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Feeding ecology of the Kalahari springbok *Antidorcas marsupialis* in the Kgalagadi Transfrontier Park, South Africa

by

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I declare that this dissertation, which I hereby submit for the degree Magister Scientiae (Botany) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

F H Stapelberg
London, United Kingdom
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TABLE OF CONTENTS

LIST OF TABLES

from April 2003 to May 2004 on the South African side of the Kgalagadi Transfrontier Park

Table 5.2 A list of plant species and plant parts that were selected by springbok when feeding during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park expressed as a percentage of the total observations. The first item represents observations that did not specify any particular plant or plant part and the second a collection of plants that were only recorded twice at most. The high number of observations is due to more than one option being provided in the questionnaire for specifying selected plants or plant parts

Table 5.3 P-values of comparative tests between sets of two variables (activities) to examine independence of the frequency of different activities in springbok herds from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park. Statistical independence is where $P \leq 0.05$

Table 5.4 Relationship between herd size of springbok and rainfall on the South African side of the Kgalagadi Transfrontier Park during the study period from November 2002 to May 2004. Rainfall in the current and previous months were noted as present (1) or absent (0) respectively. Values with the same superscript do not differ significantly, $(P>0.05)$

Table 7.3 The phosphorus content (g/kg of the dry matter by mass) of five plant species that were sampled in different habitats on the South African side of the Kgalagadi Transfrontier Park from April to November 2003. The superscripts (^{x} and ^{y}) that precede the phosphorus values denote significance within one species in the same season in different habitats (within rows) and superscripts (^{a}, ^{b} and ^{c}) that follow the phosphorus values denote significance within one species in the same habitat in different seasons (within columns). Values with the same superscripts do not differ significantly ($P \leq 0.05$)

Table 7.4 The calcium contents (g/kg of the dry matter by mass) of five plant species that were sampled in different habitats on the South African side of the Kgalagadi Transfrontier Park from April to November 2003. The superscripts (^{x} and ^{y}) that precede the calcium values denote significance within one species in the same season in different habitats (within rows) and superscripts (^{a}, ^{b} and ^{c}) that follow the calcium values denote significance within one species in the same habitat in different seasons (within columns). Values with the same superscripts do not differ significantly ($P \leq 0.05$)

Table 8.1 Information on springbok from which faecal samples were collected on the South African side of the Kgalagadi Transfrontier Park during different seasons and in different habitats in the study period from April 2003 to November 2003

Table 8.2 Faecal nitrogen concentration of springbok on the South African side of the Kgalagadi Transfrontier Park, during the hot-wet, cold-dry and hot-dry seasons from April to November 2003. Concentrations are reported as a percentage of the dry matter by mass. The superscripts (^{x} and ^{y}) that proceed the nitrogen values denote significance in the same season in different habitats and superscripts (^{a}, ^{b} and ^{c}) that follow the nitrogen values denote significance in the same habitat, in different seasons. Values with the same superscripts do not differ significantly ($P \leq 0.05$)

Table 8.3 Faecal phosphorus concentration of springbok on the South African side of the Kgalagadi Transfrontier Park, during the hot-wet, cold-dry and hot-dry seasons from April to November 2003. Concentrations are reported as a percentage of the dry matter by mass. The superscripts (^{x} and ^{y}) that proceed the phosphorus values denote significance in the same season, in different habitats and superscripts (^{a}, ^{b} and ^{c}) that follow the phosphorus values denote significance in the same habitat, in different seasons. Values with the same superscripts do not differ significantly ($P \leq 0.05$)

LIST OF FIGURES

Fig. 5.4 The mean percentage of springbok per herd feeding in the sunlight or shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Fig. 5.5 The mean percentage of springbok per herd standing in the sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Fig. 5.6 The mean percentage of springbok per herd lying down in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Fig. 5.7 The mean percentage of springbok per herd sleeping in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Fig. 5.8 The mean percentage of springbok per herd walking in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Fig. 5.9 The mean percentage of springbok per herd playing in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Fig. 5.10 The mean percentage of springbok herds feeding in sunlight and the shade respectively during the hot-wet, cold-dry and hot-dry seasons from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Fig. 7.1 The nitrogen content of a. *Acacia erioloba,* b. *Grewia flava,* c. *Rhigozum trichotomum,* d. *Schmidtia kalihariensis* and e. *Stipagrostis obtusa* in different habitats on the South African side of the Kgalagadi Transfrontier Park in the hot-wet, cold-dry and hot-dry season from April to November 2003.

Fig. 7.2 The phosphorus content of a. *Acacia erioloba,* b. *Grewia flava,* c. *Rhigozum trichotomum,* d. *Schmidtia kalihariensis* and e. *Stipagrostis obtusa* in different habitats on the South African side of the Kgalagadi Transfrontier Park in the hot-wet, cold-dry and hot-dry season from March to November 2003.

Fig. 7.3 The calcium content of a. *Acacia erioloba,* b. *Grewia flava,* c. *Rhigozum trichotomum,* d. *Schmidtia kalihariensis* and e. *Stipagrostis obtusa* in different habitats on the South African side of the Kgalagadi Transfrontier Park in the hot-wet, cold-dry and hot-dry season from March to November 2003.

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Feeding ecology of the Kalahari springbok *Antidorcas marsupialis* in the Kgalagadi Transfrontier Park, South Africa

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Springbok *Antidorcas marsupialis* ecology was examined on the South African side of the Kgalagadi Transfrontier Park in the Kalahari, with the use of public questionnaires and field forms. Statistically significant differences were found between data that were collected by public respondents and the researcher when using the same questionnaire. Questionnaires are useful for gathering large amounts of data, but should be carefully structured to ensure the quality of the data.

Feeding was the most common activity of springbok and the frequency thereof varied during the day and between seasons. Environmental conditions and seasonal changes affected the feeding behaviour of springbok in the southwestern Kalahari. Springbok fed in direct sunlight in the mornings and moved into the shade during the afternoon. More time was spent feeding in the shade during the warmer months than during the colder

months, especially under northerly to northeasterly wind directions. Herd sizes were found to increase during the cold-dry season and decreased during the hot-wet season. Springbok and blue wildebeest *Connochaetes taurinus taurinus* displayed niche separation by competition avoidance. Springbok utilized natural licks.

Night-time observations of springbok were made during different seasons and habitats on the South African side of the Kgalagadi Transfrontier Park in 2003. Nocturnal feeding behaviour was described in the context of other similar studies. Feeding times were highlighted, yet the role and importance of nocturnal feeding remains unclear.

The nutritional content of some southwestern Kalahari food plant species were determined. The nutrients in the sampled plants showed a wider fluctuation range than plants in other regions. Phosphorus levels in the Kalahari were found to be low in general and calcium levels were higher than in other regions. Browse species contained higher crude protein levels than grass species. The nutritional value of the plants was lowest during the cold-dry season and highest during the hot-dry one.

The nutritional status of springbok in the southwestern Kalahari was assessed by using faecal profiling. The faecal nutritional status for springbok populations in different habitats and seasons was examined. Faecal nutrient levels confirmed springbok as mixed feeders with a diet composition that was between that of true browsers and grazers. Faecal concentrations of phosphorus and nitrogen were similar to that of springbok in other areas, but phosphorus intake was shown to be low, particularly during the cold-dry season. Phosphorus appears to be a limiting nutrient and may cause nutritional stress in springbok in the southwestern Kalahari during dry periods.

CHAPTER 1

INTRODUCTION

The Kalahari is a fragile arid ecosystem (Van Rooyen & Van Rooyen 1998). The springbok *Antidorcas marsupialis* (Zimmermann 1780) is one of the characteristic animal species found in the Kalahari and it forms an important part of the region's ecology (Van Rooyen *et al.* 1994). However, springbok numbers have been declining in the Kalahari over the past 100 years, but especially so in the past 20 years ([1]Skinner, pers. comm.; [2]Engelbrecht, pers. comm.; Skarpe 2001; Skinner & Moss 2004). This trend of declining springbok populations is not reported from elsewhere in southern Africa, while in the Karoo region of South Africa the population is on the increase (Skinner & Moss 2004).

Although the springbok has been studied in detail, with considerable research focus being placed on its morphology and physiology (Skinner & Louw 1996), in-depth ecological studies of springbok in the Kalahari are still lacking. Skinner & Louw (1996) provided a collective summary of springbok research up to 1996. Studies investigating the morphology of the springbok even suggested a Kalahari region subspecies (Bigalke 1970; Peters & Brink 1992). Other Kalahari studies investigated morphometrics and metabolism (Jackson *et al.* 1993; Nagy & Knight 1994; Skinner *et al.* 1996), thermoregulation (Hofmeyr & Louw 1987), water requirements (Child *et al.* 1971; Bigalke 1972; Hofmeyr & Louw 1987; Cooper 1993; Nagy & Knight 1994) and reproduction of the springbok (Jackson 1995; Skinner *et al.* 1996; Jackson & Skinner 1998). Ecological studies that broadly discussed the food plants (Leistner

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1959, 1967; Cooper 1993; Nagy & Knight 1994), feeding habits (Eloff 1959; Leistner 1967; Bigalke 1972; Williamson 1987), migrations (Eloff 1959; Skinner 1993), behaviour (Bigalke 1972; Cooper 1993; Jackson 1995), herd size (Skinner *et al.* 1996), depredation (Mills 1984; Jackson 1995), territoriality (Bigalke 1972; Jackson *et al.* 1993; Jackson 1995; Skinner *et al.* 1996; Jackson & Skinner 1998), habitat use (Parris 1970; Bothma 1971; Mills & Retief 1984; Vorster 1996; Bergström & Skarpe 1999), and response to rainfall (Bothma 1972; Bothma & Mills 1977) of the springbok have been done, but some of these studies were brief and do not provide much detail.

Natural springbok habitats have recently undergone significant changes (Vorster 1996). In general, the springbok appears to be adapted to a life in arid areas, and is able to cope well with changing environmental pressures (Louw & Seely 1982; Mills & Retief 1984; Mills & Haagner 1989; Spinage & Matlhare 1992; Skinner & Louw 1996; Skinner & Moss 2004). However, studies of the sex ratio within populations (Bednekoff & Ritter 1997), and the morphometrics and reproduction (Skinner *et al.* 1996) of the springbok do not shed any light on the observed declining numbers. Depredation can also not account for the decline in numbers because no significant increase in predator numbers or shifts in prey selection have been recorded ([2]Engelbrecht, pers. comm.; Skinner & Moss 2004). Basic ecological studies have described some aspects of springbok behaviour (Bigalke 1972) but no substantial follow-up research has since been done. Little is also known of the nutritive value of some commonly found plants that springbok use in their Kalahari habitat, and it is uncertain whether their feeding behaviour has changed during the last several

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decades. The springbok population decline in the Kalahari therefore remains a mystery.

The feeding ecology of springbok was examined by various researchers, mostly as a part of their broader research interests. Bigalke (1972) made feeding-related observations which formed part of a study on springbok behaviour. Van Hoven *et al.* (1984) reported on the digestibility of some food plants of the Kalahari, some of which are used by springbok. Nagy & Knight (1994) investigated the metabolic rates and diet composition of springbok in the Kalahari. The nutritional contents of the springbok's diet were studied by Vorster (1996) as part of habitat evaluation research, and the effect of seasonal diet quality fluctuation on springbok reproduction was also investigated.

The hypotheses that were tested in the present study were:

1. Springbok feeding behaviour is significantly affected by environmental and seasonal conditions.
2. Food plants in the southwestern Kalahari have a low nutritional value.
3. Springbok in the southwestern Kalahari experience nutritional stress during dry periods as a result of the nutritionally depleted food plants.
4. Phosphorus intake is low and hence, phosphorus is a limiting nutrient of springbok in the southwestern Kalahari.

Understanding the ecology of an animal is fundamental to effective conservation of that animal. Effective conservation of the Kalahari and its springbok populations can therefore only be achieved by gaining insight into its region-specific ecology and by putting sound management practices into place. The present study does not endeavour to provide a succinct explanation for the decline of the springbok population in the Kalahari. The main objective of the research was to address the lack of knowledge on the specific feeding ecology of springbok in the southwestern Kalahari.

Three key questions were therefore investigated. Firstly, the feeding habits were examined and activity was recorded under different environmental circumstances by means of a questionnaire to determine the effect of some environmental and seasonal factors on springbok feeding behaviour. Secondly, the prevalence of nocturnal feeding was examined to establish whether it could be a behavioural adaptation to increase moisture intake. Thirdly, the seasonal changes in nutritive value of some of the commonly used plant species and the faecal nitrogen and phosphorus concentrations of the springbok were determined, to establish whether springbok were under nutritional stress during dry periods. The analyses of the questionnaire survey generated some interesting results. This led to a spin-off evaluation of how satisfactory a questionnaire approach is for investigating the feeding ecology of the Kalahari springbok.

The major part of this dissertation has been written in article format. The articles have been prepared for different journals and the format of each article follows the guidelines for that particular journal. In doing so, some repetition was impossible to prevent because each article is preceded by a general description of the study area, and contains a general discussion. Headings and subheadings within articles are numbered for ease of cross-referencing.

CHAPTER 2

STUDY AREA

The Kalahari System is an arid savanna or semidesert, relatively unspoiled within the national parks of South Africa, even though it occurs in an ecologically fragile environment (Van Rooyen & Van Rooyen 1998). It is some 2.5 million km² in extent and is a continuous stretch of sand, stretching diagonally across southern to central Africa (Main 1987; Thomas & Shaw 1991). The area between the Nossob and Auob riverbeds, northwards up to the Namibian border was proclaimed as the Kalahari Gemsbok National Park on 31 July 1931 (Mills & Haagner 1989). In 1972, the adjacent area in Botswana was designated the Gemsbok National Park and in 2000 the two across-border parks were officially joined to form one park, the Kgalagadi Transfrontier Park (Donaldson 2000). The resulting park forms the largest conservation area within the southern Kalahari and one of the largest national park systems in the world (Mills & Haagner 1989) (Fig. 2.1). The present study focused on the South African side of the Kgalagadi Transfrontier Park, which covers an area of 9 700 km² (Knight 1995). Together with the Botswana side the transfrontier park represents some 36 300 km² of conservation area. The South African side of the Park is situated between 24°15'S and 26°30'S, and 20°00'E and 20°45'E (Fig. 2.1). Within the Kgalagadi Transfrontier Park there are no border fences between the two countries involved.

2.1. Topography

The South African side of the Kgalagadi Transfrontier Park consists predominantly of red sand dunes (Castley *et al.* 2002), underlain by calcareous stone which is noticably

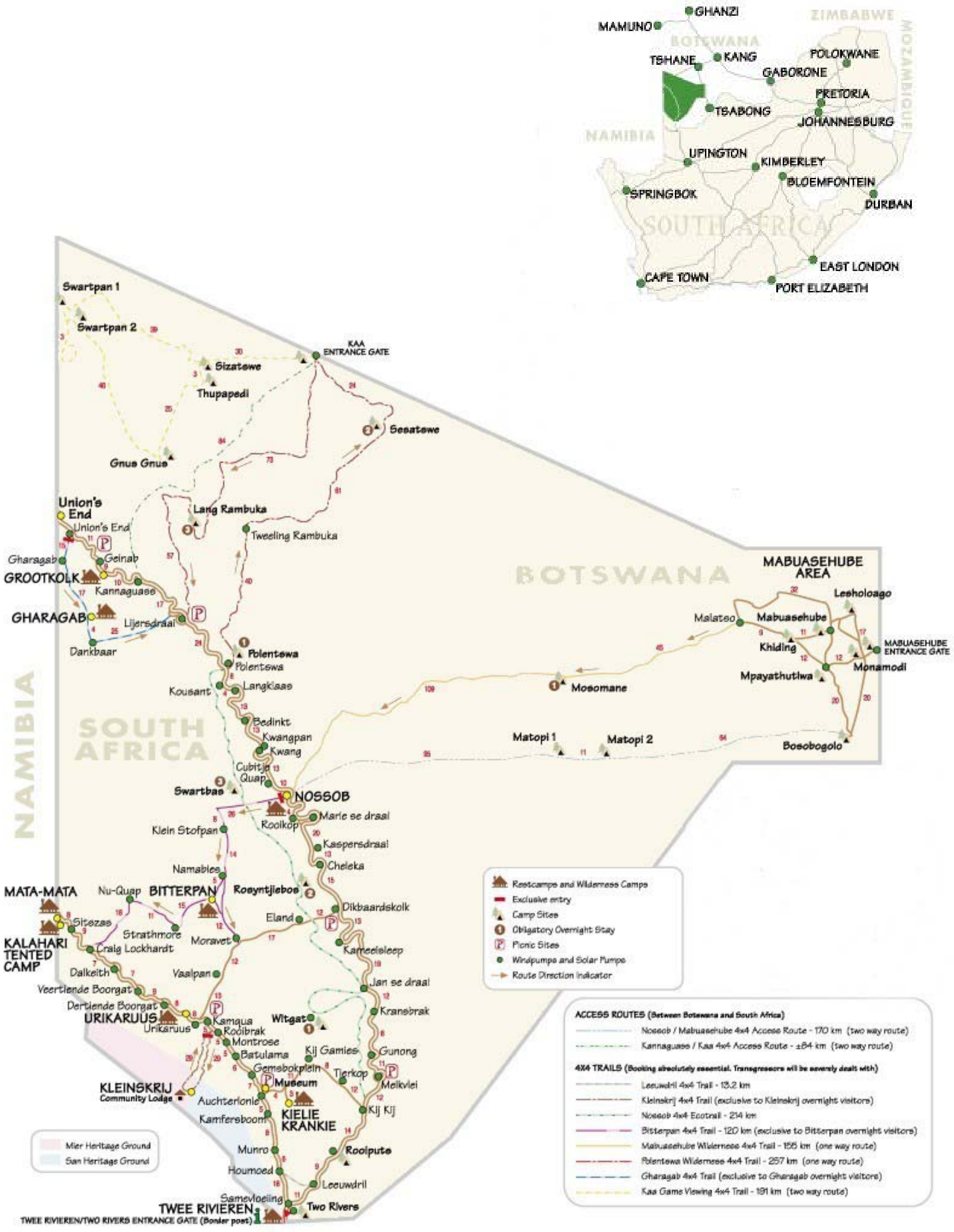

Fig 2.1 The location of the research area between the Auob and Nossob Rivers on the South African side of the Kgalagadi Transfrontier Park and the location of the park within southern Africa (adapted from http://www.sanparks.co.za/parks/kgalagadi/ tourism/map.php).

exposed in the two main dry riverbeds of the Auob and Nossob Rivers (Jackson 1995; Van Rooyen & Van Rooyen 1998). These two dry riverbeds run through the dunes to converge just north of Twee Rivieren in the south. Pans are dispersed throughout the Park (Parris 1976), increasing in number northwards and eastwards into Botswana. Some 86 artificial waterholes are distributed throughout the park (Bothma *et al.* 1993), some of which have subsequently been closed down. The altitude varies between 870 and 1080 m above sea level.

2.2 Geology

Four main geological units have been identified in the southwestern Kalahari, namely basal gravels and clays, calcareous clays, calcareous sandstones, and aeolian sands which are most extensively present (Smit 1977). Kalahari sand consists predominantly of quartz grains with some heavy minerals and derives its origin from locally weathered rock, supplemented by material transported into the region from elsewhere (Thomas & Shaw 1991).

Kalahari soils develop on Kalahari sands and are characterised by moderate acidity and poor fertility, with low levels of phosphorus, potassium and nitrogen (Thomas & Shaw 1991). Where the overlying sand layer is thin enough to expose the underlying calcrete, calcic horizons are formed, such as those that are found in the pans and along the drainage lines.

2.3 Climate

The Kalahari falls within a summer rainfall area with a mean annual rainfall that varies significantly by region, but which usually amounts to around 170 to 400 mm annually (Jeltsch *et al.* 1997). The rainfall is erratic (Skarpe 1986; Tyson 1986; Mills & Haagner 1989) and from 1980 to 2006, the mean annual rainfall as measured at the Nossob Rest Camp, Mata-Mata Rest Camp, Twee Rivieren Rest Camp and the Van Zylsrus Town weather station was 180.5 mm[3] (Table 2.1). Drought years are common (Knight 1995).

Different seasonal classifications have been proposed, but it is generally agreed that three ecological seasons occur in the Kalahari (Leistner 1967; Mills & Retief 1984; Van Rooyen & Van Rooyen 1998). These can be defined as the hot-wet season (January to April), the cold-dry season (May to August) and the hot-dry season (September to December). During the study period the rainfall did not follow this long-term trend, with a significant proportion (63%) of the precipitation occurring from September to November 2003. The temperature variation is extreme, with recorded winter lows of around -10°C and summer highs of around 45°C (Van Rooyen *et al.* 1990). Dust storms sometimes occur (Mills & Haagner 1989).

2.4 Vegetation

The vegetation of the southwestern Kalahari has been described by various researchers over the past several decades. In a phytogeographical context, the southern Kalahari was first included under the Karoo-Namib Region (Leistner 1967). Werger (1973) gave a broad scale review of the southern Kalahari's phytogeographical affinities, and he discussed the merits of including this area into the Karoo-Namib Region as opposed to the Zambezian Domain of the Sudano-Zambezian Region. In 1978, Werger refined his phytogeographical classification and

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[3] Electronic data supplied by the South African Weather Bureau, 2005.

Table 2.1

Mean annual precipitation (mm) in the southwestern Kalahari of South Africa from 1980 to 2005 based on data as supplied electronically by the South African Weather Bureau, 2005

Weather station	Mean annual precipitation (mm)
Twee Rivieren Rest Camp	182.5
Nossob Rest Camp	179.3
Mata-Mata Rest Camp	159.7
Van Zylsrus Town	200.4
Regional mean	**180.5**

reclassified and described the southern Kalahari as a distinct subdomain of the Karoo-Namib Region. Skarpe (1986), amongst others, supported this view. Later, Werger (1986) produced a map of the vegetation of southern Africa in which he included the present study area's vegetation as part of the "Open *Acacia* savanna of the southern Kalahari".

According to the regional classification of Acocks (1953), the southern Kalahari falls within the vegetation described as Kalahari Thornveld (Veld Type 16). The vegetation that presently falls within the South African side of the Kgalagadi Transfrontier Park, was subsequently broadly classified by Leistner (1959, 1967) into six zones. Each zone was roughly described and a list of typical plant species was compiled. The first phytosociological survey of the vegetation of the Kalahari Gemsbok National Park, today known as the South African side of the Kgalagadi Transfrontier Park, was done by Leistner & Werger (1973) and 12 plant communities were distinguished and described, however, they were not mapped. It was found that the pattern of the plant communities was determined by soil characteristics such as soil-water regime and nutrient availability. During the same period as Leistner & Werger's study, a habitat map of the Kalahari Gemsbok National Park was produced by Bothma & De Graaff (1973), again describing six major habitats, although different from those earlier described by Leistner (1967). Some smaller habitat units were also described during the study of Bothma & De Graaff (1973) based roughly on the vegetation structure and characteristic plant species.

A number of smaller scale studies followed, such as that of Van Rooyen *et al.* (1984) who reported on short-term vegetation dynamics of the southern Kalahari, noting that the herbaceous species composition changed often and sometimes on a large scale.

Low & Rebelo (1998) revised the vegetation classification of southern Africa and described seven subregions for the southern Kalahari of which the "Shrubby Kalahari Dune Bushveld" covered the main area considered in the present study. All of the above regions fall within the Savanna Biome (Low & Rebelo 1998). A thorough study of the vegetation of the southern Kalahari by Lubbinge (1999) identified 24 plant communities within the Kalahari Gemsbok National Park. Lubbinge (1999) did not map all of his communities as separate entities, but combined them into 14 mapping units. A floristic analysis and map of the vegetation of the entire Kgalagadi Transfrontier Park was produced in 2000 (Van Rooyen 2000), with 14 plant communities occurring on the South African side of the park and 13 on the Botswana side. The plant communities were grouped according to habitat type into eight groups for the South African side of the Kgalagadi Transfrontier Park (Van Rooyen 2000). The descriptions for these groups are as follows:

1. Communities of the dune crests that occur on coarse, red, loose sand and are dominated by tall grass species, in particular by *Stipagrostis amabilis*, with occasional woody species such as *Acacia haematoxylon* and *Boscia albitrunca*.
2. Communities of the grassy plains that occur on flat to undulating, deep, reddish sand. They are characterised by grass species such as *Centropodia glauca* and *Schmidtia kalihariensis*, with woody species such as *Acacia haematoxylon* and *Grewia flava*.

3. Communities of the dune slopes and valleys that occur on low dunes and plains on deep, loose, reddish sand. Plant species such as *Acacia erioloba* and *Acacia luederitzii* are characteristic of this open tree savanna, with shrubs and dwarf shrubs such as *Grewia flava* and *Rhigozum trichotomum* also abundant.
4. Communities of the plains that are found on slightly compact, pinkish sand and are structurally defined as an open to a dense tree and shrub savanna. *Acacia erioloba* and *Schmidtia kalihariensis* are the dominant plants here.
5. Communities that occur near pans and rivers, and that are also found in dune valleys on compact, pink to whitish sand with a high calcrete content. Scattered individuals of *Acacia erioloba* occur interspersed with dense stands of dwarf shrubs such as *Aptosimum albomarginatum* and *Rhigozum trichotomum*.
6. Communities of calcrete outcrops that are found on whitish sand near pans and rivers (notably the Auob and Nossob Rivers). Dwarf shrubs such as *Rhigozum trichotomum* dominate these communities, with scattered individuals of *Acacia erioloba* and *Grewia flava* present. The grass layer is poorly developed.
7. Communities of the pans that occur on white, calcareous sand to clayey soils and which often show concentric zonation. Plant species such as *Salsola etoshensis* and *Sporobolus coromandelianus* typically occur on pan floors or the periphery of pans, with plant species such as *Stipagrostis obtusa* and *Rhigozum trichotomum* further away.
8. Communities of the Auob and Nossob riverbeds that are found on silty or clayey alluvial soils. Various combinations of plant species are found in these communities, and these may include *Acacia erioloba*, *Galenia africana, Rhigozum trichotomum* and *Stipagrostis obtusa*.

Range degradation in the southern Kalahari is a serious problem and several studies have used satellite imagery to determine the severity and extent of the degradation (Palmer & Van Rooyen 1982; Choudhury & Tucker 1987; Ringrose & Matheson 1991; Verlinden & Masogo 1997).

Natural fires that are caused by lightning are known to occur, usually from September to April, and are considered part of the Kalahari ecosystem dynamics (Van Rooyen 2000; Kgalagadi Transfrontier Park Management Plan 2002). However, such fires are infrequent and generally only occur after years of exceptional precipitation (Van Rooyen 2001). The short-term effect of fire on vegetation can be severe as in the case of woody species, although most woody plants are well adapted to fire, showing a mean fire-induced mortality of <20% (Van Rooyen 2001).

2.5 Fauna

The South African side of the Kgalagadi Transfrontier Park has a rich diversity of animals including 60 species of mammal, 55 species of reptile and around 300 species of bird (Van Rooyen 2001). Seven types of antelope are indigenous to the area (Knight 1995). They are blue wildebeest *Connochaetes taurinus taurinus*, eland *Taurotragus oryx*, gemsbok *Oryx gazella gazella*, grey duiker *Sylvicapra grimmia*, red hartebeest *Alcelaphus buselaphus buselaphus*, springbok and steenbok *Raphicerus campestris*. The main predator of Kalahari springbok is the cheetah *Acinonyx jubatus*, with some kills made by lions *Panthera leo* (Mills & Haagner 1989) and probably leopard *Panthera pardus*.

CHAPTER 3

GENERAL METHODS AND MATERIALS

Following is a general description of the materials and methods that were used during the present study. More detailed descriptions are included with the chapters where they apply.

A set of observable variables relating to the activity and herd characteristics of springbok *Antidorcas marsupialis* was listed. A questionnaire was then compiled which incorporated these variables and an illustrated example was provided with each question on the questionnaire. The questionnaire was reviewed by five members of the public with limited ecological knowledge and changed according to their feedback. The questionnaire was then duplicated and distributed to staff and visitors to the South African side of the Kgalagadi Transfrontier Park from November 2002 to May 2004. During this period, the researcher collected similar data from the same area by using a field data sheet that was based on the questionnaire. The observation technique was similar to road strip counting and data collection was therefore random. Observations were made from a vehicle *en route* to various destinations. Most of the observations were made within the Nossob and Auob riverbeds, since springbok tend to concentrate there. Visibility varied but was generally up to 150 m, depending on the landscape. Binoculars and/or a spotting-scope were used when it was necessary.

The data from completed questionnaires were transformed into numerical codes, and these codes were digitally captured, by using Microsoft® Excel, into a numerical matrix. Numbers of springbok were converted into percentages of the total herd. The data were classified into ranges or categories wherever it best suited the statistical model that was used.

The Nossob riverbed, Auob riverbed, pans and the dunes were defined as the four habitat types within the study area. Five sampling sites were randomly selected within each of these habitats and *Acacia erioloba, Rhigozum trichotomum*, *Schmidtia kalihariensis*, *Stipagrostis obtusa* and *Grewia flava* leaves and twigs were collected within the habitats where they occur. Samples of these plant species were collected from 07:30 to 19:30 during the hot-wet (January to April), cold-dry (May to August) and hot-dry (September to December) seasons. All plant samples were pooled from several individual plants with at least five replicates per species.

During the same study period, 36 springbok faecal samples were also collected across all four habitat units. Faecal sampling was random and depended on encountering springbok *en route* between destinations. Faecal samples were collected from single springbok or pooled from individuals within a herd and took place from 06:30 to 17:30. Only fresh faecal samples were collected, to avoid the effects of exposure (Wrench *et al.* 1996). Faecal samples were not collected during or immediately following rain. Plant and faecal samples were placed in annotated paper bags and later oven-dried at 60°C to a constant mass.

Plant and faecal samples were milled through a 1 mm screen (Association of Official Analytical Chemists 1990) and submitted to the University of Pretoria’s Nutrilab for analyses according to the guidelines of the Association of Official Analytical Chemists (1990). Calcium, crude protein, nitrogen and phosphorus concentrations were determined for each plant and faecal sample. Nitrogen concentration was determined by using the macro-Kjeldahl method distilling with a Kjeltec system model 1026. Crude protein was calculated from the nitrogen content as a percentage. Calcium concentrations were determined by using the Perkin Elmer 2380 Atomic Absorption Spectrophotometer pp Ay II. Phosphorus concentrations were determined by using a Technicon Auto Analyzer II according to the standard photometric method.

The chemical analysis results were captured into numerical matrixes by using Microsoft® Excel. Plant and faecal samples from the same habitat were classified as repetitions of each plant species or springbok population. Data were analysed with uni- and multivariate statistical techniques and all analyses were done by using SAS®[Ψ] software. The hypothesis of independence was tested by using P-values, where $P \leq 0.05$ signified that the variables tested were not independent.

[Ψ] SAS® Software Version 8.2 supplied by The SAS Institute Inc., SAS Campus Drive, Cary, NC 27512, USA, running under z/VM 4.4.0 (RSU 0404) on the mainframe computer IBM Z800 2066/0C1 of the University of Pretoria.

CHAPTER 4

THE USE OF QUESTIONNAIRES TO COLLECT ECOLOGICAL DATA: IMPLICATIONS AND LESSONS LEARNT FROM A STUDY OF SPRINGBOK IN THE KALAHARI

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Abstract – Questionnaires were used to gather ecological information on the decreasing springbok population of the South African side of the Kgalagadi Transfrontier Park. Statistically significant differences were found between data collected by public respondents and the researcher when using the same questionnaire. In some instances, questions may have been misinterpreted or were unclear. Terms could have been ill-defined or lack of proper understanding was not identified. Requesting too much detail proved cumbersome to public respondents. Public respondents preferred observing large herds to single animals, but may have ended up with rushed and inaccurate counts. Public records were collected in a less objective manner than those of the researcher and were influenced by game-viewing opportunities and related factors.

Keywords: Data accumulation, Kalahari, misinterpretation, public respondents, questionnaires.

4.1 Introduction

Researchers in a variety of fields use public questionnaires as a means to collect large amounts of data. The use of questionnaires in ecology has been on the increase over the last 10 years[1], especially with regards to formulating publicly acceptable, sound ecological management processes. Such questionnaires can take on a range of different formats, but essentially, specific data are collected via direct questions. It is generally assumed that a well-compiled questionnaire provides a platform through which reliable information can be gathered[2, 3], irrespective of who collects or records it. Although a questionnaire is therefore often considered to be an effective and relatively affordable tool, this paper explores some flaws and difficulties that were discovered during an ecological questionnaire-based study on springbok *Antidorcas marsupialis* in the southwestern Kalahari.

White *et al.*[1] gave a thorough review of the use of questionnaires in ecology up to 2005. Although Reading *et al.*[4] used questionnaires to study the distribution of an adder species in Scotland, most ecological questionnaire-based studies involve an economic factor and few are purely based on ecological research. Researchers have used questionnaires to report on the economic aspect of rare and endangered species[5], investigate the management of foxes in different habitats[6], examine the economic value of grey seals in England[7] and to determine the distribution of animal[8] and invasive plant[9] species.

4.2 Materials and methods

In this study, a set of observable variables relating to the activity and herd characteristics of the springbok were listed (*Appendix A*). From these data a questionnaire was compiled. Each question of the questionnaire was illustrated by way of an example. The questionnaire was then distributed to staff and visitors to the Kgalagadi Transfrontier Park, South Africa, over a period of 19 months from November 2002 to May 2004. During the same period, the researcher collected similar data by using a field data sheet that was based on the questionnaire. Data sampling was considered random and the observation technique was related to road strip counting[10] and was carried out from a vehicle *en route* to various destinations. Most observations were made within the dry riverbeds of the Nossob and Auob Rivers, since this is where springbok tend to concentrate[11]. Visibility varied, but was generally up to around 150 m depending on the topography of the landscape. Binoculars and/or a spotting-scope were used when necessary.

The researcher considered the habitat to be a plain wherever the landscape was a sizeable flat area. A grass-dominated habitat was considered to constitute a habitat where the grass layer contributed most to the canopy cover. Playing behaviour was considered as any recreational interaction of immature springbok with each other and it usually involved pushing and chasing each other with their horns. The researcher considered a waterhole as being close to a springbok herd, when the waterhole could be seen from the position where the observation was made. However, windmills at waterholes in the study area are gradually being replaced with inconspicuous solar pumps, which will complicate future estimation of animal proximity to water.

The data from completed questionnaires were transformed into numerical codes and these codes were captured into a matrix by using Microsoft® Excel. Numbers of springbok were converted into percentages of the total herd. Data were classified into ranges or categories wherever it best suited the analytical model or question at hand (χ^2 close to 1). Amongst other categories, the origin of each questionnaire was specified as either 'Public respondent' or 'Researcher'. All analyses were done by using SAS®[Ψ]. Frequency tables were constructed with a Chi-square test to test the hypotheses of independence. A value of $P \leq 0.05$ signified that the variables tested were not independent.

4.3 Results and discussion

A total of 2 000 questionnaires were distributed, of which 955 (47.7%) were returned. This response rate is of the same order as that of another ecological distribution and status research project[4], and is considered to be an adequate response rate[12]. The researcher completed 303 field data sheets and public respondents completed 652 questionnaires. Upon examining the initial results, it was discovered that there was a significant dependence on the origin of the data for most variables, i.e. whether the researcher or a public respondent had collected the data (Table 4.1). Significant differences ($P \leq 0.05$) were found for reasonably simple questions and variables where inconsistency between knowledgeable and uninformed individuals had not been expected. In some instances, the observations of the researcher could be considered as ground-truthing for public observations. For example, the tree dominance at an observation location, as specified by a public respondent, can be verified or rejected by the researcher's records at the same location.

[Ψ] SAS® Software Version 8.2 supplied by The SAS Institute Inc., SAS Campus Drive, Cary, NC 27512, USA, running under z/VM 4.4.0 (RSU 0404) on the mainframe computer IBM Z800 2066/0C1 of the University of Pretoria.

Table 4.1 Observer dependence of variables on springbok behaviour on the South African side of the Kgalagadi Transfrontier Park from November 2002 to May 2004. Observer dependence was based on an analysis of frequency tables with a Chi-square test for independence where P values of ≤ 0.05 signify that an observed variable was dependent on the nature of the observer

Variable	**Observer dependence**	
	Yes	**No**
Total number of springbok	<0.0001	
Observation within riverbed		0.1592
Observation within a plain	<0.0001	
Observation in duneveld		0.0527
Observation in pan		0.1457
Trees dominant within the habitat		0.1252
Grasses dominant within the habitat	<0.0001	
Shrubs dominant within the habitat		0.9149
Observation near a camp		0.1719
Observation near a waterhole	<0.0001	
Observation near a picnic spot		0.2406
Total number of blue wildebeest	0.0002	
Total number of red hartebeest		0.0699
Total number of gemsbok	<0.0001	
Distance between gemsbok and springbok (m)	<0.0001	
Distance between red hartebeest and springbok (m)		0.1540
Distance between blue wildebeest and springbok (m)		0.0565
*Percentage of springbok herd feeding in sunlight	<0.0001	
* Percentage of springbok herd feeding in shade	0.0009	
* Percentage of springbok herd standing in sunlight	<0.0001	
* Percentage of springbok herd standing in shade	<0.0001	
* Percentage of springbok herd lying down in sunlight	0.0015	
* Percentage of springbok herd lying down in shade	<0.0001	
* Percentage of springbok herd sleeping in sunlight		0.1653
* Percentage of springbok herd sleeping in shade		0.1814
* Percentage of springbok herd walking in sunlight	<0.0001	
* Percentage of springbok herd walking in shade		0.0441
* Percentage of springbok herd playing in sunlight	0.0023	
* Percentage of springbok herd playing in shade		0.1346
* Percentage of springbok herd eating grass	<0.0001	
* Percentage of springbok herd eating shrubs	0.0003	
* Percentage of springbok herd eating trees		0.5525
Direction in which springbok were moving	<0.0001	
Duration of observation (minutes)	<0.0001	

*Numbers were converted into percentages of the total herd after collection.

The most noteworthy variables where significant differences were found between data recorded by the researcher and those recorded by public respondents (Table 4.1) will now be briefly discussed.

Total number of springbok

A significant difference ($P<0.0001$; $\chi^2=78.96$; df=2) was found between data recorded by the researcher and public respondents, with regard to this variable. The researcher recorded significantly fewer large-herd counts than the public respondents. Only 28.2% of the researcher's observations consisted of herds of springbok of more than six animals as opposed to 58.9% of those made by the public respondents (Table 4.2). It therefore appears that the public concentrated specifically on larger herds.

Several explanations can be proposed. Firstly, it is assumed that large herds of animals are better for game-viewing than small herds; and secondly that public respondents may subconsciously have recorded and observed only the large herds of springbok as a result of information on posters and in presentations which stated that springbok numbers were declining in the Kalahari. It could also be assumed that public respondents did not always see single springbok. Large herds are easier to perceive than single animals.

Observations made on plains

In 5.8% of all the observations, the habitat type was positively identified as a plain or valley, while in the remainder 94.2% of the cases it had either been specified as not being a plain or was not specified at all ($P<0.0001$; $\chi^2=18.05$; df=1). The researcher recorded three positively identified plains in contrast to the 52 reported by

Table 4.2 Categorised data used to examine the differences between the researcher's and public respondents' recordings of springbok herd counts on the South African side of the Kgalagadi Transfrontier Park from November 2002 to May 2004 (χ^2=78.96; df=2)

Item	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
Single animals	152	176	46.3	53.7	51	27.0	**328**	34.5
2 - 6 animals	62	92	40.3	59.7	20.8	14.1	**154**	16.2
>6 animals	84	384	18.0	82.0	28.2	58.9	**468**	49.3
Total	**298**	**652**	**-**	**-**	**100.0**	**100.0**	**950**	**100.0**
Percentage	31.7	68.3	-	-	-	-	**-**	-

the public. Possible explanations for the significant difference between the origin of the data is that the question could have been misinterpreted or that the definition of a plain or valley was not clear to the public.

Dominant grass layer within the habitat

This variable was identified in 48.5% of the questionnaire entries, leaving 51.5% of questionnaires with unspecified or missing information. Apart from that, 55.3% of the public respondents' observations were specified to have occurred within grass dominated habitats compared with 4.8% (three observations in total) of the researcher's observations (Table 4.3). Of all observations where grass dominance was positively identified, 98.7% were derived from public respondents' questionnaires and 1.3% from the researcher. A possible explanation for the significant difference ($P<0.0001$; $\chi^2=55.79$; $df=1$) between the origin of the data relating to this variable is that the question could have been misinterpreted, or that the definition of a habitat where the grass layer is dominant was not clear or properly understood. It is suspected that the public considered most habitats with a general presence of a grass layer as being grass-dominated.

Furthermore, the canopy cover of a habitat's grass layer can easily be misjudged by untrained people when viewed from a vehicle, rather than by moving through it. Requesting a perception or judgement from public respondents could pose a risk to data accuracy[13] due to differing public opinions[14], and word choice in the question is important.

Table 4.3 Categorised data used to examine the differences between the researcher's and public respondents' recordings of grass dominance within the habitat occupied by springbok from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park ($\chi^2=55.79$; df=1)

Item	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
Grass not dominant	60	180	25.0	75.0	95.2	44.7	**240**	51.5
Grass dominant	3	223	1.3	98.7	4.8	55.3	**226**	48.5
Total	**63**	**403**	**-**	**-**	**100.0**	**100.0**	**466**	**100.0**
Percentage	13.5	86.5	-	-	-	-	-	-

Observations near a waterhole

Both public respondents (73.5%) and the researcher (92.1%) recorded most of their observations as not being close to a waterhole. Of all the observations that were recorded close to a waterhole, 87.8% were recorded by public respondents and 12.2% by the researcher (Table 4.4).

A possible explanation for the significant difference ($P<0.0001$; $\chi^2=43.77$; df=1) that was found between the origin of the data relating to this variable was that the proximity to water had not been clearly defined in the questionnaire. Therefore, the number of sightings made by public respondents who considered it to be close to a waterhole could be inflated. It is therefore recommended that future questionnaires specify a distance, e.g. within a radius of 50 m from a waterhole, to indicate the proximity to water.

Number of blue wildebeest and gemsbok in the vicinity of springbok

There was a significant difference between data recorded by the researcher and by public respondents for the number of blue wildebeest ($P=0.0002$; $\chi^2=17.48$; df=2) and gemsbok ($P<0.0001$; $\chi^2=43.51$; df=2) (Tables 4.5 & 4.6) in close proximity of springbok. Most of the researcher's observations showed that no blue wildebeest ($P=0.022$; $\chi^2=7.6$; df=2) or gemsbok occurred near springbok, followed by a count of one animal being found close to the springbok. The presence of more than one individual near springbok was even more infrequent (Table 4.5 & 4.6). Public respondents also mostly recorded no gemsbok or blue wildebeest near springbok, but these were followed by records of more than one blue

Table 4.4 Categorised data used to examine the difference between the researcher's and public respondents' observations of springbok near a waterhole, from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park (χ^2=43.77; df=1)

Item	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
Waterhole nearby	279	479	36.8	63.2	92.1	73.5	758	79.4
Waterhole not nearby	24	173	12.2	87.8	7.9	26.5	197	20.6
Total	**303**	**652**	**-**	**-**	**-**	**100.0**	**955**	**100.0**
Percentage	31.7	68.3	-	-	-	-	-	-

Table 4.5 Categorised data used to examine the difference between the researcher's and public respondents' observations of blue wildebeest counts close to springbok, during the study period from November 2002 to May 2004 in the South African side of the Kgalagadi Transfrontier Park (χ^2=17.48; df=2)

Item	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
No blue wildebeest	279	563	33.1	66.9	94.9	86.6	842	89.2
One blue wildebeest	11	36	23.4	76.6	3.7	5.5	47	5.0
>1 blue wildebeest	4	51	7.3	92.7	1.4	7.9	55	5.8
Total	**294**	**650**	**-**	**-**	**100.0**	**100.0**	**944**	**100.0**
Percentage	31.7	68.3	-	-	-	-	-	-

Table 4.6 Categorised data used to examine the difference between the researcher's and public respondents' observations of gemsbok counts close to springbok, during the study period from November 2002 to May 2004 in the South African side of the Kgalagadi Transfrontier Park (χ^2=43.51; df=2)

Item	Number of observations		Percentage distribution across rows		Percentage distribution across columns		Total	Percentage
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
No gemsbok	283	511	35.6	64.4	95.3	79.0	794	84.1
One gemsbok	10	46	17.9	82.1	3.4	7.1	56	5.9
>1 gemsbok	4	90	4.3	95.7	1.3	13.9	94	10.0
Total	**297**	**647**	**-**	**-**	**100.0**	**100.0**	**944**	**100.0**
Percentage	30.8	69.2	-	-	-	-	-	-

wildebeest (7.9% of observations) and gemsbok (13.9% of observations) respectively, while records of a single blue wildebeest (5.5% of observations) and gemsbok (7.1% of observations) were recorded with the lowest frequency. The same general pattern was found for red hartebeest counts close to springbok, but the difference between the observations of public respondents and the researcher was not significant ($P=0.0699$; $\chi^2=5.32$; $df=2$). Possible explanations for the difference in blue wildebeest and gemsbok counts for public respondents and the researcher could be that public respondents subjectively avoided or ignored single animals because of the labour involved with filling in the questionnaire just for a single animal. Also, as mentioned before for springbok, large herds of animals are better for game-viewing than small herds and consequently could have been noticed more often.

Distance between gemsbok and springbok

A significant difference was found in the recorded distance between gemsbok and springbok when the data of the public respondents were compared with those of the researcher ($P<0.0001$; $\chi^2=36.16$; $df=3$) (Table 4.7). Both public respondents and the researcher's observations followed the same ranking in terms of the proportions of observations falling within each category of no data, 0–20 m apart, 21–50 m apart and >50 m apart (Table 4.7).

The most pronounced difference was found for the no data category, where public respondents recorded proportionally fewer (79.4%) observations than the researcher (94.7%). An analysis of proximity data of blue wildebeest and red hartebeest to springbok found the origin of the data not to be significant ($P=0.154$; $\chi^2=5.26$; $df=3$). A possible explanation for the abovementioned difference

Table 4.7 Categorised data used to examine the differences between the researcher's and the public respondents' observations of the distance between gemsbok and springbok, from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park (χ^2=36.16; df=3)

Item	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
No data	284	512	35.7	64.3	94.7	79.4	796	84.2
0-20 m apart	6	41	12.7	87.3	2.0	6.4	47	5.0
21-50 m apart	3	28	9.7	90.3	1.0	4.3	31	3.3
>50m apart	7	64	9.9	90.1	2.3	9.9	71	7.5
Total	**300**	**645**	**-**	**-**	**100.0**	**100.0**	**945**	**100.0**
Percentage	31.8	68.2	-	-	-	-	-	-

is that public respondents avoided counting solitary springbok, thus having more gemsbok proximity recordings overall. Solitary springbok were counted in the presence of gemsbok only in 26.2% of cases (P=0.0072; χ^2=9.86; df=2) compared with >1 springbok.

A problem with aggregated data such as those that were examined here is that it was not possible to correlate variables at the level of individuals. This is a phenomenon that is known as an 'ecological fallacy'[15]. The fact that the distance between springbok and gemsbok was similar in most recordings is questionable because it is likely that different springbok and gemsbok individuals would respond differently to variable environmental and social factors.

Springbok activities

The origin of the data significantly affected the springbok activity counts. Many different activities were specified and an in-depth technical discussion of the differences due to origin is beyond the scope of this paper. However, some influential factors are discussed. Differences between data recorded by the researcher and the public respondents could possibly be ascribed to the public avoiding filling in forms for single animals and large herds. Besides public game-viewing preferences, filling in the questionnaires for single animals may have been considered monotonous, because many single springbok are present in the Kgalagadi Transfrontier Park[16]. Although it appears that larger herds were preferred to single animals for public reporting, counting large herds may also have been considered too tiresome.

Public respondents may have had more pleasant viewing times than the researcher, i.e. they only did observations when weather conditions were favourable. This could affect the recordings specified as being in sunlight or shade and illustrates subjective data collection by public respondents. Most springbok activity observations on the questionnaires compiled by public respondents were zero or missing. This may be attributed to the length and number of questions in the questionnaire[2]. Respondents may have selected one or two apparent activities to represent the activities of a particular herd, disregarding the rest of the options available on the questionnaire. These so-called nonresponses are known to affect survey results considerably and may lead to incorrect interpretation of data[17, 18, 19]. The questionnaire may also have been too detailed for public use, generating some nonresponses.

Direction in which springbok were moving

In the majority of both the researcher and the public respondents' observations, springbok were recorded as not moving in a particular direction (80.4% and 69.9% respectively). Public respondents' and the researcher's observations switched rankings between east- and westward movement, being 7.8% eastward and 5.7% westward in the case of the public respondents and 0.7% westward and 0.3% eastward in the case of the researcher ($P<0.0001$; $\chi^2=37.48$; df=4) (Table 4.8). In the Nossob riverbed, the researcher recorded most observations on actual movements as being in a southerly direction (10.9%) followed by a northerly direction (7.3%), whereas the public respondents switched rankings and recorded most movements to be in a northerly (9.7%) followed by a southerly (8.8%) direction (Table 4.9). The difference between the rankings was found to be statistically significant ($P=0.0104$; $\chi^2=13.20$; df=4).

Table 4.8 Categorised data used to examine the difference between the researcher's and public respondents' observations of the directions in which springbok were found to move, from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park (χ^2=37.48; df=4)

Movement	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
Springbok not moving	242	451	34.9	65.1	80.4	69.9	693	73.2
Northward	29	52	35.8	64.2	9.6	8.1	81	8.6
Eastward	1	50	2.0	98.0	0.3	7.8	51	5.4
Southward	27	55	32.9	67.1	9.0	8.5	82	8.7
Westward	2	37	5.1	94.9	0.7	5.7	39	4.1
Total	**301**	**645**	**-**	**-**	**100.0**	**100.0**	**946**	**100.0**
Percentage	31.8	68.2	-	-	-	-	-	-

Table 4.9 Categorised data used to examine the difference between the researcher's and public respondents' observations of the direction in which springbok were found to move within the Nossob Riverbed of the South African side of the Kgalagadi Transfrontier Park, from November 2002 to May 2004 (χ^2=13.20;df=4)

Movement	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
Springbok not moving	88	217	28.9	71.1	80.0	68.0	305	71.1
Northward	8	31	20.5	79.5	7.3	9.7	39	9.1
Eastward	1	24	4.0	96.0	0.9	7.5	25	5.8
Southward	12	28	30.0	70.0	10.9	8.8	40	9.3
Westward	1	19	5.0	95.0	0.9	6.0	20	4.7
Total	**110**	**319**	**-**	**-**	**100.0**	**100.0**	**429**	**100.0**
Percentage	25.6	74.4	-	-	-	-	-	-

In the Auob riverbed, most of the researcher's observations on springbok movements indicated a northward trend (11.2%), followed by a southward one (7.2%), a westward one (0.6%), with no observations of an eastward nature. The public recorded most actual movements to be in a southerly direction (8.3%), followed by an easterly one (8.0%), a northerly one (6.5%) and then a westerly one (5.6%). The difference between the recordings of the researcher and the public was found to be significant ($P<0.0001$; $\chi^2=26.62$; df=4). The Nossob riverbed predominantly flows from north to south, while the Auob riverbed is more orientated in a northwest to southeast or an east-west direction. A possible explanation for the difference between the public respondents' observations and those of the researcher for this particular variable could be that public respondents were less accurate with respect to the correct compass direction at a particular point. This may be the reason for the higher proportion of herds in the Nossob riverbed which were reported as moving east- and westward when recorded by the public, particularly because springbok usually remained in this riverbed, which mainly runs from north to south.

There could also be a question of scale as springbok could have been observed moving a short distance east when in actual fact on a larger scale, they were in the process of moving north. This particular question of scale is supported when taking into account the mean duration of observations, approximately 26.0% of which lasted only a single minute (Table 4.11).

Duration of observations

Significant differences were found between the duration of observations by the researcher as opposed to those by the public ($P<0.001$; $\chi^2=57.00$; df=4). Of the

Table 4.10 Categorised data used to examine the difference between the researcher's and public respondents' observations of the direction in which springbok were found to move within the Auob Riverbed of the South African side of the Kgalagadi Transfrontier Park, from November 2002 to May 2004 (χ^2=26.62; df=4)

Movement	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
Springbok not moving	145	232	38.5	61.5	81.0	71.6	377	74.9
Northward	20	21	48.8	51.2	11.2	6.5	41	8.1
Eastward	0	26	0.0	100.0	0.0	8.0	26	5.2
Southward	13	27	32.5	67.5	7.2	8.3	40	8.0
Westward	1	18	5.3	94.7	0.6	5.6	19	3.8
Total	**179**	**324**	**-**	**-**	**100.0**	**100.0**	**100.0**	**100.0**
Percentage	35.6	64.4	-	-	-	-	-	-

researcher's observations, 29.1% lasted from >1–2 minutes, while 35.9% of those of the public lasted from >3–10 minutes (Table 4.11). The second longest duration of observations was 0–1 minute (24.5% by the researcher and 26.8% by the public). The difference between the duration of the observations possibly reflects a difference in approach between the researcher and the public. Overall, the public possibly recorded longer observations because their approach could have been more leisurely of nature, being focussed on viewing game. Public respondents also recorded fewer single springbok observations (27.0%) than the researcher (51.0%), which required less time to complete a questionnaire.

4.4 Conclusions

A public questionnaire can be an effective and affordable tool for gathering large amounts of data within a relatively short period. However, the tenet that the quantification of public observations is central to formulating sound ecological management processes[1], is questioned in this investigation. The analysis of researcher's versus public respondents' observations revealed clear statistical differences for several variables.

Questions asked in questionnaires should be worded and stated clearly and definitions and multiple answer options well-defined[20]. Questions should be asked in such a way that they are fully understood by the respondent. Constructing meaningful and interpretable questions is a complex process and requires careful word selection[21].

Table 4.11 Categorised data used to examine the difference between the duration of observations that were made by the researcher and those that were made by the public, from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park (χ^2=57.00; df=4)

Duration (minutes)	**Number of observations**		**Percentage distribution across rows**		**Percentage distribution across columns**		**Total**	**Percentage**
	Researcher	**Public**	**Researcher**	**Public**	**Researcher**	**Public**		
0–1	74	170	30.3	69.7	24.5	26.8	244	26.0
>1–2	88	102	46.3	53.7	29.1	16.0	190	20.3
>2–3	59	59	50.0	50.0	19.5	9.3	118	12.6
>3–10	63	228	21.6	78.4	20.9	35.9	291	31.1
>10	18	76	19.2	80.8	6.0	12.0	94	10.0
Total	**302**	**635**	**-**	**100.0**	**100.0**	**100.0**	**937**	**100.0**
Percentage	32.2	67.8	-	-	-	-	-	-

Examples of answers help to illustrate the questions posed better. The shorter the questionnaire and the less detail required, the better[2]. Whenever a public questionnaire is used to collect data in conjunction with a researcher, public respondents' answers should be checked for differences against the researcher's answers and ground-truthed, where possible[1]. Properly applied statistics are invaluable for filtering such data.

Apart from the statistical difference between some of the variables observed by the researcher and those by the public, the use of questionnaires in the present study was successful. This conclusion is based on the resulting amount of data that was collected and that was not found to differ statistically between the researcher and the public. Furthermore, it was possible to provide sound explanations for most of the observed differences allowing the use of the data, once those differences were described and understood. Questionnaires provided a non-intrusive method of gathering ecological data on springbok populations on the South African side of the Kgalagadi Transfrontier Park. Questionnaires could be used in future to collect ecological data, provided that the flaws that were explored in the present paper are considered.

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Appendix A

A list of the variables that were recorded by Kgalagadi Transfrontier Park staff, the researcher and visitors from November 2002 to May 2004 to study springbok behaviour on the South African side of the Kgalagadi Transfrontier Park

1. Date
2. Location
3. Time when observation starts
4. Total number of springbok
5. Riverbed habitat (yes or no)
6. Plains habitat (yes or no)
7. Duneveld (yes or no)
8. Pan type habitat (yes or no)
9. Tree dominated habitat (yes or no)
10. Grass dominated habitat (yes or no)
11. Shrub dominated habitat (yes or no)
12. Other (3 alternative dominant habitat features recorded)
13. Near a camp (yes or no)
14. Near a waterhole (yes or no)
15. Near a picnic spot (yes or no)
16. Other (none specified)
17. Total number of blue wildebeest
18. Total number of red hartebeest
19. Total number of gemsbok
20. Total number of other species (13 other animal species recorded)
21. Distance between springbok and blue wildebeest (0-20 m, 21-50 m and >50 m specified)
22. Distance between springbok and red hartebeest (0-20 m, 21-50 m and >50 m specified)
23. Distance between springbok and gemsbok,(0-20 m, 21-50 m and >50 m specified)
24. Distance between springbok and other animal species (0-20 m, 21-50 m and >50 m specified)
25. Percentage of the springbok herd eating in sunlight[*]
26. Percentage of the springbok herd eating in the shade[*]
27. Percentage of the springbok herd standing in sunlight[*]
28. Percentage of the springbok herd standing in shade[*]
29. Percentage of the springbok herd lying down in sunlight[*]
30. Percentage of the springbok herd lying down in shade[*]
31. Percentage of the springbok herd sleeping in sunlight[*]
32. Percentage of the springbok herd sleeping in shade[*]

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[*] Numbers were converted into percentages of the total herd after collection.

33. Percentage of the springbok herd walking in sunlight[*]
34. Percentage of the springbok herd walking in shade[*]
35. Percentage of the springbok herd playing in sunlight[*]
36. Percentage of the springbok herd playing in shade[*]
37. Percentage of the springbok herd doing something else[*] (19 alternative actions recorded)
38. Percentage of the springbok herd feeding on grass[*]
39. Percentage of the springbok herd feeding on shrubs[*]
40. Percentage of the springbok herd feeding on trees[*]
41. Percentage of the springbok herd feeding on something else[*] (22 alternative options recorded)
42. Direction in which animals are moving (North, Northeast, East, Southeast, South, Southwest, West and Northwest specified)
43. Time when observation ends
44. Sheet number
45. Total number of male springbok in the herd[ϕ]
46. Total number of female springbok in the herd[ϕ]
47. Total number of immature springbok in the herd[ϕ]
48. Springbok are feeding on flowers (yes or no) [ϕ]
49. Springbok are feeding on fruit (yes or no) [ϕ]
50. Nearest waterhole (47 waterholes specified) [ϕ]
51. Habitat type (4 options specified) [ϕ]

[ϕ] Although variable numbers 45 to 51 did not appear on the questionnaire, it was recorded as additional notes by the researcher, as well as some of the visitors / staff.

CHAPTER 5

FEEDING ECOLOGY OF THE KALAHARI SPRINGBOK *ANTIDORCAS MARSUPIALIS*

Prepared for Koedoe

Abstract – Springbok ecology in the Kalahari was examined with the use of public questionnaires and field forms. Feeding was the most common activity and varied during the day and between seasons. Springbok fed in direct sunlight in the mornings and moved into shade during the afternoon. More time was spent feeding in the shade during the warmer months than during the colder months, especially under northerly to northeasterly wind directions. Natural licks were commonly utilised. Herd sizes were found to increase during the cold-dry season and decrease during the hot-wet season. Springbok and blue wildebeest displayed niche separation by competition avoidance.

Keywords: *Antidorcas marsupialis,* ecology, feeding, Kalahari, questionnaire, springbok

5.1 Introduction

The Kalahari plays host to a range of herbivores of which springbok *Antidorcas marsupialis* (Zimmermann, 1780) are characteristic (Van Rooyen *et al.* 1994). It has even been suggested that the Kalahari springbok be declared a distinct subspecies (Bigalke 1970; Peters & Brink 1992). Recent declining springbok populations in South Africa have only been reported from the Kalahari while other areas such as the Karoo have shown a significant increase in recent times (Skinner & Moss 2004). Historical records describe numerous massive migrations (Eloff 1961; Child & Le Riche 1969) which are well reviewed by Skinner (1993). However, the population numbers of springbok have been declining in the Kalahari over the past 50 years, and rapidly so in the past 20 years (Skinner, pers. comm[4].; Engelbrecht, pers. comm.[5]; Skarpe 2001; Skinner & Moss 2004). Studies of sex ratios within springbok populations (Bednekoff & Ritter 1997) and of morphometrics and reproduction (Skinner *et al.* 1996) do not account for the decline in numbers, and no significant increase in depredation or major predator numbers such as that of the cheetah *Acinonyx jubatus* have been recorded (Engelbrecht, pers. comm.[2]).

Springbok morphology and anatomy have been studied in detail (Skinner & Louw 1996), but there are few in-depth ecological studies of springbok in the Kalahari. Morphology and anatomy show that springbok comfortably fit in arid areas and are able to cope well with changing environmental pressures (Louw & Seely 1982; Mills & Retief 1984; Spinage & Matlhare 1992; Skinner & Louw 1996; Skinner & Moss 2004). Springbok are selective feeders (Bothma *et al.* 2002) and the quality of their

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diet is a significant driving force behind their behaviour and movements (Mills & Retief 1984). They have an exceptionally high rate of reproduction (Mills & Haagner 1989).

The reason for the decline of the springbok population in the Kalahari remains a mystery, highlighting the need for more information on the ecology of this species to ensure its conservation within that area. Effective conservation of the Kalahari and its springbok can only be achieved by a thorough understanding of its region-specific ecology and by adopting an adaptive management process. This study aims to address the first of these two issues.

The focus of this paper is on the feeding behaviour of springbok on the South African side of the Kgalagadi Transfrontier Park. The hypothesis that was put forward was that springbok feeding and food selection are significantly affected by environmental and seasonal conditions. To test the hypothesis, data were gathered by means of public questionnaires and researcher observations. Properly designed questionnaires can be used as an effective tool for research (Hague 1993).

5.2 Study area

The Kalahari consists of the largest continuous stretch of sand in the world, located more or less diagonally across southern to central Africa (Van Rooyen 2001). The southwestern Kalahari is considered a relatively unspoilt, ecologically fragile, arid savanna or semidesert (Van Rooyen & Van Rooyen 1998, Van Rooyen 2001). The largest conservation unit within the Kalahari ecosystem covers around 20% of its surface area and is shared across the borders of South Africa and Botswana (Van

Rooyen 2001) and it is known as the Kgalagadi Transfrontier Park. The present study was carried out on the South African side of the park, an area which covers some 9 600 km² (Jackson 1995). The total size of the combined park is approximately 36 200 km² (Mills & Retief 1984).

The southwestern Kalahari consists mainly of red sand dunes that are underlain by calcrete, with two main dry riverbeds, the Auob and the Nossob (Jackson 1995; Van Rooyen & Van Rooyen 1998). These riverbeds cut through the red sand dunes, exposing calcrete outcrops and converge just north of the Twee Rivieren Rest Camp. Amongst the dunes are some dispersed pans, increasing in abundance from around the centre of the park northwards and eastwards into Botswana.

The South African side of the Kgalagadi Transfrontier Park is located between 24° 15’ S and 26° 30’ S, and 20° 00’ E and 20° 45’ E with an altitudal range from 870 to 1 080 m above sea level. It receives the majority of its rain during summer and has a highly erratic (Skarpe 1986, Tyson 1986) annual rainfall of around 180 mm in the southwest to 400 mm in the northeast (Jeltsch *et al.* 1997) with occasional drought years (Knight 1995). During the study period, the mean rainfall amounted to 213.6 mm over 19 months across all weather stations within the South African side of the Kgalagadi Transfrontier Park (Kgalagadi Transfrontier Park 2004). Three ecological seasons occur, namely the hot-wet season (January to April), cold-dry season (May to August) and hot-dry season (September to December; Leistner 1967; Mills & Retief 1984, Van Rooyen & Van Rooyen 1998). The temperature range is immense, with recorded winter lows of around -10°C and summer highs of around 45°C (Van Rooyen *et al.* 1990).

The southwestern Kalahari environment is relatively homogeneous because of the predominance of a sand mantle covering the area. The same plant species occur in most of the landscape units, and the difference between units can often only be ascribed to terrain morphology, soil characteristics and changes in dominance and structure of the plant species present (Van Rooyen *et al*. 2006).

5.3 Materials and methods

A public questionnaire and field data sheet were compiled of observable variables relating to springbok behaviour (Appendix A). The questions consisted of factual information (such as date and time), closed format questions (where choices were given) as well as open-ended questions about animal activity. Some questions relied on personal perception and judgement of observable variables, such as dominant habitat features. The questionnaire was distributed to staff and visitors of the Kgalagadi Transfrontier Park over a period of 13 months. During this time, informative talks were also held at the main rest camp, Twee Rivieren, explaining the project and the questionnaire.

One questionnaire per herd (solitary springbok were also considered as a herd) had to be completed and collection boxes were positioned at the reception office of every camp and emptied periodically. During the same period, the researcher collected data by using a field data sheet that was based on the public questionnaire but also recorded some additional variables. Observations were mostly conducted at random within strips (Bothma 2002), and were done from a vehicle *en route* between destinations. Most observations were made within the dry riverbeds of the Nossob and Auob Rivers, since this is where the springbok tend to congregate. Visibility varied, but was generally up to around 150 m on either side of the vehicle. Binoculars and/or a spotting-scope were used when necessary. Rain was accepted as being present, only when a minimum of 10 mm had fallen in a particular month. This was to ensure that a sufficient amount of water had been recieved to induce vegetation sprouting ([3]Skinner, pers. comm.).

After collecting the completed questionnaires, the data were transformed into numerical codes and these numerical codes were captured into a matrix using Microsoft® Excel. Data were classified into ranges or categories wherever it best suited the analytical model or question at hand and were analysed with uni- and multivariate statistical techniques. All analyses were done using SAS®[Ψ] software. Chi-square tests for independence were conducted to examine the independence of variables. The hypotheses of dependence were expressed by P-values, where $P \leq 0.05$ indicated that the variables being tested were not independent. Generalised Linear Models were also used to examine the data, incorporating either classed or continuous independent variables. In most cases the independent variable used in the Generalised Linear Models was time. Repeated measures analyses of variance were sometimes used in Generalised Linear Models to consider differences between dependent variables at independent variable intervals. Logistic procedures were used to calculate odds ratios for binary variables. Where necessary, regression analyses were used to clarify trends. Where the means for collective data were used, these were calculated as least square means so as to equalize the data for a more accurate mean

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[Ψ] SAS® Software Version 8.2 supplied by The SAS Institute Inc., SAS Campus Drive, Cary, NC 27512, USA, running under z/VM 4.4.0 (RSU 0404) on the mainframe computer IBM Z800 2066/0C1 of the University of Pretoria.

representation. Analyses of variance (ANOVA) were used to distinguish the various attributes of the variables.

Analyses of activity data generally involved two steps. First, the activity data were compared with and without the influence of a specified variable to investigate the effect of said variable. Thereafter, the means of the activity data were determined according to each class of the specified variable and compared with each other.

5.4 Results and discussion

Two thousand questionnaires were distributed and 955 (47.7%) were returned. The researcher collected 31.7% and public respondents the balance (68.3%). Observations lasted from 1–>10 minutes, most observations not continuing >3 minutes.

Food item selection

The scale at which habitat use is examined may greatly affect any research results obtained (Morris 1987). In this section, food item selection was considered at growth form level. Observations were therefore made of springbok feeding either on grass, shrubs or trees at different times of the day.

Feeding on grass, shrubs and trees could not be explained effectively by using time as a continuous independent variable. Even when time was reclassified into hourly categories a linear model could not be fitted appropriately for feeding on grass (R^2=0.03; df=12), shrubs (R^2=0.02; df=12) or trees (R^2=0.01; df=12). Consequently, the hourly mean percentages of the herds that were observed to feed on grass were compared (Fig. 5.1). The same analysis was repeated for springbok feeding on shrubs

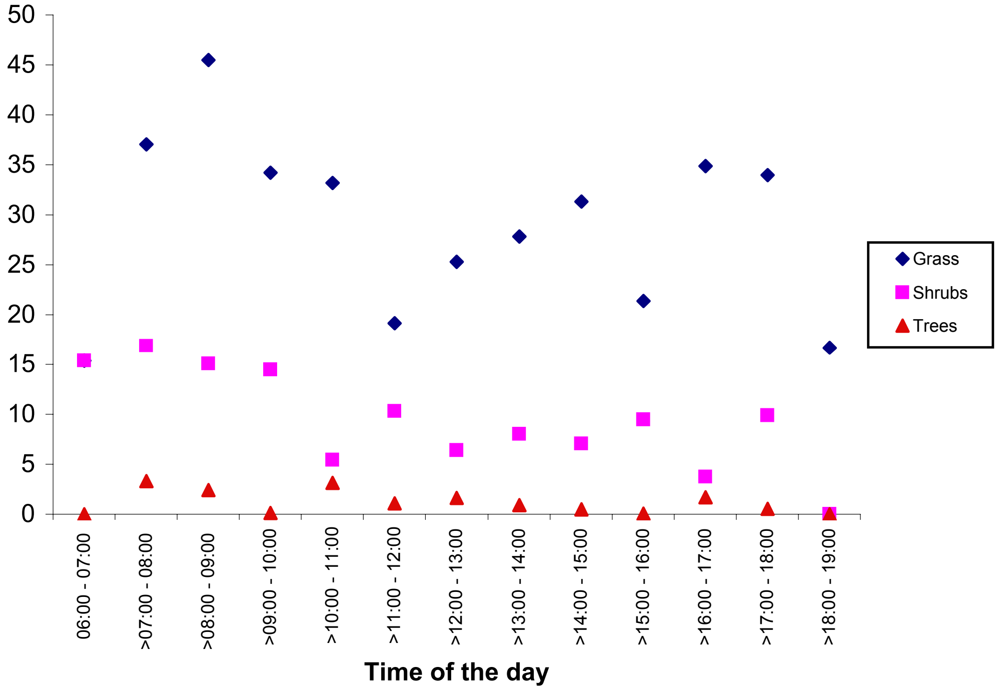

Fig. 5.1 Mean percentage of springbok herd feeding on grass, shrubs and trees at hourly intervals from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park, to show the hourly trends of diet selection.

and trees. The increase in percentage of animals feeding on grass, from 06:00-07:00 to >08:00-09:00 was found to be statistically significant (P=0.025) as was the decrease from >08:00-09:00 to >11:00-12:00 (P=0.0002) (Fig. 5.1), and the subsequent increase from >11:00-12:00 to >16:00-17:00 (P=0.029). The percentage of springbok feeding on shrubs decreased from >07:00-08:00 to >16:00-17:00 (P=0.019). A statistically significant increase in the percentage of springbok feeding on trees was observed from >09:00-10:00 to >10:00-11:00 (P=0.027).

Springbok favoured grass overall more than shrubs and trees (Table 5.1, Fig. 5.1). The percentage of the herd feeding on grass reached a maximum in the morning from >07:00-08:00 to >09:00-10:00. This trend is supported by other research (Nagy & Knight 1994) and is likely related to the increased moisture content of grass during the late night and early morning (Taylor 1968). Tree leaf consumption remained low throughout the day, however, the relative consumption of tree leaves reached a peak at mid-morning (>10:00-11:00) (Table 5.1). Shrubs were consumed at a lower rate the later in the day it became, possibly due to decreasing moisture content. The relative consumption of shrubs, however, reached a peak at >11:00-12:00 and again at >15:00-16:00.

Essentially, the study of animal ecology involves not only the animal's utilization of its habitat, but in particular the food that it consumes and the nature of the habitats it occupies (Johnson 1980). When food availability increases, animals feed more selectively to optimise nutritional quality intake, but as food availability decreases, animal selectivity of food decreases (Melton 1987). Plant selection by animals is influenced by a plant's palatability, which in turn is affected, amongst others by its

Table 5.1

The frequency of springbok (as a percentage of feeding individuals) feeding on tree leaves, shrubs or grass on an hourly basis, during the study period from April 2003 to May 2004 on the South African side of the Kgalagadi Transfrontier Park

Time interval	**Percentage of springbok feeding on**		
	Grass	**Shrubs**	**Trees**
06:00 - 07:00	50.0	50.0	0.0
>07:00 - 08:00	64.7	29.5	5.8
>08:00 - 09:00	72.2	24.0	3.8
>09:00 - 10:00	70.2	29.6	0.2
>10:00 - 11:00	79.2	13.2	14.8
>11:00 - 12:00	62.6	33.8	3.6
>12:00 - 13:00	75.9	19.2	4.9
>13:00 - 14:00	75.7	21.8	2.5
>14:00 - 15:00	80.4	18.2	1.4
>15:00 - 16:00	69.2	30.8	0.0
>16:00 - 17:00	86.6	9.2	4.2
>17:00 - 18:00	69.8	20.3	9.9
>18:00 - 19:00	100.0	0.0	0.0

physical structure and nutritional value (Owen-Smith & Cooper 1988). Different plant parts could also have different nutritional qualities (Owen-Smith & Novellie 1982), which may also affect the food selection process. It has further been suggested that particular animal features, such as mouth size, also play a role in plant selection (Owen-Smith & Cooper 1988). The springbok has a narrow mouth which is suited to fine selection and it is thus able to feed off thorny branches and can reach leaves that are inaccessible to other herbivores (Skinner & Louw 1996). This further implies that springbok are able to select highly nutritional forage.

Although springbok were observed to be selective in their feeding, no significant correlations between specific plant species eaten and time of the day or season could be found (Table 5.2). However, the data collection was limited to a few observations where specific plants or plant parts were specified. The selection list is based on few recordings where specific plant species or components were specified in the questionnaire (mostly by the researcher). It has been found that large trees, in particular *Acacia erioloba*, play an extremely important role in the Kalahari ecosystem (Dean *et al*. 1999). It is notable that in the present study, *Acacia erioloba* pods were specified most on the springbok selection list (Table 5.2), suggesting that springbok may play a role in seed dispersal of this plant species. Seeds pass through the herbivore's alimentary canal unharmed (Leistner 1961) and may benefit from the nutritional boost that the faeces impart on the soil of the immediate vicinity. It has also been reported that springbok consume plant underground storage organs as a source of moisture (Williamson 1987), but that could not be confirmed during the present study.

Table 5.2

A list of plant species and plant parts that were selected by springbok when feeding during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park expressed as a percentage of the total observations. The first item represents observations that did not specify any particular plant or plant part and the second a collection of plants that were only recorded twice at most. The high number of observations is due to more than one option being provided in the questionnaire for specifying selected plants or plant parts

Item	**Number of observations**	**Percentage**	**Accumulative percentage**
No preference	1544	95.5	95.5
Other plant material	25	1.5	97.0
Forbs (unknown)	15	0.9	98.0
Acacia erioloba pods	11	0.7	98.7
Cullen obtusifolium	7	0.4	99.1
Acacia erioloba leaves	6	0.4	99.5
Tribulus zeyheri leaves/flowers	5	0.3	99.8
Rhigozum trichotomum leaves	4	0.2	100.0

Springbok were observed to eat *Rhigozum trichotomum* leaves throughout the year, but especially so when the leaves were fresh new sprouts. This supports previous research by Bothma (1971) who described a rapid response by springbok to newly emerging green sprouts of *Rhigozum trichotomum*. This species was not specifically selected as food by springbok during times when a diversity of fresh plant growth was present, except when in flower. When flowering, springbok were observed to move through *Rhigozum trichotomum* thickets, only feeding on the flowers. Generally, however, *Rhigozum trichotomum* was recorded as being specifically selected by springbok in only 0.2% of all the observations (Table 5.2).

Nocturnal feeding

During the present study, springbok were observed to feed at night during all three seasons of the year. No data were collected on this facet by the public respondents because of tourist travel restrictions and the data collected by the researcher were mostly qualitative instead of quantitative. A detailed discussion of nocturnal feeding observations on springbok can be found in Chapter 6. In brief, a minimum of two fairly distinct night-time feeding sessions were recorded. Usually not all the animals of a herd participated in such a feeding session.

Licks

Areas where animals lick hardened, clayish soil, appropriately referred to as “natural licks”, occur in several places throughout the Kgalagadi Transfrontier Park. These licks are mostly associated with pans (Van Rooyen *et al.* 1994). In the present study, utilization of such licks was especially prominent around the Kannaguass waterhole in the Nossob riverbed (see Fig. 5.2). Licks are a common phenomenon in the Kalahari

Fig. 5.2 Natural licks found at Kannaguass waterhole in the Nossob riverbed of the Kgalagadi Transfrontier Park during April 2003. A matchbox is shown for size reference. It measures 50 mm x 35 mm.

and clear evidence of the presence of clay has been found in the guts of springbok that were shot close to pans in the Kalahari in Botswana (Bergström & Skarpe 1999). Springbok are reportedly sometimes attracted to artificial waterholes more for the licks than the water itself (Van Rooyen *et al.* 1994). It is unclear whether this was the case in the present study, as springbok were observed to drink water intermittently while also utilizing licks. The licks that were observed did, however, all occur within the piosphere zone (Jeltsch *et al.* 1997) around waterholes and could therefore have a degrading effect on the environment. It has been estimated that once piosheres become shrub-encroached, natural recovery could take well in excess of 100 years (Jeltsch *et al.* 1997).

Springbok feeding times

Although only 21 activities were listed in the questionnaire, up to 31 different activities were specified by respondents. The mean percentage of springbok involved in these activities, over all time periods during the whole study period showed that feeding in sunlight occurred most often (38.6%). The mean percentage of springbok herds feeding in sunlight and in shade during the whole study period is given in Fig. 5.3. In general, the mean percentage of the springbok per herd engaged in different activities ranged from <0.1 to 38.6%.

Six of all the recorded activities related directly to feeding. They were: feeding in sunlight, feeding in the shade, feeding on grass, feeding on shrubs, feeding on trees, and feeding on something else. The latter four were only rarely recorded. Neither feeding in the sunlight (P=0.220; χ^2=0.003; df=2;) nor feeding in the shade

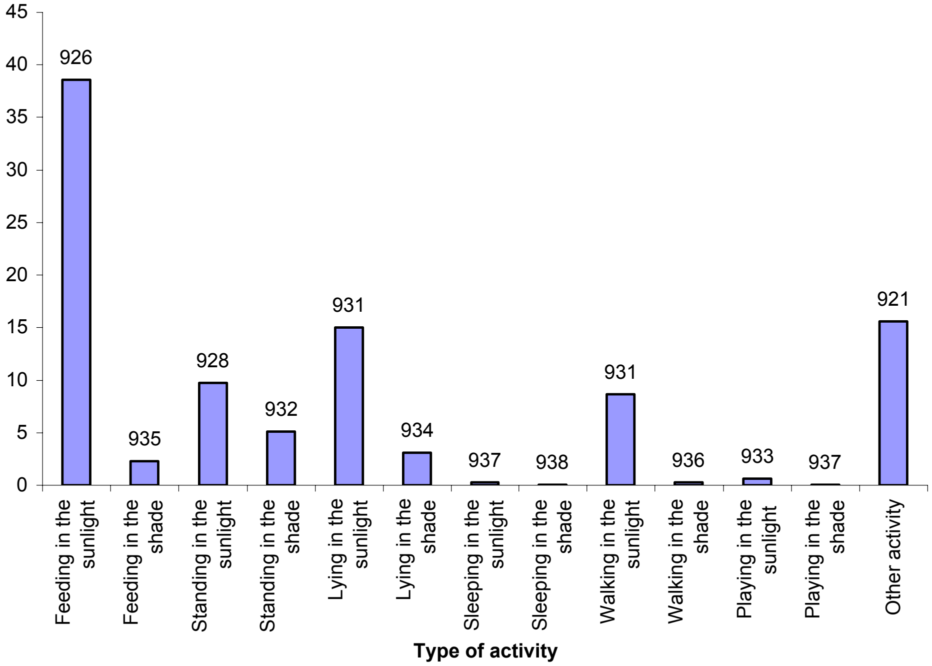

Fig. 5.3 The mean percentage of springbok herds involved in different activities, over all time periods, during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park. The "Other activity" category contains a collection of activities, all of which were recorded infrequently. The value on each bar in the graph indicates the sample size being used to calculate the percentage for that particular activity.

(P=0.150; df=2; χ^2=0.004) showed any significant changes in frequency of occurrence across different seasons. When these two activities were compared with the rest of the activities by Analysis of Variance of Contrast Variables, it was found that feeding in the sunlight was significantly more frequent than all other activities, including feeding in the shade (P<0.0001; df=1) (Table 5.3). Frequency of feeding in the shade (2.3%) was also significantly different from most other activities, but not from standing in the shade (5.1%; P=0.265; df=1), lying down in the shade (3.1%; P=0.712; df=1), sleeping in the sunlight (0.3%; P=0.097; df=1), walking in the shade (0.3%; P=0.084; df=1) and playing in the sunlight (0.7%; P=0.2745; df=1) (Fig. 5.3; Table 5.3).

The lack of a significant difference in the frequency of shade-related activities (feeding, standing, lying down and walking in the shade) indicate that the time spent in the shade is divided equally between these activities. Springbok herds were often observed to rest in the shade during the heat of the day. During such resting periods, different animals in the herd would be involved in different activities, such as standing, walking and feeding. The main objective of spending time in the shade other than feeding is assumed to be to rest.

The mean percentage of a herd involved in each activity was calculated per hourly interval and the daily trends of these activities are presented in Figs 5.4 to 5.9. Fewer springbok were observed to be feeding in the sunlight the later in the day it became up to approximately 16:00. Significantly more springbok per herd were feeding in the sunlight at >07:00-08:00 than at >10:00-11:00 (P=0.0002; df=1) or >15:00-16:00 (P<0.0001; df=1). In contrast a significantly larger percentage of the herd was

Table 5.3

P-values of comparative tests between sets of two variables (activities) to examine independende of the frequency of different activities in springbok herds from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park. Statistical independence is where $P \leq 0.05$

	Feeding in sunlight	**Feeding in the shade**	**Standing in sunlight**	**Standing in the shade**	**Lying down in sunlight**	**Lying down in the shade**	**Sleeping in sunlight**	**Sleeping in the shade**	**Walking in sunlight**	**Walking in the shade**	**Playing in sunlight**	**Playing in the shade**	**Other activity**
Feeding in the sunlight	-	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Feeding in the shade		-	0.0051	0.2654	0.0002	0.7124	0.0969	0.0462	0.028	0.0842	0.2745	0.0493	<0.0001
Standing in the sunlight			-	0.1035	0.2074	0.0173	<0.0001	<0.0001	0.6265	<0.0001	0.0002	<0.0001	0.2406
Standing in the shade				-	0.0074	0.4442	0.015	0.0074	0.2796	0.0141	0.0434	0.0089	0.0005
Lying down in the sunlight					-	0.0005	<0.0001	<0.0001	0.1075	<0.0001	<0.0001	<0.0001	0.6604
Lying down in the shade						-	0.0564	0.0275	0.069	0.0535	0.1618	0.0333	<0.0001
Sleeping in the sunlight							-	0.2869	0.0006	0.9124	0.3252	0.5393	<0.0001
Sleeping in the shade								-	0.0003	0.5665	0.0968	0.6795	<0.0001
Walking in the sunlight									-	0.0005	0.0016	0.0003	0.0712
Walking in the shade										-	0.3112	0.6864	<0.0001
Playing in the sunlight											-	0.1353	<0.0001
Playing in the shade												-	<0.0001
Other activity													-

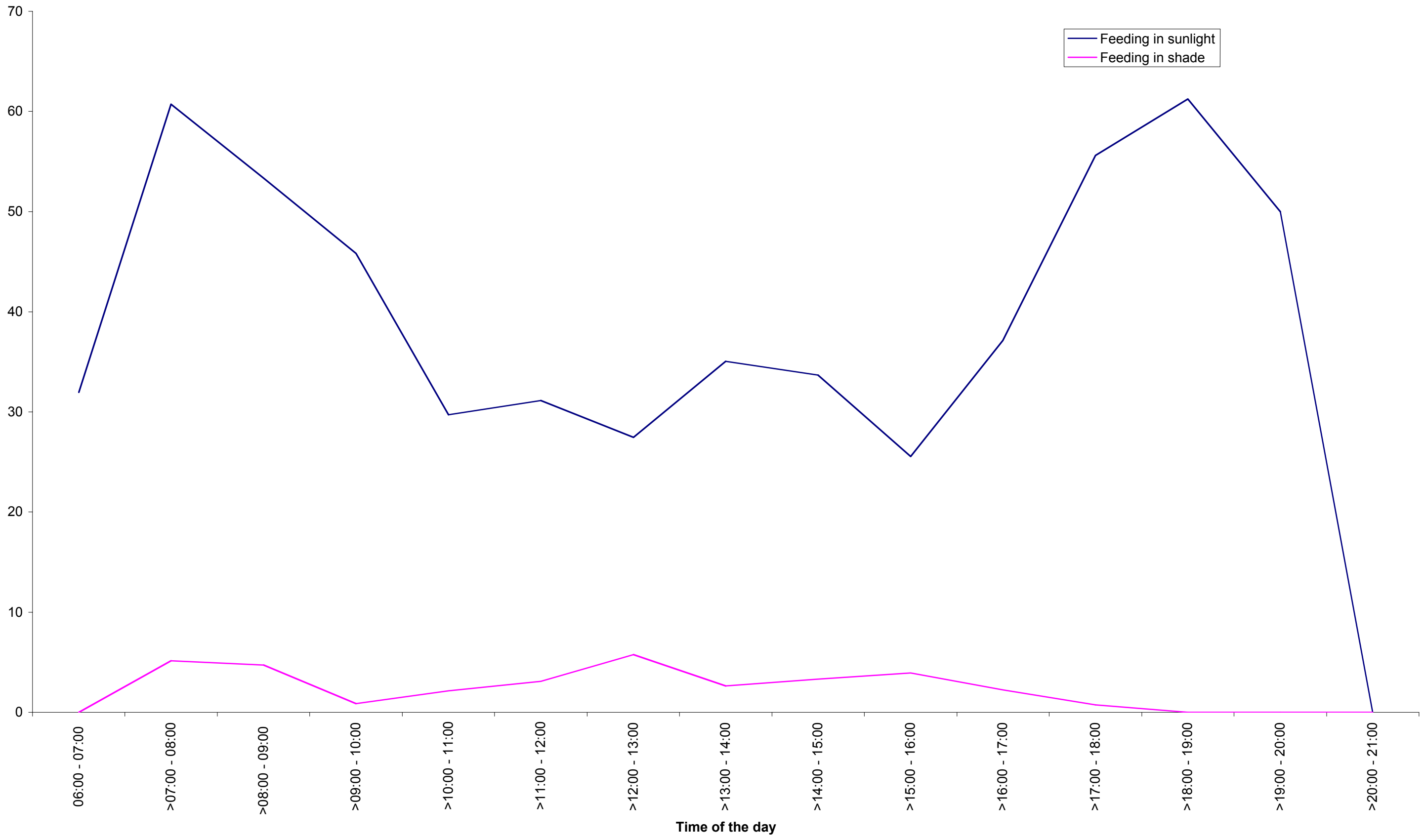

Fig. 5.4 The mean percentage of springbok per herd feeding in the sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

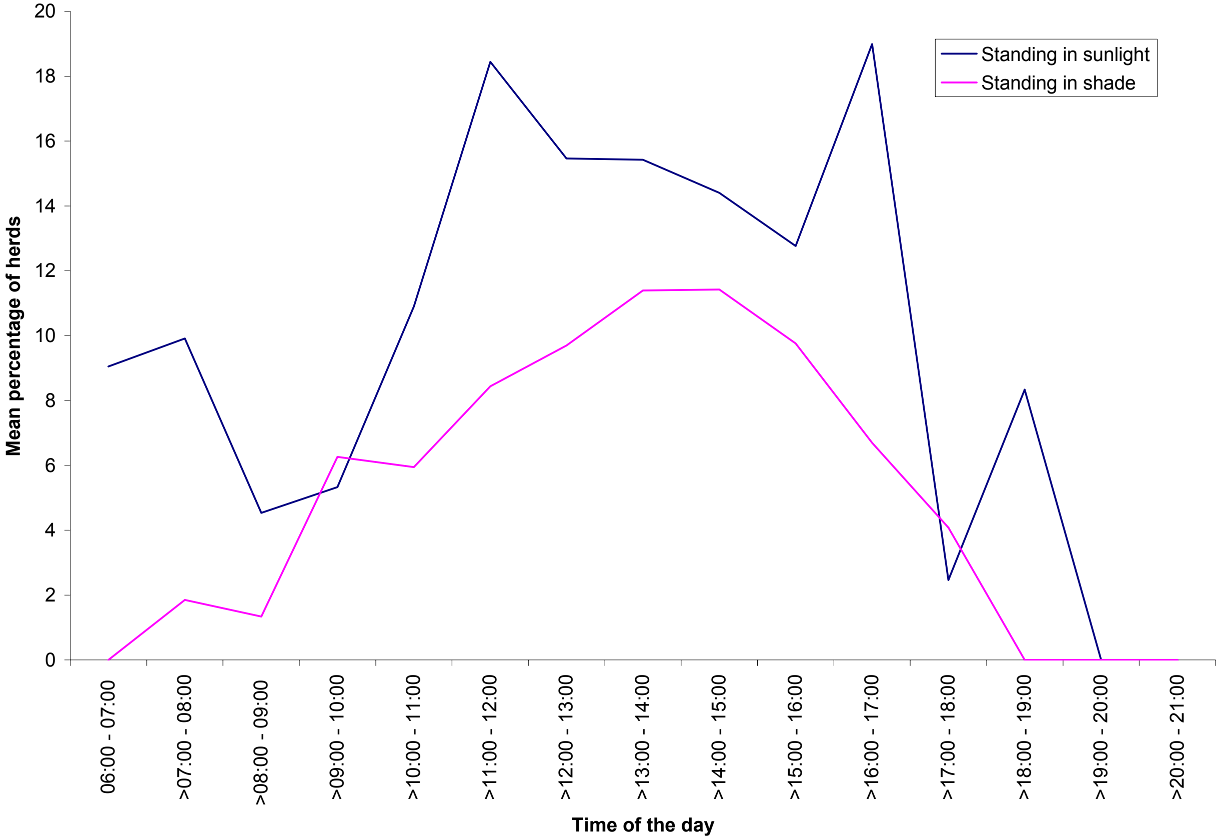

Fig. 5.5 The mean percentage of springbok per herd standing in the sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

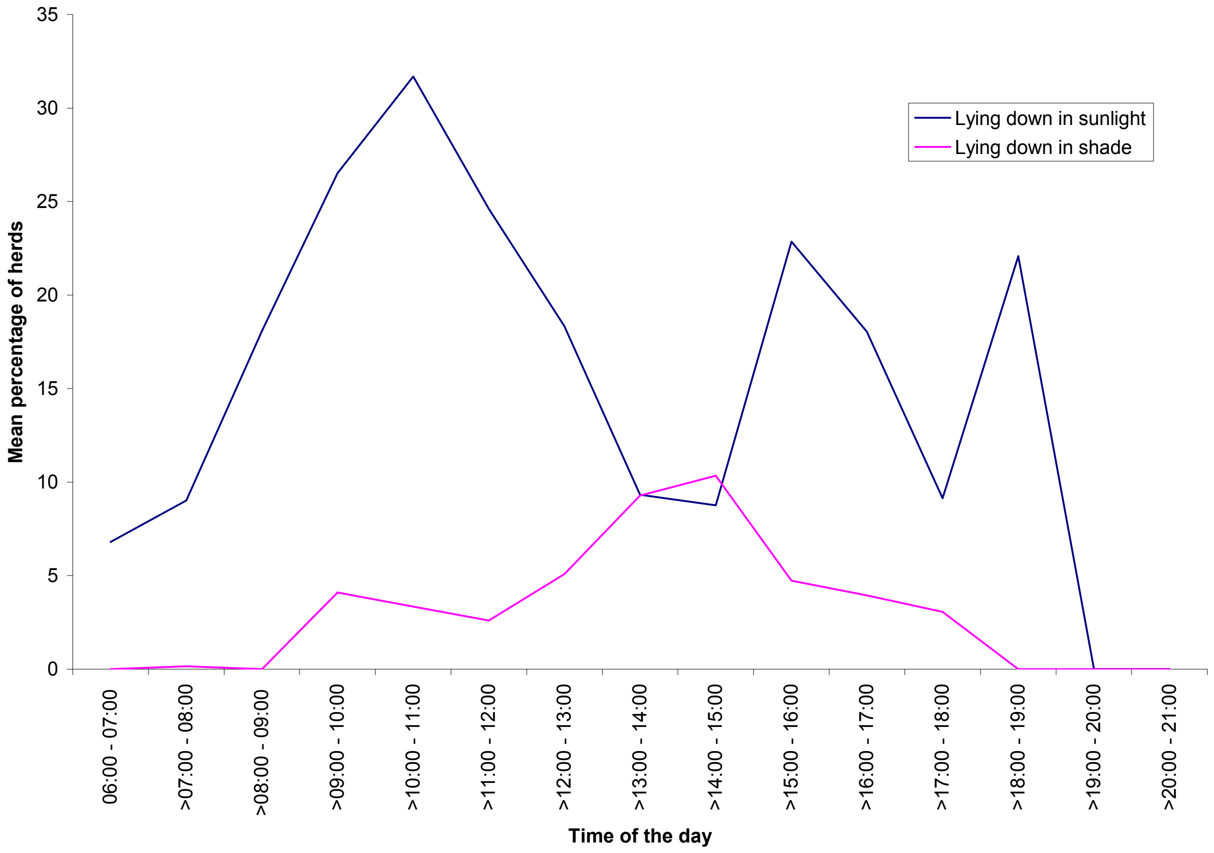

Fig. 5.6 The mean percentage of springbok per herd lying down in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

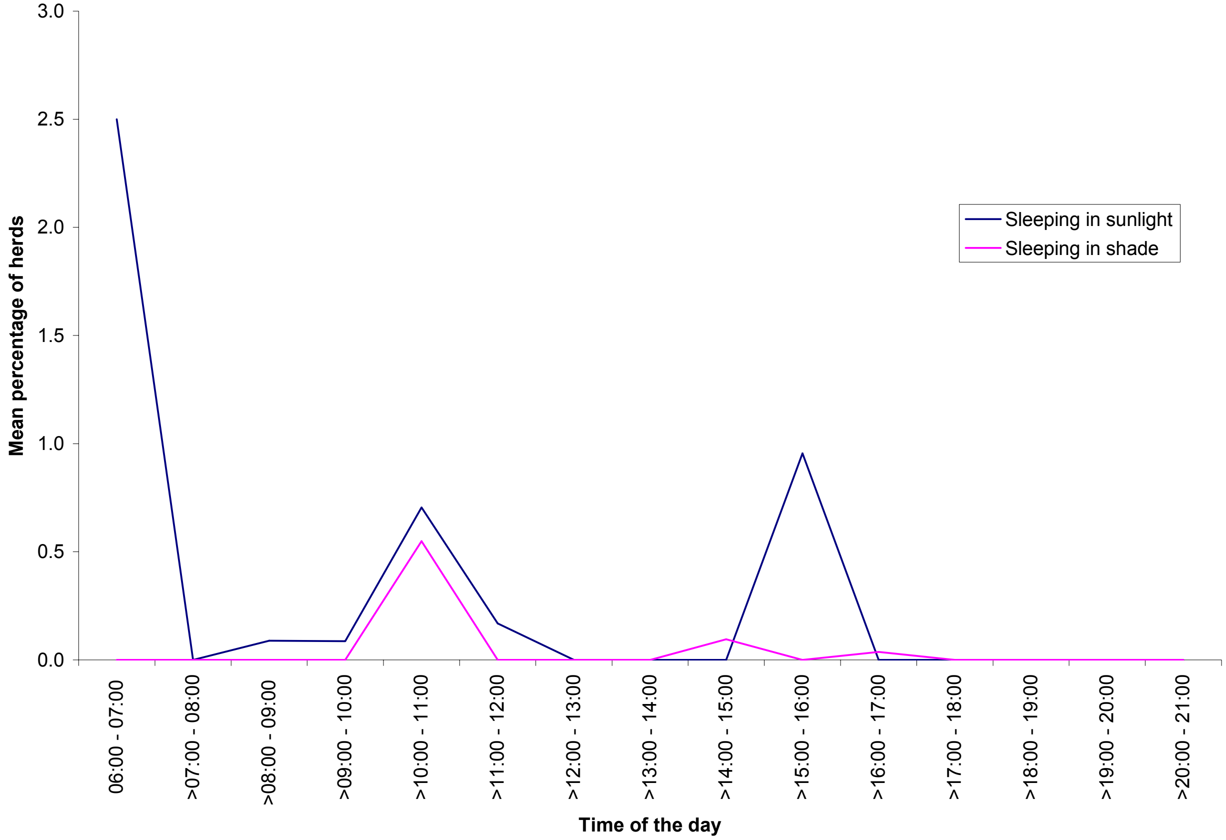

Fig. 5.7 The mean percentage of springbok per herd sleeping in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

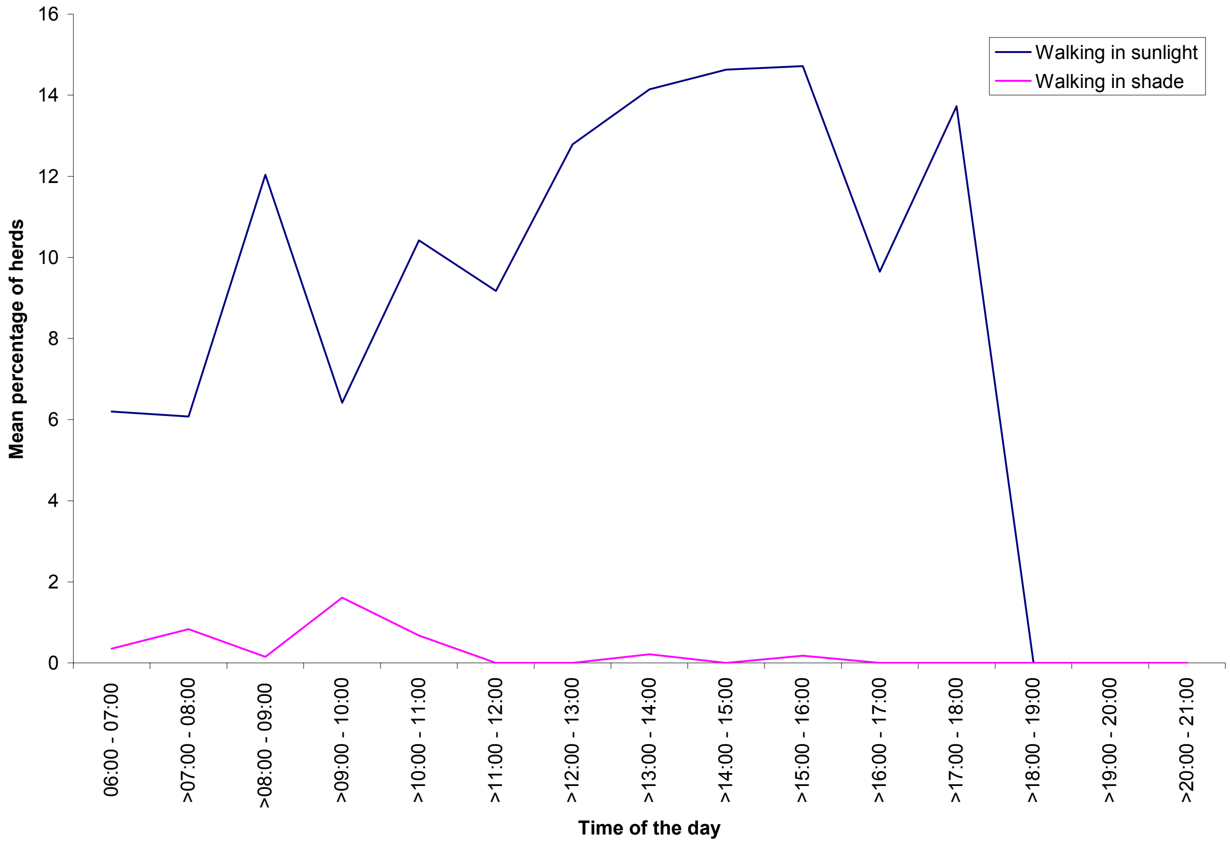

Fig. 5.8 The mean percentage of springbok per herd walking in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

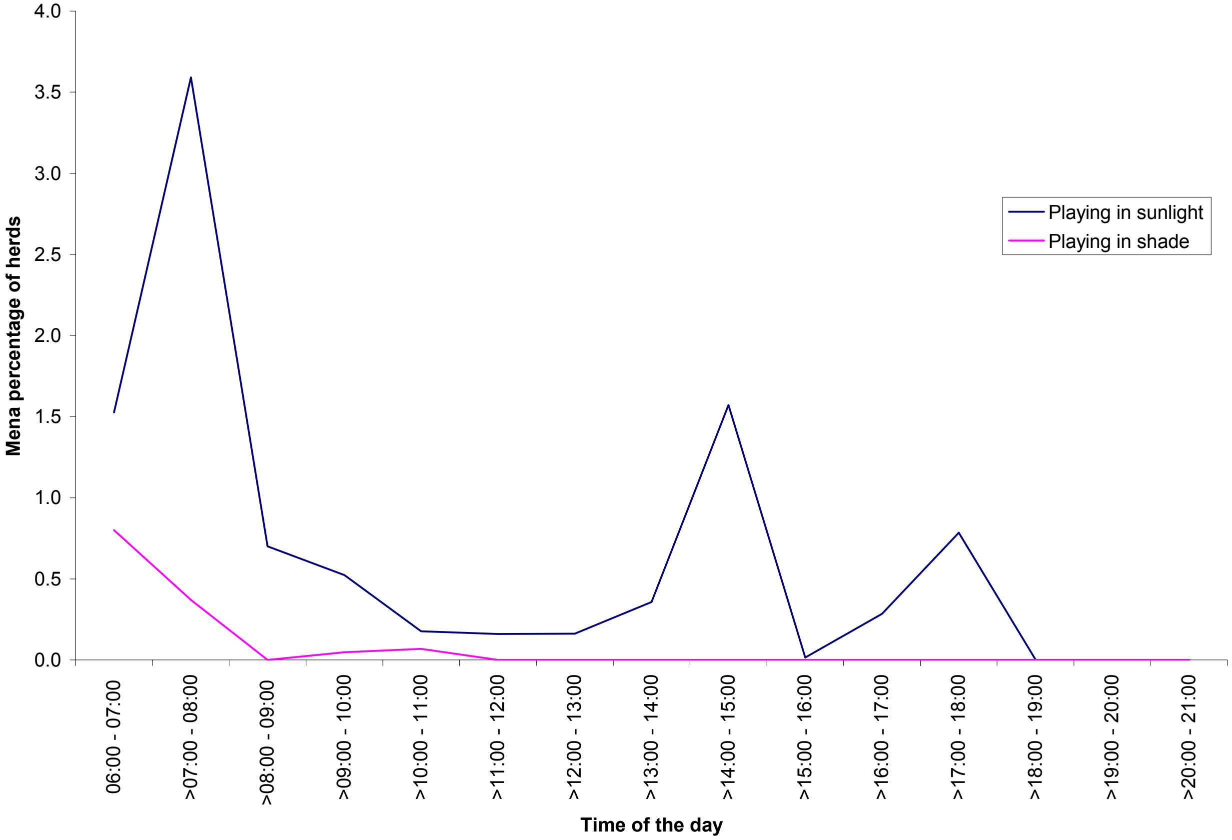

Fig. 5.9 The mean percentage of springbok per herd playing in sunlight and shade at hourly time intervals during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

feeding in the shade at midday >12h00-13:00 than at >09:00-10:00 (P=0.032; df=1), and no significant decrease (P=0.068; df=1) was observed from >12h00-13:00 to >17h00-18:00.

Activities that reached their peak frequency in the hour during sunrise included sleeping in direct sunlight and playing in the shade (Figs 5.7 and 5.9). Feeding in the direct sunlight (Fig. 5.4) and playing in the direct sunlight (Fig. 5.9) reached their peak frequency during early morning, while lying down in the shade (Fig. 5.6) and playing in the shade (Fig. 5.9) occurred at their lowest frequency then. Lying down in the direct sunlight (Fig. 5.6), sleeping in the shade (Fig. 5.7) and walking in the shade (Fig. 5.8) reached their peak frequency of occurrence during the late morning, while feeding in the shade (Fig. 5.4) and standing in the direct sunlight (Fig. 5.5) occurred at their lowest frequency of occurrence then. Feeding in the shade (Fig. 5.4) and standing in the direct sunlight (Fig. 5.5) reached their peak frequency of occurrence during midday, while feeding in the direct sunlight (Fig. 5.4), sleeping in the direct sunlight (Fig. 5.7), sleeping in the shade (Fig. 5.7) and walking in the shade (Fig. 5.8) reached their lowest frequency of occurrence then. Activities that reached their peak frequency of occurrence during the early afternoon included standing in the shade (Fig. 5.5), lying down in the shade (Fig. 5.6) and walking in the direct sunlight (Fig.5.8), while lying down in the direct sunlight (Fig. 5.6) reached its lowest frequency of occurrence then.

Feeding by season

A Generalised Linear Model was used to test the null hypothesis that the frequency of an activity in springbok herds did not differ significantly between the three different seasons. The results showed that none of the feeding-related activities produced either a good linear model fit or a significant dependence when analysed by season ($P>0.130$ and $R^2<0.005$ in all cases). Although fewer animals were found to feed in the direct sunlight in the hot-dry season than in the hot-wet season this difference was not significant ($P=0.087$; $R^2=0.003$). It appeared that more animals fed in the shade during the hot-dry season compared with the cold-dry season, but again this difference was not significant ($P=0.075$; $R^2=0.004$) (Fig. 5.10).

Season had no significant overall effect on all the feeding-related activities ($P=0.118$), even though these activities were distinctively different from each other when the effect of season was not included in the model ($P<0.0001$; df=1). The effect of season became apparent when the feeding activities were compared with some of the other activities such as lying down in sunlight ($P=0.003$; df=2), compared with feeding in the sunlight; and with feeding in the shade ($P<0.0001$; df=2).

The effect of wind on feeding

Wind strength

Analyses of data relating to wind strength were based on relatively few observations (n=97). Nonetheless, it showed a few notable results. Although the fit was poor, standing in the shade was positively linearly related to wind strength ($R^2=0.225$; $P<0.0001$). Feeding in the sunlight did not show a good linear model fit ($R^2=0.034$; $P=0.352$), while there were no data to analyse for feeding in the shade. None of the feeding activities seemed to be influenced by wind strength ($P>0.160$ in every case), nor did the feeding activities differ significantly from each other with the overall effect of wind strength taken into account ($P=0.352$; df=3).

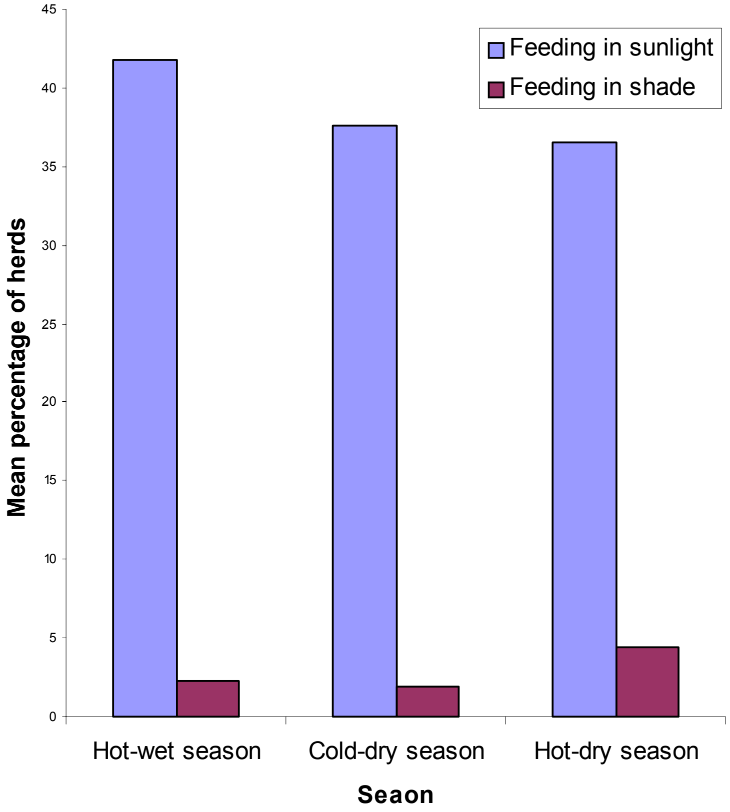

Fig. 5.10 The mean percentage of springbok herds feeding in sunlight and the shade respectively during the hot-wet, cold-dry and hot-dry seasons from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park.

Wind direction

A larger percentage of the herd fed in the sunlight when there was no wind, a southeasterly, or a random wind than when there was a northerly wind (P=0.022, P=0.043 and P=0.016, respectively). A larger percentage of the herd was observed feeding in the shade in northeasterly wind conditions than in northwesterly or no wind (P=0.009 and P=0.022 respectively). This may suggest that winds from the north to northeast are hotter winds that add to thermoregulation stress in springbok. Springbok may subsequently adapt by changing their feeding behaviour to specifically feed in the shade.

There was no effect of wind direction when the feeding activities were compared with each other (P=0.315; df=3) and most other activities, except when feeding in the shade was compared with standing in the sun (P=0.047). This could, however, be attributed to other factors such as direct or indirect sunlight, as a comparison between these two activities without the effect of wind direction proved that they were still statistically different from each other (P<0.0001).

Herd-size and rainfall

Rainfall is a key environmental factor in the southern Kalahari (Van Rooyen *et al.* 1990) and consequently, the effect of rainfall on herd size was examined. The Generalised Linear Model incorporated a lag effect in order to accommodate a response time for vegetation after the occurrence of rain.

A total of 17 rainfall stations are located on the South African side of the Kgalagadi Transfrontier Park. A geo-referenced grid was created to match specific rainfall stations with herd locations. Herd sizes varied between seasons and months. Significantly larger mean herd sizes were recorded during months of no rain, but where it had rained in the previous month, compared with when it had not rained for two consecutive months ($P=0.047$); and when it had rained during the surveying month, but not during the previous month ($P=0.012$); and when it had rained during both consecutive months ($P=0.014$; $R^2=0.13$; $F=3.05$; $df=3$) (Table 5.4). The present research results agree with those of Mills & Retief (1984). As only the monthly rainfall was used in this model, the herd size response could only be examined on a rough scale.

The largest mean herd sizes were recorded during June 2003 at 102.1 animals (n=25) and the smallest during November 2002 at 9.1 individuals (n=57) (Table 5.5). The largest herd recorded during the study period consisted of 476 springbok. This herd was found in the far northern part of the Nossob riverbed, close to Kannaguass waterhole, in April 2003. Mean herd sizes by season were largest during the cold-dry season (40 springbok, n=329), and declined slightly during the hot-wet season (35, n=294) and were smallest during the hot-dry season (19 springbok, n=326) (Table 5.5). These springbok herd sizes coincided roughly with those reported by other researchers in the same area (Mills & Retief 1984; Jackson *et al.* 1993), as having a peak from February to May and a trough from October to November

Springbok herd sizes therefore increased during the cold-dry season and decreased during the hot-dry season. This phenomenon appeared to be linked to specific rainfall patterns rather than to rigid seasonal boundaries. These results also support the results of other studies (Bigalke 1972; Nagy & Knight 1994; Bergström & Skarpe

Table 5.4

Relationship between herd size of springbok and rainfall on the South African side of the Kgalagadi Transfrontier Park during the study period from November 2002 to May 2004. Rainfall in the current and previous months were noted as present (1) or absent (0) respectively. Values with the same superscript do not differ significantly, (P>0.05)

Previous month	Current month	Mean herd size
0	0	40.915^{a}
0	1	24.189^{a}
1	0	71.413^{b}
1	1	15.099^{a}

Table 5.5

Mean herd sizes of springbok by month for the period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park

Season	**Month and year**	**Mean herd size ± Standard deviation**	**Number of observations**
Hot-dry	November 2002	9.1 ± 20.97	57
	December 2002	.	.
Hot-wet	January 2003	.	.
	February 2003	.	.
	March 2003	43.7 ± 76.67	73
	April 2003	31.1 ± 69.36	209
Cold-dry	May 2003	53.4 ± 83.43	58
	June 2003	102.1 ± 85.47	25
	July 2003	56.2 ± 75.07	48
	August 2003	23.0 ± 36.45	180
Hot-dry	September 2003	17.2 ± 25.47	141
	October 2003	13.5 ± 21.05	51
	November 2003	34.6 ± 59.88	73
	December 2003	29.7 ± 13.25	4
Hot-wet	January 2004	.	.
	February 2004	49.2 ± 76.48	10
	March 2004	74.0 ± 36.77	2
	April 2004	.	.
Cold-dry	May 2004	31.9 ± 55.63	18
Total	**.**	**40.6 ± 25.26**	**949**

1999), and are probably due to the rainfall-lambing concurrence. Bothma & Mills (1977), although using total counts instead of herd sizes, reported similar trends.

Springbok and other animals

Springbok are known to associate with blue wildebeest (*Connochaetes taurinus*) and gemsbok (*Oryx gazella*) (Skinner & Louw 1996). However, during the present study period, blue wildebeest were rarely recorded within close proximity of springbok herds, but were sometimes witnessed to feed in conjunction with springbok, as if moving in a convoy. The distance from the blue wildebeest to the springbok herds was mostly recorded at >50 m away (5.2%), followed by 0–20 m away (4.0%) and then by 21–50 m away (2.3%; $P=0.060$; $\chi^2=7.4$; $df=3$) (Table 5.6). In 88.5% of all the observations, blue wildebeest were either not present or were some distance away from the springbok herds studied. Gemsbok proximities showed similar trends ($P=0.007$; $\chi^2=9.86$; $df=2$) (Table 5.6). Moreover, gemsbok were close to springbok more often than blue wildebeest.

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, Begon *et al.* 1999). However, in the case of springbok and blue wildebeest, competition is avoided through niche separation. The blue wildebeest is a bulk, high-level grazer that seems to precede springbok as selective low-level grazers (Knight 1995). Qualitative observations confirmed this during the study period. Blue wildebeest have wide muzzles that are suited for grazing relatively close to the ground. Springbok have narrow muzzles suited for selective feeding (Skinner & Louw 1996) and were often observed tasting forage, but not consuming it.

Table 5.6

The proximity of springbok to blue wildebeest and gemsbok during the study period from November 2002 to May 2004 on the South African side of the Kgalagadi Transfrontier Park

Item	**Type of animal**			
	Blue wildebeest		**Gemsbok**	
	Number of observations	**Percentage**	**Number of observations**	**Percentage**
No data	841	88.5	796	84.2
0–20 m apart	38	4.0	47	5.0
21–50 m apart	22	2.3	31	3.3
>50 m apart	49	5.2	71	7.5
All observations	950	100.0	945	100.0

The results of the present study suggest that springbok and blue wildebeest coexist in the Kalahari by avoiding competition through niche separation. They also suggest that although these two types of animal are together, springbok and blue wildebeest more often prefer not to feed in close proximity. A similar trend has been described between Burchell's zebra (*Equus burchellii*), white-bearded wildebeest (*Connochaetes mearnsi*) and Thomson's gazelle (*Gazella thomsoni)* in the Serengeti in Tanzania (Sinclair & Norton-Griffiths 1982). The Thomson's gazelle has a similar morphology to the springbok and is also a selective feeder. In their study, Sinclair & Norton-Griffiths (1982) however, concluded that the white-bearded wildebeest population was regulating the Thomson's gazelle population in the Serengeti through competition. Competition may therefore be an important regulatory factor of the springbok population in the Kalahari and more research on this aspect is required.

Gemsbok were found to feed with springbok often. Gemsbok are considered roughage feeders and the majority of their diet consists of grass. It is not a strongly territorial animal and is believed to be fairly water independent (Bothma 2002). Few similarities between the preferred plant species selected for by springbok and gemsbok could be found in the literature (Leistner 1959).

5.5 Conclusions

The diet of Kalahari springbok is highly variable and diet selection is influenced by season and time of day. Kalahari springbok make regular use of natural licks, presumably to supplement their dietary requirements. This may have an environmentally degradable effect, especially due to lick locations, but may not be so serious as to require conservation efforts. Compared to other activities, feeding was the most important activity of springbok and had the highest frequency of occurrence, during all seasons and at all times of the day in the present study. Climate and weather conditions were found to have a significant effect on the feeding behaviour, as did shade and direct sunshine. In general, the springbok fed in the direct sunlight in the mornings and the frequency of feeding in the shade increased towards the midday. They also spent more time feeding in the shade during the hot-dry season than during the cold-dry and hot-wet ones. Wind strength did not affect feeding behaviour, although wind direction did. Springbok fed in the shade more often under northerly and northeasterly wind directions. Rainfall was found to influence herd sizes, and a relationship between herd size and feeding behaviour is proposed. The hypothesis of environmental and seasonal conditions affecting springbok feeding behaviour significantly can therefore be accepted. The ecological relationship between springbok and blue wildebeest was investigated and evidence was found of competition avoidance through niche separation.

5.6 Acknowledgements

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Appendix A

A list of the variables that were recorded by Kgalagadi Transfrontier Park staff, the researcher and visitors from November 2002 to May 2004 to study springbok behaviour on the South African side of the Kgalagadi Transfrontier Park

1. Date
2. Location
3. Time when observation starts
4. Total number of springbok
5. Riverbed habitat (yes or no)
6. Plains habitat (yes or no)
7. Duneveld (yes or no)
8. Pan type habitat (yes or no)
9. Tree dominated habitat (yes or no)
10. Grass dominated habitat (yes or no)
11. Shrub dominated habitat (yes or no)
12. Other (3 alternative dominant habitat features recorded)
13. Near a camp (yes or no)
14. Near a waterhole (yes or no)
15. Near a picnic spot (yes or no)
16. Other (none specified)
17. Total number of blue wildebeest
18. Total number of red hartebeest
19. Total number of gemsbok
20. Total number of other species (13 other animal species recorded)
21. Distance between springbok and blue wildebeest (0-20 m, 21-50 m and >50 m specified)
22. Distance between springbok and red hartebeest (0-20 m, 21-50 m and >50 m specified)
23. Distance between springbok and gemsbok,(0-20 m, 21-50 m and >50 m specified)
24. Distance between springbok and other animal species (0-20 m, 21-50 m and >50 m specified)
25. Percentage of the springbok herd feeding in sunlight[*]
26. Percentage of the springbok herd feeding in the shade[*]
27. Percentage of the springbok herd standing in sunlight[*]
28. Percentage of the springbok herd standing in shade[*]
29. Percentage of the springbok herd lying down in sunlight[*]
30. Percentage of the springbok herd lying down in shade[*]
31. Percentage of the springbok herd sleeping in sunlight[*]
32. Percentage of the springbok herd sleeping in shade[*]

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[*] Numbers were converted into percentages of the total herd after collection.

33. Percentage of the springbok herd walking in sunlight[*]
34. Percentage of the springbok herd walking in shade[*]
35. Percentage of the springbok herd playing in sunlight[*]
36. Percentage of the springbok herd playing in shade[*]
37. Percentage of the springbok herd doing something else[*]
38. (19 alternative actions recorded)
39. Percentage of the springbok herd feeding on grass[*]
40. Percentage of the springbok herd feeding on shrubs[*]
41. Percentage of the springbok herd feeding on trees[*]
42. Percentage of the springbok herd feeding on something else[*] (22 alternative options recorded)
43. Direction in which animals are moving (North, Northeast, East, Southeast, South, Southwest, West and Northwest specified)
44. Time when observation ends
45. Sheet number
46. Total number of male springbok in the herd[ϕ]
47. Total number of female springbok in the herd[ϕ]
48. Total number of immature springbok in the herd[ϕ]
49. Springbok are feeding on flowers (yes or no) [ϕ]
50. Springbok are feeding on fruit (yes or no) [ϕ]
51. Nearest waterhole (47 waterholes specified) [ϕ]
52. Habitat type (4 options specified) [ϕ]

Additional variables, only recorded by the researcher

53. Springbok are feeding on fresh, new plant growth (yes or no)
54. Springbok are feeding on old plant growth (yes or no)
55. Wind direction (North, Northeast, East, Southeast, South, Southwest, West and Northwest specified)
56. Wind strength (None, breeze, moderate, strong, extreme)

[ϕ] Although variable numbers 45 to 51 did not appear on the questionnaire, it was recorded as additional notes by the researcher, as well as some of the visitors / staff.

CHAPTER 6

A QUALITATIVE ASSESSMENT OF NOCTURNAL FEEDING BEHAVIOUR IN SPRINGBOK *ANTIDORCAS MARSUPIALIS*

Short communication, prepared for Koedoe

Night-time observations of springbok Antidorcas marsupialis *were made during different seasons and in different habitats on the South African side of the Kgalagadi Transfrontier Park in 2003. Springbok feeding behaviour was described in the context of other similar studies. Two peak feeding times were reported during the hot-dry season as opposed to one in the cold-dry and hot-wet seasons. In general, feeding periods were longer in the two dry seasons than in the wet season. These observations could indirectly be seen as supporting the hypothesis that animals feed on plant material at night because of elevated moisture levels then.*

Key words: Moisture, nocturnal feeding, Kalahari, springbok.

Springbok are considered largely water-independent (Skinner 1993; Bothma *et al.* 2002) and possess innovative abilities to obtain water from their environment to make up for their slightly above-average water requirements (Nagy & Knight 1994). Water is obtained either by drinking or feeding related activities. Nocturnal feeding is possibly an adaptation for increased water intake, but limited research has been done on this topic (Bigalke 1972; Mills & Haagner 1989; Skinner & Louw 1996).

Taylor (1968) proposed that plants (especially hygroscopic plants) absorb moisture at night when it is cooler and the relative humidity of the air is higher than during the daytime (Taylor 1968; Louw & Seely 1982; Skinner & Louw 1996). Taylor (1968) hypothesised that nocturnal feeding would result in a higher moisture intake for the herbivore and that nocturnal feeding is a realistic behavioural activity for herbivores in terms of increased moisture intake. Taylor (1968) measured the change in moisture content of plants under different relative humidity and temperature conditions and showed an increase of up to 40% moisture content under rather typical desert evening conditions. Louw & Seely (1982) effectively demonstrated the logic behind animals feeding during nighttime when plants had elevated moisture levels, but gave no account of existing supportive evidence. Two nighttime observations that were made during a previous study (Bigalke 1972) noted springbok herds feeding up to 21:30 and reports from the same study recorded grazing from around 5:00 on summer mornings. No further details were provided of exactly where and when the observations were made, or if any other feeding activity was recorded during the night.

During a research project in the Kalahari, five nighttime observations on springbok were made during the hot-wet (January – April), cold-dry (May – August) and hot-dry seasons (September – December) of 2003 in three different habitats in the Kgalagadi Transfrontier Park. These habitats were: the Auob riverbed, Nossob riverbed and at Bayip Pan (Table 6.1). Springbok were observed with a spotlight and spotting scope

Table 6.1

Some observations on nocturnal feeding behaviour by springbok Antidorcas marsupialis *in three different habitats during three seasons on the South African side of the Kgalagadi Transfrontier Park*

Season and item	Habitat		
	Auob riverbed	Nossob riverbed	Bayip pan
Cold-dry:			
Number of animals:	150: Estimated	-	-
Peak feeding time:	21:40-23:50	-	-
Food source:	Mostly unidentified and *Acacia erioloba* leaves	-	-
Hot-dry			
Number of animals:	220: Estimated	200: Estimated	-
Peak feeding time:	22:30-23:00 and 01:10-02:00	22:40-23:20 and 02:20-03:50	-
Food source:	Mostly unidentified and some young new growth and *Rhigozum trichotomum*	Mostly unidentified and some young new growth	-
Hot-wet			
Number of animals:	-	200: Estimated	15
Peak feeding time:	-	24:40-01:30	20:50-21:30
Food source:	-	Fresh new growth (after recent rain); unidentifiable grass seedlings with the roots attached; *Rhigozum trichotomum; Radyera urens*	Fresh new growth (after recent rain)

from a vehicle rooftop and their behaviour was recorded at intervals ranging from 5 to 30 minutes throughout the entire night. Exact observation locations varied depending on animal presence and although larger herds (up to 220 animals) were preferred, observations were also made on smaller herds (15 animals). Artificial waterholes were sometimes close by.

Quantifying nocturnal feeding behaviour poses considerable difficulties, as there are always individuals that do not take part in the feeding activity or do so but at different times. Nocturnal feeding behaviour in springbok appeared unsynchronised and although, for example, most of the herd would be up and about at some point, few would actually graze while the rest would play, attempt to mate or otherwise occupy themselves with other common springbok activities. Most of the time, springbok herds, especially the all-male bachelor herds, appeared somewhat uneasy or cautious as a result of the presence of the researchers.

Nocturnal feeding sessions seemed to occur at least once, but sometimes as two feeding sessions during the night. Springbok were found to feed until after sunset, followed by a period of rest and then they fed again later at night. This late feeding session usually started at around 21:00 in the cold-dry season, but was later in the hot-dry-season. This supplements the work of Bigalke (1972) who observed that springbok fed until 21:30 and again from 05:00 on summer mornings. During the hot-dry season, another feeding session was observed early in the morning, usually falling somewhere between 01:00 and 03:00. Some animals seemed to maintain constant activity throughout the night, especially males. However this did not appear to change with season. During all observations, animals started feeding again at first light.

The major part of their diet during the nocturnal feeding sessions consisted of unidentified fresh young growth, especially grass, and sometimes included shrubs such as *Rhigozum trichotomum* and forbs such as *Radyera urens*. By feeding at first light springbok would still obtain the benefit of an increased moisture content in plant material, although they were often observed drinking water from the many artificial waterholes available to them. It was evident that a significant part of their nighttime was spent feeding. It could not be established whether food plant selection at night differed significantly from that during the day, as identification of specifically selected plant species proved difficult at night. It seems to be unnecessary for springbok to feed at night in order to increase their moisture intake as artificial water points are readily available to them. Nocturnal feeding behaviour could be a form of depredation prevention by the herd through having vigilant individuals awake while some continue resting (Siegfried 1980, Treves 2000).

This short communication highlights the importance of nocturnal feeding in the ecology of the Kalahari springbok, but the topic still requires further investigation. The fact that two peak feeding times were reported during the hot-dry season as opposed to one in the cold-dry and hot-wet seasons, as well as longer feeding periods in the two dry seasons than in the wet season could be indirect evidence supporting the hypothesis that animals feed on plant material at night because of elevated moisture levels then. Data on how much food is actually consumed, specific *nocturnal plant selection and the nighttime social behaviour of Kalahari springbok are still largely lacking.*

6.1 Acknowledgements

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CHAPTER 7

SEASONAL NUTRIENT FLUCTUATION OF SELECTED PLANT SPECIES IN THE KALAHARI

Prepared for African Journal of Range and Forage Science

Abstract – Nutrients in plant species from the southwestern Kalahari showed a wider fluctuation range than in plants from other regions. Browse species had a higher crude protein content than grass species, but the fluctuation range was similar to that of grass species. *Grewia flava* was the most nutritious plant species sampled. The nutritional value of the plants was lowest during the cold-dry season and highest during the hot-dry one, but the latter was probably due to the effects of early rain experienced during the study period. The crude protein content of the grass species was often below that which is required by springbok for sustenance. The phosphorus content of all five plant species that were sampled in all the habitats during the cold-dry season were lower than that which is required by ruminants for sustenance. The Ca:P ratio of the plant species that were sampled in the present study fell outside the range that is considered to be healthy for ruminants in all instances, with calcium in excess.

Keywords: calcium, Kalahari, nitrogen content, nutritional value, phosphorus, seasonal variation.

7.1 Introduction

The productivity of large herbivores depends on the intake of digestible energy and nutrients through food, but the nutrient levels in plants fluctuate during different seasons (Skarpe & Bergström 1986; Tolsma *et al.* 1987). Poor quality of natural food sources are known to result in reduced animal production (Lukhele 2002). However, wild herbivores such as springbok are able to adapt to these fluctuations by moving away from areas of low nutritional quality to areas of higher nutritional quality (Mills & Retief 1984).

The springbok is an indigenous antelope of the Kalahari and plays a key role in the ecology of the area (Van Rooyen *et al.* 1994). Springbok react rapidly to environmental conditions (Bothma 1971; Mills & Retief 1984; Skinner & Louw 1996; Skinner & Moss 2004) and are known to be selective feeders (Skinner & Louw 1996). The nutritional status of the vegetation is believed to act as an important driving force in springbok ecology and it has been estimated that springbok consume up to 76% of the total available dry matter in the Auob and Nossob riverbeds in the Kalahari (Nagy & Knight 1994). However, the springbok population in the Kalahari is much smaller today than 50 years ago (Skarpe 2001; Skinner & Moss 2004), despite maintaining large populations in other areas of South Africa, such as the Karoo where they have shown a significant positive growth in recent years (Skinner & Moss 2004). This decline in numbers could not be explained as yet. Springbok conservation in the Kalahari therefore requires an in-depth knowledge of the region-specific ecology and the application of sound management practices.

The mineral content of a plant is affected primarily by the mineral status of the soil in which it grows (McDowell 1985; Underwood & Suttle 1999). However, it is also affected by a range of other factors, such as the stage of maturity of the plant, genetic predisposition and the weather (Underwood & Suttle 1999; Bechaz 2000; Grant *et al.* 2000; Whitehead 2000; Lukhele 2002). Different plant parts may also have different nutritional values (Owen-Smith & Novellie 1982; Coleman & Henry 2002). By shedding their seeds, plants also lose a large amount of their minerals (Underwood & Suttle 1999).

The chemical composition of plant food is often used as an index of its quality (Badri & Hamed 2000) and it has been shown to affect springbok habitat selection (Bigalke 1972; Vorster 1996). The calcium (Ca), phosphorus (P), nitrogen (N) and crude protein contents of plants have been used as indicators of their nutritional value (Skarpe & Bergström 1986; Tolsma *et al.* 1987; Vorster 1996; Badri & Hamed 2000; Bechaz 2000; Engelbrecht 2002; Lukhele 2002; Scogings *et al.* 2004). Van Hoven *et al.* (1984) studied the *in vitro* digestion of some plant species utilised by ungulates in the Kalahari and discussed the correlation between the percentage digestibility and the protein content of the plant species that were utilised by springbok. The nutrient content and digestibility were shown to differ significantly between forage plant species, and phenology and rainfall were reported to induce seasonal variation in the Kalahari vegetation (Skarpe & Bergström 1986). The latter study also showed that woody plant species were more nutritious than grass species. Seasonal fluctuation of nutrients was shown for several tree and grass species in the Kalahari in Botswana by Tolsma *et al.* (1987) who also showed that the nitrogen concentration in the leaves of shallow rooted *Acacia* species was higher than that of deep-rooted *Acacia* species. They also described the movement of nutrients in plants.

The present study aims to address the details of the region-specific ecology of the Kalahari springbok by partially investigating the relative nutritional quality of some of the commonly utilised plant species of the region. By doing so, the nutritional stress that is experienced by springbok, especially during dry periods, may be understood better. The hypotheses that were tested were:

1. Food plants in the southwestern Kalahari have a depleted nutritional value.
2. The nutritionally depleted food plants of the southwestern Kalahari place nutritional stress on springbok during dry periods.

7.2 Study area

The Kalahari is an arid savanna or semi-desert (Van Rooyen & Van Rooyen 1998) which is characterised by a lack of permanent water sources (Thomas & Shaw 1991) and deep aeolian sands (Totolo & Chanda 2003). The Kgalagadi Transfrontier Park is a large conservation area within the southwestern Kalahari, which is spread across the borders of South Africa and Botswana, and covers some 36 300 km^2. The South African side of the Park consists of a range of plant communities and habitats of which the Auob and Nossob riverbeds are the areas most heavily utilised by herbivores (Mills & Retief 1984). The substrate in the southwestern Kalahari is made up primarily of red sands, resting on calcrete which is unmistakably exposed in the Auob and the Nossob riverbeds (Jackson 1995; Van Rooyen & Van Rooyen 1998).

Some pans occur across the Park, increasing in abundance northwards and eastwards into Botswana. The South African side of the Park is situated from 24°15'S to 26°30'S, and 20°00'E to 20°45'E. The altitude ranges from 870 to 1 080 m above sea level. The area receives the bulk of its rain during summer, with a highly variable annual rainfall (Skarpe & Bergström 1986). The mean rainfall in the southwestern Kalahari, from 1980 to 2005 was 180.4 mm[6] as measured at Nossob Rest Camp, Mata-Mata Rest Camp, Twee Rivieren Rest Camp and the Van Zylsrus Town weather stations. Rainfall during the study period is given in Table 7.1. Drought years are known to occur (Knight 1995). Three clear ecological seasons can be distinguished *viz.* the hot-wet season (January to April), the cold-dry season (May to August) and the hot-dry season (September to December) (Leistner 1967; Mills & Retief 1984; Van Rooyen & Van Rooyen 1998). Extreme temperature variations have been recorded, such as winter lows of around -10°C and summer highs of around 45°C (Van Rooyen *et al.* 1990).

7.3 Procedure

The study area was divided into four broad habitat types, namely the Nossob riverbed, the Auob riverbed, the pans and the dunes. Five randomly selected sample sites were chosen within each of these habitat types, and were verified for

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[6] Electronic data supplied by the South African Weather Bureau 2005.

Table 7.1

Rainfall (mm) records from various localities on the South African side of the Kgalagadi Transfrontier Park during April to December 2003. Plant samples were collected for nutritional analysis during the shaded months[2]

Weather station	**April**	**May**	**June**	**July**	**August**	**September**	**October**	**November**	**December**
AUCHTERLONIE	11.1	0.0	0.0	0.0	0.0	8.0	17.4	4.0	0.0
BAYIP	10.5	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0
BITTERPAN	13.0	0.0	0.0	0.0	0.0	27.5	22.0	10.0	0.0
DIKBAARDSKOLK	14.5	0.9	0.0	0.0	0.0	10.3	12.2	0.0	0.0
DRIEFENDAS	14.5	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0
GROOTBRAK	4.5	0.0	0.0	0.0	0.0	8.5	0.0	7.6	0.0
KAMQUA	13.5	13.5	0.0	0.0	0.0	0.0	23.5	3.5	0.0
KLEIN SKRIJ	8.8	0.0	0.0	0.0	0.0	0.0	15.5	9.5	0.0
KRANSBRAK	25.9	1.4	0.0	0.0	0.0	3.0	17.0	5.5	0.0
KIJ KIJ	20.0	14.0	0.0	0.0	0.0	5.7	17.6	0.3	0.0
MATA MATA	9.3	0.0	0.0	0.0	0.0	11.5	18.0	36.5	0.0
MORAVET	12.0	0.0	0.0	0.0	0.0	19.5	13.2	1.8	0.0
NOSSOB	16.2	0.2	0.0	0.0	0.0	8.9	32.3	9.7	4.4
O'KUIP	6.5	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
SEWEPANNE	8.5	0.0	0.0	0.0	0.0	6.0	0.0	0.6	0.0
TWEE RIVIEREN	18.0	1.0	0.0	0.0	0.5	5.7	21.5	11.5	2.0
UNIE-END	13.5	0.0	0.0	0.0	0.0	7.5	0.0	4.1	0.0

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[2] Electronic data supplied by the South African Weather Bureau 2005.

representivity by field investigation. *Acacia erioloba, Rhigozum trichotomum* and *Schmidtia kalihariensis* occurred in all the habitats, *Stipagrostis obtusa* was collected in all but the dunes, and *Grewia flava* occurred in all but the Auob Riverbed. Sample sites were geo-referenced and samples of these plant species were collected during the hot-wet, cold-dry and hot-dry seasons. Sampling took place between 07:30 and 19:30.

Grazing material was collected to 20 mm above the soil surface and browse consisted of the last 300 mm of branch tips. This was done to simulate springbok selection on a broad scale. All samples were taken from several individual plants with at least five replicates per species. In the hot-wet season, sampling was done during April 2003, during July or August 2003 in the cold-dry season and during November 2003 in the hot-dry season. All the plant samples were collected and stored in marked paper bags. Samples were oven-dried in a convection oven at 100ºC to a constant mass. Dry matter mass estimation was then determined according to the method described by the Association of Official Analytical Chemists (1990).

All mass measurements were made using a Precisa 12100D Superball series scale with one decimal specified. At least two individual mass determinations were done and their mean was calculated. Samples were then milled to a maximum particle size of 1 mm and submitted for chemical analyses. All chemical analyses were done in duplicate, by the University of Pretoria's Nutrilab according to the guidelines of the Association of Official Analytical Chemists (1990). Calcium, crude protein, nitrogen and phosphorus contents were determined. Nitrogen content was determined by the macro-Kjeldahl method (Association of Official Analytical Chemists 1990) using a block digester and distilling with a Kjeltec system model 1026. Nitrogen was calculated as follows:

Percentage N = [Factor x (sample titration – blank titration)] / sample mass (g)] x 100

The percentage N was then given as a percentage of the dry mass of the sample.

According to Boyazoglu (1997), the mean nitrogen content of protein is 16%. Nitrogen values are thus multiplied by 6.25 to get a ‘crude protein’ value which includes non-nitrogenous protein products. The concentration of the minerals calcium and phosphorus was determined by first digesting the plant material through a wet digestion system by taking 1 g of sample material and digesting it in a block digester at 230°C. The concentration of calcium was determined by using a Perkin Elmer 2380 Atomic Absorption Spectrophotometer pp Ay II. The concentration of phosphorus was determined by using a Technicon Auto Analyzer II according to the standard photometric method (Association of Official Analytical Chemists 1990). With every digestion, an internal laboratory standard with known concentrations of minerals was included. The standard was kept in a refrigerator. Calcium and phosphorus content were calculated as follows:

Percentage of Ca or P = [n g/kg x X / Y] / 1000

Where: X = dilution factor

Y = sample mass (g)

The n g/kg ratio was a reading given by the atomic absorption apparatus.

The percentage Ca and phosphorus were both reported as a percentage of the dry mass of the sample.

The results of the chemical analyses were captured into a numerical matrix by using Microsoft® Excel. Material from each of the five sample sites within the same habitat were classified as repetitions for each plant species. Data were analysed with uni- and multivariate statistical techniques and all analyses were done using SAS®[Ψ] software. Generalised Linear Models were applied, sometimes with repeated measures analyses of variance. Least square means were used wherever the means for collective data were determined. ANOVA tests were done to examine the relationships between habitat, species and season.

7.4 Results

Habitat had a significant effect on nutritional value (Wilks' Lambda <0.0001; F=4.04; df=18), and so did season (Wilks' Lambda <0.0001; F=47.27; df=12) and species (Wilks' Lambda <0.0001; F=25.79; df=24). The woody plant species were generally found to produce higher nutritional values than the grass species, while the shrub *Grewia flava* contained the highest level of nutrients of all the food plants, and the grass *Stipagrostis obtusa* the lowest. Of the two riverbeds, the Nossob riverbed's vegetation was generally of higher nutritive value (Tables 7.2, 7.3 and 7.4).

Nitrogen (N) and crude protein (CP)

In general, the concentration of nitrogen in the plant samples decreased from the hot-wet to the cold-dry season, but in most cases this decrease was not significant (Table

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[Ψ] SAS® Software Version 8.2 supplied by The SAS Institute Inc., SAS Campus Drive, Cary, NC 27512, USA, running under z/VM 4.4.0 (RSU 0404) on the mainframe computer IBM Z800 2066/0C1 of the University of Pretoria.

Table 7.2

The nitrogen percentages of five plant species that were sampled in different habitats on the South African side of the Kgalagadi Transfrontier Park from April to November 2003. The superscripts (^{x} and ^{y}) that precede the nitrogen values denote significance within one species in the same season in different habitats (within rows) and superscripts (^{a}, ^{b} and ^{c}) that follow the nitrogen values denote significance within one species in the same habitat in different seasons (within columns). Values with the same superscripts do not differ significantly ($P \leq 0.05$)

Species		**Season**	
Habitat	**Hot-wet**	**Cold-dry**	**Hot-dry**
Acacia erioloba			
Nossob riverbed	$^{x}2.6^{a}$	$^{x}2.5^{a}$	$^{x}3.0^{b}$
Pans	$^{x}2.7^{a}$	$^{x}2.5^{a}$	$^{x}3.2^{b}$
Dunes	$^{x}2.7^{a}$	$^{x}2.4^{a}$	$^{x}3.0^{b}$
Auob riverbed	$^{x}2.5^{a}$	$^{y}2.1^{b}$	$^{y}2.6^{a}$
Grewia flava			
Nossob riverbed	$^{x}3.0^{a}$	$^{x}2.1^{b}$	$^{x}3.4^{c}$
Pans	.	.	.
Dunes	$^{x}2.9^{a}$	$^{x}2.1^{b}$	$^{x}3.3^{c}$
Auob riverbed	$^{x}2.5^{a}$	.	$^{y}2.7^{a}$
Rhigozum trichotomum			
Nossob riverbed	$^{x}2.4^{a\,b}$	$^{x}1.9^{a}$	$^{x}2.8^{b}$
Pans	$^{x}2.3^{a}$	$^{x}2.1^{a}$	$^{x}2.4^{a}$
Dunes	$^{x}2.4^{a}$	$^{x}2.2^{a}$	$^{x}2.8^{a}$
Auob riverbed	$^{x}2.3^{a}$	$^{x}1.9^{b}$	$^{x}2.7^{a}$
Schmidtia kalihariensis			
Nossob riverbed	$^{x}1.8^{a\,b}$	$^{x}1.0^{a}$	$^{x}2.4^{b}$
Pans	$^{x}1.7^{a}$	$^{x}1.0^{b}$	$^{x}0.8^{b}$
Dunes	$^{x}1.6^{a}$	$^{x}1.3^{a}$	$^{x}2.1^{b}$
Auob riverbed	$^{x}1.4^{a}$	$^{y}0.5^{a}$	$^{x}1.6^{a}$
Stipagrostis obtusa			
Nossob riverbed	$^{xy}1.4^{a}$	$^{x}1.0^{a}$	$^{x}2.1^{b}$
Pans	$^{x}1.1^{a}$	$^{x}0.8^{a}$	$^{x}1.6^{a}$
Dunes	.	.	.
Auob riverbed	$^{y}1.5^{a}$	$^{x}1.0^{b}$	$^{x}1.9^{c}$

Table 7.3

The phosphorus content (g/kg of the dry matter by mass) of five plant species that were sampled in different habitats on the South African side of the Kgalagadi Transfrontier Park from April to November 2003. The superscripts (^{x} and ^{y}) that precede the phosphorus values denote significance within one species in the same season in different habitats (within rows) and superscripts (^{a}, ^{b} and ^{c}) that follow the phosphorus values denote significance within one species in the same habitat in different seasons (within columns). Values with the same superscripts do not differ significantly ($P \leq 0.05$)

Species	**Season**		
Habitat	**Hot-wet**	**Cold-dry**	**Hot-dry**
Acacia erioloba			
Nossob riverbed	$^{x}0.18^{a}$	$^{y}0.09^{a}$	$^{y}0.19^{a}$
Pans	$^{x}0.10^{a}$	$^{y}0.09^{a}$	$^{y}0.19^{b}$
Dunes	$^{x}0.10^{a}$	$^{xy}0.08^{a}$	$^{xy}0.16^{b}$
Auob riverbed	$^{x}0.19^{b}$	$^{x}0.07^{a}$	$^{x}0.12^{b}$
Grewia flava			
Nossob riverbed	$^{y}0.20^{b}$	$^{y}0.13^{a}$	$^{x}0.24^{b}$
Pans	.	.	.
Dunes	$^{x}0.13^{b}$	$^{x}0.09^{a}$	$^{x}0.20^{c}$
Auob riverbed	$^{y}0.21^{a}$	.	$^{x}0.20^{a}$
Rhigozum trichotomum			
Nossob riverbed	$^{x}0.14^{b}$	$^{x}0.10^{a}$	$^{x}0.19^{c}$
Pans	$^{x}0.13^{b}$	$^{x}0.09^{a}$	$^{x}0.17^{c}$
Dunes	$^{x}0.23^{a}$	$^{x}0.10^{a}$	$^{x}0.16^{a}$
Auob riverbed	$^{x}0.15^{b}$	$^{x}0.11^{a}$	$^{x}0.19^{c}$
Schmidtia kalihariensis			
Nossob riverbed	$^{x}0.19^{b}$	$^{y}0.08^{a}$	$^{y}0.16^{ab}$
Pans	$^{x}0.13^{b}$	$^{xy}0.06^{a}$	$^{x}0.05^{a}$
Dunes	$^{x}0.13^{a}$	$^{y}0.08^{a}$	$^{xy}0.13^{a}$
Auob riverbed	$^{x}0.16^{b}$	$^{x}0.04^{a}$	$^{xy}0.14^{ab}$
Stipagrostis obtusa			
Nossob riverbed	$^{y}0.09^{a}$	$^{x}0.06^{a}$	$^{x}0.14^{b}$
Pans	$^{x}0.06^{ab}$	$^{x}0.05^{a}$	$^{x}0.10^{b}$
Dunes	.	.	.
Auob riverbed	$^{y}0.11^{b}$	$^{x}0.06^{a}$	$^{x}0.14^{b}$

Table 7.4

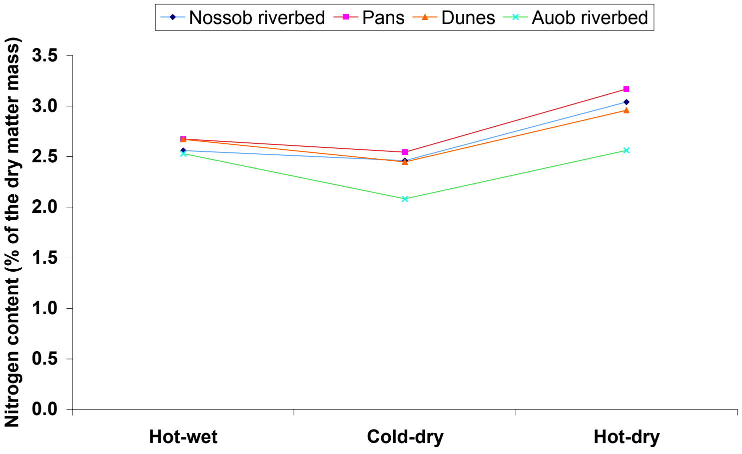
The calcium contents (g/kg of the dry matter by mass) of five plant species that were sampled in different habitats on the South African side of the Kgalagadi Transfrontier Park from April to November 2003. The superscripts (^{x} *and* ^{y}*) that precede the calcium values denote significance within one species in the same season in different habitats (within rows) and superscripts (*^{a}, ^{b} *and* ^{c}*) that follow the calcium values denote significance within one species in the same habitat in different seasons (within columns). Values with the same superscripts do not differ significantly (*$P \leq 0.05$*)*

Species		**Season**	
Habitat	**Hot-wet**	**Cold-dry**	**Hot-dry**
Acacia erioloba			
Nossob riverbed	$^{x}1.2^{a}$	$^{x}1.9^{b}$	$^{xy}0.8^{a}$
Pans	$^{x}1.0^{a}$	$^{x}1.8^{b}$	$^{x}0.5^{a}$
Dunes	$^{x}1.2^{b}$	$^{x}1.9^{c}$	$^{xy}0.7^{a}$
Auob riverbed	$^{x}1.4^{a}$	$^{x}2.3^{b}$	$^{y}1.1^{a}$
Grewia flava			
Nossob riverbed	$^{z}2.2^{b}$	$^{x}2.5^{c}$	$^{y}1.3^{a}$
Pans	.	.	.
Dunes	$^{x}1.5^{a}$	$^{x}2.1^{b}$	$^{x}1.1^{a}$
Auob riverbed	$^{y}1.9^{b}$	.	$^{y}1.4^{a}$
Rhigozum trichotomum			
Nossob riverbed	$^{x}1.2^{a}$	$^{x}1.7^{b}$	$^{x}1.1^{a}$
Pans	$^{x}1.2^{ab}$	$^{x}1.7^{b}$	$^{x}0.7^{a}$
Dunes	$^{x}0.9^{a}$	$^{x}1.2^{a}$	$^{x}0.9^{a}$
Auob riverbed	$^{x}1.2^{a}$	$^{x}1.6^{b}$	$^{x}1.0^{a}$
Schmidtia kalihariensis			
Nossob riverbed	$^{y}0.9^{a}$	$^{y}1.1^{a}$	$^{x}0.9^{a}$
Pans	$^{xy}0.7^{a}$	$^{xy}0.6^{a}$	$^{x}0.5^{a}$
Dunes	$^{x}0.4^{a}$	$^{x}0.5^{a}$	$^{x}0.6^{a}$
Auob riverbed	$^{xy}0.8^{a}$	$^{xy}0.6^{a}$	$^{x}0.8^{a}$
Stipagrostis obtusa			
Nossob riverbed	$^{x}0.8^{a}$	$^{x}0.7^{a}$	$^{x}0.7^{a}$
Pans	$^{x}0.7^{a}$	$^{x}0.6^{a}$	$^{x}0.6^{a}$
Dunes	.	.	.
Auob riverbed	$^{x}0.7^{a}$	$^{x}0.6^{a}$	$^{x}0.7^{a}$

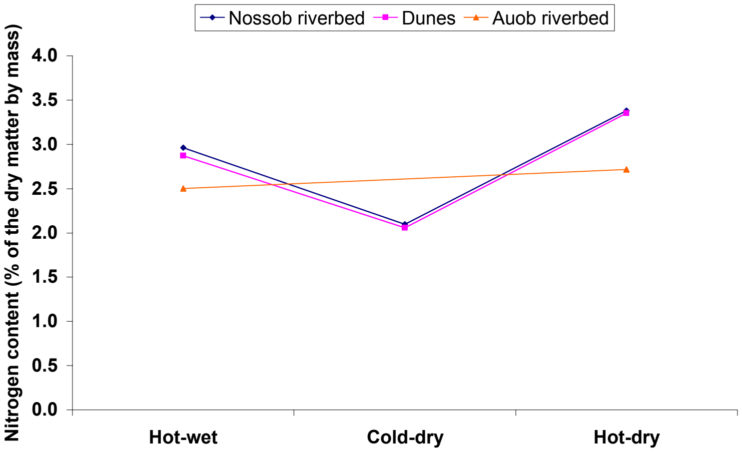
7.2; Figs. 7.1). The decrease was followed by an increase to a peak in the hot-dry season. In many instances this peak value in the hot-dry season was significantly higher than those of the other two seasons (Table 7.2). The browse plant species contained higher nitrogen concentrations than the grasses (Table 7.2; Figs. 7.1), while *Acacia erioloba*, *Grewia flava*, and *Rhigozum trichotomum* consistently contained higher levels of nitrogen than the comparable values of *Schmidtia kalihariensis* and *Stipagrostis obtusa* in all habitats and seasons. Measured nitrogen and crude protein values for *Acacia erioloba* in the present study were amongst the highest of the species sampled (Table 7.2; Fig. 7.1a). The crude protein values measured for *Acacia erioloba* in the present study fluctuated from 13.0 to 18.8% with a mean of 15.0% over all habitats during the cold-dry season, when crude protein values were at a minimum. Values for the hot-dry season were significantly higher than in the other seasons, except in the Auob riverbed. Habitat did not have a significant effect on nitrogen concentrations of *Acacia erioloba* in the hot-wet season, but in both the cold-dry and hot-dry seasons the values for the Auob riverbed were significantly lower than those of the other habitats (Fig. 7.1a).

The highest nitrogen concentration in the Nossob riverbed was found in *Grewia flava* during the hot-dry season (Table 7.2; Fig. 7.1b) with crude protein content ranging from 13.1% to 21.2% of the dry mass. The nitrogen values for the cold-dry season of *Grewia flava* were significantly lower than for the other seasons whereas the hot-dry season values were significantly highest, except for the Auob riverbed (Fig. 7.1b). Habitat had little effect on the nitrogen concentrations of *Grewia flava*, except in the hot-dry season when the value for the Auob riverbed was significantly lower than for the other habitats (Table 7.2; Fig. 7.1b).

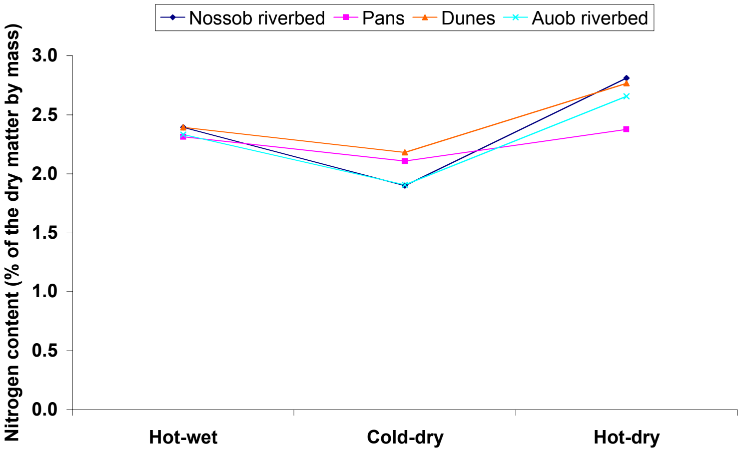
a.

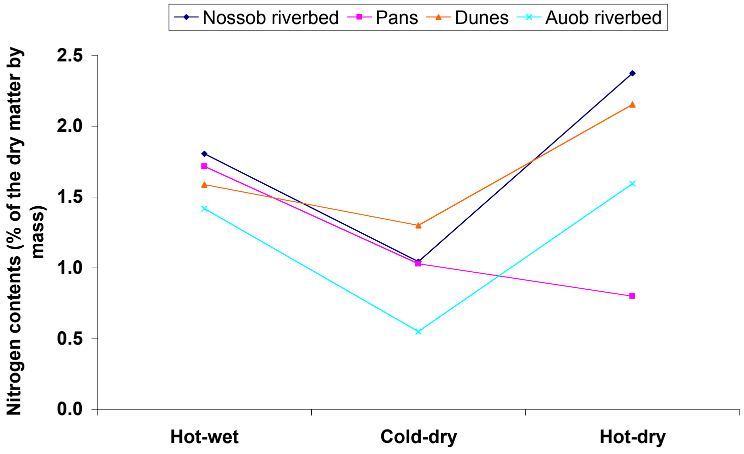

Nossob riverbed
Pans
Dunes
Auob riverbed
Nitrogen content (% of the dry matter mass)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Hot-wet
Cold-dry
Hot-dry

b.

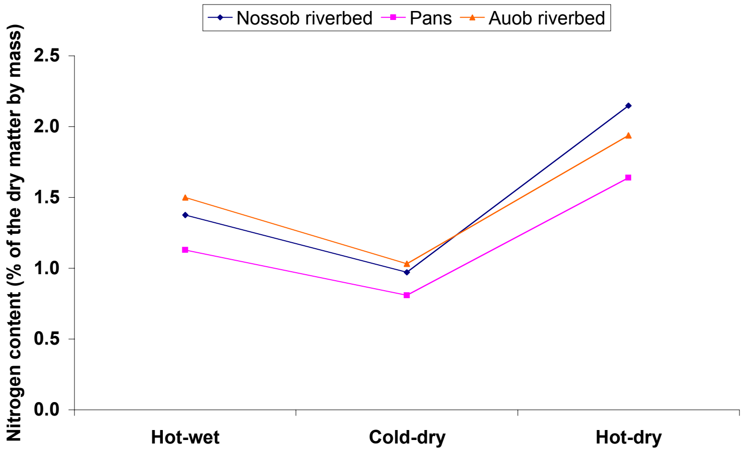

Nossob riverbed
Dunes
Auob riverbed
Nitrogen content (% of the dry matter by mass)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Hot-wet
Cold-dry
Hot-dry

c.


Nossob riverbed
Pans
Dunes
Auob riverbed
Nitrogen content (% of the dry matter by mass)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Hot-wet
Cold-dry
Hot-dry



d.



e.

Fig. 7.1 The nitrogen content of a. *Acacia erioloba,* b. *Grewia flava,* c. *Rhigozum trichotomum,* d. *Schmidtia kalihariensis* and e. *Stipagrostis obtusa* in different habitats on the South African side of the Kgalagadi Transfrontier Park in the hot-wet, cold-dry and hot-dry season from April to November 2003.

Habitat had no significant effect on the nitrogen concentration of *Rhigozum trichotomum* and significant seasonal effects were only found for the Nossob and Auob riverbeds (Table 7.2; Fig. 7.1c). The crude protein content of *Rhigozum trichotomum* ranged from 11.9 to 17.5% of dry mass.

The lowest nitrogen concentration of all plant species examined in all seasons and habitats was found in the Auob riverbed in *Schmidtia kalihariensis* during the cold-dry season (Table 7.2; Fig. 7.2d). Habitat had a significant effect only in the case of the cold-dry season with the value of the Auob riverbed once again being lower than that of the other habitats. During the hot-dry season, the lowest overall nitrogen concentration was found in the pans in *Schmidtia kalihariensis* (Table 7.2). It was also the only species and habitat where the nitrogen concentration was lowest during the hot-dry season.

The nitrogen content of *Stipagrostis obtusa* in the southern Kalahari was found to fluctuate from 0.8 to 2.1% of the dry matter by mass (Table 7.2; Fig. 7.1e). Nitrogen content was generally the highest in the hot-wet season and the lowest in the cold-dry one. Habitat only had a significant effect in the case of the hot-wet season, and in this instance the value of the Auob riverbed was significantly higher than that of the pans.

Minerals

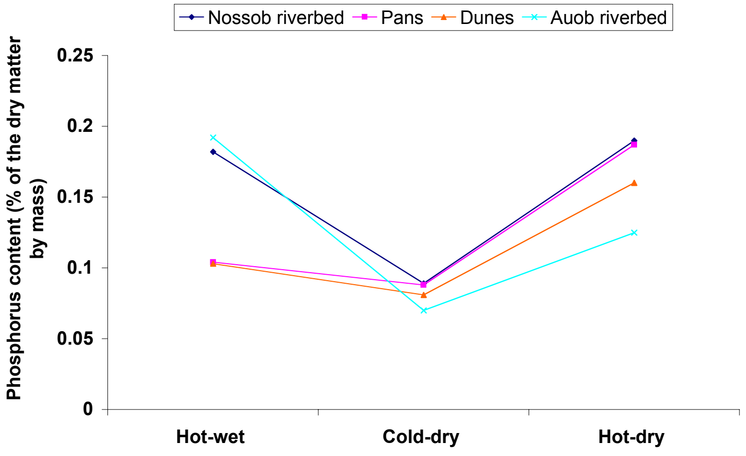
Phosphorus (P)

Across all habitats and plant species sampled, the phosphorus concentration fluctuated from 0.05 to 0.24% of the dry matter by mass (Table 7.3). The effect of season ($P<0.0001$; $F=42.4$; $df=2$) and plant species ($P<0.0001$; $F=9.33$; $df=4$) on the phosphorus content of a plant species was more significant than that of habitat (P=0.0081; F=4.03; df=3; R^2=0.41). There was a decline in the phosphorus content of all the plant species in all habitats from the hot-wet to the cold-dry season and in most cases, the phosphorus values differed significantly (Table 7.3; Figs. 7.2).

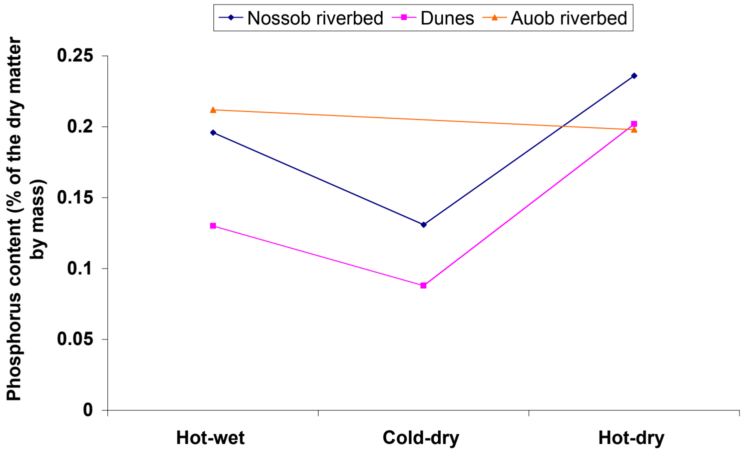
The phosphorus content of *Acacia erioloba* in all the habitats and seasons ranged from 0.07 to 0.19% of the dry matter by mass and represented the narrowest phosphorus range of the browse species in this study (Table 7.3). A general peak was measured in all habitats during the hot-dry season and the lowest concentrations occurred during the cold-dry one, but this difference was not always significant between seasons (Fig. 7.2a; Table 7.3). Habitat rarely affected the concentration of phosphorus in *Acacia erioloba* in the same season (Table 7.3).

The phosphorus concentration of *Grewia flava* ranged from 0.09 to 0.24% (Table 7.3). The highest phosphorus content of 0.24% overall was found in *Grewia flava* in the Nossob riverbed during the hot-dry season. Phosphorus concentrations in *Grewia flava* also generally reached a peak in the hot-dry season with the lowest levels measured during the cold-dry one (Fig. 7.2b), but the difference was not always significant (Table 7.3). The influence of habitat on phosphorus concentrations in *Grewia flava* during the same season was rarely significant (Table 7.3).

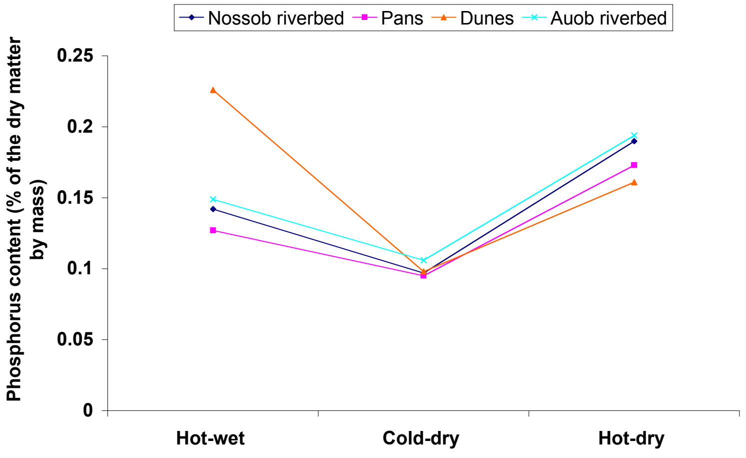
Rhigozum trichotomum's phosphorus content was the second highest overall, with a range from 0.09 to 0.23% of the dry matter by mass (Table 7.3). The seasonal change of the phosphorus content in *Rhigozum trichotomum* was statistically significant in most habitats (Table 7.3), generally with a peak during the hot-dry


Nossob riverbed
Pans
Dunes
Auob riverbed
Phosphorus content (% of the dry matter by mass)
0.25
0.2
0.15
0.1
0.05
0
Hot-wet
Cold-dry
Hot-dry

a.


Nossob riverbed
Dunes
Auob riverbed
Phosphorus content (% of the dry matter by mass)
0.25
0.2
0.15
0.1
0.05
0
Hot-wet
Cold-dry
Hot-dry

b.


Nossob riverbed
Pans
Dunes
Auob riverbed
Phosphorus content (% of the dry matter by mass)
0.25
0.2
0.15
0.1
0.05
0
Hot-wet
Cold-dry
Hot-dry

c.

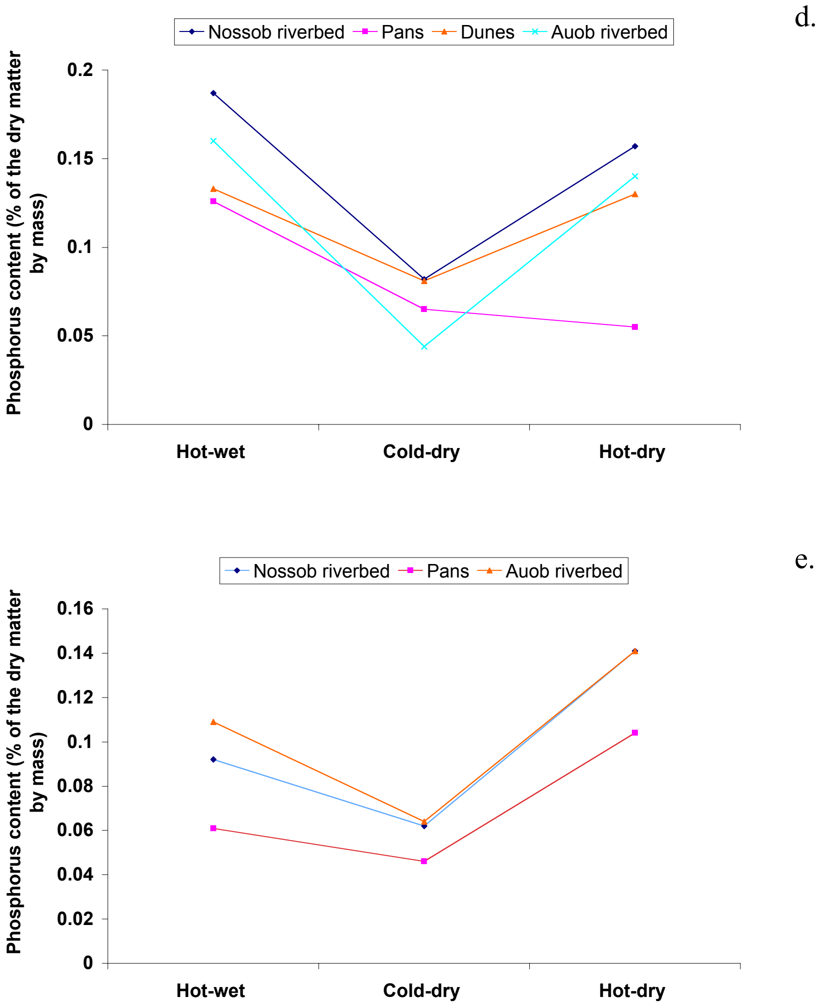


Fig. 7.2 The phosphorus content of a. *Acacia erioloba,* b. *Grewia flava,* c. *Rhigozum trichotomum,* d. *Schmidtia kalihariensis* and e. *Stipagrostis obtusa* in different habitats on the South African side of the Kgalagadi Transfrontier Park in the hot-wet, cold-dry and hot-dry season from March to November 2003.

season and the lowest levels measured during the cold-dry one (Fig. 7.2c). Habitat had no effect on the phosphorus levels of *Rhigozum trichotomum* in the same season (Table 7.3).

The lowest phosphorus content overall was found in *Schmidtia kalihariensis* in the Auob riverbed in the cold-dry season (0.04%). The phosphorus concentrations in *Schmidtia kalihariensis* ranged from 0.04% to 0.19%, generally reaching a peak in the hot-wet season and its lowest concentrations in the cold-dry one (Table 7.3; Fig. 7.2d) and the difference was often significant. Habitat influenced phosphorus concentrations in *Schmidtia kalihariensis* in the cold-dry and hot-dry season, but not in the hot-wet one (Table 7.3).

The phosphorus concentration of *Stipagrostis obtusa* ranged from 0.05 to 0.14% (Table 7.3). The lowest phosphorus concentrations were measured during the cold-dry season and the highest during the hot-dry one (Fig. 7.2e), with the difference between seasons often significant (Table 7.3). The phosphorus concentration of *Stipagrostis obtusa* was influenced by habitat only within the hot-wet season.

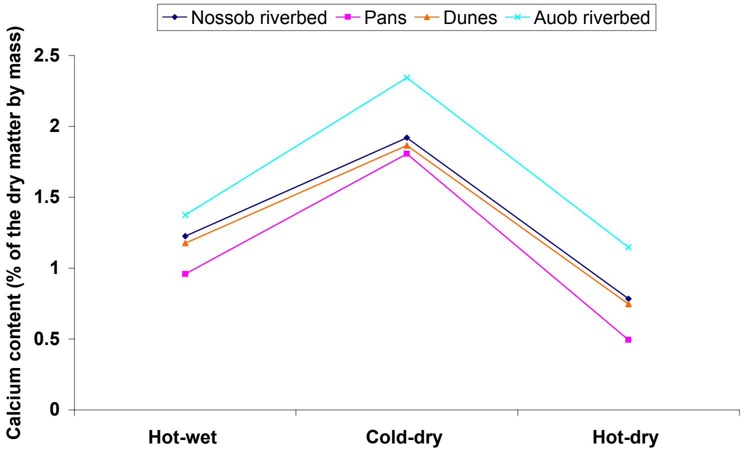
In general, the variation between seasons within species was most often significant in the Auob riverbed and least often within the dunes.

Calcium (Ca)

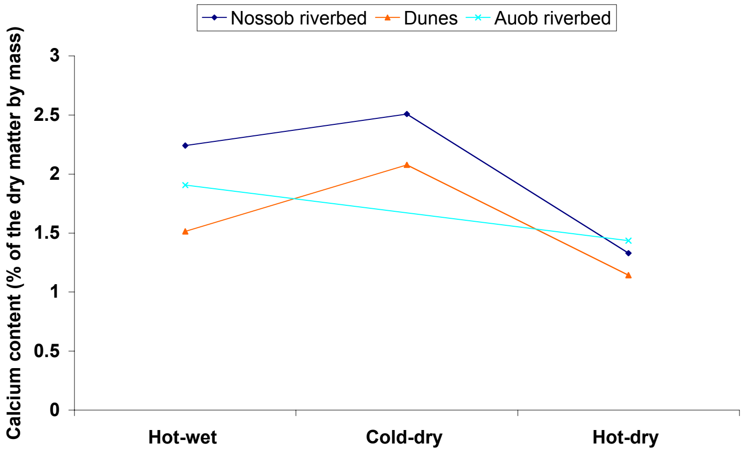
The calcium content of all the woody plant species in all the habitats reached a peak during the cold-dry season and a low during the hot-dry season (Table 7.4). However, the difference between the Ca content in the hot-wet season and the hot-dry one was only significant in three instances (Table 7.4). The Ca concentration of the browse plant species was noticably higher than those of the grass species, and the grass species also had a narrower fluctuation range across seasons, compared with the wider fluctuation range measured for browse species during the same time (Fig. 7.3). Across all habitats and plant species sampled, calcium levels fluctuated from 0.5 to 2.5 % (Table 7.4).

The Ca concentration of *Acacia erioloba* ranged from 0.5 to 2.3 % of the dry matter by mass (Table 7.4). A general peak was measured in the cold-dry season and the lowest concentrations occurred during the hot-wet one (Fig. 7.3a). The Ca content differences between *Acacia erioloba* in different habitats within the same season were rarely significant, but the differences within the same habitat across different seasons were often significant (Table 7.4).

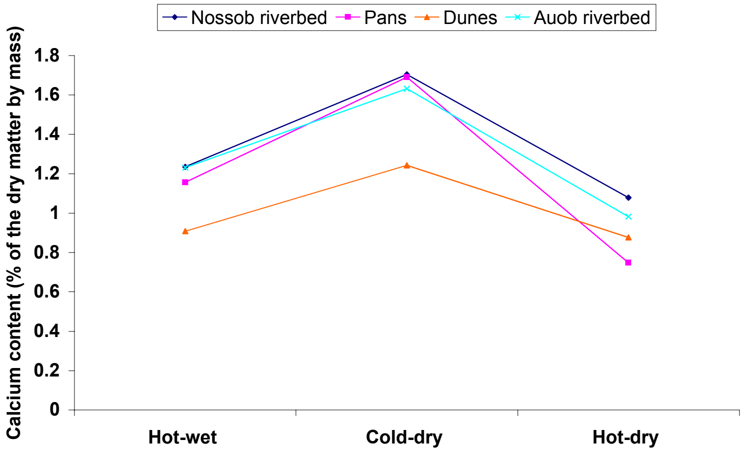
The Ca content fluctuation of *Grewia flava* showed similar trends to that of *Acacia erioloba*. Calcium concentration in *Grewia flava* ranged from 1.1 to 2.5% of the dry matter by mass (Table 7.4). The lowest concentrations were measured during the hot-dry season and a general peak occurred during the cold-dry one (Fig. 7.3b; Table 7.4). *Grewia flava* had the highest Ca content of all species examined in the present study during the cold-dry season in the Nossob riverbed (Table 7.4; Fig. 7.3b). Differences in the Ca concentration of *Grewia flava* in the same habitat during different seasons were frequently significant and habitat was also often found to affect the Ca concentration within the same season significantly (Table 7.4).


Nossob riverbed
Pans
Dunes
Auob riverbed
Calcium content (% of the dry matter by mass)
2.5
2
1.5
1
0.5
0
Hot-wet
Cold-dry
Hot-dry

a.


Nossob riverbed
Dunes
Auob riverbed
Calcium content (% of the dry matter by mass)
3
2.5
2
1.5
1
0.5
0
Hot-wet
Cold-dry
Hot-dry

b.


Nossob riverbed
Pans
Dunes
Auob riverbed
Calcium content (% of the dry matter by mass)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Hot-wet
Cold-dry
Hot-dry

c.

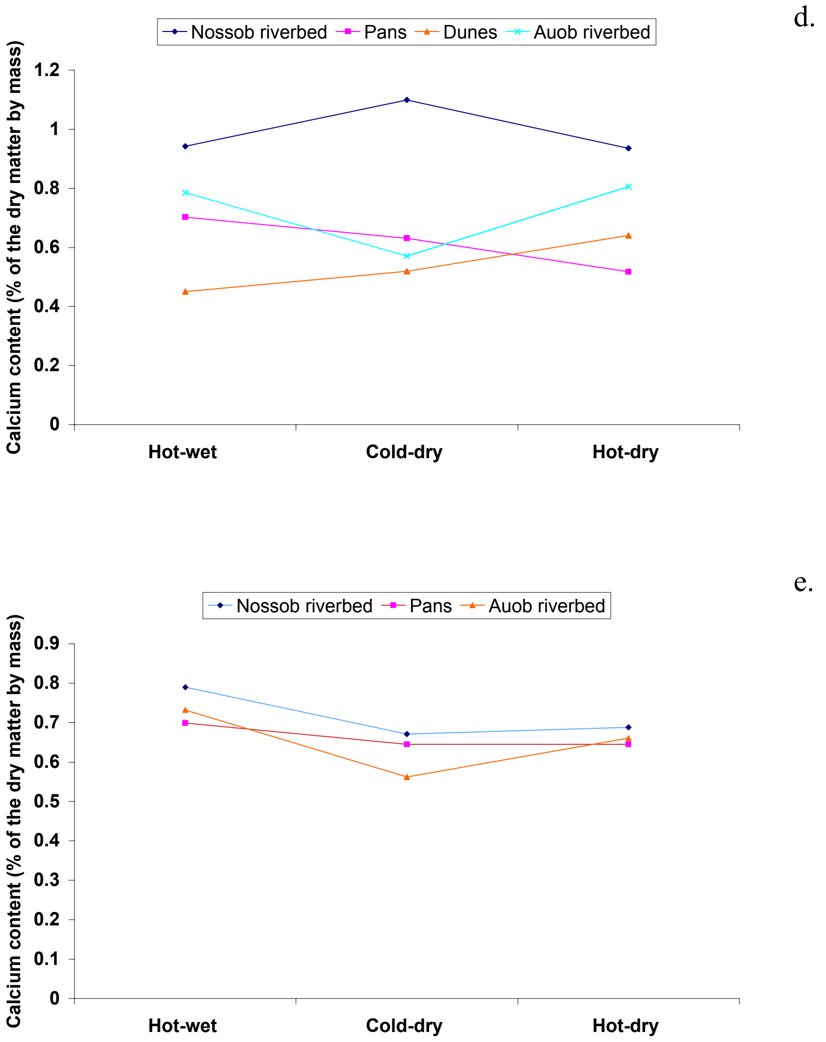


Fig. 7.3 The calcium content of a. *Acacia erioloba,* b. *Grewia flava,* c. *Rhigozum trichotomum,* d. *Schmidtia kalihariensis* and e. *Stipagrostis obtusa* in different habitats on the South African side of the Kgalagadi Transfrontier Park in the hot-wet, cold-dry and hot-dry season from March to November 2003.

Rhigozum trichotomum showed similar Ca fluctuation trends to the other browse species in the present study, generally having a peak in the cold-dry season and being at its lowest in the hot-dry one (Fig. 7.3c). Calcium concentrations in *Rhigozum trichotomum* ranged from 0.7 to 1.7% of the total dry matter by mass (Table 7.4). Habitat had no significant influence on the Ca content of *Rhigozum trichotomum* in the same season, although season did sometimes affect Ca concentration in the same habitat significantly.

The Ca content fluctuation trends were less apparent in the grass species than in the browse species that were examined in the present study. *Schmidtia kalihariensis* showed no clear seasonal Ca concentration trend (Fig. 7.3d) and although there were significant differences between Ca concentrations across habitats in the hot-wet and cold-dry seasons, the overall effect of season on the Ca concentration was not significant (Table 7.4). The Ca concentration in *Schmidtia kalihariensis* across all habitats and seasons ranged from 0.4 to 1.1% of the dry matter by mass.

The Ca concentration in *Stipagrostis obtusa* had a narrow range of variation from 0.6 to 0.8% of the dry matter by mass (Table 7.4). *Stipagrostis obtusa* showed a marginal peak of Ca concentration during the hot-wet season and its lowest in the cold-dry one (Fig. 7.3e), but these concentrations were not significantly different from those in the other seasons (Table 7.4). Habitat had no significant effect on the Ca concentration of *Stipagrostis obtusa* in the same season (Table 7.4).

7.5 Discussion

Nitrogen and crude protein

Browse species generally contain a higher crude protein concentration than grasses (Minson 1990; Lukhele 2002), as was found in the present study too. African ungulates require a minimum of 5% crude protein (equal to 0.8% N) in their food (Van Hoven 2002). All the plant species that were sampled in the present study, with the exception of *Schmidtia kalihariensis* during the cold-dry season in the Auob riverbed and during the hot-dry one in the pans; and *Stipagrostis obtusa* in the pans in the cold-dry season, contained an adequate concentration of crude protein to sustain springbok in the southwestern Kalahari (Table 7.2). Under typical weather conditions in the cold-dry season the crude protein in the grass species may therefore be a limiting nutrient in the Kalahari springbok's diet. However, the faecal nitrogen concentration of springbok in the present study was above the critical range required for sustenance of normal metabolic processes (Chapter 8) and springbok may therefore avoid the food plant species with inadequate nitrogen contents.

Minerals

The variable mineral contents contained in plants have a direct effect on the nutritional value of such plants, to the point where it could be toxic for consumption by animals (Underwood & Suttle 1999).

Phosphorus (P)

Although soluble minerals such as phosphorus are usually susceptible to leaching, it has been found elsewhere that plants contain elevated levels of phosphorus during wet seasons (White *et. al* 1981; Kiatoko *et. al* 1982). There was a decline in the phosphorus content of all the plant species in all habitats examined in the present study from the hot-wet to the cold-dry season and in most cases, the phosphorus values differed significantly (Table 7.3; Fig. 7.2). The phosphorus content tends to decline in forage as the plant matures (McPherson 2000; Whitehead 2000). This appeared to be evident in the decline in phosphorus levels in some of the plant species examined here, the decline progressing from the hot-wet to the cold-dry season when the plants tend to mature (Table 7.3; Fig. 7.2). The observed phosphorus increase in the plant species from the cold-dry to the hot-dry season may be due to the effect of early rain and subsequent fresh growth, as regular rainfall occurred from September to December 2003 in various parts of the Kgalagadi Transfrontier Park (Table 7.1). Phosphorus concentrations between leaves and stems are in general relatively similar and it has been found that a high proportion of phosphorus is absorbable from both dry and fresh plant material (Ternouth 1989; Ternouth & Coates 1997).

A phosphorus content of 0.1 to 0.6% is considered characteristic for grass species (Whitehead 2000) and in South African food plants, the phosphorus content generally ranges from 0.03 to 0.58% of the dry matter by mass (Boyazoglu 1997). According to The National Ruminants Research Council, most ruminants require from 0.18 to 0.48% phosphorus of dry matter by mass (McDowell 1992, 1997). Overall, the phosphorus concentration in all the plant species that were sampled in the present study were low, and below ruminant requirements, in all habitats during the cold-dry season. The woody plant species marginally reached the minimum requirement for ruminants in the hot-dry season, whereas the grass species were almost always deficient in phosphorus.

South Africa is known for its widespread phosphorus deficiencies, with natural herbage values as low as 0.005% phosphorus of the dry matter by mass having have been reported (Boyazoglu 1997; Whitehead 2000; Van Hoven 2002). Phosphorus is known to be a most limiting nutrient in the arid-savannas such as the Kalahari (Skarpe & Bergström 1986; Tolsma *et. al* 1987). The phosphorus concentration of springbok food measured in the southwestern Kalahari in the present study is lower compared with that reported by Vorster (1996) for springbok in Kimberley, South Africa. The faecal phosphorus concentration of springbok in the present study was below the critical range during the cold-dry season (Chapter 8). Although no physical symptoms of such a deficiency were encountered, the diet of springbok in the southwestern Kalahari appears to be phosphorus deficient.

Calcium (Ca)

All the sampled plant species fell within the fluctuation range of South African natural herbage: from 0.1 to 2.9% calcium of dry matter by mass (Boyazoglu 1997). The calcium levels in plants are influenced by soil properties such as acidity and higher Ca concentrations in plants may be found on alkaline soils (Whitehead 2000). Legumes are known to contain more Ca than grasses (Underwood & Suttle 1999) and the results of the present study support this. Browse species that were analysed in the present study showed a peak in calcium concentration during the cold-dry season, similar to the forage species sampled by Vorster (1996). In general, ruminants require from 0.18 to 0.82% calcium of dry matter by mass for maintenance, according to The National Ruminant Research Council (McDowell 1992, 1997) and all the sampled plant species in the present study fell within this minimum range.

The availability of Ca and phosphorus to animals depends on their association with other compounds present in the forage (McDowell & Valle 2000). A Ca:P ratio of 1:1 to 2:1 is generally believed to be advantageous for absorption of these minerals and for metabolic processes (Boyazoglu 1997). However, prolonged exposure to a Ca:P ratio where Ca is highly in excess and phosphorus is deficient is known to cause disorders in animals (Boomker 2002). The Ca:P ratio in the present study was found to be in excess of the 2:1 ratio, with a ratio of up to 32:1 found in *Acacia erioloba* in the Auob riverbed during the cold-dry season (Table 7.3 and 7.4). In another study involving Ca and phosphorus contents of plants in the Kalahari, a Ca:P ratio of 10:1 was measured (Skarpe & Bergström 1986). The high Ca:P ratio in food plants from the southwestern Kalahari could possibly cause disorders in springbok. However, it was not verified whether springbok showed symptoms of a Ca:P imbalance and more research is required on the subject.

Comparison by plant species

Browse species generally show less seasonal fluctuation in chemical composition than tropical grasses (Lukhele 2002). However, in the present study, browse was found to fluctuate as much, if not more than the grass species sampled, but in general maintained a higher level of nutrients. In most plant species examined in the present study, seasonal trends in the composition of browse and grasses were similar, although calcium values for grasses showed no significant seasonal changes.

Acacia erioloba

A range of browse plants have been shown to contain adequate protein and phosphorus concentrations to maintain livestock during the dry season (Le Houerou

1980) and *Acacia* species have been shown to play an important role in wildlife nutrition (Sauer *et al.* 1982; Sauer 1983a, 1983b). Browsing pressure on *Acacia* species has been shown to cause an increase in the presence of thorns on the branches (Cooper & Owen-Smith 1985), reducing its attraction as a browse plant. However, springbok have narrow muzzles that are well suited to removing leaves from thorny branches (Skinner & Louw 1996) and are therefore not necessarily deterred by such physical defence systems. *Acacia erioloba* may therefore be an important browse plant for springbok in the southwestern Kalahari.

In research done in the Kalahari from 1977 to 1979, it was found that *Acacia erioloba* had a crude protein range from 12.2 to 16.9% of the dry matter by mass, with a mean value of around 13.5% during July (Skarpe & Bergström 1986). These values are similar to those that were found in the present study. In their research, Skarpe & Bergström (1986) measured a phosphorus range from 0.08 to 0.14% of the dry matter by mass, with a mean of 0.08% during July. This is also similar to current results where a range of from 0.07 to 0.19% and a mean of 0.08% were found during the cold-dry season. Skarpe & Bergström (1986) reported a Ca fluctuation range of from 0.8 to 2.0% with a mean of 0.9% during July. The current research found a wider fluctuation range from 0.5 to 2.3% with a mean of 2.0% during the cold-dry season across all the habitats.

Grewia flava

Grewia flava was the most nutritive plant species that was sampled, across all habitats and seasons, with only *Acacia erioloba* having a higher overall nitrogen content during the cold-dry season. Crude protein values reported in this study ranged from

13.1 to 21.0% and were slightly higher than the 14.0 to 14.1% of the dry matter by mass that was found in the Kalahari in Botswana (Skarpe & Bergström 1986), while Van Rooyen (2002) described a mean of 11.5% in the arid savannas of South Africa. In southern Africa, the calcium content of *Grewia flava* leaves have been found to range from 1.4 to 2.5% of the dry matter by mass during all seasons, and phosphorus from 0.07 to 0.20% of the dry matter by mass (Boyazoglu 1997). In their study, Skarpe & Bergström (1986) reported a Ca range for *Grewia flava* from 1.2 to 1.3% and phosphorus range from 0.12 to 0.14%. The results from the present study were similar to that of the above research, but with a wider range.

Rhigozum trichotomum

Rhigozum trichotomum had the lowest nutritional ranking of the browse plant species and in no instance did the habitat affect the nutritional value.

Schmidtia kalihariensis

On average, *Schmidtia kalihariensis* was the more nutritious of the grass species sampled. However, it was rarely observed to be consumed by springbok and during its flowering stage it is covered completely with a sticky residue from glandular hairs that would protect it from being eaten (Van Rooyen 2001).

Stipagrostis obtusa

Although, it had higher nitrogen and phosphorus contents than *Schmidtia kalihariensis* during the hot-dry season, *Stipagrostis obtusa* had the lowest nutritional value of the plant species sampled in the other seasons. Research on *Stipagrostis obtusa* in the Karoo found that its nitrogen content ranged from 0.5% of the dry matter by mass during dry season to 1.7% during wet season (Louw 1969) and in the Free State province, it was reported to have a crude protein content of 5.0% (Van Rooyen 2002). In the present study higher values and a wider range was reported, compared with the above research results.

7.6 Conclusions

The browse plant species examined here contained higher concentrations of crude protein, phosphorus and calcium than the grass species but the fluctuation range was as wide or wider than that of the grass species. The five plant species of the southwestern Kalahari which were examined here were found to have wider nutritional variation than similar or identical species reported elsewhere. *Grewia flava* was the most nutritious plant sampled in the southwestern Kalahari and *Schmidtia kalihariensis* and *Stipagrostis obtusa* were the least nutritious plants species. The crude protein content was found to be below ruminant requirements in the cold-dry season for the grass species and phosphorus content was below ruminant requirements in all plant species, in all habitats during the cold-dry season.

The overall nutritional value of all the plant species examined was lowest during the cold-dry season and highest during the hot-dry season, probably as a result of new growth following early rain in the latter season. However, calcium concentrations peaked in the browse plant species examined, during the cold-dry season.

The first hypothesis tested in this study was that the food plants in the southwestern Kalahari have a low nutritional value. This hypothesis was found to be false for

Acacia erioloba, *Grewia flava* and *Rhigozum trichotomum*, but true for *Schmidtia kalihariensis* and *Stipagrostis obtusa*. The second hypothesis that was tested was that nutritionally depleted food plants place nutritional stress on springbok during dry periods. This hypothesis was found to be true. Faecal phosphorus concentrations of springbok in the present study supported these findings and fell below the critical range during the cold-dry season. Nitrogen and phosphorus levels in plant food were especially low during the cold-dry season and in general, the Ca:P ratio was higher than recommended (McDowell 1992, 1997), and has been reported by similar research in the southern Kalahari (Skarpe & Bergström 1986).

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CHAPTER 8

FAECAL PROFILING OF SPRINGBOK IN THE KALAHARI

Prepared for The South African Journal of Wildlife Research

Abstract – The nutritional status of springbok in the Kalahari was assessed in different habitats and seasons with faecal profiling. Faecal nutrient levels confirmed springbok to be mixed feeders with a dietary composition between that of browsers and grazers. Faecal concentrations of phosphorus and nitrogen were similar to that of springbok in other areas, but faecal phosphorus was below the critical range during the cold-dry season. Springbok in the southwestern Kalahari may experience nutritional stress during dry periods.

Key words: faecal nitrogen, faecal phosphorus, springbok, Kalahari.

8.1 Introduction

Animal productivity is directly linked to the nutritional status of the population (Wrench *et al.* 1997; Van der Waal *et al.* 2003), which in turn depends on the intake of digestible energy and nutrients through food plants (Skarpe & Bergström 1986). Common problems that hamper the determination of diet quality and animal condition include animal selectivity, and the cost, ethics and duration of using intrusive methods such as oesophageal fistulae (Leslie & Starkey 1985; Wrench *et al.* 1997; Botha & Stock 2005). These factors make dietary quality one of the most difficult aspects of range nutrition to study (Wofford *et al.* 1985). Consequently, surrogate measures have been investigated to provide a cost-effective, indirect estimation of range nutrition and animal condition.

The use of the chemical composition of faecal samples as an indicator of an ungulate's physical condition has been discussed by several researchers (Erasmus *et al.* 1978; Holecheck *et al.* 1982; Grant *et al.* 1995, 1996; Van der Waal *et al.* 2003) as has been using faecal phosphorus concentration as an indication of the phosphorus intake of an animal (Belonje 1978, Belonje & van den Berg 1980; Holechek *et al.* 1985; Grant *et al.* 1996; Wrench *et al.* 1997).

It has been demonstrated that faecal nitrogen and phosphorus concentrations can be used as indicators of the nutritive value of the plants that a herbivore utilises (Wrench *et al.* 1997; Botha & Stock 2005) and that comparing the faecal components of animals in different habitats could be of assistance in understanding their nutritional ecology (Erasmus *et al.* 1978; Wofford *et al.* 1985; Wrench *et al.* 1997; Van der Waal *et al.* 2003). Researchers have used faecal nutrient concentration studies in African buffalo *Syncerus caffer* (Grant *et al.* 1995, 2000; Codron *et al.* 2005), African elephant *Loxodonta africana* (Codron *et al.* 2005), blue wildebeest *Connochaetes taurinus taurinus* (Grant *et al.* 1995, 2000; Wrench *et al.* 1997; Botha & Stock 2005; Codron *et al.* 2005; Mbatha & Ward 2006), Burchell's zebra *Equus burchellii* (Wrench *et al.* 1997; Grant *et al.* 2000; Codron *et al.* 2005), bushbuck *Tragelaphus scriptus* (MacLeod *et al.* 1996), bushpig *Potamochoerus porcus* (Codron *et al.* 2005), cattle (type not specified) (Holechek *et al.* 1982, 1985; Wofford *et al.* 1985; Leite & Stuth 1990; Grant *et al.* 1996; Wrench *et al.* 1997), Columbian black-tailed deer

Odocoileus hemionus columbianus (Leslie & Starkey 1985), eland *Taurotragus oryx*)(Codron *et al*. 2005), gemsbok *Oryx gazella* (Codron *et al*. 2005), giraffe *Giraffa camelopardalis* (Grant *et al.* 1995, 2000; Codron *et al*. 2005), goats (type not specified) (Mbatha & Ward 2006), impala *Aepyceros melampus* (Grant *et al.* 1995, 2000; Wrench *et al.* 1996, 1997; Botha & Stock 2005; Codron *et al.* 2005), klipsringer *Oreotragus oreotragus* (Codron *et al.* 2005), greater kudu *Tragelaphus strepsiceros* (Grant *et al.* 1995, 2000; Van der Waal *et al.* 2003; Codron *et al.* 2005), merino sheep *Aries ovis* (Erasmus *et al.* 1978; Belonje & Van den Berg 1980), nyala *Tragelaphus angasii* (Botha & Stock 2005), porcupine *Hystrix africaeaustralis* (Codron *et al.* 2005), crossbred Rocky Mountain bighorn sheep (Irwin *et al.* 1993), Roosevelt elk *Cervus elaphus roosevelti* (Leslie & Starkey 1985), springbok *Antidorcas marsupialis* (Erasmus *et al.* 1978; Vorster 1996; Mbatha & Ward 2006), square-lipped rhinoceros *Ceratotherium simum* (Codron *et al.* 2005), warthog *Phacochoerus africanus* (Botha & Stock 2005) and waterbuck *Kobus ellipsiprymnus* (Codron *et al.* 2005).

Faecal nitrogen consists of unabsorbed dietary nitrogen, undigested microbial nitrogen and endogenous nitrogen, diluted by indigestible dietary dry matter and endogenous material (Leslie & Starkey 1987). Total faecal nitrogen has been found to correlate with the soluble nitrogen fraction in faeces (Leite & Stuth 1990) however, the ratio of insoluble nitrogen in faeces increases as the forage quality decreases (Leite & Stuth 1990). Leslie & Starkey (1985) also found that faecal nitrogen concentration increases with an increase of the nitrogen concentration of the herbivore's diet.

The faecal nitrogen concentration of herbivores has been reported to be a reliable predictor of pasture digestibility, provided that the diet consists primarily of grasses which have similar chemical properties, but it is less effective when the diet consists primarily of browse (Holecheck *et al.* 1982; Wofford *et al.* 1985; Grant *et al.* 1996). Some 80% of all shrub species and 15% of all forb species contain tannins (Hobbs 1987) and tannins are reported to affect faecal nitrogen measurement (Hobbs 1987; Wrench *et al.* 1997; Grant *et al.* 1995, 1996, 2000). However, the findings of other researchers contradict this relationship and describe the effect of tannins on faecal nitrogen as insignificant or minimal (Wrench *et al*. 1997; Van der Waal 2003). It has also been argued that free-ranging herbivores avoid plants with high levels of phenolic compounds or low quality browse (Leslie & Starkey 1987; Irwin *et al.* 1993; Grant *et al.* 2000; Botha & Stock 2005).

If faecal nitrogen reflects nitrogen intake, dietary protein and mass changes of an animal (Leslie & Starkey 1985; Wofford *et al.* 1985) it may be a viable index of relative inter-seasonal dietary quality fluctuation and within-season comparisons between different populations within similar habitats (Leslie & Starkey 1987). Faecal nitrogen is useful when considered with faecal phosphorus because they are similarly excreted (Grant *et al.* 1995, 1996) but faecal phosphorus concentration is not affected by the tannin content of the herbivore's diet (Mbatha & Ward 2006).

In the present study faecal analysis was used as an efficient, cost-effective and non-invasive method to investigate the nutritional status and dietary quality of springbok in the southwestern Kalahari. Two hypotheses were tested:

1. Springbok in the southwestern Kalahari experience nutritional stress during dry periods.

2. Phosphorus intake of springbok in the southwestern Kalahari is low and hence phosphorus is a limiting nutrient.

8.2 Study area

The study area is located on the South African side of the Kgalagadi Transfrontier Park, a large conservation area within the southwestern Kalahari which is spread across the borders of South Africa and Botswana. The park has a combined total surface area 36 300 km². The South African side of the Kgalagadi Transfrontier Park is an arid savanna (Van Rooyen & Van Rooyen 1998) characterised by deep aeolian sand (Totolo & Chanda 2003). The park consists of a range of plant communities and plant associations but most herbivores concentrate in the Auob and Nossob riverbeds (Mills & Retief 1984). The mean annual rainfall in the study area as measured at the Nossob Rest Camp, Mata-Mata Rest Camp, Twee Rivieren Rest Camp and Van Zylsrus Town weather station from 1980 to 2005 was calculated as 180.4 mm[7], with the bulk of its highly variable rain occurring in summer. Drought years are known to occur (Knight 1995). Three ecological seasons occur, known as the hot-wet (January to April), cold-dry (May to August) and hot-dry one (September to December) (Leistner 1967; Mills & Retief 1984; Van Rooyen & Van Rooyen 1998). Temperature variations can be extreme, with winter lows of -10°C and summer highs of 45°C that have been reported (Van Rooyen *et al.* 1990).

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[7] Electronic data supplied by the South African Weather Bureau 2005.

8.3 Materials & methods

Faecal samples were collected from springbok on the South African side of the Kgalagadi Transfrontier Park in four different habitats (Table 8.1) *viz.* the Auob riverbed, the Nossob riverbed, the pans and the dunes. Sampling was done in the hot-wet season (April 2003), in the cold-dry season (July/August 2003), and in the hot-dry one (November 2003). Sampling was done at random and depended on encountering springbok *en route* between destinations. Wherever possible, five repetitions per habitat and per season were collected (Table 8.1). Faecal samples were either collected from single animals, or samples from different individuals within a herd were pooled into one. Collection took place between 06:30 and 17:30. Faecal samples from immature springbok were only included if they had been weaned. Only fresh faecal samples of less than ten minutes old were collected to avoid the effects of exposure on the nutrient contents (Wrench *et al.* 1996). Samples were not collected if it rained, because rain has been found to decrease the phosphorus concentration of faeces by leaching (Wrench *et al.* 1996). Samples were placed in marked paper bags and were later oven dried in a convection oven at 100°C to a constant mass.

After drying the samples, they were milled through a 1 mm screen and sent to the University of Pretoria's Nutrilab for analyses. All chemical analyses were done in duplicate, according to the guidelines of the Association of Official Analytical Chemists (1990). Faecal crude protein, nitrogen (N) and phosphorus (P) concentrations were determined. The faecal nitrogen concentration was determined using the macro-Kjeldahl method with a Tector Kjeltec system model 1002. Faecal phosphorus concentrations were determined with the standard spectrophotometer

Table 8.1 *Information on springbok from which faecal samples were collected on the South African side of the Kgalagadi Transfrontier Park during different seasons and in different habitats in the study period from April 2003 to November 2003*

Habitat	**Season**		
	Hot-wet	**Cold-dry**	**Hot-dry**
Nossob riverbed			
	1 male	Not specified	5 Not specified
	Not specified	1 male	2 Not specified
	Not specified	Not specified	1 male
	Not specified	-	1 female
	Not specified	-	-
Auob riverbed			
	Unknown # male	1 female, 1 immature	3 unknown
	Unknown # male	1 male	2 females, 1 male
	Unknown # male	2 males	2 unknown
	Not specified	Not specified	1 male
	1 female	5 males	1 male
Pans			
	1 male	-	-
	2 male	-	-
	6 male	-	-
	-	-	-
	-	-	-
Dunes			
	Unknown # mixed	3 Not specified	-
	Unknown # mixed	-	-
	Unknown # mixed	-	-
	Unknown # mixed	-	-
	Unknown # mixed	-	-

= number

technique, using a Technicon Auto Analyzer II. Faecal nitrogen and faecal phosphorus are both reported as a percentage of the dry matter by mass. The mean nitrogen content was multiplied by a factor of 6.25 to get a crude protein value (Boyazoglu 1997). Chemical analysis results were organised into a numerical matrix with Microsoft® Excel and the data were analysed with uni- and multivariate statistical techniques using SAS®[8] software. The least square means were used for collective data.

8.4 Results and discussion

Thirty six faecal samples were collected and analysed in the present study. None of the collected samples showed any signs of dung beetle activity. Seasonal differences in faecal nitrogen content were only found within the Nossob riverbed, where the faecal nitrogen was significantly higher in the hot-dry season than in the hot-wet and cold-dry seasons (Table 8.2). Habitat did not significantly affect faecal nitrogen contents in the hot-wet or hot-dry seasons, but in the cold-dry season faecal nitrogen concentrations were significantly higher in the Auob riverbed than in the Nossob riverbed or in the dunes. Faecal phosphorus, on the other hand, showed more significant seasonal variation. In both the Nossob riverbed and dunes the values of the cold-dry season were significantly lower than the other seasons and in the Nossob riverbed the values in the hot-dry season were significantly higher than in the other seasons (Table 8.3). Faecal phosphorus was not significantly affected by habitat in any season.

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[8] SAS® Software Version 8.2 supplied by The SAS Institute Inc., SAS Campus Drive, Cary, NC 27512, USA, running under z/VM 4.4.0 (RSU 0404) on the mainframe computer IBM Z800 2066/0C1 of the University of Pretoria.

Table 8.2 *Faecal nitrogen concentration of springbok on the South African side of the Kgalagadi Transfrontier Park, during the hot-wet, cold-dry and hot-dry seasons from April to November 2003. Concentrations are reported as a percentage of the dry matter by mass. The superscripts (*^{x} *and* ^{y}*) that proceed the nitrogen values denote significance in the same season in different habitats and superscripts (*^{a}*,* ^{b} *and* ^{c}*) that follow the nitrogen values denote significance in the same habitat, in different seasons. Values with the same superscripts do not differ significantly (*$P \leq 0.05$*)*

Habitat	**Season**		
	Hot-wet	**Cold-dry**	**Hot-dry**
Nossob riverbed	$^{x}1.6^{a}$	$^{x}1.4^{a}$	$^{x}2.0^{b}$
Pans	$^{x}1.5$	.	.
Dunes	$^{x}1.8^{a}$	$^{x}0.9^{a}$	.
Aoub riverbed	$^{x}1.5^{a}$	$^{y}1.9^{a}$	$^{x}1.5^{a}$

Table 8.3 *Faecal phosphorus concentration of springbok on the South African side of the Kgalagadi Transfrontier Park, during the hot-wet, cold-dry and hot-dry seasons from April to November 2003. Concentrations are reported as a percentage of the dry matter by mass. The superscripts (^{x} and ^{y}) that proceed the phosphorus values denote significance in the same season, in different habitats and superscripts (^{a}, ^{b} and ^{c}) that follow the phosphorus values denote significance in the same habitat, in different seasons. Values with the same superscripts do not differ significantly (P≤ 0.05)*

Habitat	**Season**		
	Hot-wet	**Cold-dry**	**Hot-dry**
Nossob riverbed	$^x0.42^a$	$^x0.19^b$	$^x0.67^c$
Pans	$^x0.38$	.	.
Dunes	$^x0.37^a$	$^x0.15^b$	.
Aoub riverbed	$^x0.34^a$	$^x0.22^a$	$^x0.45^a$

An inverse relationship exists between the protein and fibre content of food plants and when the protein content of a food plant falls below 4 to 8% it becomes uneconomical for herbivore digestion (MacLeod *et al.* 1996). Grant *et al.* (1995) described a critical faecal nitrogen concentration for ruminants of 11 to 12 g/kg dry matter (1.1 to 1.2%) to maintain rumen fermentation, but suggested that short grass feeders, selective feeders and browsers seldom reach this critical level. Wrench *et al.* (1997) suggested a critical faecal nitrogen concentration for grazers of 14 g/kg dry matter (1.4% of the dry matter by mass), as around 80% of faecal nitrogen originates from dietary nitrogen. In 2000, Grant *et al.* adjusted the critical range from 13 to 16 g/kg (1.3 to 1.6% of the dry matter by mass) nitrogen. In the present study, springbok in the southwestern Kalahari had a mean faecal nitrogen concentration of 1.6% of the dry matter by mass (standard deviation ±0.3). It therefore exceeds the critical levels proposed by Grant *et al.* (1995) and Wrench *et al*. (1997) and falls within the critical range proposed by Grant *et al.* (2000). The mean faecal nitrogen concentration in the present study was higher than that measured for blue wildebeest and African buffalo, but lower than that reported for impala, kudu and giraffe in the Kruger National Park (Grant *et al.* 1995, 2000; Wrench *et al* 1996; Van der Waal *et al.* 2003), and nyala and impala in the Hluhluwe-Umfolozi Park (Botha & Stock 2005). In the present study, the mean crude protein concentration of springbok in the southwestern Kalahari (10% of the dry matter by mass) was lower than that reported for bushbuck in the Eastern Cape (12.6% dry matter; MacLeod *et al.* 1996). These comparisons indicate that the faecal concentration of the springbok lies between that of bulk grazers (African buffalo and blue wildebeest) and strict browsers (kudu and giraffe). This seems to confirm the mixed feeding status of springbok in the southwestern Kalahari. The diet of impala appears to contain more browse than the diet of springbok. The faecal crude protein content of the springbok in the present study was similar to that reported for springbok in a South African arid savanna elsewhere (Mbatha & Ward 2006) and in the Karoo (Vorster 1996). The research of Erasmus *et al.* (1978) on springbok faecal nitrogen concentration could not be used for comparative purposes with the present study, as it did not involve free-ranging animals selecting their own diet.

It has been found that elevated levels of faecal nitrogen may occur during a dry season due to the secretion of urea through the intestinal wall back into the gut lumen (Thornton *et al.* 1970). Higher levels of faecal nitrogen may also be due to a 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 & Ward 2006). It is possible that the significantly higher faecal nitrogen concentration of springbok in the Nossob riverbed during the hot-dry season may be due to either of these factors, but the latter is a more likely explanation because it relates to seasonal change (Table 8.2). The correlation between faecal nitrogen concentration and dietary quality deteriorates when dietary nitrogen levels are >2.4% (>15% crude protein) of the dry matter by mass (Wofford *et al.* 1985; Irwin *et al.* 1993). The browse species that were examined in the present study frequently exceeded this value, although the grasses did not (Table 7.2). The mixed feeding status of the springbok in the present study therefore complicates the interpretation of their faecal nitrogen levels, however, at the the least, it can be stated that nitrogen is not a limiting factor in the diet of the springbok in the southwestern Kalahari (see also Chapter 7).

Faecal nitrogen and phosphorus should be considered together, because faecal phosphorus can predict dietary digestibility (Wrench *et al.* 1997) and may aid in the interpretation of faecal nitrogen changes. Phosphorus, and to some extent nitrogen, are deficient in most natural pastures (Grant *et al.*1996; Wrench *et al.* 1997; Boomker 2002). However, a low faecal phosphorus concentration may be indicative of a low phosphorus intake or of efficient phosphorus utilisation (Grant *et al.* 1995). Wrench *et al.* (1997) described a critical faecal phosphorus concentration of 2 g/kg (0.2%) for most herbivore species. More recently, Grant *et al.* (2000) reported a faecal range of between 1.90 and 2.00 g/kg phosphorus over a long period of time to lead to deficiencies in animals and hence to reduced production. In the present study, springbok in the southwestern Kalahari had faecal phosphorus levels below 1.9 g/kg (0.19%) of the dry matter only during the cold-dry season in the dunes (0.15%), while the faecal phosphorus in the Nossob riverbed reached a low of 0.19% in the cold-dry season. The food plant species that were examined in the present study reached their lowest phosphorus levels during the cold-dry season (Fig. 7.2), a time when their phosphorus concentration fell below the requirements for the maintenance of a ruminant in all habitats (Chapter 7). The phosphorus concentration of the grass species in the present study was always lower than that required by ruminants for maintenance (Table 7.3). The phosphorus concentration of the food plant species in the present study also had the least seasonal variation in the dunes (Chapter 7).

Phosphorus deficiency is usually distinguishable by symptoms such as pica (Boomker 2002) and pica has not yet been reported in wildlife in southern Africa (Grant *et al.* 2000). In the present study, springbok had a mean faecal phosphorus content of 0.35% (standard deviation ±0.16) of the dry matter by mass, which is similar to that of springbok on Pniel Estates within the arid savanna in South Africa (Mbatha & Ward 2006) and springbok in the Karoo (Vorster 1996).

8.5 Conclusions

Faecal analysis proved to be an efficient, cost-effective and non-invasive way to gather information on the dietary quality of springbok in the Kalahari. It was found that the faecal concentration of phosphorus and nitrogen were similar to that of springbok in other arid savanna areas. Based on faecal crude protein content, the mixed feeding guild of springbok was confirmed. The faecal nutritional status for springbok populations in different habitats in the present study only differed significantly for nitrogen concentration in the cold-dry season.

The mean faecal nitrogen and phosphorus content of springbok in the southwestern Kalahari were not lower than the proposed critical ranges. However, faecal phosphorus and in some instances faecal nitrogen concentration were below the critical threshold in the cold-dry season. This indicates that springbok in the southwestern Kalahari experience nutritional stress during dry periods and that the first hypothesis cannot be rejected. Although faecal phosphorus concentrations in the hot-wet and hot-dry seasons indicate that phosphorus intake is sufficient, the critically low values in the cold-dry season suggest that the phosphorus content in the diet of the springbok is not sufficient during this period. The low phosphorus concentration of the food plant species in the present study during the cold-dry season confirms this. The hypothesis that phosphorus intake of springbok in the southwestern Kalahari is low and hence that phosphorus is a limiting nutrient can therefore not be rejected.

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CHAPTER 9

GENERAL DISCUSSION

Questionnaires are increasingly used for involving members of the public in ecological management decisions and it is frequently assumed that the often large amounts of data which are collected by using questionnaires are accurate. In the present study, questionnaires proved to be a good method of collecting large amounts of data. However, the value of the collected data was found to be compromised by several factors, such as complicated questions and assumptions about respondents' understanding. In the present study there were significant differences between some of the data that were collected by public respondents and by the researcher. By carefully considering each difference and proposing sound explanations for them, it is possible to filter through the data and still discern trends. The proposed explanations should follow scientific reason and hold true for the specific field of study as well as in more general terms. However, such a process is tedious and time consuming and is best avoided by proper survey preparation. Survey questions should be short, simple, well-defined and clearly explained by means of examples. Public bias should be limited by ground-truthing as far as possible. In the present study, the questionnaire survey proved to be an efficient quantitative, yet less efficient qualitative data collection method, because a large part of the public respondents' data differed significantly from that of the researcher.

The ecology of Kalahari springbok is fine-tuned to the prevailing environmental conditions of the region. The most important of these is rainfall (Mills & Retief 1984), which has a direct effect on herd dynamics on a small scale, and population dynamics on a larger scale (Bothma 1972). Rainfall also has an indirect influence on springbok through the associated changes in nutritive value of the vegetation (Mbatha & Ward 2006). Springbok sometimes travel long distances in response to rainfall and food availability (Skinner & Moss 2004). Springbok response to rainfall is dependent on many factors which include the amount, timing and locality of the rainfall. Another important factor affecting springbok behaviour and their feeding strategies during different seasons is sunlight (Chapter 5). Minor factors such as wind, both strength and direction, may further shape springbok behaviour. The hypothesis that was tested for environmental and seasonal conditions affecting springbok feeding and food selection significantly could therefore not be rejected (Chapter 5).

Springbok are selective mixed feeders (Skinner & Louw 1996) that make use of grass and browse (Boomker 2002; Chapter 8). They have a preference for green plant material, especially that which is in an active growing phase (Mills & Haagner 1989; Chapter 4) and can adapt their diet according to the availability of quality food plants, sometimes feeding predominantly on grass (Vorster 1996) and other times predominantly on browse (Bothma 2002). Most of their daytime is spent feeding (Chapter 5). They have the ability to consume only the highest quality food available to them and are able to survive with little or no water at all, provided that their diet contains enough moisture (Boomker 2002). Irrespective of their water independence, they have access to multiple waterholes on the South African side of the Kgalagadi Transfrontier Park and make regular use of natural licks to supplement their diet (Bergström & Skarpe 1999; Chapter 5). Springbok were regularly recorded feeding within close proximity of other animals, such as blue wildebeest, but avoided direct competition with them. Springbok also show a substantial amount of nocturnal activity (Chapter 6), the purpose of which is not yet fully understood. It may be related to depredation avoidance, but requires further investigation. Nighttime activities frequently included feeding, but the quantification thereof was not always possible and it could therefore not be compared with daytime feeding.

Springbok prefer plains and flat areas, with a low vegetation structure and low basal cover (Bigalke 1972; Vorster 1996). The South African side of the Kgalagadi Transfrontier Park provides a suitable macro-habitat for springbok, and in some respects it may be more suitable for springbok than the macro-habitat of the Karoo. Yet, this contradicts the observed decline of springbok numbers in the Kalahari and a growing population in the Karoo. Springbok in the Kalahari are larger in size than springbok in the Karoo and it has been suggested that the springbok from the Karoo and the Kalahari are two different subspecies (Bigalke 1970). The scope of the present study could not address the reasons for the observed size difference, but research by Peters & Brink (1992) suggest that size is not the only significant difference between springbok in the Kalahari and springbok in the Karoo as they also showed a significant osteological (postcranial skeleton) difference between the springbok from these two areas.

The nutrients in the five food plant species of the southwestern Kalahari which were analysed had a wider fluctuation range there than in other regions. Browse species had higher crude protein contents than the grass species and *Grewia flava* was the most nutritious food plant that was sampled. The nutritional value of some of the food plants in the southwestern Kalahari was found to be adequate for springbok maintenance and production (Chapter 7). However, the nitrogen concentration of the grasses was below ruminant requirements and the phosphorus level of the food plants was generally low (Chapter 7). Faecal profiling confirmed that the phosphorus intake by the springbok in the area was below the critical level during the cold-dry season, but the faecal crude protein concentration was too high to reflect crude protein intake accurately (Chapter 8). The calcium level of the food plants that were sampled in the southwestern Kalahari was higher than in regions outside the Kalahari (Chapter 7). The hypothesis that that the food plants of the springbok in the southwestern Kalahari have a low nutritional value held true for the grass species, but false for the browse plants. The hypothesis that the springbok in the southwestern Kalahari was being nutritionally stressed during the dry season due to poor quality food was found to be true. These hypotheses were further complemented by the hypotheses that were examined using faecal profiling, both of which could not be rejected. Therefore it was found that springbok experience nutritional stress during dry periods and that phosphorus is a limiting nutrient in the diet of the southwestern Kalahari. Furthermore, faecal profiling results showed a higher faecal nutrition level for springbok in the Karoo (Vorster 1996) than for springbok in the Kalahari (Chapter 8) and in terms of the available food plants and dietary quality, the Karoo appears to be a better habitat for springbok than the South African side of the Kgalagadi Transfrontier Park. This nutritional difference between the two regions may have contributed to the observed increase of the springbok population in the Karoo and the decline of springbok numbers in the southwestern Kalahari over a long term.

The main predators of springbok in the Kalahari are the cheetah *Acinonyx jubatus*, with some kills being made by lion *Panthera leo* (Mills & Haagner 1989). However, the lion population of the southwestern Kalahari has shown a decline over the past 20 years (Castley *et al.* 2002) and cheetah numbers have remained low over the past several decades ([1]Funston, pers. comm; Skinner & Moss 2004). Predator-prey interactions are complex relationships (Begon *et al.* 1999*)* and the long-term effects of the predator-prey relationship between springbok and cheetah, on their respective population dynamics in the southwestern Kalahari have not yet been studied in detail. Irrespective of the long-term effect of the predator-prey relationship of cheetah and springbok on their population dynamics, the South African side of the Kgalagadi Transfrontier Park provides a habitat for springbok which is low in predator numbers. It is not known what the predator dynamics are of springbok in the Karoo, where the large predators have been virtually exterminated, but it is likely to be different in different regions.

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CHAPTER 10

MANAGEMENT RECOMMENDATIONS

A simplified questionnaire could provide continual monitoring data on specified, observable variables. A significant proportion of visitors to the Kgalagagadi Transfrontier Park are believed to be repeat-customers who have a keen interest in the Park's affairs ([1]Engelbrecht, pers. comm). Questionnaires could provide such visitors with an opportunity to participate actively in conservation efforts, whilst providing the management staff with additional data to aid in their management decisions. Many students from different educational institutions also visit the Park annually. Such students could assist in collecting and capturing questionnaire data as part of their learning experience. Questions could include:

1. Date
2. Location
3. Time
4. Total number of springbok
5. In the vicinity of a camp (yes or no, specify)
6. In the vicinity of a waterhole (yes or no, specify)
7. Any other animals present (yes or no, specify)
8. [ϕ]What is the majority of the herd doing?
9. Habitat (specify Auob riverbed, Nossob riverbed, pans or dunes)
10. Presence of lambs (yes or no)
11. Sheet number

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The plant species that were examined in the present study on the South African side of the Kgalagadi Transfrontier Park were found to be somewhat nutritionally limiting on springbok. Springbok conservation management should take this into account and caution should be excercised not to place any additional stress on the southwestern Kalahari springbok population. Future management decisions should be aimed at maintaining free springbok movement within the Kgalagadi Transfrontier Park and access to drinking water should be ensured during drought years when the moisture content of the springbok's diet may not be sufficient for proper metabolism. Monitoring the nutritional value of the springbok's food plants and verifying trendusing faecal profiling could also assist in the understanding of the changing springbok ecology. Faecal profiling is non-intrusive and may provide a valuable index of the nutritional status of individuals, herds and populations.

In addition to monitoring the aspects which were adressed in the present study, future research on springbok in the southwestern Kalahari can be aimed at addressing at least the following issues:

1. The role and importance of nocturnal feeding in the springbok's ecology, with reference to predator avoidance.
2. The predator-prey interaction between cheetah and springbok in the Kalahari and the effect thereof on springbok population dynamics.

Further issues that require attention are the effect of the mineral contents of the water in the Kgalagadi Transfrontier Park, as well as the genetic dynamics and reproduction strategy of the springbok. Conservation management involves two related fundamental concepts, namely monitoring and reviewing. Detailed databases are of little use if they are not continually updated. Similarly, updated databases are of little use if they are not analysed, reviewed and understood. The present study provides an updated review of the feeding ecology of the Kalahari springbok and should ideally be continually updated, reviewed and analysed in the long-term for an in-depth understanding of the springbok ecology of the region.

CHAPTER 11

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