner. The new owner introduced more game species than what was previously present.

9.3 UTILIZATION AND CURRENT MANAGEMENT

A young manager, under the supervision of the owner who resides in the southern part, runs the Wag-‘n-Bietjie Private Nature Reserve (PNR). Only the large predators (lions, wild dogs and tigers) are fenced off in camps, otherwise there are no camps and game can move freely through the entire area available as PNR, with the exception of cultivated lands and the areas occupied by human settlements in the southern part. Feed, mostly lucerne, is cultivated in an area behind the homestead and baled to supply to the game in winter months.

At the time of the study, commercial game ranching in the form of small-scale meat-, biltong- and trophy hunting, as well as auctioning (live sales) of game species (including rare species and large predators) were the main forms of utilisation. The PNR is usually not open to the public for game-viewing and no public accommodation is available. Funding is supplied by the owner of the PNR who has an additional income, as well as from income of auctions and hunting.

9.4 INFRASTRUCTURE

Roads: There is an all-weather gravel road that runs almost through the centre of the study area and allows access to the waterholes and adjacent feeding areas. Other roads are hard soil roads that are also usually easily accessible and well maintained. Some of the roads in the more remote areas are twin-tracks that are not often used. Twin-track roads are also present along the border fences for fence patrol purposes. In general, poorly planned roads in the wrong areas may lead to erosion and habitat deterioration.

Fences: The PNR has an Adequate Fencing Certificate issued by the provincial Department of Economic development, Tourism and Environmental Affairs. The fences should thus be capable of containing the animals, but fences still need to be checked regularly and maintained to keep them in good condition. Game ranches with Adequate Fencing Certificates may qualify for a three-year exemption period that entitles the holder to hunt, capture and sell approved/specified species for 12 months of the year. Without such a certificate, legislation restricts the use and ownership of wildlife (NAMC 2006).

Buildings: The owner's house, barns/sheds and staff accommodation are situated in the southern side of the PNR. The 'farmyard' and approximately 8 predator camps with electrified fences are located in the vicinity of the farmstead. These will not be discussed in the management plan, because it falls outside the main study area.

Waste management: The establishment of a waste accumulation site normally needs an environmental impact assessment. Waste streams need to be determined, regarding their origins and flow. This is, however, more applicable to large game ranches that cater for public game viewing and accommodation (lodges).

9.5 NATURAL RESOURCES

Wildlife-based tourism, hunting, wildlife meat trade and game auctions are in general the prime forms of resource use on a game ranch. Other secondary uses may include wood harvesting, clay collection, thatch harvesting, harvesting of medicinal plants and fishing where possible. The local community can benefit greatly from such secondary uses of resources available on a game ranch. Fishing and clay collecting from the Modder River are unexplored resource uses in the PNR – the river is fenced off from the rest of the reserve which makes it more practical. Wood collection already takes place and tree thinning (discussed later in this chapter) can create a great opportunity to supply more wood for this purpose.

9.6 OPERATIONAL GUIDELINES FOR EFFECTIVE VELD MANAGEMENT

9.6.1 Monitoring of veld condition

Hardy *et al.* (1999) described different methods of veld condition assessment. Some of these are easy to apply and do not need a high level of scientific knowledge, except for the identifying of plant species. In the step point method, for example, a person can walk in a straight line for 200 m and note the plant species present at the shoe tip of every step (Van Rooyen 2010). Alternatively a 200 m rope that is marked every meter can be placed in the veld like a transect at different points in each vegetation unit. A metal rod can be used to determine which plants are hit where it touched the soil at meter intervals. The percentage of each species should then be calculated to determine plant species composition and percentage frequency. It is advised to use fixed transects for monitoring purposes. If the grassland deteriorates over time and a lower percentage of palatable species with high grazing values (listed in the appendix of Van Rooyen 2010) are available, the herbivore numbers should be reduced. Monitoring required to determine grazing and browsing capacities are discussed under the heading 'Carrying capacity' (9.8.2), as well as in Chapter 8.

Fixed-point photographs of certain areas can be taken annually at the same date and on the same position/spot. The GPS (Global Positioning System) position of specific spots can be stored and markers can be used to indicate the exact spot where photographs are taken. Comparing photographs of different years can help to determine if the grassland is deteriorating (more bare patches appear), or if encroachment of trees into the open thickets and grassland is occurring. If this is the case, steps must be taken to prevent further deterioration of the veld by initiating tree thinning, and/or by reducing grazer numbers, or luring grazers to other areas by means of licks or water points.

Fixed transects can be placed on the superficial border between open thickets and grassland, and on borders between open thickets and dense thickets, that mark the position of the trees at the point where the vegetation changes to open areas. Markers of transects can be in the form of short metal rods holding a weather resistant rope in position that is stretched on ground level in such a way that it can not cause any injuries to animals or humans travelling in the area. The position of the rods and rope should be marked with the aid of a GPS in order to locate it again. It can assist in determining whether the woody component increases into the grassland (discussed under 'Thinning of trees' (9.6.4). This may influence the veld condition and the stocking density of game, since habitat and available grass resources will change with higher densities of trees.

9.6.2 Soil erosion

Geological erosion is a natural process, but the human induced acceleration of soil loss due to unsustainable land use practices, like prolonged overgrazing and the injudicious use of fire, must be minimized. Other causes of soil erosion are highly erodable soils, steep slopes, high rainfall intensities, animal hoof action by means of trampling, etc. (Snyman 1999). Van Rooyen (2010) graphically illustrated the relationships between veld, soil and water, where proper veld management leads to the protection of the soil surface, stabilization of the topsoil, increased soil fertility, more nutritious grazing and ultimately a higher grazing capacity. Unfortunately the opposite leads to soil erosion, poorer grazing and lower production per animal.

The grassland in the study area was found to be in relatively good condition and showed little evidence of overgrazing when this study commenced in 2004. At the end of the study in 2009, however, degradation was already visible in the grassland and bare patches were increasing. Plant cover protects the soil surface from raindrop impact and from the consequent splash erosion and surface sealing (Snyman 1999). It further improves the rate of water infiltration into the soil, thereby reducing erosion wash. Grass plants protect the soil against sheet erosion that arises directly from raindrop impact. Wind erosion is also reduced by vegetation cover (Snyman 1999).

The grazing pressure on overutilized veld can be eased by planting pastures consisting of indigenous grasses of good quality (Van Rooyen 2010). Naturally occurring grass seed can be harvested elsewhere in the area. More seed can be included of preferred highly palatable grass species such as *Themeda triandra* (red grass) and *Digitaria eriantha* (finger grass). On large bare patches a tractor can be used to scarify the soil surface and seed can be sown in the ploughed soil. However, this method is usually not recommended in areas where soil disturbance can lead to bush thickening. Sandy soils should be cultivated when wet and clay soils when dry. It can be covered by grass cuttings so that the soil can maintain moisture to aid in seed germination (Snyman 1999). Different implement types and procedures of rehabilitation were discussed by Snyman (1999), depending on specific conditions of the area.

9.6.3 Burning of veld

Most authors advise against the burning of sweetveld, because with regular burning in late autumn or winter the density of the cover of these grasslands declines and susceptibility of the soil to erosion increases (Tainton and Mentis 1984, Everson 1999). Burning can, however, be considered for achieving specific objectives, like the removal of old, moribund grasses, to prevent encroachment of trees by killing saplings or to possibly reduce ticks (Everson 1999, Van Rooyen 2010). Burning may also be used after a series of wet seasons to reduce the density of invading pioneer dwarf karroid shrubs, but the veld then needs to be rested until late summer (Everson 1999). Burning certain patches can help to create habitats suited to specific game species or to induce game to graze otherwise non-preferred areas in order to rest heavily grazed areas (Janecke 2002, Van Rooyen 2010). Burning is necessary to ensure that enough young, green grass shoots are available for animals that need grass with high nutritional value, like bontebok and tsessebe, for example (Furstenburg 2006 b & c). Many game species are in general attracted to new growth on recently burned areas. It is of utmost importance that the negative effects of severe defoliation of this regrowth are minimised, because regrowth draws on the plant's store of reserves. The total area burned should be large enough to support the expected influx of herbivores without causing severe defoliation pressure (Grossman *et al.* 1999).

Certain regulations need to be adhered to when consideration is given to burning of a game ranch. The Fire Act (Act 101 of 1998 on veld and bush fires in South Africa) needs to be complied to that specifies it compulsory to be a member of an official fire protection committee and that official permission must be obtained before any burning is done on a game ranch (Van Rooyen 2010). There must be fire-breaks, fire-fighting equipment, water and trained manpower available and it should be a controlled fire. The fire can be kept under control using knapsack sprays, water carts ("bakkie sakkies"), rubber beaters, rakes and shovels (Cheney 2005). It is advised to consult a professional ecologist at first to help with the planning of a burning program and burning procedures.

The four main components of the fire regime are type and intensity of fire, season and frequency of burning (Trollope 1984). To obtain the type of fire needed (hot fire or cool fire), the wind speed and –direction, as well as fuel load available in the veld and humidity in the air need to be known (Trollope 1984, 1999, Cheney 2005, Van Rooyen 2010). Trollope (1999) and Van Rooyen (2010) described the pasture disc meter method to determine fuel load available in the veld and some equipment for safe ignition of the fire. Head-fires that burn with the wind should be used in controlled burning, because less damage to the grass layer is caused than with back-fires that burn against the wind and cause maximum damage to herbaceous vegetation. When the aim is to remove moribund grass material, cool, low intensity fires are recommended, while high intensity fires are required to control undesirable plants (Trollope 1984, Everson 1999, Cheney 2005, Van Rooyen 2010). The area must be inspected after a fire to put out burning logs and to move burning or smouldering dung well into the burned area to ensure that it cannot be blown into adjacent areas and ignite a fire there (Cheney 2005).

The time of year of burning is extremely important, with a good time mostly being after the first 10 mm of spring rain fell during September/October in the central Free State (H. van Niekerk, *pers. comm.*[1]). Grasslands burned in July will green up by October and protect the soil from the heavy summer rains. Burning in late October will mostly not allow grasslands enough time to recover until late November, meaning that the soils are exposed to the storms that typically occur in October and November (Everson 1999). There should be follow-up rain predicted by the Weather Service after burning and other climate conditions should also be checked. It is recommended to burn the sweetveld every five to seven years in different mosaic patches and not all at once, or annually (H. van Niekerk, *pers. comm.*[1]). Patch burning gives a mosaic of newly-burned, recently burned and unburnt areas (Grossman *et al.* 1999) that can allow patches of the veld enough time to rest between burns and will probably result in the local movement of herbivores between these patches.

9.6.4 Tree thinning

Riparian areas where *Acacia karroo* occurs are usually prone to the thickening of trees and shrubs. The presence of *Acacia karroo* next to the grassland unit of the study area may be the result of a spread from the drainage lines. If this is the case, care should be taken not to overgraze the grassland and transitional open thickets, because it may lead to increasing numbers of this tree species. A higher occurrence of *A. karroo* would in turn lead to denser thicket areas and may even reduce the size of the grassland unit by intruding into it. Some causes of bush thickening are the incorrect use of fire, prolonged overgrazing, climatic changes and human disturbances. A detailed discussion on this topic is presented in the literature review of Chapter 8. Methods to determine the extent of bush thickening into the grassland or open areas were discussed under the heading 'Monitoring of veld condition' (9.6.1).

Tree thinning will result in a drastic and immediate change in the competition regime, which mainly controls the growth and structure of the plant community. It is important to take into consideration that in *Acacia* species, establishment of seedlings are limited to between canopy environments, thus tree thinning might result in establishment of many new individuals that failed to establish previously under the tree canopies (Smit *et al.* 1999). It is important to decide beforehand how the veld should look after tree thinning, how many trees should remain and what size they should be. There is a difference between tree/bush thinning and bush clearing where all woody components are

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[1] Major Hugo van Niekerk, Regional Environmental Manager of the game ranches of South African National Defence Force, based at Army Support Base, Bloemfontein.

removed. If it can be managed by the workers on the game ranch, some money can be saved. Establish the height or width of trees in areas that need thinning. If, for example, most tree trunks are 10 – 20 cm thick, a caliper can be made of the desired cross-section (20 cm) to enable the workers to cut trees with a smaller diameter. In this way only the smaller, younger trees can be removed. Alternatively, certain trees can be marked and then felled by the workers. Fire wood can be made of the felled trees and sold for extra income. Stumps of trees that have been sawn off should be treated with arboricide chemicals to prevent regrowth.

Other control methods include the strictly controlled use of appropriate soil applied arboricides (poisons) early in the growing season that can for example be applied as water soluble liquid or powder or granules around the base of tree trunks. This method is expensive, slow to act (may take up to 2 years to kill trees), dependent on the clay content of the soil and generally not advised due to their non-selective nature and negative impact on the environment. Most of these products remain active in the soil for up to four years. Herbicides, that have immediate results, can rather be applied on specific plants but are labour intensive (Smit *et al.* 1999, Van Rooyen 2010).

Tractors with brush cutters, as well as other mechanical means are also available to do the thinning, but should preferably not disturb the soil. The stumps should be treated immediately with a chemical after mechanical treatment (Van Rooyen 2010). Another option is that thinning can be contracted out to companies that specialize in bush thinning. Small-scale entrepreneurs using labour intensive methods for bush thinning are encouraged in order for local communities to benefit from wildlife activities in support of conservation in general.

Tree thinning is not a once-off operation as establishment of woody plants is a continuing process. Stocking densities need to be adapted to ensure enough rest for the grass layer to establish after tree thinning. Factors that usually lead to the spread and thickening of trees and bush in the first place, like overgrazing and patch-selective overutilization, should be managed to delay a rapid spread. Follow-up spot applications of chemicals will often be necessary (Smit *et al.* 1999).

9.7 OPERATIONAL GUIDELINES FOR EFFECTIVE ANIMAL MANAGEMENT

9.7.1 General aspects in managing animal species

In addition to aspects such as stocking densities, game species selection, food and habitat preferences there are other essential aspects that need to be considered, such as the following.

- **Exotic species:** These species often reproduce quickly and outcompete indigenous species for habitat and food. They often cause more damage to the veld than indigenous species. It is strongly advised not to introduce any exotic species on game ranches.
- **Cross-breeding:** Hybridization and contamination of the gene pool of species are becoming serious concerns. Du Toit *et al.* (2010) listed the following hybrids between wild herbivores:

  Fertile hybrids: Bontebok and Blesbok
  Blue- and Black Wildebeest
  Red Lechwe and Waterbuck
  Black-faced- and Common Impala
  Infertile hybrids: Tsessebe and Blesbok
  Red Hartebeest and Blesbok
  Roan and Sable antelopes
  Eland and Kudu
  Possible hybrids: African savanna buffalo and Indian water buffalo
  Burchell's and Cape Mountain Zebra

  Introduced exotic species in the Free State, like the Arabian- and Scimitar-horned Oryx can cross-breed with the indigenous gemsbok, while the Red-, Sambar- and Sika deers can hybridize with each other (*vid.* Chapter 2).
- **Inbreeding:** When all the animals on a fenced property are from the same local genetic pool, it is advisable to obtain breeding males from another genetic source from time to time. This will prevent development of localized genetic species/subspecies. Owners of neighbouring ranches can exchange healthy breeding animals to prevent inbreeding in their own herds. It is also strongly recommended that game ranchers form breeding clubs in order to conserve pure genetic lines (Du Toit *et al.* 2010). Le Roux (2010) stated that the principle of 'survival of the fittest' is being circumvented by inbreeding (for horn length, body mass, colour mutations, etc.), the supply of feed and the medicinal treatment against parasites. These aspects are normally responsible for the strongest and best genetic material being selected for transmission to the next generation, while weaker, ill animals (irrespective of horn length or colour) are not breeding. Important aspects, such as selecting breeding stock

for higher parasite resistance, usually do not have a high priority and become secondary to economic considerations in animal breeding (Le Roux 2010).

- **Rare species vs common species:** Rare species, like roan, sable and tsessebe, should be able to increase at their maximum biological potential. These species are habitat specific, mostly prefer areas of medium to tall grasses and are very sensitive to competition from other species. The more common species are often selective short grass grazers and have the ability to alter habitats to such an extent that they are unsuitable to these rare species. In addition these short grass grazers are often high density species that increase their potential to compete negatively with rare species. This necessitates that the numbers of these high impact common species be regularly monitored and controlled to reduce competition for habitat and food.
- **Bones and carcasses:** Leave some bones of disease-free dead animals in the veld for osteophagial behaviour where animals chew on bones to reduce their nutritional deficiencies. It is not advisable to poison problem causing animals such as jackal by means of poisoned meat and bones. It will affect other non-target species, like giraffe (known for osteophagial behaviour), fish eagles, vultures and carrion feeders.
- **Ticks and diseases:** Ticks carry large numbers of diseases that can spread from the neighbouring farms' cattle to the game species, especially buffalo, or *vice versa*. Ticks can further reduce the physical condition of animals and their resistance to diseases. The Duncan applicator has been used successfully with game. The animals are lured to the apparatus by a lick and while eating on the lick, the neck, head and ears come into contact with a pole down which a pour-on dip runs. This contact is sufficient to kill many of the ticks on the animal (Boomker and Horak 2010). Another method (Tick-Off Applicator) involving a buried pressure plate that weighs the animal and a spray mechanism delivering the correct dosage after forcing the animal through a narrow passage to reach a waterhole, is described by Boomker and Horak (2010) and illustrated as an advertisement in Furstenburg's article (2006a). Le Roux (2010) described various defense mechanisms against parasites of animals in natural conditions, without any medicinal treatments needed. He further stated that the strongest animals have a natural resistance to parasites due to natural selection.

9.7.2 Hunting

The decision needs to be made as to what kind of hunting practices will be allowed on the game ranch and what kind of hunters, e.g. professional hunters, local and/or foreign hunters. For example, European hunters prefer game in a natural environment, American hunters prefer the presence of game in large open veld with no obstruction, and so forth (H. van Niekerk, *pers. comm.*[1]) also, the reason for the hunt is important to determine stocking density. For trophy hunting, the population should consist of more male animals that are charged per head and for biltong more female and young animals are needed. For the meat or venison market the price is calculated per kilogram and a normal male:female ratio (like for livestock) should be maintained, but more animals need to be stocked for rapid population growth to meet the demand. For bird hunting a large population of game birds should be present with ostriches that can also be included as hunting birds. Viljoen (2010) gives a short description of the counting techniques used to establish harvesting game bird quotas, major hunting methods, the use of hunting dogs and equipment necessary for game bird hunting. There is a vast market for game bird hunting in South Africa that can provide an important additional income with relatively little expenditure and effort (Viljoen 2010).

Most casual local hunters that hunt for venison wish to pay per animal or item, instead of for a package hunt (Van Rooyen and Du Toit 2010). A shooting range is required by most hunters to set up their rifles on arrival. Many hunters prefer an overnight camp with the minimum facilities, since they want to experience a wilderness atmosphere. Minimum facilities may consist of water, shade trees, trackers, skinners and the use of a four-wheel-drive vehicle. Hunters normally pay a daily hunting fee and a limit of four hunters is usually allowed per group. It is advantageous for the game rancher to get to know a small group of reliable hunters who will return to hunt year after year (Van Rooyen and Du Toit 2010).

Bow-hunting is allowed in the study area and mostly occurs from two permanent wooden hides located at the waterholes. Rifle hunting also takes place. No specific portion or area is permanently used for hunting due to the small size of the PNR, but are conducted under controlled conditions. Hunting should not have a negative impact on population growth rates. Ensure that the strong, dominant males are not targeted because of their solitary nature. It is essential that the social structure of animals are known (summarized in Table 7.2 for the study area) and taken into account when deciding which individuals are to be removed by hunting, including trophy hunting.

9.7.3 Waterholes

It is important to take the topography, geology, vegetation, soil type, as well as the habitat preferences and drinking habits of different types of wildlife into consideration when planning the cite of an artificial waterhole on a game ranch (Van Rooyen 2010). There are two waterholes in the form of earth dams present in the study area. The one is permanent, but the other dries up occasionally (*vid.* Chapter 3). The permanent waterhole is located in a disturbed area that are distinguished from the surrounding vegetation by a carpet of the creeper grass *Cynodon transvaalensis* underneath the dominant *Acacia karroo* trees (*vid.* Chapter 4), as well as by the presence of old ruins and a row of *Pinus* and *Eucalyptus* tree species. This waterhole is accessible to all animals and is less than 2 km distance away from any point in the study area (Figure 7.21).

All the game species present in the study area, except the common duiker, will drink if water is available (Table 7.1). According to Grossman *et al.* (1999) and Furstenburg (2006a), water independent species that can go without water for long periods include gemsbok, eland, steenbok, common duiker and klipspringer. Grossman *et al.* (1999) reported that the non-mobile water dependent species that require water regularly will usually not venture beyond 5 – 6 km from water and include impala, bushbuck and warthog. Mobile water dependent species can occur at a distance of 10 km or more from water and include zebra, wildebeest, white rhino, sable, roan and red hartebeest (Figure 7.22). The monitoring of water quality is very important to ensure the health of animals. The different water requirements of game species, their drinking patterns and drinking behaviour are discussed by Du Toit (2010b) and Du Toit and Ebedes (2010).

Piospheres that result from trampling and heavy use of veld around waterholes, along with a diminishing grazing intensity with increasing distance from the waterhole, are common on game ranches (Grossman *et al.* 1999). The piosphere effect is discussed in detail in the General Discussion of Chapter 7. It may be considered to create a non-permanent watering point in the western part of the study area to temporarily replace one of the waterholes. This will reduce the impact that animals have on the current piospheres, aid in better dispersion of animals to areas that are not so often used and also give the current surrounding veld a chance to rest.

9.7.4 Supplied- and supplementary feed

The main problem in low rainfall regions like the Free State is lack of sufficient forage and inadequate energy intake during late winter and spring. Feed should only be supplied when the vegetation cannot sustain the animals through the critical period in the dry season, if animal numbers are not reduced to make the area sustainable. In this thesis, supplied feed (“voer”) refers to lucern bales and game pellets that are provided due to a lack of food in the critical period, while supplementary feed (“byvoeding”) refers to licks and other supplements to the animal’s diet that can be provided any time of the year. Supplementation becomes necessary when nutritional deficiencies affect the productivity and health of herbivores. Dry season supplementation involves energy supplements, protein supplements and provision of mineral licks (Schmidt and Snyman 2010).

The main sources of energy supplements are maize, grain sorghum, barley, wheat and oats, as well as byproducts of these grains such as maize bran, maize germ meal, maize gluten and wheat bran. Molasses is high in energy, a good source of calcium, magnesium, potassium and sulphur, but is low in crude protein. It is a good binding agent and highly palatable (Meissner 1999, Schmidt and Snyman 2010). Lucerne hay can be used as a plant-based source of protein, while other sources include industrial by-products such as fishmeal, carcass meal, bloodmeal and brewer's grain (Meissner 1999, Schmidt and Snyman 2010). It must be realized that wild herbivores, especially grazers, cannot consume fresh lucerne due to its high content of prussic or hydrocyanic acid ("blousuur"). When the lucerne is dried, the acid contents are reduced and animals can no longer incur prussic acid poisoning from it (H. van Niekerk, *pers. comm.*[1]). Urea, sometimes included in cattle feed, is toxic to ruminants when consumed in excess (Schmidt and Snyman 2010).

Salt licks are the most widely used form of mineral supplementation in summer and winter. Salt is an essential nutrient for all herbivores. It is useful in supplementing protein and trace elements like selenium, manganese and possibly phosphorous. The best known nutritional deficiency in the Free State that occurs during the summer growing season is phosphorous. Bulk grazers have a high need for phosphorous supplements, but concentrate feeders seldom have a need for phosphorous supplementation (Schmidt and Snyman 2010). Salt licks should be provided in early winter to avoid overconsumption due to animals developing a hunger for salt. Salt licks can also be used to encourage rotational grazing by placing them in areas that are not readily grazed. These licks should not be placed in areas with soils that are susceptible to erosion (Van Rooyen 2010).

It was a management decision to supply feed to game species during the dry season in the study area instead of reducing animal numbers or species. It was done in order to help animals maintain body condition due to a decline in quality and quantity of browse (deciduous woody plants) and grass (sweetveld, *vid.* 'Vegetation overview' in Chapter 4) during this period. Feed consisted of lucerne hay, lucerne game pellets, game licks and salt licks. The best time to supply feed in the study area would be from middle June/beginning of July to middle October after the spring rain (*vid.* Chapter 8). It is advised to test game supplement products carefully in controlled experiments before investing heavily in them. Schmidt and Snyman (2010) gave contact details of companies that supply commercially produced licks and supplements for wild herbivores. Determination of faecal nitrogen can be useful to evaluate when animals need supplementation (*vid.* Chapter 6).

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[1] Major Hugo van Niekerk, Regional Environmental Manager of the game ranches of South African National Defence Force, based at Army Support Base, Bloemfontein.

9.8 SPECIES MIX AND STOCKING CONSIDERATIONS

9.8.1 Available resources and space

There are certain factors that need to be taken into consideration when the species mix of a game ranch is determined. These are dealt with in detail in Chapter 7, namely the animal's habitat and food preferences, normal social structure, space requirements and consequent competition with other species. The food resources available will determine for the largest part the types of game species that can be stocked. If there are abundant trees and shrubs present, browser- and mixed feeder game species might be considered. It is extremely important to determine if such woody plants are palatable and known to be able to maintain the introduced animal's nutritional status. It is also essential to determine if there are only deciduous plants available or if semi-deciduous and evergreen plants are also present that can act as a food resource during the winter months. Grazers feed at specific grazing heights, such as short, medium or tall grass grazers.

Joubert (2010) stated that: "There are primarily three social systems that regulate the relationship among individuals of the same type, namely: i) a loose grouping of individuals without clearly defined associations (eland, buffalo, giraffe); ii) a dominance hierarchy according to which the individuals in the same herd act according to a set order of rank, often with separate hierarchies for the males and females; iii) a territorial system according to which fixed parts of the range are marked and defended against intrusion by other individuals of the same type." Territorial animals of which the breeding herd's home range falls in the herd bull's territory, normally occur at low densities and need plenty of space, like roan, sable and tsessebe. The young males should be removed if the herd is kept in a small, limited area, otherwise the continued presence of young males will lead to violent conflicts, injury or death. A few solitary bulls can be kept in a separate camp to periodically replace the herd bull (Joubert 2010). Space is also a prerequisite for animals that have a loose herd structure, since they mostly have large home ranges (Table 9.1).

In general, the animal's social unit size is directly related to habitat structure. Animals are usually found alone, in pairs or small family groups in dense vegetation as a result of tall grass or the presence of dense shrubs and trees. The social unit size decreases as the habitat becomes less dense. Animals that are present in the largest herds usually prefer large open, grassy plains (Joubert 2010). In the study area, herd sizes are controlled through management. Numbers of animals that are known to form large herds are kept at approximately 20 individuals, except the springbok (±50) and impala (±40).

Table 9.1 Population size and -growth, regeneration characteristics, spatial occupation, carrying capacity equivalents and dietary intake, as well as impact, density and auction prices of game species present in the study area. Information from Furstenburg (2006a), except rows or columns indicated by a number: [1]Smit (2006), [2]Smit (2002), [3]Eloff (2006), [4]Cloete and Taljaard (2010), [5]Anonymous (2010), [6]Furstenburg (2006b), [7]Furstenburg (2005a), [8]Furstenburg (2005b).

		Blue Wildebeest	Bontebok[6]	Buffalo (African/Cape)	Burchell's (plains) Zebra	Common Duiker	Eland	Gemsbok	Giraffe
Minimum numbers for establishing new populations	M	2	3	2	1	1	1	3	1
	F	3	5	3	3	2	2	2	1
Minimum viable population size	M	3		3	3	2	3	3	2
	F	8		8	5	4	7	7	3
Expected annual population growth (%)	Min	28	3	6	21	35	11	15	7
	Max	35	52	18	35	60	38	35	16
	Aver	30	25	16	27	45	20	25	12
Expected longevity (years)	M	16	9-10	24	22	12	18	20	25-28
	F	18	9-10	20	22	12	18	18	22-25
Age of sexual maturity (months)	M	36	20	30-36	36	12	18	18-24	36-42
	F	18-27	27	36-42	16-20	8-9	18	20-24	42-48
First mating (months)	M	54-66	48-60	84-96	60	14-16	60	60-84	96
	F	30	36	48	24-30	9-12	27	24-30	48-60
Gestation period (months)		8.5	8	11	12.5	6.5	9	9	15
Interval between lambing/calving (months)		10-18	10-14	20-26	16	8	10-12	9-10	18-20
Lambing/calving season		Nov-Jan,May	Sep-Dec	March-May	Whole year	Whole year	Whole year	Whole year	Whole year
Age at weaning (months)		8	4-5	5-7	9-14	3-4	4-5	3.5	8-10
Territorium (ha)	M	0.5-1.5	4-30	None	None	1.9-3.8	None	420-980	None
	F	None	None	None	None	1.3-3.2	None	None	None
Home range (ha)	M	600-1800	?	100-400	10 000-26 000	1.9-18	unlimited	unlimited	3 000-16 000
	F	1 000-2 500	350-600	5 000-40 000	10 000-26 000	1.5-20	unlimited	unlimited	2 000-7 000
Animal unit (AU) [1]		0.5	0.2	2	1.0	0	0.4	0.7	0
Grazer unit (GU) [1]		1.0	0.4	3.8	1.9	0	0.7	1.3	0
Browser unit (BU) [1]		0	0	0	0	0.2	2.2	0	5.2
% Grass in diet		95	97	78	93	12	50	75	1
% Browse in diet		5	3	22	7	88	50	25	99
Impact on the veld		High	High	Moderate	Low	Low	Moderate	High	High
Density (from winter to summer) [2]		High	Interm-High	High	Interm-High	Low	Interm-High	Intermediate	Low-Interm
Average game auction price 2004 [3]		R 1 631	R 9 300	R 148 867	R 4 590	R 2 191	R 4 390	R 3 519	R 13 993
Average game auction price 2009 [4]		R 2 439	R 5 500	R 246 878	R 5 248	R 1 183	R 6 879	R 4 762	R 13 647
Average game auction price 2010 [5]		R 1 738	--	R 139 600	R 4 518	R 800	R 3 960	R 3 942	--

Game auction prices for 2004 and 2009 are averages of 47 and 45 national auctions, respectively. Averages for 2010 will only be available in 2011and thus prices of one auction in the Free State is indicated.

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Table 9.1 continued

		Impala	Kudu	Red Hartebeest	Red Lechwe[7]	Roan Antelope	Southern Reedbuck	Springbok	Steenbok	Tsessebe	Waterbuck	Ostrich[8]
Minimum numbers for new populations	M	2	1	2	1	2	1	2	2	3	3	1
	F	3	2	3	3	3	2	3	2	2	2	2
Min. viable population	M	5	3	3	1	3	2	5	3	3	3	1
	F	12	9	5	8	7	4	12	3	5	5	4
Population growth (%)	Min	23	13	20	20	7	18	28	21	12	15	8
	Max	48	28	32	28	25	25	42	32	25	35	75
	Aver	35	19	23	18	22	12	33	27	17	28	23
Longevity (years)	M	10-12	12-16	15	10-12	15-19	9	8-10	9	15	18	15-20
	F	10-12	7-9	11	9-10	12-15	9	8-10	6-8	12	16	15-20
Sexual maturity (months)	M	16	21-24	30	30	30-36	?	11-12	9	40-42	14	36-48
	F	13	15-19	18	18	20-24	10-14	6-12	6-7	22	13	24-36
First mating (months)	M	36	60	36-42	36-48	60-72	48	30	13-18	54	60-72	48
	F	18	36	28	24	24-28	18	10-12	7-9	26-30	30	36
Gestation (months)		6.5	8.5	8	7.6	9.2	7.5	5.5	5.6	8	8.5	42 days*
Lamb interval (months)		12-16	10-15	11-12	10-14	10-11	9	8-14	8-10	12	14-16	6 **
Lamb season		Oct-Dec	Dec-May	Feb-Apr	Area specific	Whole year	Whole year	Jul-Jan	Sep-Dec	Sep-Dec	Whole year	Jun-Jan***
Weaning (months)		3	4.5 - 5.5	6-7	5	5-6	3	3	3-4	4	7	7 ****
Territorium (ha)	M	4-10	None	10-30	2-14	non-static	35-60	2-6	5-15	150-400	40-150	1 500
	F	None	None	None	None	None	35-60	None	5-15	200-400	None	None
Home range (ha)	M	200-400	90-600	2 000-8 000	Unknown	1 500	50-100	100	12-30	200-400	150-750	1 500
	F	250-700	90-600	2 000-12 000	Unknown	1 500	50-135	300-800	12-30	200-400	250-750	Unknown
Animal unit (AU) [1]		0.1	0	0.4	---	0.8	0.2	0.09	0.03	0.4	0.7	---
Grazer unit (GU) [1]		0.2	0	0.7	0.5	1.5	0.4	0.2	0.05	0.7	1.3	0.49
Browser unit (BU) [1]		0.1	1.0	0	0	0	0	0.1	0.07	0	0	0
% grass in diet		45	12	80	95	85	95	32	34	95	84	85
% browse in diet		55	88	20	5	15	5	68	66	5	16	15
Impact on the veld		Very high	Low	Low	Low	Low	Low	High	Low	Low	Low	High
Density [2]		Interm-High	Intermediate	Interm-High	Interm-High	Intermediate	Low	Interm-High	Low	Intermediate	Intermediate	Low-Interm
Auction price 2004 [3]		R 638	R 2 032	R 3 336	R 14 009	R 149 521	R 4 419	R 523	R 1 305	R 19 123	R 4 989	R 1 193
Auction price 2009 [4]		R 1 099	R 4 894	R 4 409	R 10 175	R 62 993	R 4 218	R 866	R1 761	R 11 280	R 6 006	R 1 285
Auction price 2010 [5]		R 1 250	R 3 020	R 3 044	--	--	R 4 300	R 754	--	R 12 270	R 4 130	R 598

*Incubation period ** Interval between chicks (months) ***Breeding season ****Chicks independent (months)

Table 9.2 Numbers of animals stocked in the study area were converted to grazer and browser units (GU & BU) based on substitution values listed by Smit (2006). Advised minimum viable population numbers of these species were also converted to GU and BU. The study area can support an average of 122 GU and 4 - 6.7 BU at the 0 - 1.5 m and 0 - 2 m height strata, respectively. The 0 - 5 m stratum, where giraffe feed, can support 16 BU. Species grouped under mixed feeders usually include a high percentage of karroid shrubs, or tree and shrub leaves along with herbaceous material in their diet.

	No. animals stocked	Grass in diet (%)	No. animals x % grass in diet	Browse in diet (%)	No. animals x % browse in diet	Grazer unit (GU)	Browser unit (BU)	No. animals x % grass x GU	No. animals x % browse x BU
GRAZERS									
Bulk grazers									
Buffalo	20	100	20	0	0	3.80	0.00	76.00	0.00
Burchell's zebra	10	100	10	0	0	2.00	0.00	20.00	0.00
	30		**30**	**0**	**0**			**96.00**	**0.00**
Selective grazers									
Bontebok	25	100	25	0	0	0.40	0.00	10.00	0.00
Blue wildebeest	20	100	20	0	0	1.00	0.00	20.00	0.00
Gemsbok	20	100	20	0	0	1.30	0.00	26.00	0.00
Lechwe	20	100	20	0	0	0.50	0.00	10.00	0.00
Red hartebeest	10	100	10	0	0	0.70	0.00	7.00	0.00
Roan antelope	6	100	6	0	0	1.50	0.00	9.00	0.00
Southern reedbuck	6	100	6	0	0	0.40	0.00	2.40	0.00
Waterbuck	20	100	20	0	0	1.30	0.00	26.00	0.00
Tsessebe	2	100	2	0	0	0.70	0.00	1.40	0.00
	129		**129**	**0**	**0**			**111.80**	**0.00**
MIXED FEEDERS									
Eland	20	30	6	70	14	0.70	2.20	4.20	30.80
Impala	40	70	28	30	12	0.20	0.10	5.60	1.20
Ostrich	20	100	20	0	0	0.49	0.00	9.80	0.00
Springbok	50	70	35	30	15	0.20	0.10	7.00	1.50
Steenbok*	5	50	3	50	3	0.05	0.07	0.13	0.18
	135		**92**	**180**	**44**			**26.73**	**33.68**
BROWSERS									
Giraffe*	6	0	0	100	6	0.00	5.20	0.00	31.20
Kudu	15	0	0	100	15	0.00	1.00	0.00	15.00
Common grey duiker*	10	0	0	100	10	0.00	0.20	0.00	2.00
	31		**0**	**200**	**21**			**0**	**46.2**
TOTAL	**325**		**251**	**380**	**65**	**0**	**0**	**235**	**80**

* Not included in the calculations of GU or BU, because of a too small contribution or in the case of the giraffe another feeding height used

Continued on next page…

Table 9.2 Continued

	Total units stocked (BU+GU)	Advised minimum viable number	Advised min. no. x % grass in diet	Advised min. no. x % browse in diet	Advised min. no. x % grass x GU	Advised min. no. x % browse x BU	Minimum no. stocking totals
GRAZERS					**Total GU**	**Total BU**	**Sum total**
Bulk grazers							
Buffalo		15	15	0	57.00	0.00	
Burchell's zebra		5	5	0	10.00	0.00	
	96.00	**20**	**20**	**0**	**67.00**	**0.00**	**67.00**
Selective grazers							
Bontebok		10	10	0	4.00	0.00	
Blue wildebeest		0	0	0	0.00	0.00	
Gemsbok		12	12	0	15.60	0.00	
Lechwe		15	15	0	7.50	0.00	
Red hartebeest		0	0	0	0.00	0.00	
Roan antelope		10	10	0	15.00	0.00	
Common reedbuck		6	6	0	2.40	0.00	
Waterbuck		0	0	0	0.00	0.00	
Tsessebe		0	0	0	0.00	0.00	
	111.80	**53**	**53**	**0**	**44.50**	**0.00**	**44.50**
MIXED FEEDERS							
Eland		10	3	7	2.10	15.40	
Impala		15	11	5	2.10	0.45	
Ostrich		6	6	0	2.94	0.00	
Springbok		25	18	8	3.50	0.75	
Steenbok*							
	60.40	**56**	**37**	**19**	**10.64**	**16.60**	**27.24**
BROWSERS							
Giraffe*		4	0	4	0.00	20.80	
Kudu		8	0	8	0.00	8.00	**8.00**
Grey duiker*							
	46.20	**12**	**0**	**12**	**0.00**		
TOTAL		**141**	**110**	**31**	**122**	**25**	**147**

9.8.2 Carrying capacity

It is very important to determine the correct browsing- and grazing capacity (*vid.* Chapter 8), since the unscientific stocking of game ranches often has serious consequences in the form of animal losses and/or environmental degradation. Knowledge of habitat, food and water preferences, as well as other ecological requirements of herbivorous animals, like their social structure and space needed, distribution, abundance, hybridization possibilities with other species, the density at which they can be stocked and what species can be re-introduced, is basic to any management programme (Trollope 1990, Dekker *et al.* 1996, Van Rooyen 2010). Large herbivores are not evenly distributed while foraging, but rather favour certain habitat types over others (*vid.* Chapter 7). Failure to consider the spatial components of herbivory in calculations of carrying capacity can contribute to overgrazing, failed ecosystem persistence and declines of wildlife populations (Coughenour 1991).

Joubert (2010) stated that: "Every animal species has its own characteristic density under optimal habitat conditions. In sub-optimal conditions, the social structure of animal populations may be affected to such an extent that it can lead to a decline in numbers or even cause extinction". The upper limit of all game species should be adjusted regularly depending on changes in the environment and increasing ecological knowledge (Joubert 2010). The weather pattern follows a cycle of approximately 7 – 10 years from peak to peak. A wet cycle is usually followed by a dry cycle. The stocking density should be kept lower than the maximum carrying capacity so that veld can be spared for dry cycles and loss of animals does not occur (H. van Niekerk, *pers. comm.*[1]).

Annual surveys of the veld condition at the end of the rainy season are needed to adjust animal numbers to the seasonal variation in available grazing (Van Rooyen 2010). Grazing capacity is influenced by rainfall totals. Numbers in the study area changed from 116 to 128 to 158 grazer units (GU) from dry to wet to extremely wet (flooding conditions) years. The average between the wet and dry years, excluding the flooding conditions, was taken as the grazing capacity of the study area, namely 122 GU (3.6 ha/GU). Overgrazing will play a role in the decrease of GU numbers that can be stocked between different years, depending on the veld condition.

Numbers of grazing- and browsing animals should be strictly regulated in the dry season to keep within seasonal variation in food resources. It is further important to determine leaf carriage- and other phenological patterns of each palatable woody species in different vegetation types (*vid.* Chapter 5), especially for deciduous species. This will help to determine browse availability and

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[1] Major Hugo van Niekerk, Regional Environmental Manager of the game ranches of South African National Defence Force, based at Army Support Base, Bloemfontein.

also when the critical period, when browse becomes too scarce to sustain browsing animals, occurs each year for a specific vegetation type.

It is not advisable in the Free State to use the total dry leaf mass (LMAS) available on the ranch as calculated with the BECVOL-program (Smit 1989a) to determine browsing capacity, since it indicates the leaf production of the total browse available from ground level to higher than 5 m. Only elephant can reach >5m and giraffe bulls can reach up to 5 m. For the other browsing species the dry leaf mass total of up to 2 m (LM-20) and up to 1.5 m (LM-15) should be used to determine the browsing capacity of the ranch (*vid.* Chapter 8). The maximum browsing capacity of the study area is 4 BU (146 ha/BU) at the 0 – 1.5 m height stratum and 7 BU (71 ha/BU) at the 0 – 2 m height stratum.

The connecting tunnel underneath the road (that connects the two parts of the PNR) is occasionally blocked until newly introduced species, that should not mix with present species, have settled. The area available for game to move unhindered should be as large as possible. The connecting tunnel should ideally not be blocked during the dry season so that browsing game species can reach food resources closer to the Modder River that could sustain them through the critical period when other browse becomes scarce and browsing pressure in the northern part of the PNR becomes unbearable. The critical period for the study area is from July/August to middle October (*vid.* Chapter 5).

9.8.3 Species mix

Dekker (1996) calculated the overlap for spatial distribution (plant community preferences), habitat variables and diet composition (grass : tree ratios) in order to calculate substitution values for different game species based on potential competition for the same food source. These substitution values (Dekker 1996, Smit 2006) for browser- and grazer units were used in the calculation of the numbers of each animal species that can be supported by the vegetation of the study area, as determined by the carrying capacity. These were compared with the substitution values listed by Van Rooyen (2010) and certain discrepancies were found between the two sets of values.

Both authors regard a blue wildebeest as equal to one grazer unit (GU) but, for example, according to Smit (2006), a buffalo equals 3.8 GU (Table 9.2) and according to Van Rooyen (2010) it equals 2.2 GU (Table 9.3). A kudu is taken as representative of one browser unit (BU) by both authors, but a giraffe represents 5.2 BU according to Smit (2006) and 3.8 BU according to Van Rooyen (2010). Differences between the authors are mostly due to different mean weights of animals used and differences between the percentage browse and grass included in each animal's diet (Tables 9.2 & 9.3). Van Rooyen (2010) stated that the percentage grass and browse in the diet of an animal species is an approximate value that may vary depending on the vegetation types of a specific region or habitat of the animal.

If exactly similar animal numbers to stock the study area are used for both sets of substitution values (Tables 9.2 & 9.3), the GU and BU values based on the substitution values of Smit (2006) are at the carrying capacity determined, namely 122 GU and 8 BU (eland and giraffe excluded), while that of Van Rooyen (2010) add up to 86 GU and 35 BU (eland and giraffe excluded). Eland was excluded from the calculation of BU, since they were mostly present in the southern side of the PNR and not in the study area, while giraffe was excluded from the number of BU that can be supported by the 0 – 2 m height stratum that are used for these calculations, since they can also feed at higher strata where more browse is available.

The assumption was made that, due to the deciduous nature of plant species present, browse that would normally be included in the grazer diet during the winter months, was not available to grazers in the study area. Therefore, it was decided to use the substitution values listed by Smit (2006), since he reported zero percentage browse in the diet of the grazer species. Van Rooyen (2010) made a finer distinction between the percentage grass and browse included in a herbivore's diet and used higher browse percentages in the calculation of substitution values for grazers. Table 9.3 clearly illustrates the competition that can exist between grazers and browsers when grass should become scarce, for example due to overgrazing, and grazers start to include more browse in their diet, thereby elevating the number of BU needed. Using Van Rooyen's substitution values, but ignoring the contribution of grazers to the browser units (43.8 BU), a higher number of bulk- and selective grazers can be considered. A total number of 182 individual animals can then be stocked equivalent to 122 GU, since 1 GU equals the weight of one blue wildebeest (Table 9.3). In comparison, a total of 141 individual animals equivalent to 122 GU were calculated by means of Smit's substitution values. However, if the grazers do not include a high percentage of browse in their diet, like Van Rooyen implied, their diet will most probably require more grass to make up the deficit. In that case the calculations will not have made provision for a higher percentage grass included in the diet of the number of grazers stocked. This might lead to overstocking and consequent overgrazing for the specific conditions of the study area. Therefore it is concluded that the percentage of grass and browse included in the diet of a herbivore is very important to determine the number of individuals that can be stocked at carrying capacity.

Table 9.3 Numbers of animals stocked in the study area were converted into grazer and browser units (GU & BU) based on the substitution values listed by Van Rooyen (2010). The advised minimum viable population numbers of these species were also converted to GU and BU. The study area can support an average of 122 GU and 4 - 6.7 BU at the 0 - 1.5 m and 0 - 2 m height strata, respectively. The 0 - 5 m stratum, where giraffe feed, can support 16 BU. Species grouped under mixed feeders include a high percentage of karroid shrubs, or tree and shrub leaves along with herbaceous material in their diet.

	No. animals stocked	Grass in diet (%)	No. animals x % grass in diet	Browse in diet (%)	No. animals x % browse in diet	Grazer unit (GU)	Browser unit (BU)	No. animals x % grass x GU	No. animals x % browse x BU
GRAZERS									
Bulk grazers									
Buffalo	20	78	16	22	4	2.21	2.68	34.48	11.79
Burchell's zebra	10	93	9	7	1	1.32	1.60	12.28	1.12
	30		**25**		**5**			**46.75**	**12.91**
Selective grazers									
Bontebok	25	90	23	10	3	0.44	0.53	9.90	1.33
Blue wildebeest	20	87	17	13	3	1.00	1.21	17.40	3.15
Gemsbok	20	75	15	25	5	1.12	1.36	16.80	6.80
Lechwe	20	95	19	5	1	0.41	0.50	7.79	0.50
Red hartebeest	10	75	8	25	3	0.74	0.89	5.55	2.23
Roan antelope	6	85	5	15	1	1.24	1.50	6.32	1.35
Sable antelope		85	0	15	0	1.16	1.40		
Southern reedbuck	6	95	6	5	0	0.41	0.50	2.34	0.15
Warthog		70		30		0.26	0.31		
Waterbuck	20	84	17	16	3	1.10	1.33	18.48	4.26
Tsessebe	2	95	2	5	0	0.77	0.92	1.46	0.09
	129		**111**		**18**			**86.04**	**19.84**
MIXED FEEDERS									
Eland	20	50	10	50	10	2.02	2.44	20.20	24.40
Impala	40	45	18	55	22	0.33	0.40	5.94	8.80
Ostrich	20	80	16	20	4	0.49	0.59	7.84	2.36
Springbok	50	32	16	68	34	0.31	0.37	4.96	12.58
Steenbok*	5	34	2	66	3	0.11	0.14	0.19	0.46
	135		**62**		**73**			**39.13**	**48.60**
BROWSERS									
Giraffe*	6	1	0	99	6	3.15	3.80	0.19	22.57
Kudu	15	15	2	85	13	0.83	1.00	1.87	12.75
Common grey duiker*	10	12	1	88	9	0.19	0.22	0.23	1.94
	31		**2**		**19**			**2.0565**	**35.322**
TOTAL	**325**		**200**		**115**			**174**	**117**

* Not included in the calculations of GU or BU, because of a too small contribution or in the case of the giraffe another feeding height used.

Continued on next page…

Table 9.3 Continued

	Total units stocked (BU+GU)	Advised minimum viable number	Advised min. no. x % grass in diet	Advised min. no. x % browse in diet	Advised min. no. x % grass x GU	Advised min. no. x % browse x BU	Minimum no. stocking totals
GRAZERS					**Total GU**	**Total BU**	**Sum total**
Bulk grazers							
Buffalo		15	12	3	25.86	8.84	
Burchell's zebra		5	5	0	6.14	0.56	
	59.66	**20**	**16**	**4**	**32.00**	**9.40**	**41.40**
Selective grazers							
Bontebok		10	9	1	3.96	0.53	
Blue wildebeest		0	0	0	0.00	0.00	
Gemsbok		15	11	4	12.60	5.10	
Lechwe		15	14	1	5.84	0.38	
Red hartebeest		0	0	0	0.00	0.00	
Roan antelope		10	9	2	10.54	2.25	
Sable antelope							
Common reedbuck		6	6	0	2.34	0.15	
Warthog							
Waterbuck		0	0	0	0.00	0.00	
Tsessebe		0	0	0	0.00	0.00	
	105.89	**56**	**49**	**7**	**35.28**	**8.41**	**43.68**
MIXED FEEDERS							
Eland		10	5	5	10.10	12.20	
Impala		15	7	8	2.23	3.30	
Ostrich		6	5	1	2.35	0.71	
Springbok		25	8	17	2.48	6.29	
Steenbok*							
	87.73	**56**	**25**	**31**	**17.16**	**22.50**	**39.66**
BROWSERS							
Giraffe*		4	0	4	0.13	15.05	
Kudu		8	1	7	1.00	6.80	**7.80**
Grey duiker*							
	37.38	**12**	**1**	**11**	**1.12**	**21.85**	
TOTAL	**291**	**144**	**91**	**53**	**86**	**62**	**133**

In general, bulk grazers should preferably be stocked at a high proportion of the carrying capacity, selective grazers and mixed feeders at intermediate proportions and browsers at a low proportion. It is advised that bulk grazers in the study area should be stocked at 45% of the sum total of GU and BU that the study area can support (Table 9.2), selective grazers at 30%, mixed feeders at 20% and browsers at 5% (E. Schulze, *pers. comm.*[1]). Large herbivores should be stocked at a level between their ecological and economical values. Utilization factors that were used to calculate grazing and browsing capacities (*vid.* Chapter 8) have already made provision for lower values than the maximum that the study area can carry, should all the vegetation be available and within reach of the animals.

In Table 9.4 the stocked numbers of each species during the study period are summarized, as well as the recommended numbers that are required to meet the available carrying capacity. The values on which these calculations and recommendations were based are presented in Table 9.2. A brief report on the economic value, impact on the veld and rate of reproduction of each species (more detail are provided in Table 9.1) is included in Table 9.4 to explain the recommendations. The minimum viable population of a species was used as a starting point in determining the numbers that can be maintained, accompanied by the economical and ecological value of the species (Table 9.4). The general recommendation is that there should be a reduction in animal numbers, since the study area was overstocked with approximately 113 GU and 79 BU during the study period. Some animals, like lechwe, eland, waterbuck and tsessebe, mostly occurred in the southern part of the PNR and should be kept out of the study area, or removed from the PNR, in order to meet the ecological carrying capacity (Table 9.4).

Duiker, steenbok and reedbuck have a very low impact on the environment and are low density species that are present in relatively low numbers in the study area. Therefore their numbers do not need adjustment at this stage (Table 9.4), but should be monitored in future when space might become a problem due to their population growth. A method on how to determine the density of duikers by using dung heap counts is described by Lunt *et al.* (2006). The calculated densities in the Matobo National Park, Zimbabwe ranged from 1 – 18 duikers/km^2. Additional small mammals such as hares, suricates, ground squirrels and other rodents also occur throughout the PNR, but have a low impact in general on the environment and are thus not incorporated in any calculations.

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[1] Erika Schulze, Principle Nature Conservation Scientist, DETEA head office, Bloemfontein.

Table 9.4 Stocked number of animals per species present in the northern part of Wag-'n-Bietjie Private Nature Reserve and the recommended number that can be supported by the vegetation in the study area, using substitution values of Smit (2006). Abbreviations used: GU = grazer unit, BU = browser unit, PNR = private nature reserve.

	Stocked number	Advised number	Recommendation
Blue wildebeest	20	0	The owner removed all the wildebeest at the end of the study period. Their numbers were kept on zero, otherwise the GU that the study area can support would be exceeded. They have a high impact on the veld and a rather low economic value, except for biltong hunting.
Bontebok	25	10	Although they seem to have adapted well in the area, they were not historically present. Their numbers should be reduced to keep within the grazing capacity of the study area. They have a high impact on the veld, an expected 25% annual population growth rate and are no longer permitted at game auctions in the Free State.
Buffalo (African/Cape)	20	15	This species has a high economic value. They have a moderate impact on the veld, because of their large home range that includes the southern side of the PNR. This bulk feeder's numbers should be reduced in order to accommodate the selective grazers in the study area.
Burchell's zebra (Plains zebra)	10	5	Zebra has a medium economic value. They have an expected 27% annual population growth and are bulk feeders with a low impact on the veld. Their numbers have to be reduced to five or if all the bontebok are removed, 2 more zebra can be added for a total of 7.
Common duiker (grey)	±10	±10	Duiker has a low impact on the veld. At this stage their numbers can be left unchanged. It has to be monitored in future due to space available, since they have an expected 45% annual population growth. They have a low economic value at auctions, up to R 1 000.
Eland	20	10	Eland have a moderate impact on the veld and a medium economic value. They have a 20% annual population growth and are mixed feeders. They mostly occur in the southern side of the PNR, but should they be present in the study area, their numbers will exceed the BU available. Their numbers should be reduced to conform with the available grazing capacity.
Gemsbok	20	12-15	Their numbers should be reduced, since they have a high impact on the veld. They have a medium economic value and are sought after for hunting purposes. Their expected annual population growth is 25%.
Giraffe	6	4	Giraffes were not historically present in the Free State, but seem to have adapted well. Feed should be supplied in winter due to deciduous browse plants. A reduction in their numbers is advised in order to allow for young animals to have sufficient browse available. Expected population growth is 12% annually Their numbers should be kept between 4 and 6. Five is their minimum viable population size. They have a high economic value, but also a high impact on the veld.
Impala	40	15	Their numbers should be reduced drastically because of the very high impact they have on the veld and their expected 35 – 48% population growth annually. They have a low economic value at auctions. It is believed that they were not historically present in the Free State. These mixed feeders have low GU and BU values, therefore many must be removed to make a difference.

Continued on next page...

Table 9.4 Continued

	Stocked number	Advised number	Recommendation
Kudu	±15	8	There is not enough browse available to sustain more than 8 kudus. Only half of the total herd of approximately 15 – 20 kudus was observed in the study area at a time. They have large home ranges and move closer to the river when browse reserves in the study area become scarce. They have a low impact on the veld, a medium economic value at auctions and are sought after for hunting purposes.
Ostrich	±20	6	Ostrich numbers should be reduced drastically because of their high impact on the veld and their expected 23 – 75% population growth annually. They have a low economic value at auctions, but their hide and feathers are sought after for commercial use. Six individuals represent their minimum viable population size.
Red hartebeest	10	0	The owner removed almost all ten hartebeest at the end of the study period. The remaining 3 – 4 escapees should also be removed to reach grazing capacity. They have a low impact on the veld and a medium economic value at auctions. (See lechwe recommendation)
Red lechwe	20	15	They were not historically present in South Africa, but seem to have adapted well to the Free State environment. Their numbers should be reduced to accommodate the other grazers as well. They have a high live economic value, a low impact on the veld and an expected 18% population growth annually. If lechwes are kept out of the study area and contained in the south, they can be replaced with ten red hartebeest.
Roan antelope	6	10	Roan have a very high live economic value, since it is one of the rare species and have a low impact on the veld. Their numbers should be increased slightly. They have an expected annual population growth of 22%, specific habitat requirements and need a lot of space.
Southern reedbuck	±6	6	They have a low impact on the veld, a low annual population growth rate (12%) and a medium economic value at auctions. Their numbers can remain as it is.
Springbok	50	25	Their numbers should be halved. They have a high impact on the veld and a population growth rate of up to 42%. They have a very low economic value at auctions and is mostly used for biltong and meat hunting.
Steenbok	±5	±5	They have such low GU and BU values that they can almost be left out of the calculation. They have a very low impact on the veld, can reach up to R 1 000 at auctions and an annual population growth rate of 27%.
Tsessebe	2	0	They were not historically present in the Free State. The remainder of the herd of ±20 individuals is resident in the southern side of the PNR. These two individuals joined the bontebok herd and should rather be removed. They have a low impact on the veld and a high economic value, since they are also a rare species.
Waterbuck	20	0	They were not historically present in the Free State. These animals are not always present in the study area, but concentrate in the southern side and should be kept out of the study area to ensure enough grass is available for the other grazers. They have a low impact on the veld and a medium economic value at auctions, with an expected population growth of 28% annually.
TOTAL	**325**	**156**	

9.9 MANAGEMENT TOOL FOR THE NORTHERN PART OF WAG-‘n-BIETJIE PRIVATE NATURE RESERVE

A CD is included at the back of the thesis that contains different data sets that have been illustrated as overlays on the vegetation map of the PNR. Data is indicated for each 150 m^2 grid block (Figure 8.1) that have been overlaid on the vegetation map and the darker the colour of the block, the higher the value. Data sets included, are browser units (per block and per vegetation unit) that can be sustained in summer and winter in each of the different height strata (<1.5 m, <2 m, <5 m); grazer units that can be sustained by each vegetation unit in a wet and a dry year; Canopied Subhabitat Index values < 2 m per block; density of woody plants, of trees and of shrubs per block; and the number of times the giraffe, kudu, impala, eland and grazers were observed in a grid block in summer and winter months. The overlays were created with ArcGIS 9.3 and ArcPUBLISHER 9.3 was used to convert the file to be able to view it in ArcREADER 9.3. The ArcREADER software (ESRI 2008) is available as freeware from the internet and is included on the CD.

To view a layer, select it by clicking in the box ☐ next to the name and then on the + next to it. The legend will appear in the ‘table of contents’. A layer has to be turned off by deselecting it, before the next one can be opened, or else one layer’s data will be covered by the next where data is present in similar blocks. With this management tool, for example, the specific number of browser units per block can be compared to density of woody plants and the number of times browsing animals have been observed in that block to give an indication of why an animal species preferred a specific area when compared with its preferred habitat types (Table 7.1). The low values of the BU per block combined with density data for trees and shrubs clarify why only ±7 BU can be sustained in the study area. Any other combination of comparisons can be made by viewing different layers.

A Windows Excel (Microsoft Corporation 2002) worksheet is also included on the CD that can help with the determination of the number of individuals of each species that can be stocked in the study area if certain changes need to be made to the species mix. The column with the heading ‘New number per species’ can be changed and it will calculate the new total GU and BU, but it is important to stay in the limits of the determined carrying capacity (indicated at the top of the table). As mentioned earlier, the grazing capacity needs to be adjusted annually according to the total rainfall. Warthogs are already present along certain stretches of the Modder River (E. Schulze *pers. comm.*[1]) and are thus included along with nyala and sable antelope that are present in the southern side of the PNR, should their numbers need to be included in the species mix calculation for the study area in future.

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[1] Erika Schulze, Principle Nature Conservation Scientist, DETEA head office, Bloemfontein.

9.10 LEGISLATION

Wildlife ranching has to function in a specific legislative framework. NAMC (2006) lists the following 18 Acts that affect wildlife management, depending on the kind of activities that take place on the ranch: Agricultural Product Standard Act, No. 119 of 1990; Animal Health Act, No. 7 of 2002; Animal Improvement Act, No. 62 of 1998; Animal Identification Act, No. 6 of 2002; Animals Protection Act, No. 71 of 1962; Conservation of Agricultural Resources Act, No. 43 of 1983; Environment Conservation Act, No. 73 of 1989; Fencing Act, No. 31 of 1963; Firearm Control Act, No. 60 of 2000; Marketing of Agricultural Products Act, No. 47 of 1996; Meat Safety Act, No. 40 of 2000; National Environment Management Act, No. 107 of 1998; Perishable Products Export Control Act, No. 9 of 1983; National Environmental Management: Biodiversity Act, No. 10 of 2004; National Environmental Management: Protected Areas Act, No. 57 of 2003; South African Abattoir Corporation Act, No. 120 of 1992; Tourism Act, No. 72 of 1993; and Veterinary and Para-veterinary Professions Act, No. 19 of 1982**.** The Fire Act, No. 101 of 1998 is also applicable (Cheney 2005). The National Environmental Management: Biodiversity Act in combination with the National Environmental Management: Protected Areas Act constitute a set of laws in which the full range of conservation efforts are recognised, regulated and empowered (NAMC 2006).

The threatened or protected species (TOPS) regulations apply only to those species that are listed as Threatened (Critically Endangered, Endangered, Vulnerable) or Protected (section 56(1) in terms of the National Environmental Management: Biodiversity Act (Act 10 of 2004). No restricted activity may be carried out involving a TOPS specimen without a TOPS permit. More detail is given in Chapter 2. TOPS species present in the Wag-‘n-Bietjie Private Nature Reserve, are bontebok, tsessebe, roan antelope and reedbuck, while African wild dog, cheetah and lion are present in another fenced off part in the southern side of the PNR.

9.11 FINAL RECOMMENDATIONS

Monitoring of all components of the system is indispensable to measure success and to adapt management actions where necessary. Different components that need monitoring include the fauna, flora, rainfall, fire, erosion, hydrological processes, natural resources and infrastructural aspects. A practical work plan for the year should be compiled in which specific dates are set to monitor different aspects like when an evaluation of the veld will be done, when animals will be counted, when to manage animal population sizes (live capture and cropping is from March –

October), when to hunt (hunting season is May – August), when to control tree/bush thickening, when to burn the veld (if necessary) and when to plant, harvest and bale lucerne for feed. The management plan should be edited every five years to accommodate changes in veld condition and/or decisions on stocking densities. The grazing and browsing capacities should be determined annually and animal numbers adapted to the changed veld conditions.

Two different sets of substitution values per herbivore species for grazer- and browser units were compared. If the grazers include a low percentage of browse, the one set of substitution values can be used that reflect this. If grazers include a higher percentage of browse in their diet, the other set of substitution values should be used. The number of true browsers (kudu and giraffe) must then be reduced or else the available browse will not be sufficient to sustain them and feed will have to be supplied. The number of grazers should also be reduced to minimize the impact on trees, shrubs and grasses. The substitution values are approximate values and should scientifically be adapted to the specific region to ensure that the best stocking density for the area can be determined.

To ensure that the game ranch do not operate at a financial loss, now or in future, it is advised to draft a realistic prospective income plan for the game ranch. Then reduce both the inset costs and the running costs to achieve the expected profits. One way of doing this is to ensure that game is stocked at the correct density in order for them to be self sustaining without damaging the veld, that game can supply a population increase (higher income) and do not need too much feed (expenditure). Domestic animals, like sheep or cattle can also be incorporated to provide extra income to supplement income from game, especially in out-of season periods of low income.

Appointment of a part-time ecologist for the private nature reserve is recommended to help with management of the wildlife. The current manager is in charge of all aspects of management and will not be able to fully accommodate the monitoring of veld conditions and animals as well.

If conservation is to succeed, local communities and individuals should benefit from wildlife conservation and/or activities. Jobs and business opportunities that are created can help the community become actively involved in conservation. Their use of natural resources present in private game ranches can also contribute to this process.

CHAPTER 10
GENERAL DISCUSSION AND CONCLUSIONS

DISCUSSION AND CONCLUSIONS

This study represents an attempt to quantify the available food resources, habitat characteristics and adaptation of game species to the available habitat in certain vegetation types in the Free State. For the most part, published information on these aspects is very limited for the province, especially information related to browsing species. Based on this, the objectives were to determine:

i) leaf carriage patterns and other phenological aspects of deciduous woody species;
ii) vegetation types that certain species have adapted to by including it in their home ranges due to a lack of space and preferred prime habitat;
iii) habitats used by certain introduced species; shared with other common species and niche differentiation between species;
iv) animals' local, seasonal movements;
v) faecal nitrogen values to indicate the nutritional status of giraffe, kudu, eland and impala;
vi) carrying capacity of such a small game ranch and its advised herbivore species mix in order to make the ranch sustainable; and
vii) general operational guidelines for a game ranch that can be applied throughout the province.

Vegetation types of Wag-'n-Bietjie Private Nature Reserve generally consist of grassland, dense thicket associated with two dry drainage lines of the Modder River and thicket-grassland transitional areas, or open thickets. Woody areas are characterized by trees and shrubs normally associated with riparian thickets in the province. A wet-dry gradient and a tree-grass gradient were distinguished with distance from the drainage lines towards the grassland surrounding it.

Areas with similar vegetation to that of the study area are popular for game ranches and nature reserves, because of the presence of trees and shrubs. In August 2010 there were 343 private game ranches with Adequate Fencing Certificates in the Free State province, 13 proclaimed provincial nature reserves and 16 municipal areas that are stocked with game. These numbers do not include all the areas that are stocked with game in the province and are only a small indication of the true number of privately owned game ranches. The presence of such a large number of game ranches indicates the necessity and value of this current study, particularly since most relevant research is done in savanna areas and very little in the Free State.

The presence of trees and shrubs is often perceived as a good motivation to introduce browser and mixed feeder species, in such areas of the province. However, most of the woody species associated with this type of vegetation are deciduous and shed their leaves in the dry season. All the tree species in the study area are leafless for about 2 to 3 months, with the exception of some dry leaves retained on trees. The shrub species present in the study area are semi-deciduous and retained mature leaves for longer periods. These shrubs become important browse reserves in the middle of winter, but they have a low abundance.

Leaf litter, of especially *Ziziphus mucronata* and *Diospyros lycioides*, ripe fruits and pods mostly constituted the other food sources, along with the shrubs, available for herbivores from March to May/June. Green leaves can be stored at the beginning of autumn by the manager of a game ranch to use as additional leaf litter, along with supplied feed during winter months when browse becomes limited. The critical period for browser and mixed feeder game species in the central Free State, when available browse is insufficient to sustain these animals, was established to be from July/August to middle October. A progressive decline in browse availability due to shedding of leaves was observed during this period and continued until new-season budding leaves became more mature and contained less tannins that deter browsing. Tannins are phenolic compounds known to reduce protein and cell wall digestion of browsed leaf material and act as a chemical plant defense mechanism.

New-season leaves mostly appeared on trees in September/October and leaf senescence started in April. Differences in climate, specifically temperatures, between the years may have resulted in differences in leaf phenology patterns in the sense that phenophase changes from budding-, immature- and mature leaves to yellow- and dry leaves occurred on different dates annually. It is important to annually monitor the leaf phenology patterns of woody species in this area, especially towards the end of the growing season starting from March, in order to know when it becomes crucial to provide game with supplementary ("byvoeding") and/or supplied feed ("voer").

Supplying feed is essential since evergreen species are not available, all the trees are deciduous and shrubs and fruits are not abundant enough to sustain the numbers of browsers and mixed feeders, stocked on summer values, during the critical period. When true leaf carriage percentages of woody species were taken into account, it was calculated that the study area could support only 1 browser unit (BU), equivalent to one kudu, at the end of the critical period when the deciduous trees are leafless. Browser units based on the 0 – 2 m height stratum ranged from 1 – 6.7 BU between winter and summer, while at the 0 – 1.5 m stratum the range is from 0.8 – 4.1 BU. Therefore, if there is only enough browse to sustain 1 BU, it is obvious that feed should be supplied to the other approximately 6 BU that make up the round total of 7 BU. The alternative is to drastically reduce game numbers in order to be closer to the winter carrying capacity of the study area, or even remove some game species completely that rely more on the supplied feed. This also applies to the grazer game species. In this way, the study area can be sustainable by having enough food reserves to support game species through the winter period without damage to the environment or the animals. If the numbers of animals are reduced to 1 BU, however, it is not a sustainable population. This justifies in some way the provision of feed in order to be able to stock the minimum number that makes a population viable.

At the time of study, the management decision was to continue feeding the animals through the critical period and not to reduce numbers or remove species. Lucerne and game pellets were at first supplied from April/May to the beginning of October in an attempt to prevent game from losing condition during this period. It is concluded from this study that it will be financially advantageous to start feeding only from June/July, but at a low ration and then increase feed towards the end of the critical period in correspondence with the declining browse and grass resource. Otherwise animals ‘waste’ feed when adequate food is still available in the veld. The supply of feed can be terminated in middle October after the spring rain when good quality browse and grass become sufficient to sustain the animals during this period. Stopping the supply of feed too early may lead to animal losses due to a decrease in their nutritional status, which will have serious financial implications. It must also be taken into consideration that availability of the supplied feed is limited due to intra-species competition for obtaining feed, as well as inter-species competition between giraffe, kudu, eland, impala and the grazers.

Monitoring the nutritional status of the animals can offer the manager a useful tool to establish when more supplementary feeding may be required, like for instance when measured faecal nitrogen (N_f) concentrations approach known critical concentrations where animals will start to lose body condition. N_f was measured for the browser- (giraffe and kudu) and mixed feeder game species (impala and eland). The nutritional status of kudu was low and they were in poor physical condition during two to three months of the critical period (July to August/September) when their N_f concentrations dropped to 13 – 16 g N/kg DM. The known nitrogen value where kudus start to lose body condition is <18 g N/kg DM. The lucerne hay diet proved to be insufficient in sustaining kudu during the winter months. However, without the supplied feed the available browse in the study area, due to intense competition for it, may not be enough to sustain these animals through the winter period. Eland, impala, as well as grazers, such as African savanna buffalo, blue wildebeest, Burchell’s zebra, gemsbok, red hartebeest, roan antelope, southern reedbuck, springbok, waterbuck and ostrich may include browse in their winter diet and will then compete with kudu and giraffe that are relying almost 100% on browse.

Minimum N_f concentration of giraffes during the dry season (18.6 g N/kg DM) was above critical nitrogen levels for browsers in general (± 16 g/kg). They did not appear to be in poor condition and were reproducing every year. However, a N_f content of 20.3 g/kg were recorded for giraffe in the Kruger National Park during the severe drought of 1992 – 1993. The minimum N_f concentrations measured in this study that were lower than that of severe drought conditions should give an indication that the giraffes' nutritional status is actually low, even though they seem to be in good condition.

A seasonal pattern in N_f concentrations was observed for giraffe and kudu that correlated with the leaf phenology pattern of the trees. N_f concentrations increased until it peaked in the late summer (December – February) when trees had full leaf carriage and then decreased until it reached the lowest concentrations during winter (June – August) when trees had shed their leaves and browsing animals were relying mostly on leafless shoots, shrubs and supplied feed. In general a decrease in crude protein content has been indicated from immature leaves to yellow leaves for all the woody species, that was reflected in the animal's N_f concentrations.

A seasonal pattern was also observed for impala and eland, with the highest N_f concentrations during summer months, but lowest concentrations occurring during autumn. An increase in these mixed feeders' N_f concentrations was observed between May and July 2007 that differed from leaf phenology patterns and N_f patterns of browsers. Mixed feeders in general select higher quality food items during the critical period. They include more browse in their diets causing a further increase in N_f concentrations when changing from their predominantly grass diet in summer months.

The minimum N_f concentrations of eland in the study area were 16 – 17 g N/kg DM. These concentrations are close to known critical concentrations where grazers and browsers lose body condition, namely 14 g/kg and 16 g/kg, respectively. The minimum N_f concentration of impala during 2006 (16.9 g N/kg DM) reached the critical level indicated for impala during drought conditions in the Kruger National Park when they started to lose body condition (16.6 g/kg). Impala numbers were reduced to a quarter of the original number in the study area during 2007. This would have increased the quantity of food available for the remaining impala, leading to higher minimum N_f concentrations (21.3 g/kg) during the critical period of 2007 in comparison with 2006. Thus, faecal nitrogen can effectively be used as a management tool in deciding the optimum stocking rate of animals that can be sustained by the quantity and quality of food resources available.

The drainage lines and dense thicket associated with it, contribute largely to the number of browser units that can be stocked in the study area. The higher density of trees in these areas in return resulted in a lower grazing capacity than in open grassland areas due to the grasses not being dominant and a different plant species composition occurring in the shade of canopied subhabitats. Browsing capacity did not vary much between wet and dry years, but grazing capacity was more severely affected by rainfall – more rain means more grazer units can be sustained. As can be expected, more hectares per browser- and per grazer unit are needed in winter and early spring to sustain animals compared to summer months. This fact, combined with the small confined space of the private reserve that prevents migration in search of other food resources, are all factors that emphasize the need for supplying feed if numbers are not strictly regulated within the boundaries of the ecological carrying capacity. Animals have little need for supplied feed in their unrestricted natural environment as their free ranging habits usually enable them to search for more nutritious food elsewhere when resources become depleted.

The presence of supplied feed is also the main factor in causing local, seasonal movements of browsers and mixed feeders in the private reserve, by drawing these animals to the feeding areas. In the dry season, browsing animals mostly concentrated in areas neighbouring feeding areas, whereas they were dispersed through the dense thicket and drainage lines during the wet season. When the demand for the scarce browse resource became very high in the study area during the late dry seasons, the non-territorial kudu and eland occasionally moved through the connecting tunnel underneath the road to reach the dense riparian vegetation close to the river in the southern side of the private reserve. The higher density of trees and shrubs provided not only shelter from winter temperatures, but also proved to be a critical food resource area for these animals during the limiting, critical period. Another reason for moving out of the study area was that competition for the browse resource was also much less in the southern side. This, along with severe browsing evidence on most shrubs and karroid shrubs present clearly indicated that the browsing capacity in the study area was exceeded in winter months.

The main focus of this study was on browsing animals, how they adapted to wooded areas in the Grassland Biome of the Free State and particularly to the deciduous nature of available riparian vegetation. Grazer game species were included in general to determine their impact on browsers' habitat selection and food resources, since they compete for it indirectly with browsers and directly with mixed feeders that also include grass in their diet. Therefore, seasonal movements were only indicated in general and not studied in detail for the grazers. Most of the grazers present are territorial and were sedentary in the same local area due to lack of space in the study area.

Habitats used by each of the 17 game species were determined and certain differences were observed between vegetation units used and those avoided by the different animal species. Inter-species competition for prime habitat, in terms of space and food, proved to be high. Water is not a limiting factor because of a permanent waterhole being within 2 km from any point in the study area. Shade and shelter are sufficient as habitat requirements, since trees are present in almost the entire area, except in the grassland.

Giraffes, kudus and impalas were only observed in the open thickets in transit and preferred habitats with a higher density of trees, while eland made use of the grassland, open- and denser thickets. These four species had large home ranges and spaced themselves in order to reduce interspecies competition for browse. Grazers compete for habitat in the dense thicket, due to lack of space in open areas and the grassland, with browsers- and mixed feeders that need the presence of trees for food. When grazer species are introduced into an area, their need for space to set up territories and their possible non-sharing behaviour towards other species should be taken into consideration. Certain grazer species can co-exist in the same area, because they prefer the same habitat and grass height for feeding, while this is not the case for other species that have different needs and cannot co-exist. There is often also a grazing succession in progress where certain grazer species prepare areas for successive species by changing the height of grasses. Thus, the total space available is divided into areas where each species' own needs and preferences can be accommodated as far as possible and is not available in its entirety to every species present in the environment.

The area with the highest use in the study area by all game species is that between the big drainage line and the disturbed area around the main waterhole. The open thickets, being transitional between riparian thicket and grassland, were favoured by a large number of grazer species. Reasons for this might be that it provides shade and shelter that are absent in the grassland, contains palatable herbaceous species associated both with shady areas and grasslands and is not as dense as the thicket that allows for easy access of all vegetation. Care must be taken not to overgraze, trample or erode open thickets, since that will allow for a spread of *Acacia karroo*. Woody seedlings should also be monitored and controlled to prevent the change of these open habitats into dense thicket.

The open thickets were differentiated from the thicket and grassland by the co-dominance of woody species and herbaceous species, instead of being dominated by either one of these two groups of species. The study area falls in a transitional zone because the presence of the Modder River's drainage lines resulted in riparian thicket vegetation to occur in the Grassland Biome. Under normal circumstances, ecotonal areas like this would usually be omitted from a dataset due to their transitional nature. However, the differences in vegetation in these ecotones and their distinct habitat characteristics, compared to the dense thicket and grassland, contributed to these areas being included in this study as a management unit of its own. This was also the case with the disturbed area that is characterised by its carpet of creeper grasses.

It is anticipated that the results of this study will provide crucial information for effective management of similar game ranches in the Free State. It can also serve as a means to create a benchmark for other similar areas. It must be taken into consideration that game areas in the province that include rocky hills or accessible river vegetation are characterized by the presence of different, mostly evergreen, woody species than those present in the study area. Evergreen woody species in general are not as palatable or acceptable as leaved deciduous species associated with drainage lines. Consequently, it is possible that fewer browser units can be sustained by an area with only evergreen species present, because the quality of browse will be less sufficient. Those evergreen woody species would, nevertheless, be a valuable browse resource in the dry season when they can substitute deciduous species that become leafless. Local, seasonal movements of browsing animals towards such areas in the dry season and away from it in the wet season towards areas dominated by deciduous species will most probably be observed. These aspects should be taken into consideration when carrying capacities of other localities are determined. A conservative stocking density should be used when the emphasis is on rare species or veld reclamation. A less conservative density, without exceeding the carrying capacity limits, is appropriate when the emphasis is on high production of animals for hunting or venison production. Two approaches to determine the individual numbers of a species from carrying capacity equivalents were tested, one includes more browse in a grazer’s diet and the other no browse. Thus, it has to be adapted to the herbivore’s diet preferences in a specific area or region for calculations to be accurate.

The manager of a game ranch plays a vital role in sustainable utilisation of fenced properties used in game production for commercial purposes by ensuring that enough space and food resources are available for all the animals stocked. Important decisions that he has to make include placement of waterholes, feed supplied, choice of animal species and the regulation of their numbers. Regular monitoring of all components of the system is indispensable to measure success and to adapt management actions where necessary. Different components that need monitoring include the wildlife, veld condition, rainfall, fire, erosion, natural resources and infrastructural aspects. Certain management suggestions have been made, regarding these subjects in the management plan created for the northern part of the private nature reserve. Some of these ideas and suggestions can also aid the ever increasing number of game ranches in the province in their management.

SUMMARY

OPSOMMING

A PLANT BASED STUDY OF THE FEEDING ECOLOGY OF INTRODUCED HERBIVORE GAME SPECIES IN THE CENTRAL FREE STATE

by

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Key terms: Browsers; carrying capacity; faecal nitrogen; game ranch; giraffe, kudu, eland, impala; habitat; leaf phenology; management plan; mixed feeders; seasonal movements.

Wag-‘n-Bietjie Private Nature Reserve is situated ±30 km north of Bloemfontein in the summer rainfall area. The northern part is 437 ha in size and represents a transition between grassland and riparian vegetation. Vegetation types present are grassland, open thickets, dense thicket, drainage lines of the Modder River, a wetland and disturbed area.

Phenology (seasonal leaf carriage) of plants formed the basis of this study. Percentage leaves in each phenophase (Budding-, Immature-, Mature-, Yellow- and Dry leaves) was noted fortnightly for specific marked trees and shrubs representing each vegetation type. The deciduous nature of woody species influenced quality and quantity of browse available for herbivores. Consequently the nitrogen concentration in faeces (N_f) of four game species was determined to indicate their nutritional status through the different seasons. The rise and fall of N_f values corresponded to the seasonal increase and decrease of leaves (phenology pattern). N_f ranged during four years from 18 – 37 gN/kgDM for giraffe, 14 – 33 g/kg for kudu, 16 – 35 g/kg for eland and 17 – 28 g/kg for impala. Abovementioned minimum concentrations are close to, and in the case of kudu below known critical values where animals start to lose body condition. Nitrogen is the most limiting nutrient in the dry, cool season and is linked to protein percentage present in browse. Browse becomes a limited resource in the winter, therefore certain game species moved seasonally to different areas inside the private reserve in search of food. It was decided to supply feed in order to sustain animals

and help them maintain body condition during the critical period that was established to be from July/August to middle October. The duration of feeding is important and it is recommended to start feeding from July at a low ration and then gradually increase feed towards the end of the critical period in correspondence with the declining browse and grass resources.

Average monthly leaf carriage percentages were used to calculate browsing capacity per month in each vegetation type and in the study area as a whole. Browser units that could be sustained on browse resources within the 0 – 2 m stratum ranged from 1 – 6.7 BU between winter and summer due to the deciduousness of all woody plants present in the study area. This justifies in some way the provision of feed, or else the numbers of animals would need to be reduced to 1 BU which does not represent sustainable populations. Viable population numbers, economic value, diet and reproduction rates were used in determining the numbers of individual animals that can be stocked. Grazing capacity of the area differed according to annual rainfall and increased with higher rainfall. Consequently it needs to be recalculated annually.

Habitat occupied by all 17 herbivore species was determined. Some species did not historically occur in the province. Most of them have adapted to the central Free State conditions over time, while others were introduced more recently. Inter-species competition for space and food resources proved to be high in the study area. A reduction in animal numbers has been recommended to limit competition.

There is an ever increasing number of private game ranches in the province, >343 in August 2010, that will benefit from this research. Some general, operational guidelines have been presented that are applicable to the management of other game ranches in the province as well. When calculating individual animal numbers equivalent to carrying capacity values of other areas, the percentage grass and browse that herbivores include in their diet need to be adjusted to the specific area for accurate stocking densities.

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Sleutelterme: Bestuursplan; blaarfenologie; blaarvreters; drakrag; gemengde vreters; habitat; kameelperd, koedoe, eland, rooibok; seisoenale bewegings; stikstof in mis; wildplaas.

Wag-'n-Bietjie Privaat Natuurreservaat is ±30 km noord van Bloemfontein in die somer-reënvalstreek geleë. Die noordelike gedeelte is 437 ha groot en verteenwoordig 'n oorgangsone tussen grasveld en rivierplantegroei. Die volgende plantegroeitipes is verteenwoordig: grasveld, oop bos, digte rivierbos, spruite verbind aan die Modderrivier, 'n vleiland en versteurde area.

Fenologie (seisoenale blaredrag) van plante het die uitgangspunt van die studie gevorm. Die blaarpersentasie in elke fenofase (Bottende-, Onvolwasse-, Volwasse-, Geel- en Droë blare) is twee-weekliks bepaal vir spesifieke, gemerkte bome en struike wat elke plantegroeitipe verteenwoordig. Die bladwisselende aard van houtagtige spesies het die kwaliteit en kwantiteit van beskikbare blaarvoedsel vir herbivore beïnvloed. Gevolglik is die stikstofkonsentrasie in die mis (N_f) van vier wildspesies bepaal om hulle voedingstatus deur verskillende seisoene aan te dui. Die styging en daling in N_f waardes het ooreengestem met seisoenale toename en afname in blare (blaarfenologie-patroon). Die N_f-waardes het oor vier jaar gewissel tussen winter en somer van 18 – 37 gN/kgDM vir kameelperde, 14 – 33 g/kg vir koedoes, 16 – 35 g/kg vir elande en 17 – 28 g/kg vir rooibokke. Bogenoemde minimum konsentrasies grens aan bekende kritiese waardes waar diere kondisie begin verloor en in die geval van koedoes was dit selfs laer as kritiese waardes. 'n Tekort aan stikstof ontstaan in die koel, droë seisoen. Stikstof word geassosieër met die persentasie proteïen teenwoordig in die blaarvoedsel. Blaarvoedsel raak skaars in die winter, dus het sekere spesies

seisoenaal verskuif na ander dele in die privaat natuurreservaat op soek na kos. Daar is besluit om diere te voer om sodoende te verhoed dat hulle liggaamskondisie verloor tydens die kritieke periode wat strek vanaf Julie/Augustus tot middel Oktober, soos vasgestel. Die tydperk waarin voer verskaf word is belangrik. Daar word aanbeveel dat daar met ‘n lae rantsoen voer begin word vanaf Julie en dat die voer hoeveelheid geleidelik vermeerder word tot aan die einde van die kritieke periode in ooreenstemming met die afnemende blaar- en grasvoedselbronne.

Gemiddelde maandelikse bladedrag-persentasies is gebruik om die blaarvoer-drakrag per maand vir elke plantegroeitipe en vir die studiegebied as geheel te bereken. Van winter na somer het die blaarvretereenhede (BE) wat op blaarvoedsel in die 0 – 2 m hoogteklas onderhou kan word, verander van 1 – 6.7 BE as gevolg van bladwisseling van al die houtagtige plante teenwoordig in die studiegebied. Dit regverdig in ‘n sekere mate die voorsiening van voer, waarsonder die dieregetalle verminder sou moes word tot 1 BE, wat nie lewensvatbare populasies verteenwoordig nie. Lewensvatbare populasie-getalle, ekonomiese waarde, dieët en voortplantingstempo’s is gebruik om die getalle van individuele diere wat aangehou kan word te bepaal. Grasvoer-drakrag het verskil na gelang van die jaarlikse reënval en was meer wanneer die reënval hoër was. Gevolglik noodsaak dit jaarlikse herberekening van die grasvoer-drakrag.

Die habitat wat deur al 17 dierspesies gebruik word, is bepaal. Sommige van hierdie spesies het nie histories in die provinsie voorgekom nie. Meeste van hulle het mettertyd aangepas by die sentrale Vrystaat toestande, terwyl ander meer onlangs ingebring is. Sterk inter-spesiekompetisie vir spasie en voedselbronne het in die studiegebied voorgekom. ‘n Vermindering in dieregetalle is aanbeveel om kompetisie te beperk.

Die groot aantal privaat wildplase in die provinsie wat reeds 343 in Augustus 2010 oorskry het en steeds toeneem, sal kan baat vind by hierdie navorsing. Algemene bedryfsriglyne wat ook van toepassing is in die bestuur van ander wildplase in die provinsie is voorgestel. Indien individuele dieregetalle, gelykstaande aan drakrag-waardes, vir ander areas bereken word moet die blaarvoer- en graspersentasies wat die herbivore in hulle dieët insluit, aangepas word by die spesifieke area om akkurate drakrag digthede te verseker.

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