Habitat suitability and behaviour of springbok (*Antidorcas marsupialis*) at Augrabies Falls National Park, South Africa

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Abstract

Habitat selection may be considered a behavioural consequence of an individual actively selecting where it lives or passively persisting in a certain habitat. There are a variety of approaches to assessing habitat selection, including relating densities to predefined habitats and the characteristics of these habitats, measuring the behaviour of animals within predefined habitats in order to assess the relative benefits to the animal and comparing these between habitats, and using optimality theory to allow the animal to provide measures of its preference for particular habitats or patches. Each approach provides different perspectives on an animal's choice and use of habitat, with some approaches working more effectively with certain species or habitats than others. There have, however, been no attempts to apply all these approaches to a single species at a single site. The objective of this study was therefore to apply the three above-mentioned approaches to assess habitat use and quality to a single species, the springbok (*Antidorcas marsupialis*) at the Augrabies Falls National Park (AFNP), on the northern bank of the Orange River, in order to provide the basis for further work on comparing and integrating these approaches. The relative abundance of springbok in Augrabies Falls National park was used to develop a habitat suitability model for the park, and thus determine the habitat variables that influenced habitat suitability. Isodar analysis revealed information on the mechanisms underlying habitat preference. Behavioural models were developed to improve our understanding of how springbok behaviour changes in relation to the habitat, and incorporated the variables identified in the habitat suitability model. The different spatial and temporal scales influencing springbok habitat selection were determined using optimal foraging theory and giving-up densities. Springbok preferred open habitats providing high food quality. Springbok behaviour was related to the foraging and predation risk characteristics of the habitat, and springbok varied their temporal and spatial utilisation so as to minimise their risk of predation and maximise their food intake. The habitat suitability model, behaviour models and giving-up densities were compared for ease of use and applicability. Using giving-up densities to reveal habitat suitability had greater applicability and was both efficient and objective.

Keywords: Habitat suitability, isodar, giving-up density, behaviour, springbok, vigilance, predation risk.

Chapter 1

Introduction

Habitat suitability

Habitat is one of the most widely used terms in ecology (Morris 2003b). It represents a central tenet in ecological thinking, linking an organism to its environment (Henley 2001). Habitat influences individual behaviour, affecting activity patterns (Belovsky 1981), reproduction (Deutsch 1994), territoriality (Itzkowitz 1979), antipredator behaviour (Repasky 1996), and foraging behaviour (Roese *et al.* 1991; Rosenzweig 1991; Krasnov *et al.* 2000). Differential use of habitats by species influences species richness (Vernier & Fahrig 1996) and community composition (Morris 1990; Danielson 1991; Ziv 1998). Our understanding of wildlife ecology is strongly influenced by the habitat concept (Henley 2001).

Habitat characteristics influence the behaviour of a species, including activity patterns (Belovsky 1981), territoriality (Itzkowitz 1979), foraging behaviour (Rosenzweig 1991; Duncan & Gordon 1999) and anti-predator behaviour (Repasky 1996). Acquiring food and avoiding predators are considered to be the two principal components of the survival strategies of most animals (Cowlishaw 1997). However, in order to maximise fitness, many animals are forced to trade-off these components (see Fraser & Huntingford 1986; Lima & Dill 1990 for reviews) through the strategic use of habitats and appropriate shifts in behavioural patterns (Cowlishaw 1997).

Despite its importance, habitat remains one of the most ambiguous terms in ecology (Morris 2003b). Depending on the context, habitat has been used to represent biome, ecosystem, community, spatial mosaic and foraging patch (Morris 2003b). It is seldom defined, and those definitions that do exist are often broad generalisations that refer to an organism's habitat either as the place where it occurs (Black 1954; Begon *et al.* 1990), or its association with a plant community (Grzimek 1973; Smithers 1983; Hutto 1985). Neither offers much insight into the relationship between an animal and its environment. For the purposes of this study, a more rigorous definition of habitat will be used, referring to habitat as that place which provides for the life needs of an organism (Harris & Kangas 1988; Owen-Smith 1988; Fabricius 1989).

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The way in which an animal perceives and uses its environment is central to studies of animal ecology (Johnson 1980). Since the environment in which an animal lives contains habitats that vary in quality both in terms of the costs and the benefits, this can influence an individual's ability to survive and reproduce (Melton 1987). The classification of habitats into discrete categories (and measurement of their relative availability) from which an animal chooses allows one to determine if the use of habitat is selective (Arthur *et al*. 1996). The use of habitat and habitat selection may be considered a behavioural consequence of an individual actively selecting where it lives or passively persisting in a certain habitat (Boyce & McDonald 1999). The selection of habitats by animals can be viewed as a multilevel, hierarchical process acting at different scales that should permit individuals to avoid effects of those factors most able to limit their individual fitness (Johnson 1980). At a macro-habitat scale the selection of habitat may be influenced by factors such as substrate and vegetation type. At the smallest micro-habitat scale, factors such as the extent of cover within a patch may influence habitat selection. The extent of habitat use suggests the quality and abundance of resources, which in turn affects the fitness in that habitat (Boyce & McDonald 1999).

Assessing habitat

There are a variety of approaches to assessing habitat, including relating densities of the study species to predefined habitats and the characteristics of these habitats (Schamberger & O'Neil 1986), measuring the behaviour of animals within predefined habitats in order to assess the relative benefits to the animal (feeding opportunities, etc) and comparing these between habitats (Siegfried 1980), and using optimality theory to allow the animal to provide measures of its preference for particular habitats or patches (typically in terms of measuring feeding opportunities that are not utilized) (Brown 1988). Each of these approaches provide different perspectives on an animal's choice and use of habitat, and some approaches work more effectively with some species or habitats than others. There have, however, been no attempts to apply all these approaches to a single species at a single site.

The objective of this study was therefore to apply the three above-mentioned approaches to assessing habitat use and quality to a single species, in order to provide

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the basis for further work on comparing and integrating these approaches. The chosen study species was the springbok, *Antidorcas marsupialis*, a medium-sized antelope occurring in open, semi-arid habitat in southern Africa. This species was selected due to its relative abundance, visibility on the landscape, as well as the fact that it has been reasonably well studied, providing background information (see Chapter 2) to develop hypotheses regarding its habitat selection. The study was undertaken at the Augrabies Falls National Park (AFNP, see Chapter 2 for details), on the northern bank of the Orange River. This conservation area provided a relatively undisturbed population of springbok (tourism is limited in the section of the AFNP where the study was undertaken) as well as a reasonable variety of habitats (open plains – woodlands) within the centre of the distribution range of springbok.

Aims and hypotheses

One of the aims of this study was to contribute towards a standardised and comparable set of criteria for evaluating springbok habitat in AFNP by applying three different approaches to assessing habitat use by this species.

A secondary aim of this study was to make a contribution towards the effective management of springbok within AFNP. This was achieved through

a) improving our understanding of springbok association with their habitat by developing a habitat model to account for the variation in springbok abundance across habitats, and by using isodar analysis to reveal information on the mechanisms underlying habitat preference by springbok,

b) improving our understanding of how springbok behaviour changes in relation to their habitat by developing behaviour models to account for changes in springbok behaviour according to the foraging and predation risk characteristics of the habitat as well as individual and group factors,

c) improving our understanding of how they perceive differences in their habitats at different temporal and spatial scales using optimal foraging theory and giving up densities.

The following general hypotheses were addressed (see Chapter 2 for background information that was used to develop these hypotheses):

1. Springbok prefer open habitats that allow early predator detection and fast escape as they rely on detection and running to reduce predation (Shortridge 1934; Leistner 1967; Bigalke 1972; Bednekoff & Ritter 1994). This habitat preference can be described by habitat models (which measure their association with habitat variables) and isodar analysis (which measure their density in adjacent habitats). The habitat model and isodar analysis were used to test the predictions arising from the hypothesis, namely that

   - the maximum number of springbok would be found in open areas with high food quality, and
   - the minimum number of springbok would be found in densely vegetated, rocky areas.

2. Springbok behaviour changes across the landscape in a non-random fashion that can be described by behaviour models which measure how the time spent in each activity (Novellie 1978; Davies & Skinner 1986a,b; Liversidge & Gubb 1994), groups of different size (Novellie 1978; Skinner *et al*. 1996), choice of diet (Leistner 1967; Bigalke 1972; Cooper 1993; Nagy & Knight 1994; Vorster 1994), and the sex ratio (Jackson *et al.* 1993; Bednekoff & Ritter 1994) varies according to the habitat. These models were used to test the predictions arising from the hypothesis, namely that

   - springbok would spend more time being vigilant in areas of greater predation risk,
   - springbok would feed more in areas of low predation risk with high quality food items,
   - springbok would move more in areas of high predation risk
   - springbok would move more in areas with low quality food items,
   - springbok would spend more time resting or grooming in areas with low predation risk,
   - the adult sex ratio would differ between habitats, since males and females have different requirements associated with reproduction,

- springbok would spend more time feeding and less time vigilant with increasing group size,
- the greater the proportion of adults in the group, the more time would be spent vigilant and less time feeding as subadults would feed more and be less vigilant than adults,
- males would be more vigilant and feed less than females since males exhibit territoriality and may be found alone, due to the presence of territorial individuals, and finally
- the time spent moving and grooming would be greater for females to meet the nutritional requirements of their offspring and keep them free of parasites than for males.

3. Springbok perceive differences in their habitats at different temporal and spatial scales that can be evaluated using optimal foraging theory and giving up densities (Brown 1988; Brown & Kotler 2004). Foraging theory was used to test the prediction that springbok prefer feeding at night in order to obtain more water from their diet (Louw & Seely 1982; Nagy & Knight 1994), and in open, non-rocky habitats on ridges away from drainage lines (Shortridge 1934; Leistner 1967; Bigalke 1972; Bednekoff & Ritter1994). As a result, giving-up densities would be
- higher during the day than at night,
- higher on rocky substrates than on sandy substrates,
- higher in the drainage lines than on ridges, and
- higher under a bush than in the open.

Chapter 2

Study site and study species

Study site

Augrabies Falls National Park (AFNP), covering 55 365 ha along the Orange River, is the largest conservation area in the Orange River Nama Karoo (Hoffmann 1996). The Orange River Nama Karoo, synonymous with Acock's (1975) Orange River Broken Veld (ORBV) Type is the second largest veld type in the Nama Karoo Biome (Scheepers 1983). The Nama Karoo, Succulent Karoo and Desert Biomes comprise the Karoo-Namib Region which is the largest phytochorion in southern Africa (Rutherford & Westfall 1986). The Nama Karoo biome is the largest of the three and occupies 22.7% of the southern African region (Palmer 1997). The vegetation is characterised as a dwarf open shrubland (Campbell *et al.* 1981), or open dwarf-shrub steppe (Werger 1980). Vegetation is dominated by *Acacia mellifera*, *Rhigozum trichotomum* and *Zygophyllum suffruticosum* (Palmer 1997). Where the terrain becomes hilly, at the higher elevations, *Aloe dichotoma* and *Euphorbia avasmontana* occur (Palmer 1997). The bedrock consists of highly reflective stony surfaces (quartzites and calc-silicates) derived from the Namaqualand complex (Palmer 1997). In terms of ecology, it is one of the least studied of southern Africa's biomes (Palmer 1997).

Only 1.5% of the ORBV is conserved, of which AFNP occupies 1.0% (Hoffmann 1996). AFNP is situated in the Gariep Center of Endemism, and 54% of its flowering plant species have not been recorded in any of the three nearest major conservation areas, namely the Goegap Nature Reserve, Kalahari Gemsbok National Park and Vaalbos National Park (Zeitsman & Bezuidenhout 1999). The park is approximately 120 km west of Upington and extends from 28°25' S to 28°38' S and from 19°53'E to 20°24' E. The Orange River divides the park into a northern and southern section (Bezuidenhout 1996).

The study area, known as the Waterval section, is in the northern section of AFNP and comprises 7532 ha of the park (Fig 2.1). Most of this area was declared a "Schedule One" National Park in 1982. The western part had livestock on it until

1974, while the north-eastern part had livestock on it until 1992. Eleven vegetation communities with one community sub-division have been identified in the study area (Fig. 2.2) (Buk 2004) (see Appendix 1 for a description of these communities). These vegetation types proved useful in delineating springbok habitats as shown in Chapter 3. According to Land Type Survey Staff (1986), four land types are represented in the study area (Table 2.1) (see Appendix 2 for the geographical location of these land types).
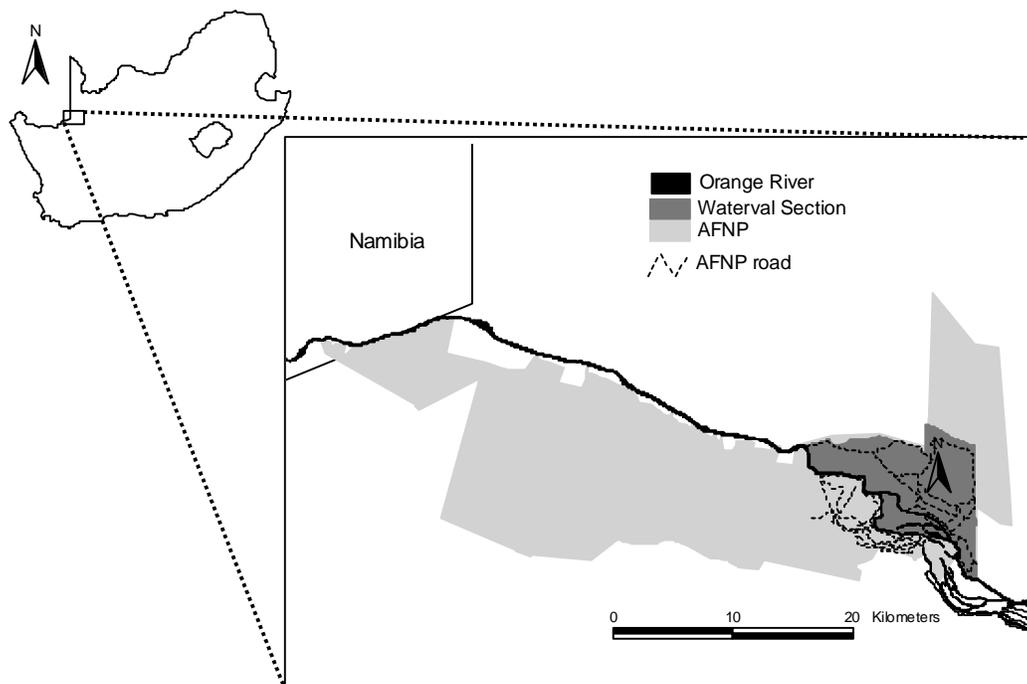
Figure 2.1: The location of the Waterval section in Augrabies Falls National Park (AFNP) in relation to the rest of South Africa.

The altitude in the study area varies from 420 to 750 m above sea-level. AFNP has a tropical, arid climate with summer rainfall. The annual precipitation (1945 to 1999) at Augrabies Waterfall averaged 123 ± 72.57 mm with a coefficient of variation of 59% (Buk 2004). The rainfall for the period during which data were collected (August 2002 - November 2003) was 45.6mm. The majority of the rain falls between November and April, with a peak in March (Fig. 2.3). The three major seasons are the hot/wet season (January to April), the dry/cold season (May to August), and the hot/dry season

(September to December) (Fig. 2.3) (Schulze 1997). The absolute maximum and minimum temperatures (1984-1990) were 46.0 °C and - 2.0 °C respectively (Buk 2004). Mean monthly humidity ranges from 10 - 40% (Buk 2004).

Table 2.1: The location and geology of the four land types represented in the study area (Land Type Survey Staff 1986). Quartzite granite outcrops occur in the three latter land types.

Land Type	Location	Geology
Ia1a	The gently sloping upper river valley ranging in height from 610-630m.	Intrusive rocks, primarily granite, overlain with silt and fine sand
Ic3a	The lower river valley and incised gorge area ranging in height from 420-620 m, and the north-eastern mountainous area ranging in height from 610-750 m.	Comprised mostly of exposed red biotite granite gneiss
Ag2d	The central basin generally sloping south and west ranging in height from 550-610 m.	Same as Ic3a, overlain with sand and gravel
Ae110b	A small area of high-lying plain in the far north ranging in height from 705-725 m.	Tectonic intrusive rock

Vegetation communities
Acacia erioloba - Schmidtia kalahariensis short, closed woodland
Acacia erioloba - Zygophyllum microcarpum short, closed woodland
Acacia karroo - Ziziphus mucronata short, riverine forest
Acacia mellifera - Euphorbia spp. tall, open shrubland
Acacia mellifera - Stipagrostis hochstetteriana tall, open shrubland
Acacia mellifera - Zygophyllum dregeanum - Euphorbia rectirama tall, open shrubland
Acacia mellifera - Zygophyllum dregeanum - Monechma spartioides tall, open shrubland
Adenolobus garipensis - Boscia albitrunca tall, open shrubland
Euphorbia gregaria - Osteospermum microcarpum tall, open shrubland
Schotia afra - Indigofera pechuelii low, open woodland
Sisyndite spartea - Forskaolea candida tall, open shrubland
Tamarix usneoides - Maytenus linearis tall, open shrubland

Figure 2.2: Distribution of the eleven vegetation communities (Buk 2004) within the study area.

Augrabies Falls National Park is an ideal location for this study since the relative simplicity of the ecological interactions within desert ecosystems greatly facilitates

ecological analyses and the construction of predictive models (Louw 1982). The paucity of vegetative cover in AFNP improves sitelines, facilitating the ability to observe animals and making AFNP ideal for studying animal behaviour. AFNP also provides a reasonable variety of habitats, from open plains to woodlands, within the centre of the distribution range of springbok. The extreme spatial and temporal heterogeneity within AFNP allow one to separate the system into component parts. Finally, this conservation area also provides a relatively undisturbed population of springbok since tourism is limited in this section of AFNP.
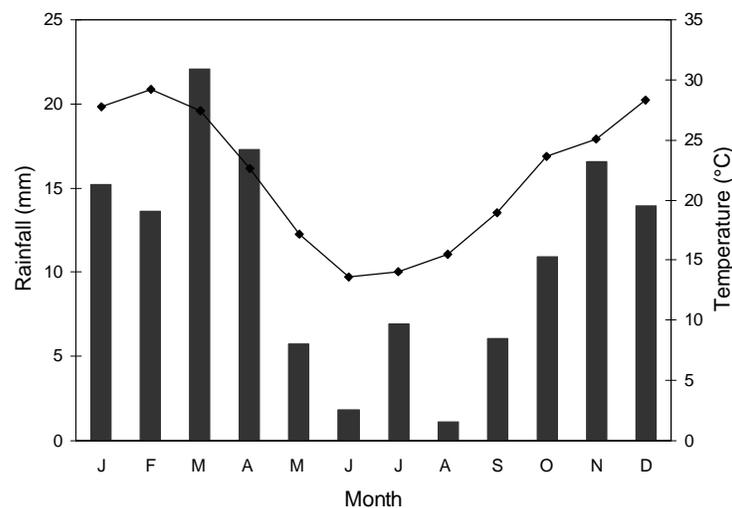
Figure 2.3: Simplified composite climatic diagram for data collected at the AFNP weather station from 1995 to 2003 (Weather Bureau 2004). Temperature is indicated by the line and rainfall is revealed in the bars.

Study species

The springbok, *Antidorcas marsupialis* (Zimmerman 1780), is an indigenous ungulate species with widespread distribution throughout the arid regions of southern Africa. The shoulder height of springbok is approximately 750 mm, with their hindquarters appearing higher than their forequarters (Skinner & Louw 1996). This gives them a sloping appearance. Body mass varies with geographic location (Robinson 1979); the mean mass for males is 41.0 kg (range: 31.3 - 47.6 kg), and the mean mass for females is 37.1 kg (range: 26.5 - 43.5 kg) (Skinner & Smithers 1990). Both males and females possess horns, however the horns of males are heavily ridged and slope

backwards then diverge outwards, and in older males the horns curve sharply inwards in a hook at the tip. Female horns are more lightly ridged, smaller, more slender and wider apart at the base (Skinner & Louw 1996).

Historically springbok occurred throughout much of Africa but widespread and indiscriminate hunting of this species has resulted in a reduced distribution. Springbok are adapted to an arid habitat with unpredictable food resources (Nagy & Knight 1994). Springbok are highly mobile, capable of moving large distances in search of food or water, responding rapidly to rainfall and the subsequent growth of herbaceous plants (Knight *et al* 1988; Vorster 1994). The energy requirements of springbok are unusually low, as is characteristic of many desert mammals (Nagy & Peterson 1988). Instead of having reduced water requirements, springbok have enhanced abilities to obtain water from their environment (Nagy & Knight 1994). These include drinking water when it is available, selecting succulent foods over drier food types, or perhaps if neither of these is available, feeding at night after drier food items have taken up water from humid night air (Nagy & Knight 1994).

The digestive system of the springbok is functionally adapted to the environment in which they live (Nagy & Knight 1994; Skinner & Louw 1996). They have been described as an intermediate type or mixed-dicotyledonous feeder (Hofmann 1989). They forage selectively (Davies & Skinner 1986a; Fairall *et al*. 1990; Cooper 1993; Liversidge & Gubb 1994), usually selecting a mixed diet and avoiding high-fibre diets, and are able to increase their food intake two- to three-fold when forage is plentiful (Hofmann 1989). According to Hofmann *et al*. (1996), the digestive tract of springbok provides them with a high potential for digesting mixed forage. Springbok appear to prefer plants undergoing relatively active growth, because of the succulence and higher nutrient content of such vegetation (Skinner & Louw 1996). Springbok feed on grasses mainly when the grass is young and tender but the major portion of the diet of springbok consists of short, karoid vegetation as well as the leaves of several tree species (Leistner 1967; Bigalke 1972; Fairall *et al*. 1990; Liversidge & Gubb 1994). Karoid shrubs, according to Louw (1969), contain sufficient protein to provide for the maintenance requirements of ruminants during winter. Springbok

spend long periods feeding due to their selective feeding habits (Novellie 1978; Davies & Skinner 1986b).

Population size, food availability and day length (Davies & Skinner 1986b; Cooper 1993) influence the daily activities of springbok. As high-quality food becomes scarcer springbok spend a greater proportion of their time feeding (Davies & Skinner 1986a). When nutritional conditions are better and there is a risk of predation, springbok spend less time feeding (Cooper 1993). Springbok exhibit alternating peaks of feeding and ruminating throughout the day, with feeding peaks at dawn (05h00-07h30) and dusk (17h30-19h00), although nocturnal feeding patterns have not been described (Davies & Skinner 1986b; Bigalke 1972). There are also claims that a feeding peak at midday is indicative of environmental stress (Novellie 1975). Cooper (1993) found that rumination time decreased as the forage became more succulent and abundant and that time spent resting increased as ambient temperatures increased, particularly when there was no wind.

Springbok drink from natural water holes at all times through the day, during all seasons, but stop after rain and during cold weather (Child *et al.* 1971; Bigalke 1972). Springbok are able to survive indefinitely without free water provided that that they can get water from their diet (Nagy & Knight 1994). They acquire moisture by selecting succulent plant parts, including flowers, fruits and tubers (Cooper 1993; Nagy & Knight 1994).

The spatial dispersion pattern of springbok appears to be independent of food and water; therefore, social structure may act to influence levels of dispersion (Davies *et al.* 1986). Springbok rams maintain a social hierarchy by territorial spacing and exclude bachelor herds from these territories (Bigalke 1972). Mean territory size of rams has been calculated as 0.21 km^2 by Novellie (1975) and 0.22 km^2 by Schijf (1978). In contrast to females and non-territorial males, territorial rams do not respond as sensitively to environmental change, and as a result are exposed to greater environmental risks (Jackson *et al.* 1993). Territorial males feed less efficiently than non-territorial animals, particularly during the rut when increased physical activity aggravates this disadvantage (Jackson 1995). In addition to the nutritional stress

imposed by territoriality, solitary males are more isolated and more vulnerable to predation. Jackson (1995) suggests that greater mortality among males is due to their being more solitary, in smaller herds, having a greater neighbour distance within the herd, and having a greater tendency to be found at the periphery of herds and in areas of tall vegetation after the rain.

The breeding season in springbok, although unrestricted, is sensitive to climatic change (Skinner & Louw 1996). Rainfall appears to be the cue evoking territorial and rutting behaviour in springbok rams (Davies 1985). Territorial rams exhibit a rut that is characterised by loud vocalising, grunting and increases in male sexual activity (Skinner & Louw 1996). During the rut, anoestrous springbok ewes show a classic oestrus response to the territorial rams, known as the "ram effect" (Skinner *et al.* 1992). This response later results in a synchronised birth of lambs. This synchronisation may serve to reduce the impact of predation (Estes 1976), although it occurs in springbok in an opportunistic manner due to the unpredictability of the environment (Skinner & Louw 1996).

The majority of lambs are born in September in summer rainfall areas, although in the Kalahari Gemsbok National Park, where rainfall peaks in the second half of summer, lambs are born in February/March (Skinner & Louw 1996). The observed major peak in springbok lambing in early summer agrees with previous literature (Shortridge 1934; Bigalke & Van Hensbergen 1993) and coincides with optimal environmental conditions which may serve to maximise the chance of survival of lambs. A minor peak in lambing in autumn is thought to be a result of early summer rain (Bigalke 1970). However, springbok are known to adjust their reproductive behaviour to the unpredictable arid environment that they inhabit and can breed throughout the year (Skinner & Louw 1996; Skinner *et al*. 1996).

Although generally gregarious, sociality varies seasonally depending on food, feeding style and reproductive behaviour (Skinner & Louw 1996). Springbok herd size and composition can vary in relation to season, year, and region and appears to be influenced by ecological factors (David 1978). In summer rainfall areas springbok form small herds from about April to October when dry conditions prevail, and

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aggregate in large herds when vegetation responds to favourable conditions (Skinner & Louw 1996).

Springbok generally fit the gazelle pattern in having herds averaging 10-30 animals (Estes 1976; David 1978). Bigalke & Van Hensbergen (1993) described the following social grouping for springbok:

a. nursery herds containing females and young

b. harem herds containing a nursery herd and one adult male

c. bachelor male herd containing males from about 10 months old

d. territorial males

e. mixed herds

Harem herds and territorial behaviour are most common during the mating season.

There are a number of animals that may prey upon the springbok and their lambs, including leopards (*Panthera pardus*), caracal (*Felis caracal*), black-backed jackals (*Canis mesomelas*), African wild cats (*Felis sylvestris*), martial eagles (*Polemaetus bellicosus*) and black eagles (*Aquila verreauxii*) (Mills 1984; Hofmeyr and Louw 1987; Jackson *et al.*1993). In the Kalahari Gemsbok National Park, Mills (1984) found that cheetahs prey heavily on springbok. Leopards are ambush predators which also prey relatively heavily on springbok (Jackson *et al.* 1993). Both predators appear to influence the structure of the population and may be responsible for distorted adult sex ratios in favour of females (Jackson *et al.* 1993).

Bednekoff & Ritter (1995) recorded three instances when springbok approached predators. In the first instance, 25 ewes advanced in a wedge-shaped formation to drive off an African wild cat (Bednekoff & Ritter 1995). On the other occasions, a large group (200-250) of springbok formed a wedge and advanced to within 50-100 m of a leopard and a cheetah, respectively (Bednekoff & Ritter 1995). Bednekoff & Ritter (1995) postulated that such approaches enable the springbok to gain information which may assist them to thwart later attacks (Bednekoff & Ritter 1994). Similar approaches to large predators have been observed in Thomson's gazelle (Fitzgibbon 1994).

AFNP falls within the historical range distribution of springbok (de Graaff & Penzhorn 1976). Reports of springbok near the Augrabies Falls occur from as early as 1827 (du Plessis 1969). Census results (Fig. 2.4), uncorrected for potential bias, for the mammalian herbivores in the Waterval section show that springbok are the most numerous species in the study area and the population has been increasing in recent years (Castley pers. comm.[1]). Springbok are highly mobile and able to move throughout the study area in search of food or water, responding rapidly to changes in environmental conditions. While habitat use may be influenced by density-dependent factors, the growth and freedom of movement exhibited by springbok is assumed to mitigate this effect, thereby reducing the amount of variation in distribution which cannot be explained by models of habitat selection.
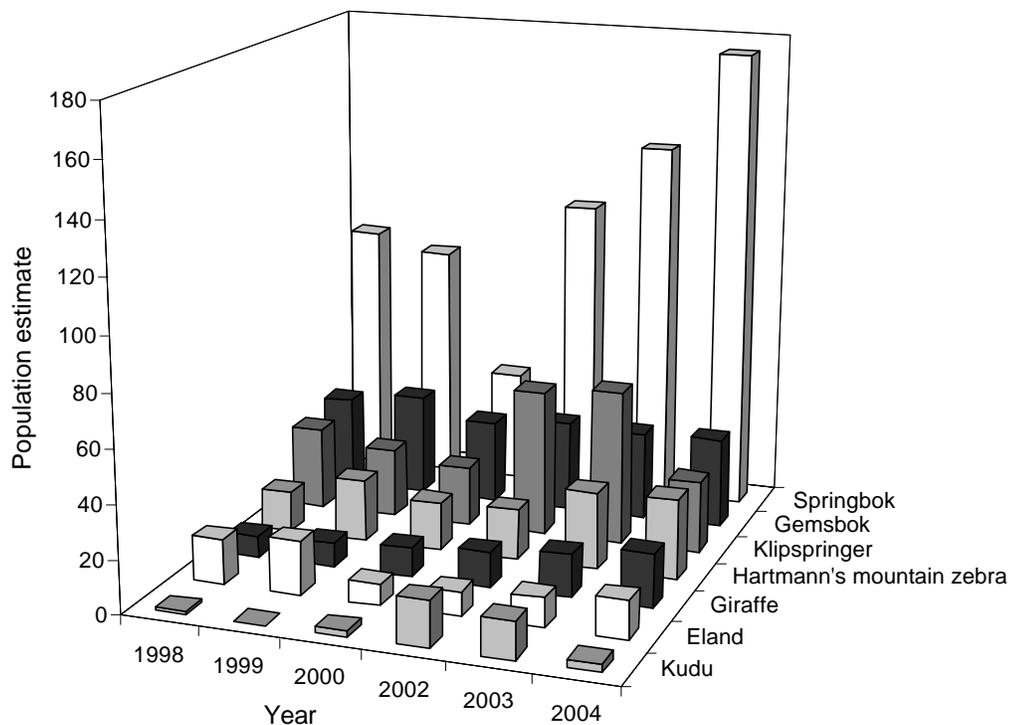
Figure 2.4: Census estimates for the herbivores in the Waterval section of AFNP (J.G. Castley pers. comm.[1]).

The benefit of using springbok for this study includes their morphological and behavioural adaptations to an arid habitat with unpredictable food resources. Springbok are able to exploit ephemerally favourable conditions, and are not limited to specific habitats by the availability of water, which results in a distribution that reflects responses to current environmental conditions. Springbok adjust their diet, microhabitat, foraging time, and social groupings in response to changes in the environment, making it possible to evaluate their perception of the environment using behaviours that are easy to read. Also, springbok generally form conspicuous, discrete groups and typically inhabit open, gently undulating country covered in short grass and scattered small bushes (Siegfried 1980) and hence are easy to observe.

Chapter 3

Habitat preferences of springbok revealed through a habitat suitability model and isodar analysis

Introduction

Habitats differ in quality for different organisms, habitat quality being governed by both the costs (e.g. risk of predation) and benefits (e.g. availability of food) associated with living in that habitat (Melton 1987). Habitat quality influences population viability and persistence (Doncaster *et al*. 1996; Root 1998). As a result, habitat evaluation has emerged as a vital component of wildlife conservation and management (Fabricius & Mentis 1991).

To effectively manage populations, the definition of a habitat should be based on a clear understanding of the environmental conditions upon which animals are dependent, and should be described in terms of the suite of environmental conditions which provide for the needs of an organism to sustain life and reduce the risk of mortality (Henley 2001). This includes a broad understanding of the life requisites of the species in question (Farmer *et al.* 1982). From a conservation and management perspective habitat should therefore be defined by measurable environmental factors that allow individuals to grow or maintain body condition, reproduce, and minimise the risk of mortality (Henley 2001). In this way, habitat is defined by a set of environmental factors which correspond with known determinants of population abundance and is consistent and comparable among habitats (Henley 2001).

The habitat concept has been used as the basis for modelling efforts to assist in planning studies since it integrates the concepts of population and carrying capacity and provides a consistent basis for baseline, impact assessment, mitigation, and monitoring studies (Fish & Wildlife Services 1980a, 1980b). Habitat suitability modelling refers to a set of models developed as part of the Habitat Evaluation Procedure (HEP), in which the suitability of an area for a species is summarised by a single unitless value or index (Whitaker & McCuen 1976; Noss & Cooperrider 1994). The Habitat Suitability Index (HSI) value is determined by combining Suitability

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Index (SI) scores which represent the organisms' response to a particular environmental condition (Schamberger & O'Neil 1986).

Habitat Suitability Models were developed and used in the context of determining habitat quality (Fish & Wildlife Service 1981a) and designed for use in situations where land use and habitat conditions were expected to change. These Habitat Suitability Index (HSI) models were intended to allow assessment of changes in habitat quality and availability for selected wildlife species (Schamberger & O'Neil 1986; Stauffer & Best 1986). HSI models are based on the premise that it is possible to link habitat suitability in terms of individual habitat variables, these relationships being described by primarily linear relationships (Fish & Wildlife Service 1981a). These separate variables can then be combined into a meaningful index that represents the suitability of a given patch of habitat for a specific wildlife species (Laymon & Barrett 1986). By definition, the HSI provides a 0-1.0 index of habitat suitability for a species at a given site and is not intended for prediction of population levels, but to indicate habitat quality (Blenden *et al.* 1986; Schamberger & O'Neil 1986). Because each model identifies key habitat variables, these models serve as a linkage to management actions that can be designed to enhance wildlife populations (Loomis 2002).

Isodars and the Ideal Free Distribution

Habitat use data document the use of, or preference for, particular areas (habitat patches) by a species and assume (based on optimality theory - Rosenzweig 1974; Charnov 1976; Pyke 1984) that individuals of a species will select and use areas best able to satisfy their life requirements and as a result, greater use will occur in high quality habitat (Schamberger & O'Neil 1986). Habitat selection is the process whereby individuals preferentially use or occupy a non-random set of available habitats (Morris 2003b). An ideal-free distribution will occur whenever individuals select habitats that maximise their Darwinian fitness, and when they are free to occupy the habitats they choose (Fretwell & Lucas 1969). In such a case the densities in different habitats are adjusted such that the mean fitness is the same in each (Morris 1987a). One way to reveal this distribution, and to measure the various interactions among species that influence it, is to plot the densities in adjacent habitats. The

relationship of the number of individuals in each habitat type when plotted in a state space of density in each habitat type produces a line along which fitness is equal in both habitats at different densities and is known as the habitat isodar (Morris 1987a, 1987b 1988, 1989). Quantitative differences between habitat features alter the intercept of the line whereas qualitative differences, that alter efficiency, modify its slope (Morris 1988). Competitive interactions as well as the degree of density dependent habitat selection are therefore revealed by the corresponding regression coefficients (Morris 1989, 1999a; Rodriguez 1995; Morris *et al.* 2000).

It thus appears that fundamental insights into the relative qualities of the habitats a species occupies can be gained simply by analysing its pattern of abundance in adjacent habitats (Morris 2003b). Factors such as spatial scale, boundaries between habitats, and source-sink dynamics may influence the distribution and abundance of species (Morris 2003b). Population determinants may override habitat features, or variation in animal numbers may be explained by considering the scale of measurement or stochastic variation in population size independent of the details of habitat and other biotic features (Rotenberry 1986). These factors have the potential to mislead estimates of habitat quality (Van Horne 1986).

Springbok habitat use

Springbok prefer open areas and are often found in grassveld or more arid plains (Shortridge 1934) although they are also able to occupy densely vegetated habitat (Bigalke 1972). They sometimes occur in fairly thick belts of bush that intersect grasslands; however, they avoid unbroken areas of bush or forest (Shortridge 1934). Tall grassland is avoided as it is too high and unpalatable, and it causes springbok to run awkwardly (Bigalke 1972). Rocky hills are avoided unless *Acacia mellifera* is present and flowering, or unless they are hard pressed during a hunt (Bigalke 1972). As a mixed forager, springbok adjust their diet, microhabitat and foraging time to the highly variable quality of the forage in arid areas (Hofmann *et al.* 1996). They are able to change from habitat opportunists and diet selectors to habitat selectors and diet opportunists as the environmental conditions dictate (Hofmann *et al.* 1996).

The factors considered most important to springbok include the availability of preferred food plants, the mineral content of plants, physical attributes of the vegetation that may affect ease of movement, and a preference for open areas (Leistner 1967; Bigalke 1972).

It is hypothesised that springbok prefer open habitats that allow early predator detection and fast escape as they rely on detection and running to reduce predation. Therefore, the objectives of this study were:

1. to identify proximate environmental features to which springbok are responsive;
2. to develop a habitat suitability index (HSI) model to account for the variation in springbok abundance across habitats;
3. to use isodar analysis to reveal information on the mechanisms underlying habitat preference by springbok;
4. to relate the component variables of these models to the biology of springbok so as to develop our understanding of their ecology.

Methods

Population density

Accurately estimating population size is difficult, and therefore ecologists often rely on indices of population size as a proxy for actual population size (Gibbs 2000). An index to population size is simply a measurable correlate of density (Caughley 1977) derived from sampling a small fraction of a population using a standardised methodology, and is expressed as individuals counted per sampling unit (Gibbs 2000).

Estimates of density for species that occur in reasonably open habitats can be obtained by counting the animals directly, normally using transect or point sampling approaches (Buckland 1993). Buckland (1993) suggests that line transect sampling of animal density is preferable to point sampling methods. This is because the time spent sampling in line transect surveys may be greater, however, often more time is spent travelling between and locating sampling points for point sampling (Bollinger *et al.* 1988). Since the present study area is large, the efficient utilisation of effort may have been an order of magnitude better for line transect surveys (Buckland 1993).

I used drive transects to determine the density of springbok in the different habitats (see Table 3.1 for habitat definitions). Springbok are most active during the morning and late afternoon, making these times ideal for sampling density and group sizes (Bigalke 1972; Davies & Skinner 1986). I therefore used these times to drive transects and utilised most of the roads in the study area. I used two observers for the drives, each of whom counted groups independently until the total from each observer was within 5% of each other. I used five different transects to cover as great an extent of the park and as many habitats as possible (Appendix 3 shows the roads of the park, the area of the park covered by each drive transect, the habitat within these drives, and the number of drives completed for each). Not all of the roads were used in the drive transects, and drive transects utilised more than one road.

During the drive transects, I recorded the date and time, the number of individuals present, the GPS position (in decimal degrees) of the vehicle, the distance and bearing to the animal from the vehicle, and habitat type for each animal or group of animals sighted. If possible, I determined the number of individuals of different age and sex classes comprising the group. I also recorded the social group type (solitary males, bachelor herds, harem herds, and nursery groups), and the behaviour of the group or individual. I also noted if no animals were sighted on a drive transect.

I determined the exact location of the springbok using the following equations:
Latitude:

latitude of vehicle + [COS(vehicle bearing + animal bearing) × distance to animal × latitude correction]   (3.1)

Longitude:

longitude of vehicle + [SIN(vehicle bearing + animal bearing) × distance to animal] × longitude correction   (3.2)

I inputted these locations into a table, along with the group size, and imported these data into the geographical information system (GIS) program ArcView®. I overlayed these locations onto a vegetation map of AFNP. I used the vegetation community map from South African National Parks (SANParks) as the basis of my habitats. This map was created with the goal of describing the Waterval section of AFNP in terms of the

20

medium to large browsers' resources and therefore describes the vegetation communities in terms of substrates, vertical availability of all browse species and the availability of shade for each community (Buk 2004). I recoded this vegetation map to reflect the habitats for the different vegetation communities (Table 3.1).

Table 3.1: Summary of the vegetation communities according to the vegetation map (Buk 2004) and the habitat codes I assigned to create the habitat map used in analyses.

Vegetation Community/Habitat	Habitat Code
Acacia erioloba - Schmidtia kalahariensis short, closed woodland	1
Acacia erioloba - Zygophyllum microcarpum short, closed woodland	2
Acacia karroo - Ziziphus mucronata short, riverine forest	3
Acacia mellifera - Euphorbia spp. tall, open shrubland	4
Acacia mellifera - Stipagrostis hochstetteriana tall, open shrubland	5
Acacia mellifera - Zygophyllum dregeanum - Euphorbia rectirama tall, open shrubland	6
Acacia mellifera - Zygophyllum dregeanum - Monechma spartioides tall, open shrubland	7
Adenolobus garipensis - Boscia albitrunca tall, open shrubland	8
Euphorbia gregaria - Osteospermum microcarpum tall, open shrubland	9
Schotia afra - Indigofera pechuelii low, open woodland	10
Sisyndite spartea - Forskaolea candida tall, open shrubland	11
Tamarix usneoides - Gymnosporia linearis tall, open shrubland	12

I determined the habitat at the location of each sighting by performing a spatial join of the habitat data and the location data. I then exported this information into the spreadsheet Microsoft Excel for further analysis. I calculated the mean number of individuals sighted per habitat for each drive completed.

In order to determine the density of individuals in the different habitats, I first had to create a visibility map for each drive in order to estimate the area sampled. A person walked perpendicular to the vehicle, away from the road until an observer in the vehicle could no longer see them (due to the uneven topography) and this was taken as the springbok visibility distance. The GPS location at this point was recorded. This was done on both sides of the vehicle at regular intervals along the transect roads. I imported these points into ArcView®, and then joined them using lines to make a polygon along all the transect roads. I separated this polygon into segments according to the drive transects. I then intersected these polygons with the habitat map of the park. This gave the habitats sampled in each transect. Because the area inside a drainage line is obscured by vegetation and not visible from the road, I excluded these from the transect areas. I did this by creating a buffer map of the drainage lines in

AFNP using a buffer of 2 m which I intersected with the habitat map for each drive transect. I selected all the areas outside the buffer and converted it into a separate map. I then updated the area of the maps using the X-tools function in ArcView®, which resulted in a table showing the area of each habitat visible from the road for each drive transect (Tables 3.1 and 3.2).

Table 3.2: Summary of the four drive transects (S1, S2, M1, L1, and L1(B)) used in the analysis. The total area of the park and the visible area of each habitat covered by transects is included. The total visual area of the habitats is less than the sum of areas in the drives since some areas of the drives overlap. See Table 3.1 for the details of the habitats.

Habitat	Area of study site in AFNP (ha)	Total visible area in all drives (ha)	Visible area in S1 (ha)	Visible area in S2 (ha)	Visible area in M1 (ha)	Visible area in L1 and L1(B) (ha)
1	31.57	18.36	–	–	4.48	17.65
2	8.15	7.50	3.42	4.45	4.63	4.63
3	83.37	4.44	0.04		3.52	3.80
4	1098.92	346.17	–		71.43	338.20
5	936.99	337.01	33.04	104.60	125.91	230.17
6	879.90	285.83	213.11	6.16	53.80	72.70
7	210.16	106.54	92.89	13.61	13.64	13.64
8	878.86	54.91	1.64	0.36	0.36	52.78
9	507.65	112.22	4.16	30.49	57.24	70.54
10	2755.43	87.75	–	6.88	19.48	84.22
11	51.74	36.72	–	–	–	36.72
12	76.19	14.06	0.09	0.07	13.98	13.98
Total	7518.93	1411.50	348.37	166.61	368.48	939.01

I incorporated this information with the sightings information obtained earlier, and thus was able to estimate the density of springbok in each habitat for each drive. In order to determine if springbok were exhibiting a preference in their habitat use, I compared their observed density with their expected density (based on a random habitat use model) using a Chi-square test. I used box-and-whisker plots showing the mean, first and third quartiles and the range to illustrate the data since the data were not normally distributed (Kolmogorov-Smirnov test, $P < 0.05$). Although outliers and extremes were used in the analysis, I have not represented them in the box plots in order to avoid cluttering and to facilitate interpretation of the trends. I made pairwise comparisons in springbok density between the 12 vegetation types using a Mann-Whitney U test, adjusted for multiple comparisons using a Bonferroni adjustment, to determine which vegetation types were significantly different from each other. The major disadvantage of the Bonferroni adjustment is that it is not an exact procedure.

The Bonferroni adjusted P value is larger than the true *P* value. Therefore, in order for the Bonferroni adjusted *P* value to be 0.05, the true *P*-value must be smaller, especially when comparing many treatment groups (Dallal 2003). I therefore considered $P > 0.1$ to indicate significant differences.

Habitat suitability model

Because the vegetation in AFNP is sparse, and often occurs in clumps, I used strip transects in order to quantify the biotic characteristics of habitat for the different habitats. Transects were randomly located within each habitat, using randomly generated numbers applied to GPS coordinates. I measured components of all woody plants inside each transect. For each plant, I measured the number and diameter of the stems, as well as the height below the canopy and the height to the top of the canopy. I also measured the longest diameter of the canopy and the diameter of the canopy at right angles to this. Where possible, the species was identified in the field and voucher specimens were collected. These voucher specimens were sent to the herbarium (SANParks Herbarium, Kimberley; MacGregor Museum, Kimberley) for verification and identification of the unknown species. From this I determined the total canopy cover, as well as the canopy cover for three plant species important to springbok, namely *Acacia mellifera*, *Boscia albitrunca* and *Ceraria namaquensis*.

Other information I collected at each line transect included the percent ground cover of boulders, rocks, stones, pebbles, grit, sand and clay. In addition to this I recorded the percent aerial and basal cover of the herbaceous layer (divided into grasses, herbs, forbs and succulents), aspect, slope, topographic position, soil texture, moisture status, shading, and protection from wind. I also estimated the type, intensity and frequency of erosion, deposition and herbivory (see Appendix 4 for a complete list of habitat variables and the codes for categorical variables).

I combined the percent cover of stones and pebbles into one category called stones, and the percent cover of grit and sand into one category called sand. Because the aerial component of herbs and forbs is more important as a source of forage, I combined the percent aerial cover of herbs and forbs into a single category and removed the basal cover of both from further analysis. The basal cover of annual

grasses is a more reliable estimate of productivity; therefore I used this parameter and removed the percent aerial cover from further analysis. Since the percent cover of succulents was less than 5% in all habitats, and 0% in most, I also removed this from further analysis. Since ungulate populations may be expected to fluctuate annually, therefore I removed those environmental variables (such as slope and aspect) which may be expected to change only on a longer time frame (Henley 2001). Next, I removed those variables highly correlated with other variables using the correlation matrix generated in Principle Component Analysis. I then combined these environmental data with the density estimates generated earlier in order to generate the habitat suitability model. I calculated the mean density per drive per habitat, as well as the mean values for the environmental variables data per habitat.

Habitat suitability models are composed of response curves that define the relationship among environmental parameters and animal abundance, and a habitat suitability index (HSI) equation which defines the relationship among the response curves and between response curves and habitat suitability.

To account for the typically non-linear nature of the relationship among environmental parameters and animal relative abundance, I used polynomial regressions to generate the HSI response curves. Because the direct effect of environmental parameters on populations is considered, the requirement of dependency is met (Gutzwiller & Anderson 1986; Ter Braak & Looman 1987). The polynomial regressions helped establish an *a priori* understanding of the relationship between environmental parameters and springbok population density (Johnson 1981a). Non-significant Durbin-Watson statistics suggest that the data did not suffer from a lack of independence of error terms, and therefore I did not correct for autocorrelation (Gutzwiller & Anderson 1986). I did not remove outliers from samples as it was not obvious whether these were the result of observer error, error in recording, miscalculation or atypical behaviour on the part of the study animal (Gutzwiller & Anderson 1986; Morrison *et al.* 1992). Environmental parameters showing the weakest relationship with springbok population density were discarded from further analysis. Given the number of environmental parameters under consideration I have included only the simplified response curves for those

environmental parameters that I considered for the model. In the retained parameters I converted the range of densities making up the y-axis to a 0 to 1 scale, with 1 corresponding to the highest density recorded. In this way, I transformed the samples into suitability index (SI) scaled from 0 to 1. I used transformed data in comparable units for the multiple regression analysis.

I used a multiple linear regression to determine the contribution of each habitat variable to the HSI equation and thus establish the best formula for defining the relationship among the habitat variables and springbok density (Morrison *et al.* 1992). This forms the basis of the linear equation that is the HSI model. Tolerance values associated with each multiple regression were used to test for multicollinearity.

Isodars

I determined the density of springbok in adjacent habitats along a drive and for each drive. I used only those habitats that showed a significant difference in their densities for the isodar analysis. I restricted isodar analysis to those situations when both habitats were occupied since inclusion of zero densities can bias the isodar calculations because they may not yield a uniquely determined density in the alternative habitat (multiple possible densities below the isodar intercept) (Morris 2003a). Adjacent habitats that met these criteria were habitats 5 and 7, and habitats 6 and 7.

Results

Population density

Springbok displayed preferential use of habitat (Chi-square test: $?^2{}_{0.05,89} = 35602.82$; *P* < 0.001), with habitats 4 (median density = 0.015 springbok/ha, range 0 – 0.40, n = 31) and 5 (median density = 0.006 springbok/ha, range 0 – 0.75, n = 54) having the greatest population density (Fig. 3.1, Table 3.3). Springbok were seen more than half of the time in these habitats and less than 30% of the time in all other habitats (Table 3.3). For this reason the median density in all habitats other than 4 and 5 is 0, while maximum densities varied between 0.12 and 12.09 springbok/ha (Fig. 3.1, Table 3.3). Springbok where never seen in habitat 1. The greatest maximum density occurred in habitat 2; however springbok were only ever seen once in this habitat (Table 3.3).
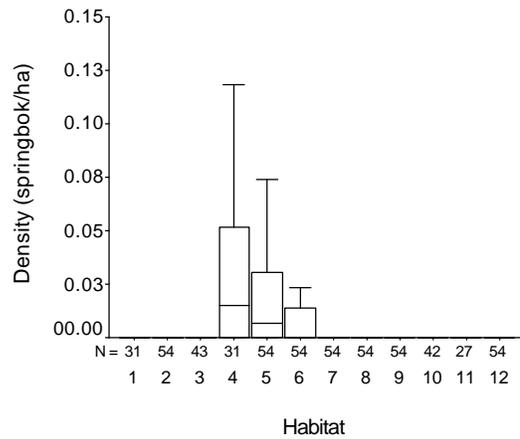
Figure 3.1: Preference in habitat use (box plots show the median, the first and third quartiles and the range of the data, excluding extremes and outliers. N = the number of times the habitat was sampled for estimating springbok density. There is a significant difference in the observed density of springbok to what would be expected if springbok were distributed randomly throughout the habitats

Table 3.3: Summaries for the density of springbok (springbok/ha) recorded alone or in groups in the different habitat types. The median, minimum and maximum density of springbok is shown, as is the number of times springbok were seen in each habitat, and as a percent of the total number of times that habitat was sampled. Springbok were never seen in habitat 1. N = number of transects sampling that habitat.

Habitat	N	Median density (springbok/ha)	Minimum density (springbok/ha)	Maximum density (springbok/ha)	Number of springbok sightings	Sightings per drive transect (%)
1	31	0.000	0.00	0.00	0	0
2	54	0.000	0.00	12.09	1	2
3	43	0.000	0.00	0.53	1	2
4	31	0.015	0.00	0.12	20	65
5	54	0.006	0.00	0.75	28	52
6	54	0.000	0.00	0.72	17	31
7	54	0.000	0.00	0.15	7	13
8	54	0.000	0.00	6.12	5	9
9	54	0.000	0.00	0.25	12	22
10	42	0.000	0.00	0.18	6	14
11	27	0.000	0.00	0.60	2	7
12	54	0.000	0.00	1.14	4	7
Total	552	0.021	0.00	12.09	103	19

Table 3.5: Comparison of springbok density in different habitats. I made pairwise comparisons using a Mann-Whitney U test and adjusted for multiple comparisons using a Bonferroni adjustment. Shown below are the Z-values of the test statistics with those showing significant differences marked with an asterisk.

Habitat	1[a,y]	2[a,y]	3[a,y]	4[b]	5[b,c]	6[c]	7[a,z]	8[a,z]	9[c]	10[a,z]	11[a,z]	12[a,z]
1		-0.758	-0.849	-5.258*	-4.742**	-3.444*	-2.078	-1.735	-2.805	-2.179	-1.529	-1.543
2			-0.148	-6.205**	-5.632**	-4.009**	-2.145	-1.633	-3.164	-2.261	-1.209	-1.333
3				-5.572**	-5.050**	-3.545**	-1.827	-1.391	-2.76	-1.936	-1.014	-1.118
4					-2.183	-4.571	-4.995**	-3.567**	-4.171**	-4.057**	-5.175**	-5.175**
5						-1.668	-4.102**	-4.438**	-2.958	-3.638**	-3.551**	-4.667**
6							-2.411	-2.746	-1.244	-2.042	-2.3	-3.006
7								-0.546	-1.213	-0.211	-0.707	-0.901
8									-1.706	-0.681	-0.278	-0.346
9										-0.955	-1.536	-2.009
10											-0.796	-1.003
11												-0.022
12												

*	Habitats showing a significant difference ($P = 0.10$).
**	Habitats showing a significant difference ($P = 0.05$).
a, b, c	Density in habitats not significantly different from each other.
y, z	Density in habitats similar and display the same differences relative to all other habitats

Table 3.4 shows the results of the pairwise comparisons of habitats. Springbok density in habitat 4 was significantly different from all habitats except habitat 5. Springbok density in habitat 5 was significantly different from all habitats except 4 and 6, while density in habitat 6 was significantly different from all habitats except for 5 and 9 (Table 3.4). None of the remaining habitats is significantly different from each other. Habitats 1, 2, and 3 display the same differences relative to other habitats as do habitats 7, 8, 10, 11, and 12 (Table 3.4).

The total area of each habitat in the Waterval section was known (Buk 2004), as was the visible area sampled by the drive transects for each habitat, and the proportion of the total that this represents (Table 3.5). Thus the density in the transect area could be extrapolated to the whole of the Waterval section and a total observed population size for the Waterval section could be estimated by multiplying the total density of springbok in the drives by the total area of the Waterval section. I estimated the expected population size by averaging the uncorrected population estimates obtained from SANParks census for 2003 and 2004 (137 and 175 springbok respectively). The observed population size (150 springbok) was not significantly different from the expected population size (156 springbok) (G-test: $?^2_{0.05,1} = 3.84$; $P < 0.05$).

Habitat suitability model

The habitat variables used in the habitat suitability model (Fig 3.2) are listed in Table 3.6 in the order in which they were entered into the model as part of the linear regression. This provides some indication of the contribution of each variable to the overall regression coefficient; those entered first generally had the greatest contribution. All variables must pass the tolerance criterion to be entered in the equation; the default tolerance level is 0.0001. Also, a variable is not entered if it would cause the tolerance of another variable already in the model to drop below the tolerance criterion. None of the variables entered had a beta coefficient that is significant at the 95% confidence level. The model had a low correlation coefficient; however, this may be due to a lack of variation in the habitat variables since they were averaged before input into the model, rather than indicating a lack of fit for the data (Morrison *et al.* 1992).

Table 3.5: Summary for the total area, the visible area covered by the drive transects, and the proportion of the total that this represents for each habitat in the Waterval section of AFNP. The density of springbok estimated in the drive transects is extrapolated to estimate a total population size for springbok in the Waterval section by multiplying the total density of springbok in the drive transects by the total area of the Waterval section.

Habitat	Area of AFNP (ha)	Visible area in all drive transects (ha)	Proportion of habitat covered in drive transects	Density in drives (springbok/ha)
1	31.57	18.36	0.58	0.00
2	8.15	7.50	0.92	0.00
3	83.37	4.44	0.05	0.00
4	1098.92	346.17	0.32	0.01
5	936.99	337.01	0.36	0.01
6	879.90	285.83	0.32	0.00
7	210.16	106.54	0.51	0.00
8	878.86	54.91	0.06	0.00
9	507.65	112.22	0.22	0.00
10	2755.43	87.75	0.03	0.00
11	51.74	36.72	0.71	0.00
12	76.19	14.06	0.18	0.00
Total	7518.93	1411.50	0.19	0.02

Table 3.6: Summary of regression statistics and constituent variables of the habitat suitability model. Incorporated variables are listed in the order in which they entered into the model.

F	*P*	r	Incorporated variables	Coefficients
0.70	0.70	0.39	Constant	-0.09
			Moisture Status	0.10
			Aerial cover of forbs and herbs	0.52
			Percent of sand	-0.06
			Percent of boulders	0.33
			Boscia albitrunca	-0.60
			Acacia mellifera	0.15
			Percent of stones	-0.27

Figure 3.2: The seven variables, and their response curves, that were included into a springbok habitat suitability model for Augrabies Falls National Park.
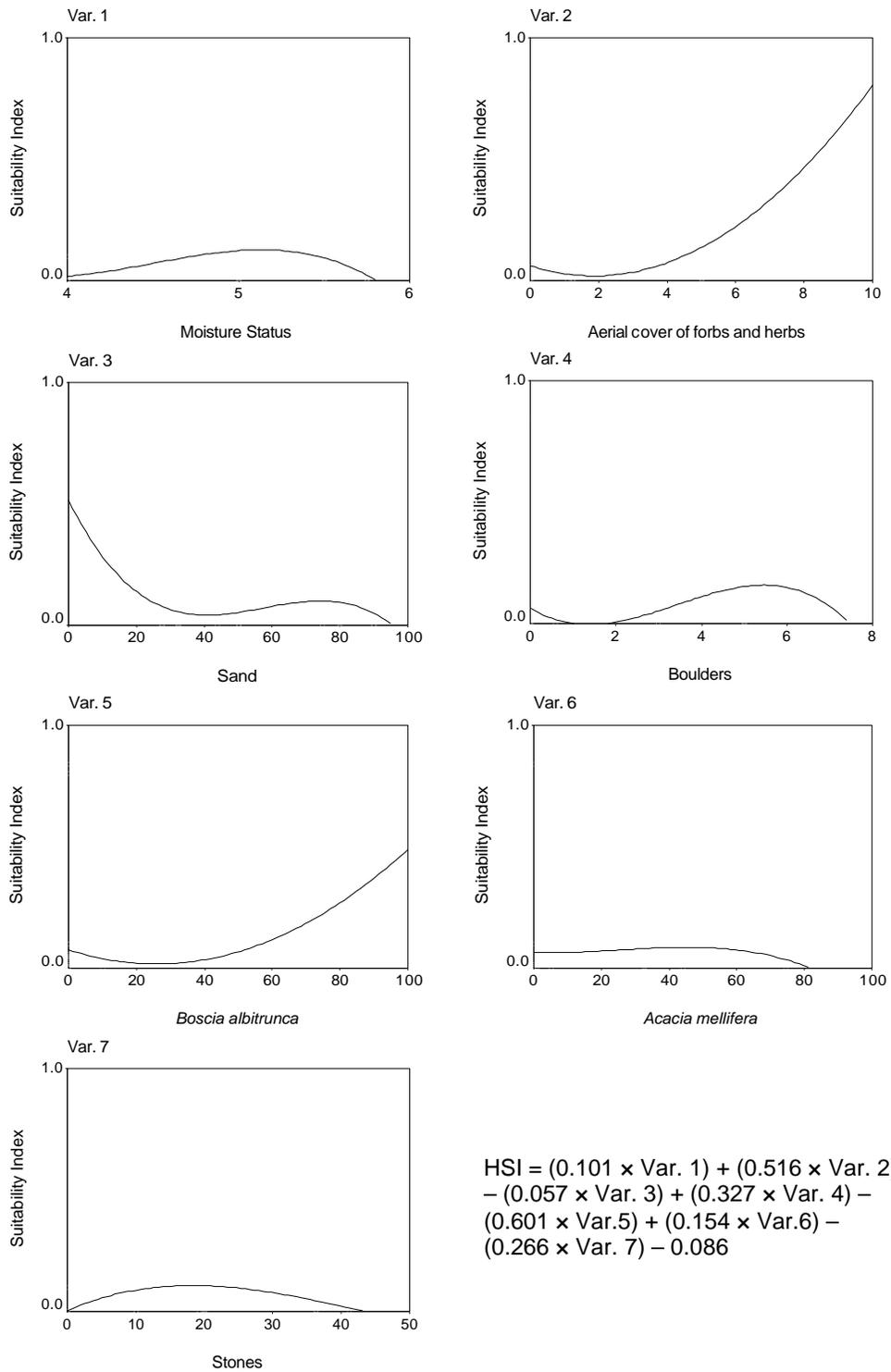
HSI = (0.101 × Var. 1) + (0.516 × Var. 2) − (0.057 × Var. 3) + (0.327 × Var. 4) − (0.601 × Var.5) + (0.154 × Var.6) − (0.266 × Var. 7) − 0.086

Isodars

Isodar regressions were analysed for habitats 5 and 7, and 6 and 7 (Table 3.7, Fig. 3.3). Density-dependent habitat selection was not evident between habitats 5 and 7, or between habitat 6 and 7 ($P > 0.05$). However, the isodar between habitats 6 and 7 is marginally significant despite the small sample size. The isodar analysis suggests that habitat 6 is quantitatively superior to habitat 7, but the two habitats are qualitatively similar. These isodars should however be interpreted with caution given that the data are so limited.
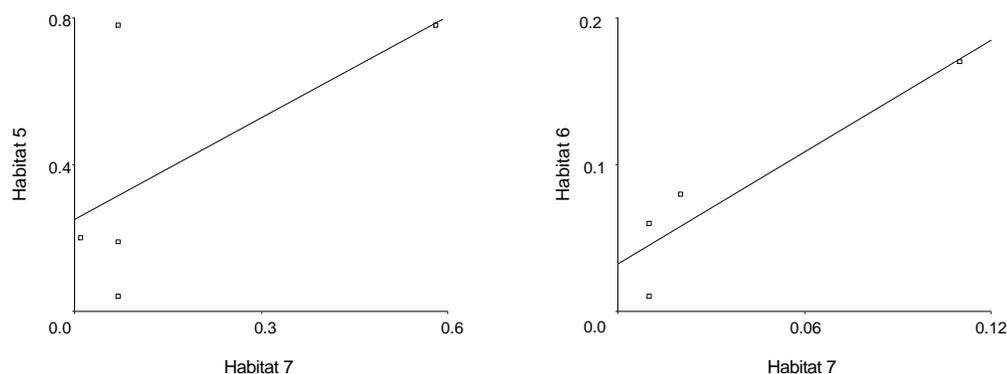
Figure 3.3: The relationship (isodars) between springbok population size in habitats 5 and 7 and habitats 6 and 7.

Table 3.7: Results of linear correlation for isodars contrasting springbok density in adjacent habitats.

Isodars	Constant	Slope	R^2	F	*P*	N
Habitat 5 ? Habitat 7	0.25	0.96	0.38	1.85	0.27	5
Habitat 6 ? Habitat 7	0.03	1.27	0.85	11.74	0.08	4

Discussion

Population distribution

The results clearly supported the hypothesis that springbok preferred open habitats with density being greatest in habitats 4 and 5 and lowest in habitat 1. Habitats 4 and 5 are open shrublands with limited shade and abundant forage provided by *A. mellifera*; whereas habitat 1 is short, closed woodland with abundant shade (Buk 2004). These habitats also provide relatively high forage resources (Buk 2004). Numerous other studies have described springbok as preferring such habitat anecdotally (Shortridge 1934; Leistner 1967; Bigalke 1972; Davies & Skinner 1986;

Milton *et al.* 1992; Skinner 1996) but this is the first attempt to quantify springbok habitat preferences. The results, therefore, agree with the previously published data on the habitat preferences of springbok, and support the prediction that the maximum number of springbok would occur in areas of high food quality.

All three habitats have sand and gravel in the substrate. The dominant substrate in habitat 4 is gravel strewn with rocks and pebbles interrupted by outcropping bedrock and sandy drainage lines, and that of habitat 5 is an almost equal mixture of sand and gravel (Buk 2004). The substrate of habitat 1 has a high percentage of sand mixed with some gravel (Buk 2004). This does not support the prediction that the minimum number of springbok would occur in rocky areas, as habitat 4 contains rocky areas while habitat 1 has none. Bigalke (1972) found that springbok would avoid rocky hills unless *A. mellifera* were growing there or they were stressed during a hunt. *A. mellifera* contributes more than double the browse in habitats 4 and 5 than in habitat 1 (Buk 2004), it is therefore possible that the preference of springbok for habitats 4 and 5 is related more to the presence of *A mellifera* than to the substrate.

Habitats 4 and 5 occupy approximately 15% and 13% of the study area, respectively; while habitat 1 makes up only 0.4% of the study area (Buk 2004). There may be a lower size limit to the area of a habitat before springbok will occupy that habitat, related to body size (Dasmuth 1981a, 1981b; Calder 1983). The average estimated spatial requirement for springbok in the Nama Karoo has been calculated as 24 ha/springbok (Boshoff *et al.* 2002). Since habitat 1 occurs in five discrete areas, the largest of which is only 11 ha (Buk 2004), one might suggest that the absence of springbok in habitat 1 is due to its small size (and hence low probability of sampling springbok present). However, on one occasion 10 springbok were seen in habitat 2, the smallest habitat occupying only 8.15 ha in one area (Buk 2004). Therefore the absence of springbok in habitat 1 must be due to factor(s) other than patch size.

Habitat suitability model
The habitat suitability model incorporates those variables that have the greatest influence on springbok density. Variables similar to those described in the vegetation community map were inputted into the model, as well as other habitat variables. None

of the variables displayed a linear relationship with habitat suitability. The feature of the habitat that most influenced habitat suitability was moisture status. Habitat suitability increased as the habitat went from seasonally moist to occasionally moist/mostly dry, and then decreased as the habitat got drier still. Springbok are able to survive indefinitely without water provided that that they can get it from their diet (Hofmeyr and Louw 1987; Nagy & Knight 1994). The next most influential variable was the percent cover of forbs and herbs - increasing cover of forbs and herbs increased the habitat suitability. Leistner (1967) found that herbs and forbs provide an excellent source of feed for springbok while they are green. The percent cover of sand and boulders had a more complex interaction with habitat suitability, although the general trend was a negative interaction for sand and a positive interaction for boulders. Springbok prefer soils with higher mineral concentrations since generally plants remain green for longer on these soils (Milton *et al*. 1992). Sandy soils have low mineral content while minerals and water may collect on boulders enabling the plants growing there to remain green for longer. Increasing canopy cover of *B. albitrunca* and *A. mellifera*, the fifth and sixth most important variables, respectively, had a positive interaction with habitat suitability. Leaves, shoots and fruits of most shrubs and trees are rich in protein and phosphate, and provide an important source of fodder during the driest months of the year (Leistner 1967; Bigalke 1972). Dicotyledonous plants form a large part of the diet of other species, such as Grant's gazelle and Thomson's gazelle (Stewart & Stewart 1971). Unlike springbok, however, grass remains an important component of their diet (Stewart & Stewart 1971). The final variable to be entered into the model is percentage of stones. This variable had an overall negative influence on habitat suitability and may relate to the ease with which springbok are able to move (Bigalke 1972; Bednekoff & Ritter1994).

Henley (2001) attempted to develop a generic habitat suitability model for ungulates, including springbok, in the Eastern Cape Thicket vegetation. He took the principle constraints on growth, maintenance and survival of an ungulate to be food, water, climatic conditions, predation and parasites and as such developed five submodels relating to forage, water, thermoregulation, predator abundance and parasites (Henley 2001). The most obvious limitation to his model was that the specific habitat requirements of some species were excluded from the model (Henley 2001). Another

limitation in the model was that the model had apparently conflicting predictions between forage and other submodels on the predicted habitat utilisation by springbok (Henley 2001). The forage submodel also failed to identify the importance of karoid shrubs in open areas in the diet of springbok (Henley 2001).

Since habitat models are simplifications of reality and lack complete information, they can therefore be expected to have a degree of inherent unreliability (Farmer *et al.* 1982). This limits their capacity to reflect reality (Henley 2001). Species-specific habitat models may be more reliable and suffer fewer limitations than more generic models. The fact that Henley's (2001) model did not appear to describe springbok habitat suitability effectively precludes its application here.

Isodars

The slopes of the isodar regressions and their y-intercepts reveal information on the mechanisms underlying preference for habitats (Morris 1987a, 1988). If the isodar slope comparing the 2 habitats does not significantly differ from 1, the habitats are considered to differ only in the abundance of resources available in each (quantitatively). If the slope is significantly greater than 1 the habitats are considered to differ in the efficiency of the foraging individuals that are present in each (qualitatively). Y-intercepts significantly greater than 0 give an indication of the relative differences in habitat suitability perceived by consumers (Morris 1987a, 1987b, 1988).

Following the procedure for isodar analysis outlined by Morris (1987a, 1988), correlation analysis implied both habitats 5 and 6 were more preferred than habitat 7, based on the isodar values, since the y-intercepts (constant) were greater than 0. Habitat 5 was seven times more suitable than habitat 6. The slope between habitats 5 and 7, and habitats 6 and 7 did not significantly differ from 1, therefore these habitats are considered to differ quantitatively.

Quantitative differences in habitat typically reflect food availability and productivity, whereas qualitative differences typically reflect risk of predation. From the habitat suitability model the components of habitat suitability for springbok that reflect these

quantitative differences are the percent cover of forbs and herbs, *B. albitrunca*, and *A. mellifera*.

Conclusion

It is possible to show that springbok show preferences in their habitat use that can be described using habitat suitability models. Isodar analysis can be used in conjunction with habitat suitability models to further increase our understanding of qualitative and quantitative differences in habitat use. Analysing patterns of abundance in adjacent habitats can reduce the risk of being mislead by density estimates alone in assessing habitat suitability.

This approach, which provides a useful way of furthering our understanding of the ecology of springbok, can be applied to other species.

Chapter 4

Behaviour of springbok varies across the landscape

Introduction

Habitats and patches often vary both in terms of foraging profitability and predation risk (Lima & Dill 1990). The primary 'goal' of any optimal forager is to maximise its reproductive fitness, which means being able to respond to the relative costs and benefits associated with foraging in a particular habitat (Ramp & Coulson 2002). If the best areas for foraging have the highest predation risk, the forager trades off energy gain against predation risk in deciding where to feed (Lima & Dill 1990). Animals therefore trade off the needs for food and safety when under the risk of predation. Some studies emphasise predation risk as the prime determinant in habitat and patch use trade-offs (Stein & Magnuson 1976; Sih 1982; Mittelbach 1984; Caldwell 1986; Fraser & Huntingford 1986; Ferguson *et al.* 1988; Repasky 1996; Kotler & Brown 1999), while others report that habitat choice is determined by profitability of foraging in a specific area (Storch 1993). Optimal behaviour, however, lies on a continuum between energy maximisation, at the expense of predator avoidance, and risk minimisation, at the expense of feeding (Lima & Dill 1990).

The ways in which individuals actively respond to the presence of predators include reducing activity or shifting activity to safer habitats (Sih 1980; Werner *et al.* 1983). Such non-lethal effects of predators on their prey may be more important than the actual killing of prey by predators (Kotler & Holt 1989). Other non-lethal effects of predators include influencing prey behaviour, intraspecific interactions, competitive interactions (Persson 1991), and interactions between the prey and its food (Abrams 1984, 1989).

Predator avoidance and food distribution patterns are the main forces that lead to sociality and the formation of groups (Hamilton 1971; Jennings & Evans 1980; Dehn 1990). Predation has long been implicated as a major selective force in the evolution of many patterns of sociality, such as colonial breeding, social mating systems, social structures, flocking and roosting (Crook 1965; Pulliam & Caraco 1984; Pitcher 1986).

Vigilance for predators as a social phenomenon is one of the most studied aspects of behaviour under the risk of predation. This has been demonstrated in mammals (Lipetz & Bekoff 1982; Risenhoover & Bailey 1985; Dehn 1986) and birds (e.g. Kenward 1978; Creswell 1994). The common observation is that individuals in a foraging group spend less time being vigilant with an increase in group size (Lipetz & Bekoff 1982; Risenhoover & Bailey 1985; Dehn 1986). The trade-off commonly thought to underlie the "group size effect" is straightforward: the act of being vigilant detracts from energy intake; thus, a change in any factor that lessens the need to be vigilant should lead to a decrease in vigilance (Lima & Dill 1990). There is an intuitive appeal to greater safety in numbers, but the precise benefit of being in a larger group is not always clear (Lima & Dill 1990). The general effect of group size on vigilance could be due to a detection effect: with many animals, predators can be spotted even if each individual looks around less; a dilution effect: if a predator attacks, the probability that it will kill a particular individual is lower; or animals in a group may practice group defence; or a combination of these effects (see Dehn 1990).

There are, however, some problems with being in a larger group, including competition for readily depletable food and the benefit of being the first to detect and/or respond to an attack (Lima & Dill 1990). Also, bigger groups are easier for the predator to detect, and the heightened rate of attacks by predators may more than offset the other benefits of being in a larger group (B.P. Kotler, pers. comm.[1]). Inglis & Lazarus (1981) suggest that the decrease in vigilance may be due to the fact that the highly vigilant individuals on the edge of the group comprise a smaller proportion of the group as its size increases. Dehn (1986) suggests that "false alarms" are a major factor in determining vigilance. Other problems with the group size effect include the object of vigilance (Knight & Knight 1986) and evolutionary stability in vigilance patterns. To make matters more complicated, some animals may reduce group size under an increased risk of predation (Caldwell 1986).

Caraco (1979b) found that group size increases with a decrease in both temperature and food abundance. Group size also increases with the distance to cover and in the presence of a potential predator (Caraco *et al*. 1980a, 1980b). After explicitly

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considering several aspects of predation risk, Caraco (1979a) developed an argument that patterns reflect the outcome of energy and predation risk-dependent decisions made both by dominant individuals (attempting to control group size) and subordinate individuals (deciding whether to remain in a group given the behaviour of the more dominant individuals).

Group composition has been shown to be an important factor in vigilance (Metcalfe 1984; Hogstad 1988). In most ungulate species, the sexes form separate groups that are spatially segregated for most of the year and come together primarily to mate (Main & Coblentz 1990; Main *et al.* 1996). Sexual segregation is a basic component of the social organisation of ungulates (Ruckstuhl1988). Several hypotheses have been proposed to explain this phenomenon, although the evolution and adaptive advantages are poorly understood (Ruckstuhl 1988).

Main *et al.* (1996) classified these hypotheses into three groups

1) sexual differences in how reproductive strategies affect the risk of predation and consequently predator avoidance strategies (reproductive strategy hypothesis: Geist 1971; Festa-Bianchet 1988; Berger 1991; Young & Isbell 1991; Bleich *et al.* 1997).

2) social factors, such as interactions with a preference for same-sex peers, and learning fighting skills (social hypothesis: Clutton-Brock *et al.* 1987).

3) sexual-specific differences in energy requirements and digestive characteristics of their guts and therefore foraging behaviour, choice of habitat types and diet (sexual dimorphism-body-size hypothesis: Shank 1982; Seip 1983; Clutton-Brock *et al.* 1987; Harris & Miller 1995; Main *et al.* 1996).

Springbok behaviour

Population size, food availability, and day length (Davies & Skinner 1986b) influence the daily activities of springbok. As high-quality food becomes scarcer springbok spend a greater proportion of their time feeding (Davies & Skinner 1986a). Springbok exhibit alternating peaks of feeding and ruminating throughout the day, with feeding peaks in the early morning and early evening (Davies & Skinner 1986b). A feeding peak at mid-day is indicative of environmental stress (Novellie, 1975). See Chapter 2 for a detailed description of springbok behaviour.

It is hypothesised that springbok behaviour will not be random across the landscape, but rather will change according to the foraging and predation risk characteristics of the habitat, the magnitude and direction of which will depend on social and individual factors. Therefore, the objectives of this study were:

1. to identify proximate environmental features to which springbok are responsive;

2. to differentiate social factors which influence the response of springbok to environmental features;

3. to distinguish age and sex related differences in response of springbok to environmental features;

4. to develop behaviour models using MANOVA to account for the variation in springbok behaviour across habitats; and

5. to relate the component variables of these models to the biology of springbok so as to develop our understanding of their ecology.

Methods

To evaluate the perception of the environment by springbok using behaviours that are easy to see, and thereby establish an indicator of habitat suitability for this species can be achieved using three observable tools;

  1. activity patterns
  2. habitat choice
  3. group size.

This can be best achieved using focal animal sampling.

Focal samples are best done on a single individual for a predetermined length of time (Altmann 1973). I performed continuous focal observations for a minimum of 2 minutes and a maximum of 10 minutes on selected individuals. In order not to influence the behaviour of the animals, I performed the focals from a distance greater than 100 m using binoculars. I recorded the date and time of the observation, the age and sex of the selected focal individual, my GPS location and the distance and bearing to the animal. If the individual was in a group, I recorded the number of individuals present, divided into the following categories: adult males, adult females, subadults, and juveniles. I recorded the category of group the focal individual was in. These were:

1) territorial males - lone adult males,

2) bachelor herds - groups consisting of adult and subadult males,

3) mixed herds - groups consisting of females, subadults, juveniles, and one or more
   males,

4) nursery herds - groups consisting of females, subadults, and juveniles (no adult
   males present).

For the focal animal (selected *a priori* to satisfy the requirements for coverage of all sex and age classes), I noted the activity that the animal was engaged in at the start of the observation period and recorded the length of time spent in different activities. Activities were divided into five categories, defined as:

Feeding - foraging in head down position or foraging with head in a bush,

Vigilant - head up, neck erect,

Moving - walking - trotting, running, 'stotting' or 'pronking',

Grooming - apparent attempts by an individual to remove parasites from its body,

Other - lying down, territorial marking, defecating or urinating.

If the animal moved out of sight, I recorded the amount of time for which it could not be seen and deducted this from the total time for the focal observation. Using the total time for the focal observation and the time spent in each activity, I was able to determine the proportion of time the animal spent in each separate activity. I square-root transformed the data for further analysis. These data were collected over the period of October 2002 - November 2003, and were only collected during daylight hours (hence these results refer only to the diurnal).

I determined the location of the springbok for each focal observation using equations 3.1 and 3.2.

I captured these location data into a table and imported it into the geographical information system (GIS) program ArcView®. I overlayed these locations onto the recoded vegetation map of AFNP (obtained from South African National Parks) to reflect the habitat codes for the different vegetation communities (see Chapter 3).

I determined the habitat at the location of each springbok focal observation by performing a spatial join of the habitat data and the location data. I then exported this information into Excel for further analysis. For each focal observation, I included the habitat data for those variables included in the habitat suitability model, in the order they were entered into the model (moisture status, cover of forbs and herbs, percent cover of sand, percent cover of boulders, cover of *Boscia albitrunca*, cover of *Acacia mellifera*, and percent cover of stones; see Chapter 3). I entered the data collected at the focal observation and the square-root transformed data for the proportion of time spent feeding, moving, vigilant, and grooming.

I used a Multivariate Analysis of Variance (MANOVA) to define the relationship between habitat variables and springbok behaviour. Because I had both fixed factors and covariates, I specified a model to include interactions between these terms. I used a model with the general form:

> (Proportion of time feeding, vigilant, moving grooming) = HSI variables + group size + group type + proportion of adults + age (of focal individual) + sex (of focal individual) + substrate + vegetation type + (substrate × vegetation type)

I did not include the proportion of time spent in other activities so that the dependent variables did not sum to 100% in order to preserve the degrees of freedom. I used Type IV Sum of Squares in the analysis since the data had missing cells. In order to determine differences among the levels of a factor, I used a difference contrast and Bonferroni confidence interval adjustment for each factor. I used Box's and Levene's tests to test the equality of covariance matrices and error variances respectively. I tested the dependent variables and the standardised residuals for normality using a Kolmogorov-Smirnov test. I performed a lack of fit test to determine if the model adequately accounted for the relationship among the dependent variables and the predictors. The model did not perform well due to multicollinearity of some of the variables. Removing the redundant variables resulted in a model that appropriately fitted the data.

I used linear regressions to generate response curves which defined the relationship among environmental parameters (HSI variables) and animal behaviour, box and whisker plots which defined the relationship between social (group size, group type, and proportion of adults) and individual (age and sex of focal individual) parameters and animal behaviour, and an equation which defined the relationship among the response curves and between response curves and animal behaviour. Although not represented in the box plots, outliers and extremes were used in the analysis as it was not obvious if these were the result of observer error, error in recording, miscalculation or atypical behaviour on the part of the study animal (Gutzwiller & Anderson 1986; Morrison *et al.* 1992).

I determined the proportion of adult males and females by dividing the number of individuals of each sex category by the total number of adults at the focal observation. Because the data were not normally distributed, I used a Wilcoxon signed-rank test to determine if the adult sex ratio differed across habitats.

Results

Based on 117 focal observation periods, springbok spent most of the time feeding ($38.8 \pm 3.1\%$). The next most important activity was being vigilant, which occupied $30.9 \pm 2.8\%$ of the time. They moved $23.0 \pm 2.1\%$ of the time and devoted significantly less (Chi Square: $?^2_{0.05,116} = 109.54$; $P < 0.001$) time to grooming ($2.8 \pm 0.5\%$) and other activities ($7.6 \pm 2.1\%$) (Fig. 4.1).

The regression model for the between-subject effects of the behaviour (Table 4.1) significantly accounts for the proportion of time feeding and vigilant, as seen by the low significance and high R Squared values. The models (Figs 4.2 - 4.5) account for only ~ 20% of the variability in the proportion of time moving and vigilant.

None of the variables considered had a significant influence on the behaviour of springbok, except the presence of breeding herds and subadults. Breeding herds significantly influenced the time spent feeding (MANOVA: $F_{0.05,1} = 4.82$; $P = 0.03$) as did subadults (MANOVA: $F_{0.05,1} = 4.64$; $P = 0.04$).
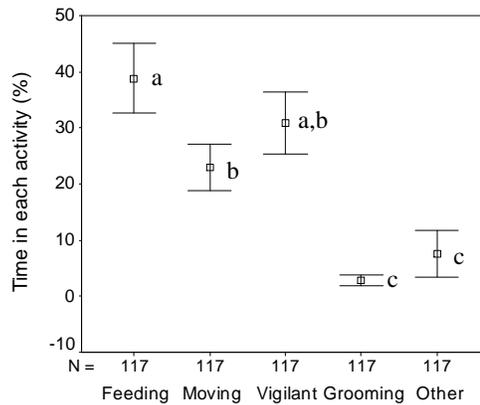
Figure 4.1: The proportion of time springbok spent in each activity (mean ± 95% confidence intervals). N = the number of individuals included in the analysis. Springbok spent approximately half of their time feeding. Blocks labelled with different letters differed significantly.

Table 4.1: Summary of regression statistics for the between-subject effects of the springbok behaviour models. The model significantly accounts for the proportion of time feeding and vigilant but not for the proportion of time moving or grooming.

Dependent Variable	Type IV Sum of Squares	df	R Squared	F	Sig.
Proportion of time feeding	3.06	12	0.42	2.84	0.01
Proportion of time moving	0.84	12	0.21	1.04	0.43
Proportion of time vigilant	1.92	12	0.36	2.25	0.02
Proportion of time grooming	0.16	12	0.21	1.03	0.44

The habitat variables do not appear to have as great an influence on the proportion of time feeding and vigilant as group size and the proportion of adults (Fig. 4.2 and Fig. 4.3), as seen by the slope of the line in the response curves. However, the habitat variables appear to have a greater influence on the proportion of time moving than group size and the proportion of adults (Fig. 4.4). In contrast, the habitat variables, group size and the proportion of adults appear to influence the proportion of time spent grooming to the same extent (Fig. 4.5). Group size, age and sex appeared to have a greater influence on the proportion of time feeding and vigilant than on the proportion of time moving or grooming, as seen by the greater degree of overlap of the error bars for these variables for the latter two behaviours (Figs 4.2 - 4.5).

Var. 1

Var. 2

Var. 3

Var. 4

Var. 5

Var. 6

Var. 7

Var. 8

Var. 9

Proportion of time feeding

Aerial cover of forbs and herbs

% Sand

% Boulders

Cover of *Boscia albitrunca*

Proportion of adults in a group

N = 58 Female 46 Male

N = 15 Territorial 18 Bachelor 46 Mixed 34 Nursery

N = 29 Subadult 85 Adult

Proportion of time feeding = 1.0787 + (0.0420 × Var. 1) + (0.0059 × Var. 2) + (0.0471 × Var. 3) – (0.0003 × Var. 4) – (0.0002 × Var. 5) + [0.1950 × (Var. 6 = Territorial male)] + [0.4092 × (Var. 6 = Bachelor herd)] + [0.5221 × (Var. 6 = Mixed herd)] + [0.7605 × (Var. 6 = Breeding herd)]* + (0.3360 × Var. 7) - [0.3172 × (Var. 8 = Adult)]* - [0.1578 × (Var. 9 = Male)]

Figure 4.2: A model for the feeding behaviour of springbok in Augrabies Falls National Park. Factors whose coefficients differ significantly are marked with an asterisk.
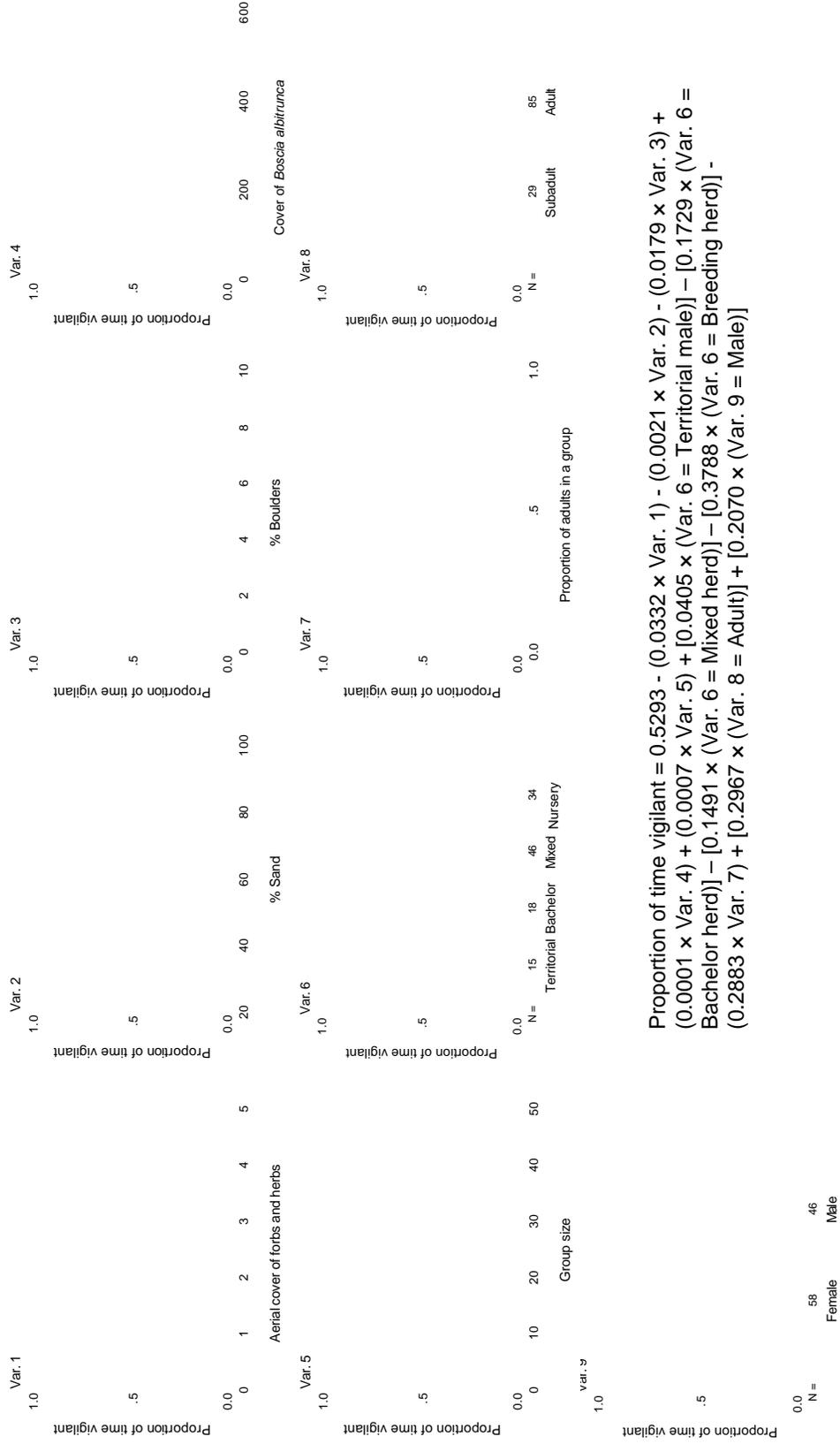
Figure 4.3: A model for the vigilance behaviour of springbok in Augrabies Falls National Park.

Proportion of time vigilant = 0.5293 - (0.0332 × Var. 1) - (0.0021 × Var. 2) - (0.0179 × Var. 3) + (0.0001 × Var. 4) + (0.0007 × Var. 5) + [0.0405 × (Var. 6 = Territorial male)] – [0.1729 × (Var. 6 = Bachelor herd)] – [0.1491 × (Var. 6 = Mixed herd)] – [0.3788 × (Var. 6 = Breeding herd)] - (0.2883 × Var. 7) + [0.2967 × (Var. 8 = Adult)] + [0.2070 × (Var. 9 = Male)]

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Var. 4

Cover of *Boscia albitrunca*

Var. 8

Var. 3

% Boulders

Var. 7

Proportion of adults in a group

Var. 2

% Sand

Var. 6

Var. 1

Aerial cover of forbs and herbs

Group size

Var. 5

Proportion of time moving

N = 15 18 46 34

Territorial Bachelor Mixed Nursery

N = 29 85

Subadult Adult

N = 58 46

Female Male

Proportion of time moving = -0.1223 - (0.0067 × Var. 1) - (0.0106 × Var. 2)* - (0.0751 × Var. 3) + (0.0006 × Var. 4) + (0.0012 × Var. 5) - [0.4525 × (Var. 6 = Territorial male)] – [0.4584 × (Var. 6 = Bachelor herd)] – [0.3820 × (Var. 6 = Mixed herd)] – [0.3916 × (Var. 6 = Breeding herd)] - (0.0019 × Var. 7) + [0.0818 × (Var. 8 = Adult)] + [0.0793 × (Var. 9 = Male)]

Figure 4.4: A model for the moving behaviour of springbok in Augrabies Falls National Park. Factors whose coefficients differ significantly are marked with an asterisk.

Proportion of time grooming = -0.6765 - (0.0046 × Var. 1) + (0.0005 × Var. 2) + (0.0077 × Var. 3) + (0.0001 × Var. 4) + (0.0036 × Var. 5) - [0.2331 × (Var. 6 = Territorial male)] – [0.2559 × (Var. 6 = Bachelor herd)] – [0.2370 × (Var. 6 = Mixed herd)] – [0.2429 × (Var. 6 = Breeding herd)] - (0.0677 × Var. 7) + [0.0230 × (Var. 8 = Adult)] + [0.0216 × (Var. 9 = Male)]
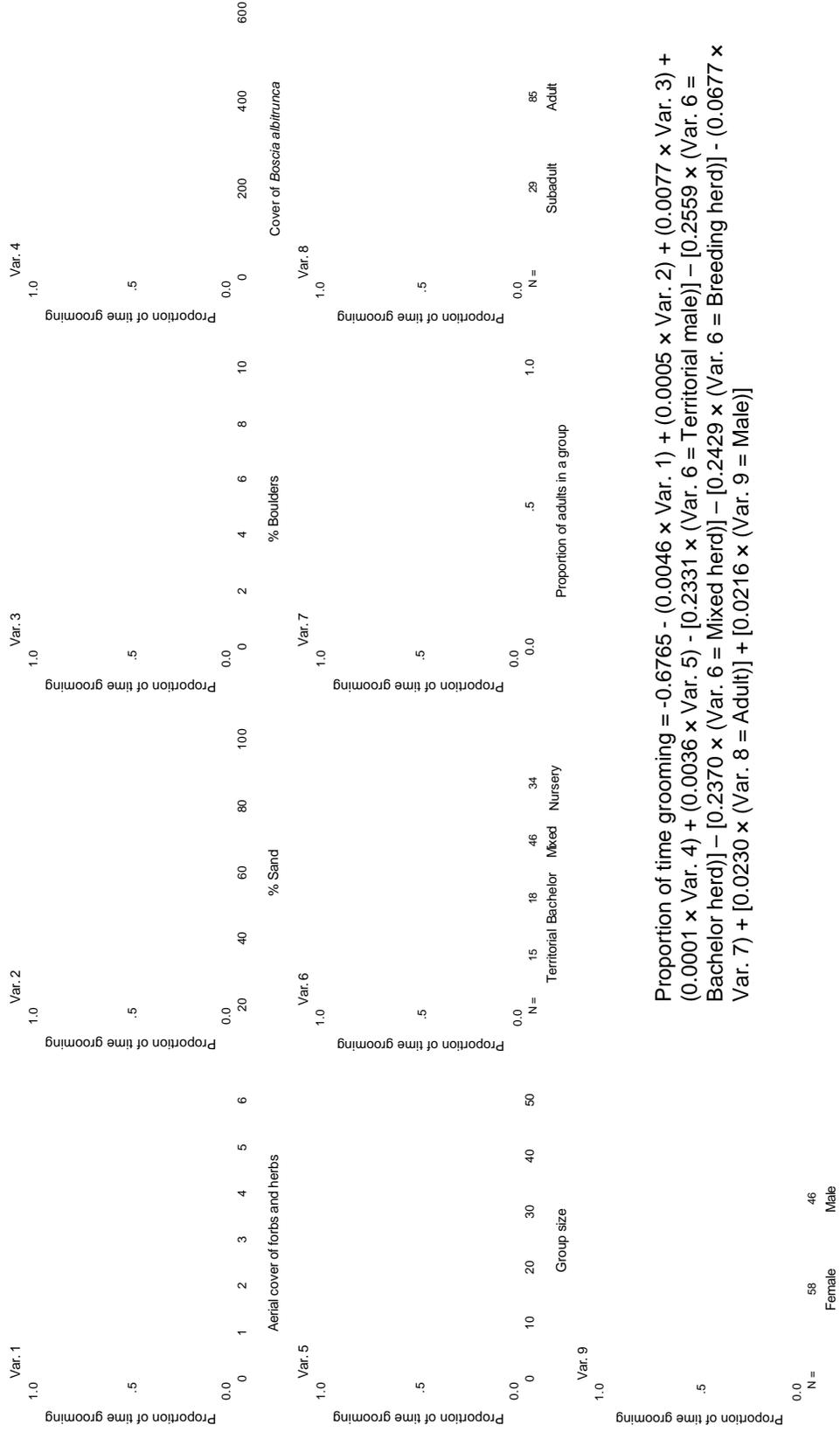
Figure 4.5: A model for the grooming behaviour of springbok in Augrabies Falls National Park

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To further analyse this apparent trend in the data, I compared the influence of habitat, group type, and the interaction between habitat and group type on the activity of springbok using a MANOVA. I was looking for trends in the data and therefore I used the broader categories rather than more specific habitat and group variables. Habitat was found not to have an overall significant effect on springbok behaviour (MANOVA: $F_{0.05,20} = 1.28$; $P = 0.19$). Multiple comparisons of behaviour across habitats using Tukey's HSD showed that the only behaviour that was significantly influenced by habitat was the proportion of time moving. Table 4.2 shows the homogeneous subsets for the proportion of time moving in the different habitats. These results indicate that springbok spend significantly more time moving in habitat 9 than in habitats 10, 5, 6 and 7. The proportion of time moving in habitat 4 is not significantly different from either subset.

Table 4.2: Homogeneous subsets for the proportion of time moving in different habitats. In the subset columns, the subsets of means not significantly different from one another are displayed in the same column. The groups are ordered by the size of their means. Springbok spend significantly more time moving in habitat 9 than in habitats 10, 5, 6 and 7.

Habitat	N	Subset 1	Subset 2
10	5	0.24	
5	28	0.36	
6	29	0.38	
7	36	0.41	
4	11	0.55	0.55
9	4		0.76
Sig.		0.06	0.33

There was an interaction between habitat and group type (Fig. 4.6), however, this interaction did not significantly influence springbok behaviour (MANOVA: $F_{0.05,44} = 1.04$; $P = 0.41$). Group type, on the other hand, did have a significant influence on springbok behaviour (MANOVA: $F_{0.05,12} = 1.94$; $P = 0.03$). Group type had a significant influence on both the proportion of time feeding (ANOVA: $F_{0.05,3} = 5.14$; $P = 0.002$) and the proportion of time vigilant (ANOVA: $F_{0.05,3} = 4.52$; $P = 0.005$). Multiple comparisons using Tukey's HSD identified which group types differed in the proportion of time feeding and

vigilant. Table 4.3 shows the homogeneous subsets for these behaviours for the different group types. These results indicate that territorial males spend significantly more time vigilant and subsequently less time feeding than individuals in nursery herds. As the proportion of adult males in a group increases from nursery herds (where there are no males) to territorial males (only males), the proportion of time vigilant increases and time feeding decreases. The increased vigilance in territorial males may be directed toward other males as well as predators. Thus social factors (competition) may be an important additional vigilance cost to males.
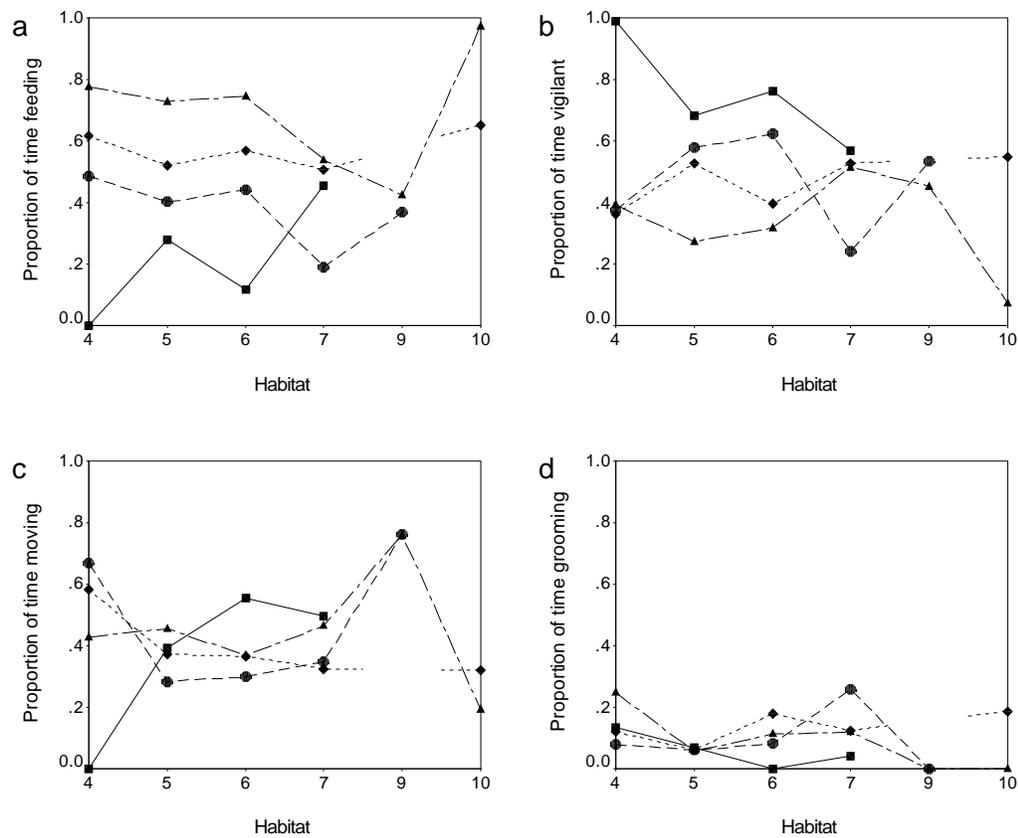
**Figure 4.6:** Profile plots showing the interaction between group type and habitat. None of the lines in the profile plots are parallel, indicating that there is an interaction between group type and habitat. I show the estimated marginal means for the proportion of time **a)** feeding, **b)** vigilant, **c)** moving and **d)** grooming. Territorial male = ──■── ; Bachelor herd = ─ ● ─ ; Mixed herd = ···◆··· ; Nursery herd = ─ ·▲ ·─.

Table 4.3: Homogeneous subsets for the proportion of time feeding and vigilant for the different group types. In the subset columns the subsets of means not significantly different from one another are displayed in the same column. The groups are ordered by the size of their means. Territorial males spend significantly more time vigilant and subsequently less time feeding than individuals in nursery herds.

Group Type	N	Proportion of time feeding Subset 1	Proportion of time feeding Subset 2	Group Type	N	Proportion of time vigilant Subset 1	Proportion of time vigilant Subset 2
Territorial male	15	0.31		Nursery herd	34	0.38	
Bachelor herd	18	0.41	0.41	Mixed herd	46	0.47	0.47
Mixed herd	46	0.55	0.55	Bachelor herd	18	0.52	0.52
Nursery herd	34		0.66	Territorial male	15		0.67
Sig.		0.07	0.06	Sig.		0.33	0.07

The significant difference in behaviour between territorial males and nursery herds may be an artefact of group size since the territorial males only occur alone whereas the mean nursery herd size consisted of 15 (minimum: 2, maximum: 29) springbok. However, the proportion of time vigilant was not significantly different between territorial males and mixed herds (mean: 23.0, minimum: 2, maximum 48 springbok), whose group size was greater than that of nursery herds. The difference between nursery herds and mixed herds is that there are no adult males in nursery herds, whereas there may be one or more adult males associated with a mixed herd. Therefore sex appears to be the major factor influencing the proportion of time vigilant and feeding.

I removed the subadults from the analysis and considered the effect of sex and group size and the interaction between sex and group size on the behaviour of only the adult springbok. Group size had no significant influence on behaviour (MANOVA: $F_{0.05,4} = 0.83$; $P = 0.51$) and nor did the interaction of group size and sex (MANOVA: $F_{0.05,4} = 1.82$; $P = 0.13$). Sex, however, did have a significant influence on behaviour (MANOVA: $F_{0.05,4} = 2.84$; $P = 0.03$), with females feeding more than males (MANOVA: $F_{0.05,1} = 7.19$; $P = 0.01$), and males more vigilant than females (MANOVA $F_{0.05,1} = 9.75$; $P = 0.002$) (Fig. 4.7).
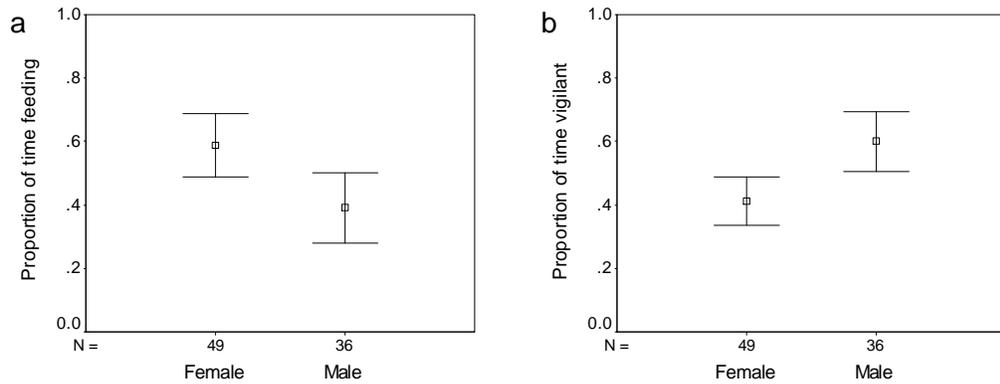
Figure 4.7: Sex differences in the proportion of time spent in different activities (mean ± 95% confidence intervals). N = the number of individuals included in the analysis. Males spent **a)** less time feeding and **b)** more time vigilant than females.

The adult sex ratio differed among habitats (Wilcoxon signed ranks test; $Z_{1,97}$ = -8.62; $P < 0.001$). Habitats 6 and 10 had a greater proportion of adult females than males while habitat 5 had a greater proportion of adult males (Fig. 4.8). Habitats 4 and 9 had almost equal proportions of adult males and adult females (Fig. 4.8).
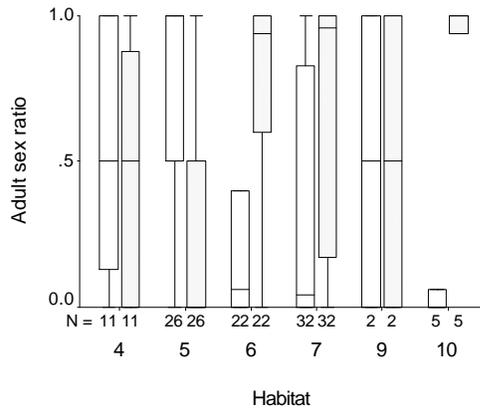
**Figure 4.8:** Sex ratio differences in habitat use. There was a significant difference in the adult sex ratio among habitats. The box plots showed the median, the first and third quartiles and the range of the data, excluding extremes and outliers. Shaded boxes represent the proportion of adult females while unshaded boxes represent the proportion of adult males in each habitat. N = the sample size.

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Discussion

As in other studies (Davies & Skinner 1986), springbok spent more time foraging than any other activity. This is not surprising since the survival of any individual depends on the acquisition of enough food to fuel metabolism (Calder 1983). A wide array of life-history characteristics such as territory, distribution, and population dynamics are directly or indirectly related to the ability of an individual to acquire adequate amounts of food (Calder 1983).

As predicted, an increase in the aerial cover of forbs and herbs results in an increase in the proportion of time feeding. This is not surprising since forbs and herbs are an excellent source of feed for springbok while they are green (Leistner 1967). There is also an increase in the proportion of time moving which may be related to obtaining more food items or moving to non-depleted patches. In contrast to this, the proportion of time feeding decreased, while the proportion of time vigilant and moving increased with an increase in the cover of *Boscia albitrunca*, a highly palatable and nutritious plant species. Springbok have been found to be more vigilant when approaching tree clumps, related to an increase in the risk of predation in these areas (Bednekoff & Ritter 1994), such that the risk of predation may outweigh the nutritional advantages of feeding on such a plant species. Underwood (1982) also found that African antelopes avoid cover that might obscure or harbour predators; for these animals, cover is not a refuge but a source of risk. As predicted, increasing the percent of boulders resulted in less time feeding. Springbok may prefer open areas away from boulders in order to lower the risk of being taken by ambush predators such as leopards (Bednekoff & Ritter 1994) and the decreased feeding (and hence more time vigilant) may be due to increased risk of predation in areas with greater cover of boulders. As predicted, increasing percent of sand ground cover led to a reduction in the proportion of time vigilant and moving Escape substrate refers to the substrate within which a food patch is found and across which a forager must flee to escape or avoid predators (Kotler & Brown 1999), and may influence the ability of a foraging animal to detect and/or evade predators (Kotler *et al*. 2001). This may influence where an animal feeds since the ability of an animal to escape predation is important in determining feeding-

site selection (Schneider 1984; Eckman 1987). Sand may be a good escape substrate for springbok which may result in a decreased risk of predation due to an increase in their ability to avoid or detect predators, and which may account for more time spent feeding and grooming and less time spent moving or vigilant in sandy areas.

As predicted, the proportion of time feeding increased as group size increased. Females spent a greater proportion of their time feeding than males. This can also be seen in the effect of group type - as increasingly more females are added to a group, from territorial males to nursery herds, the greater the proportion of time feeding and the less the proportion of time vigilant. Siegfried (1980) found that the percentage of springbok foraging with their heads down increased as group size increased, although in groups larger than 25 feeding time decreased. He concluded that group sizes of about 20 animals may be optimal for anti-predator vigilance without negatively affecting feeding rates. These observations extended over only four days, and in the long term the factors influencing group size may involve more complex factors such as the availability of food and reproductive status of the animals (Skinner & Louw 1996). In contrast to this, Bednekoff & Ritter (1994) found group size effects even in large springbok herds.

Contrary to predictions, vigilance increased with increasing group size. Males spent a greater proportion of the time vigilant than females. The increased vigilance with group size may be due to males in the larger mixed herds being vigilant for other males rather than for predators, and therefore not gaining any benefit from being in a larger group.

Also, in contrast to Bednekoff & Ritter (1994), territorial males spent significantly more time vigilant than females in nursery herds. Territorial rams do not respond as sensitively as females and non-territorial males to environmental change, and as a result are exposed to greater environmental risks (Crowe & Liversidge 1977; Jackson *et al*. 1993). They feed less efficiently than non-territorial animals, particularly during the rut when increased physical

activity aggravates this disadvantage (Jackson 1995). In addition to the nutritional stress imposed by territoriality, solitary males are more isolated and more vulnerable to predation, which may be a factor in the greater mortality among these males (Jackson 1995).

Springbok moved more when in larger groups. This may be in order for mothers to find food to meet the nutritional requirements of juveniles and subadults. It may also be due to depletion of food stocks associated with large numbers of feeding animals, since the animals must spend more time on feeding which will favour an increase in group size, because of a reduction in time spent on vigilance (Siegfried 1980). Further depletion of food stocks will contribute to an increase in the distance travelled by animals in searching for food. This should lead to further increases in group size if springbok in large herds can avoid revisiting places where they have recently fed, whereas smaller groups foraging independently may expend energy and time covering ground denuded by previous foragers (Siegfried 1980).

Age and sex also played a role in the behaviour of springbok. As predicted, adults were more vigilant than subadults. These results were similar to those of Bednekoff & Ritter (1994) who found juveniles slightly less vigilant than adults, although they concluded that this may reflect greater movement. In contrast, adults spent more time moving than subadults.

Apart from protection against predators (Duncan & Vigne 1979), and an enhanced feeding rate, there are certainly other benefits attending grouping such as courtship and mate selection (Siegfried 1980). In practice, there are many different and changing pressures, involving ecological factors and within-group interactions, operating to modify a social species' group size (Bertram 1978). Environmental factors, group factors, and individual factors all interact to influence the behaviour of springbok. Group type had a greater influence on the two main activities of springbok - feeding and vigilance - than either environmental or other group factors. Since group type is primarily defined by the presence (and absence) of adult individuals of both sexes, the age and sex of

the individuals within a group are the most important factors in determining the behaviour of springbok.

Habitat did not influence the feeding and vigilance behaviour of springbok. However, springbok spent significantly more time moving in habitat 9 than in the other habitats, except habitat 4. Habitat 9 also had an almost equal male:female ratio. This suggests, based on the data, that this habitat may provide a relatively safe corridor between habitats, that is utilised to the same extent by both sexes for movement into other habitats where foraging occurs.

Conclusion

It is possible to show that springbok behaviour is related to foraging opportunities and predation risk characteristics of the habitat which can be described by behaviour models. Social factors and age and sex related differences that influence this response can be built into the models, thus generating a more realistic output that reflects a range of factors influencing springbok behaviour.

Springbok have been shown to display preferences in their habitat use that can be related to features of the environment (Chapter 3). The environmental factors influencing habitat suitability were built into the behaviour models. Using environmental factors it may be possible to identify the preferred habitat of springbok as being the place where opportunities are maximised and risks minimised based on a suite of environmental and behavioural factors acting together to influence the habitat choice of springbok.

Chapter 5

Patch and time specific habitat use by springbok revealed through an assessment of giving-up densities

Introduction

The way in which an animal perceives and uses its environment is central to studies of animal ecology (Johnson 1980). Since the environment in which an animal lives contains habitats that vary in quality both in terms of the costs and the benefits, the use of these habitats can influence an individual's ability to survive and reproduce (Melton 1987). The classification of habitats into discrete categories from which an animal chooses allows one to determine if the use of habitat is selective (Arthur, *et al.* 1996). This can include habitat use at various spatial scales. At a macro-habitat scale the selection of habitat may be influenced by factors such as substrate and vegetation type. At the smallest micro-habitat scale, factors such as the extent of cover within a patch may influence habitat selection.

Patch use refers to those circumstances in which a foraging individual can detect spatial aggregations of resources and bias its effort towards these (Brown 2000). At the macro-patch level the forager must alternate activities between searching for patches, harvesting resources from within patches and travelling between patches too poor in resources (Brown 2000). At the micro-patch scale, the forager must place bounds on aggregations of food and bias its effort toward the more favourable food patches (Brown & Mitchell 1989).

It has been shown the optimal patch use strategy is dependent on the distribution of resources (Iwasa *et al*. 1981). Most foragers can assess the quality of a patch to some level of accuracy and bias their efforts to those patches of greater quality (Brown 2000). Once foraging in a patch, the forager must decide at which point to stop harvesting from that patch and seek another (Brown 2000). The marginal value theorem provides one possible solution for when a forager can only exploit its current patch or travel to a new one, faces diminishing returns while exploiting a patch, and depletes the patch, but never

the environment (Charnov 1976). It states that a forager should continue foraging in a depletable food patch until the harvest rate in that patch no longer exceeds the average harvest rate expected should the forager travel to and exploit another patch. Optimal patch use may be generalised to consider situations in which the forager may be exposed to predation, may perform other fitness enhancing activities, and where the quality of the environment may become depleted during foraging (Gilliam & Fraser 1987; Brown 1988). An animal's fitness may increase with the energy gained from foraging and time spent in alternative activities, however, it may decline with exposure to predators while foraging (Brown 1988). An optimally foraging individual, therefore, should forage in a patch until its harvest rate (H) in the patch (i.e. benefits) is equal to the sum of the energetic costs of foraging (C), predation risk (P) and missed opportunity costs (MOC) (Brown 1988, 1992); i.e. until

$$H = C + P + MOC \tag{5.1}$$

In a heterogeneous environment, patches that are more risky should have a higher quitting harvest rate (i.e. the individual stops foraging in that patch sooner) than those that are safe (Sih 1980, Werner *et al.*1983; Abrahams & Dill 1989; Nonacs & Dill 1990). The ability of the animal to escape predation is also important in determining feeding-site selection (Schneider 1984; Ekman 1987). Escape substrate refers to the substrate within which the food patch is found and across which the forager must flee to escape or avoid predation (Kotler & Brown 1999). It may influence the ability of the foraging animal to detect and/or evade predators (Kotler *et al.* 2001). Predation risk could promote habitat selection if a species differs in which habitats are safest (Repasky 1996).

Using equation 5.1 and controlling for the harvest characteristics of the patch, the energetic costs of foraging and the missed opportunities cost (H, C and MOC respectively), it is possible to determine how a forager perceives its environment through the cost of predation. In order to control the harvest characteristics of the patch, the forager must be given access to a number of food patches of identical food quality and structure (Brown 1988). All patches must be placed in the same microclimate to control for the energetic costs of

foraging, and all foragers must have equal access to food patches in order to control for the missed opportunity cost (Brown 1988). This allows for the cost of predation to be revealed by variation in the quitting harvest rate between patches.

In most depletable food patches in which the forager experiences diminishing returns, the food left behind by a forager (its giving-up density; GUD) can be used as a substitute for its quitting harvest rate - the more risky an environment, the higher the giving-up density should be (Brown 2000). This is because the harvest rate is a function of resource density (Brown 2000). The GUD can be used to provide insight into both the state of the forager and the state of its environment (Whelan 1989, Astrom *et al*. 1990; Shipley *et al.* 1999). GUDs have been used to assess changes in habitat characteristics in an ungulate species (mule deer - *Odocoileus hemionus*) by Altendorf *et al.* (2001).

Springbok habitat use

As a mixed forager, springbok are able to adjust their diet, microhabitat, and foraging time to the highly variable quality of the forage in arid areas and can vary their habitat use and diet selection from selective to opportunistic (Hofmann *et al.* 1996). Springbok forage selectively (Davies & Skinner 1986a; Fairall *et al*. 1990; Cooper 1993; Liversidge & Gubb 1994), usually selecting a mixed diet and avoiding high-fibre diets, and are able to increase their food intake two- to three-fold when forage is plentiful (Hofmann 1989). Although springbok do feed on grass, they avoid patches of tall grass and it has a negative influence on their ease of movement in these areas (Bigalke 1972). Springbok foraging peaks after dawn and before dusk (Davies & Skinner 1986). Springbok avoid areas that could harbour ambush predators such as leopards, and prefer to forage in the open away from cover (Bednekoff & Ritter 1994).

It is hypothesised that springbok will alter temporal and spatial utilisation of their environment according to predation risk and foraging opportunities. Therefore, the objectives of this study were:

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1. to use foraging theory and giving-up densities to reveal information on the temporal and spatial utilisation of habitat by springbok;
2. to relate this information to the biology of springbok so as to develop our understanding of their ecology.

Methods

I conducted field experiments between May and November 2003. I measured giving-up densities (GUDs; the amount of food left behind by a forager when it leaves a resource patch (Brown 1988, 1992)) using artificial food patches consisting of plastic trays (0.5 x 0.4 x 0.1 m). I filled the trays with 4 l of dried, husked corn cobs to act as an inedible substrate, and strung four wires across the top (two wires running down the length and two wires running across the width) to prevent the springbok from removing the cobs from the trays (Fig 5.1). I provisioned the trays with 300 g of pellets comprised of alfalfa and corn (cylindrical in shape, 2 cm long and 0.5 cm in diameter, and weighing approximately 1 g each) which was mixed throughout the corn cob matrix (see Appendix 5 for the nutritional information of the pellets). The wires and the corn cob substrate ensured that springbok experience diminishing returns while exploiting the trays.

Figure 5.1: Giving-up density tray was a grape tray filled with 300 g of pellets and dried corn cobs and wired across the top.

I measured GUDs at 3 spatial scales relating to macro-, meso-, and micro-habitat use, using four sites that offered either sandy or rocky substrate (two in sandy and two in rocky substrates) located approximately 1 km apart (macro-habitat). These sites were randomly located throughout the study area. At each site, I located two stations, one in the drainage line (wash) and one on a nearby ridge (ridge). These stations were approximately 10 m apart (meso- habitat). At each station I placed two trays about 1 m apart, in the open (open) and under cover (bush) (micro- habitat). Note that these habitat scales are different to the habitats (vegetation types) used in Chapters 3 and 4.

Since more than one species fed from the trays, I identified the species using each patch based on the spoor left in the sand around the tray. In the rocky habitats, I spread 2 l of sand around the trays up to a distance of 0.5 m to facilitate the identification (from their tracks) of the species using the trays. I measured GUDs twice daily, checking the trays at sunrise and sunset. I attributed the GUD measured to the last species present at the patch (Brown *et al.* 1994). If the tray had been foraged, I sieved the remaining pellets from the tray and weighed them to determine the GUD. I then reprovisioned the tray with another 300g of pellets. I recorded the date, weight of the pellets remaining, time of day and species. If no foraging occurred, I also noted this. I used controls to determine if a species had been present, but did not feed out of the trays. These controls consisted of 300g of pellets placed in a tray with no corn cob substrate. Because the food was 'free,' I expected any herbivore species present at the patch to feed from them. When the control had been foraged, but not the food patch, I recorded the GUD of all the trays at the station as equalling 300g, and I identified the species from tracks in the sand around the control. Although GUDs were recorded from a range of species, including kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), eland (*Tragelaphus oryx*), Hartmann's mountain zebra (*Equus zebra hartmannae*), klipspringer (*Oreotragus oreotragus*) and porcupine (*Hystrix africaeaustralis*), I only included springbok GUDs in the analysis here.

As the GUD data were normally distributed (Kolmogorov-Smirnov test, $P >$ 0.05), I analysed the effect of time (night or day), substrate (sandy and rocky), position (ridge and wash) and cover (bush and open) and their interactions using an ANOVA. I made pairwise comparisons among the estimated marginal means of these factors and their interactions.

I took the GPS location at each pair of trays. This I inputted into ArcView® and determined the habitat (as defined in Chapter 3) at each pair of trays using a spatial join of the tray locations and the habitat map of the park. I incorporated this with the GUD data and used an ANOVA to analyse the risk of predation across habitats and a post-hoc Tukey's HSD test for the multiple comparisons of across habitats.

Results

The giving up density is significantly related to time of day, position, cover and the interaction of time and substrate, but not to the interaction of any of the factors except time and substrate (Table 5.1). The giving-up density was higher during the day (Fig. 5.2a), in the wash (Fig. 5.2b), and under the bush (Fig. 5.2c). The interaction between substrate and time was significant, with giving up-density tending to be higher during the day on the rocky substrate than either during the night or during the day on the sandy substrate (Table 5.1; Fig. 5.2d).

For springbok, habitats 8, 4 and 9 had significantly lower giving up densities than habitats 5, 6 and 7 (Fig. 5.3). These results indicate that habitats 8, 5 and 6 are significantly different from each other, with habitat 6 having the highest and habitat 8 having the lowest giving-up density. Habitats 4 and 9 are intermediate between habitats 8 and 5, and are not different from either of these habitats in their giving up density. The giving up-density in habitat 7 is intermediate between habitats 5 and 6 and does not differ significantly from either.

Table 5.1: The influence of spatial and temporal variation on the giving-up density, together with the outcomes of the ANOVA analysis of these various factors.

Factor	df	Mean Square	F	*P*
Time	1	68952.83	10.75	0.00
Substrate	1	15633.19	2.44	0.12
Position	1	29661.61	4.62	0.03
Cover	1	37957.11	5.92	0.02
Time x Substrate	1	25165.98	3.92	0.05
Time x Position	1	12621.73	1.97	0.16
Time x Cover	1	5816.40	0.91	0.34
Substrate x Position	1	132.96	0.02	0.89
Substrate x Cover	1	20.65	0.00	0.96
Position x Cover	1	89.26	0.01	0.91
Time x Substrate x Position	1	1248.87	0.20	0.66
Time x Substrate x Cover	1	187.76	0.03	0.86
Time x Position x Cover	1	607.74	0.10	0.76
Substrate x Position x Cover	1	660.95	0.10	0.75
Time x Substrate x Position x Cover	1	4460.15	0.70	0.41
Error	325	6415.78		
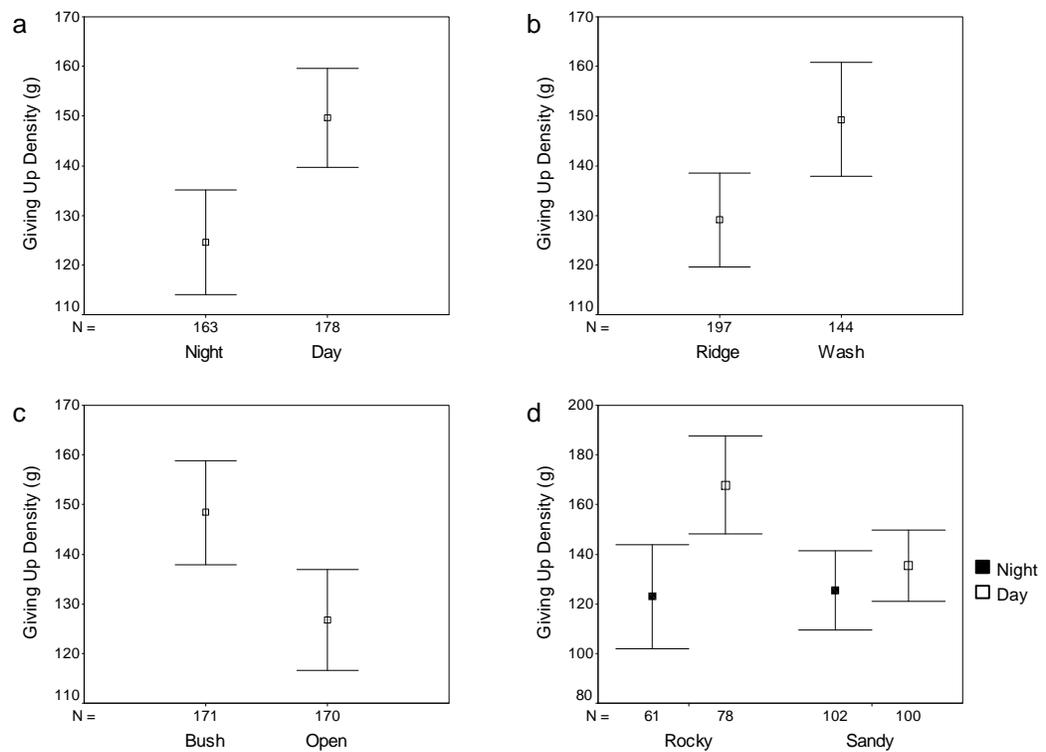
**Figure 5.2:** The effect of time, position, cover and the interaction of time and substrate on the giving up density (mean ± 95% confidence intervals). N = the sample size. The giving-up density was significantly higher **a)** during the day, **b)** in a wash, **c)** under the cover of a bush, and **d)** during the day on the rocky substrate (shaded boxes represent night while unshaded boxes represent day).
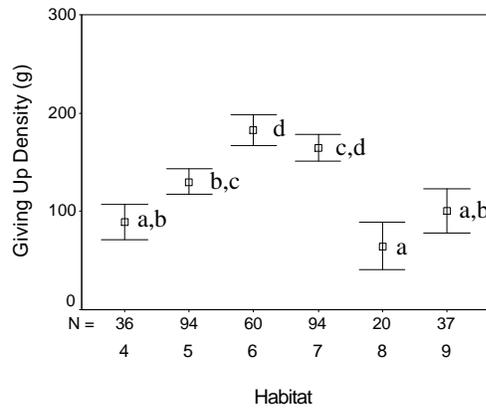
Figure 5.3: The giving up densities in the different habitats (mean ± 95% confidence intervals). N = the sample size. Means with different letters differ significantly according to a post-hoc Tukey's HSD test for multiple comparisons of across habitats.

Discussion

Springbok preferred feeding from the trays in the open, away from cover. They also preferred feeding from the trays on ridges (which are generally more open), than in drainage lines (which are more vegetated). This is in agreement with the published literature for springbok (Shortridge 1934; Leistner 1967; Bigalke 1972; Davies & Skinner 1986; Ritter & Bednekoff 1994) and supports the results obtained earlier that springbok prefer open areas (Chapter 3) and are more vigilant (and consequently feed less) in areas of increasing canopy cover (Chapter 4) in response to increasing predation risk. The effect of cover on GUDs has also been shown for rodents (Brown *et al.* 1988; Hughes & Ward 1993), crested larks (Kotler & Brown 1999), and mule deer (Altendorf *et al.* 2001).

Substrate interacted with time such that springbok fed less during the day than at night on the rocky substrate. Springbok also fed more on the sandy substrate, both during the day and at night, than on the rocky substrate during the day. This is in agreement with Bigalke (1972), who found that springbok avoid rocky areas, and supports the results obtained earlier that increasing cover of stones decreases the suitability of a habitat for springbok (Chapter 3), and increasing sand ground cover results in springbok spending less time vigilant and more time feeding (Chapter 4) in response to decreased predation risk on

sandy substrates. The effect of substrate on GUDs has also been shown for desert rodents (Hughes *et al*.1995; Kotler *et al*. 2001)

The risk of predation as revealed by springbok foraging behaviour is therefore less in the open, in areas away from drainage lines, and on sandy substrates. The actual drivers of this perceived change in predation risk cannot be revealed by the present data. It may, however, be hypothesised that this may be a function of changes in group size and increased vigilance in open habitat. Predation effects on GUDs have also been shown on rodents (Hughes & Ward 1993; Abramsky *et al.* 1996), porcupines (Brown & Alkon 1990), birds (Olsson *et al.* 2002), and deer (Altendorf *et al.* 2001).

The results show that springbok are more willing to feed more at night than during the day. This result is the first clear demonstration that springbok actively feed at night (Davies 1985; Bigalke 1972) and shows that nocturnal foraging is important in this species. As the air temperature cools at night and condensation occurs (Louw & Seely 1982; Nagy & Knight 1994), the pellets used in this study (which are highly hygroscopic and therefore efficient in absorbing atmospheric moisture) would be expected to absorb atmospheric moisture (Louw & Seely 1982). Thus, by feeding at night, the springbok would increase their water intake. Water effects on GUDs have been shown in Australian Ravens (Kotler *et al.* 1998), crested larks (J.S. Brown & B.P. Kotler, unpublished data), and Nubian ibex (Hochman & B.P. Kotler unpublished data) but not on nocturnal gerbils (B.P. Kotler pers. comm.[1]).

Differences among habitats may be due to different costs of predation, different energetic costs of foraging, different missed opportunity costs, and different marginal values of energy if foragers cannot easily pass from one habitat to the next (Kotler *et al.* 1994b). The giving up density is significantly lower in habitat 9 than habitats 5, 6 and 7. This is somewhat surprising since, based on the behavioural data, springbok spent significantly more time moving in habitat 9 than in other habitats, therefore habitat 9 was thought to be a corridor for

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[1] Prof. B.P. Kotler; Ben Gurion University of the Negev

movement to other habitats where foraging occurs (Chapter 4). One cannot dispute the amount of foraging measured directly in this habitat by the GUDs, therefore the deduction made based on the behavioural data must be incorrect, and the large amount of time spent moving in habitat 9 may rather be due to individuals moving between food patches while foraging. GUDs have been used to determine habitat preferences in a range of animals, including small rodents (Brown *et al*. 1992; Brown *et al*. 1994; Ziv *et al.* 1995; Brown *et al*. 1998; Kotler *et al*. 1998; Kotler & Brown 1999), birds (Olsson *et al.* 2002), squirrels (Schmidt *et* al. 1996), porcupine (Brown & Alkon 1990), and large herbivores such as mule deer and Nubian ibex (Kotler *et al.* 1994b; Altendorf *et al.* 2001).

Conclusion

GUD data uses one currency for patch preference assessment across space and time, and therefore provides an efficient and objective way to assess selective habitat use. From these results it can be seen that springbok vary their temporal and spatial utilisation so as to minimise their risk of predation and maximise their food intake.

Chapter 6

Concluding discussion

Habitat preferences

Springbok showed clear preferences in their habitat use. The density of springbok was greatest in open habitats of high food quality (habitats 4 and 5), and lowest in closed habitats (habitat 1). These preferences in habitat use can be described using habitat suitability models.

The habitat suitability model incorporates those variables that have the greatest correlation with springbok density in AFNP. Habitat suitability increased as the habitats varied from seasonally moist to occasionally moist/mostly dry, and then decreased as the habitats got drier still. Increases in the percent cover of forbs and herbs served to increase the habitat suitability. The percent cover of sand and boulders had a more complex interaction with habitat suitability, although the general trend was a negative interaction for sand and a positive interaction for boulders. Increasing canopy cover of *B. albitrunca* and *A. mellifera* had a positive interaction with habitat suitability. Finally, the percent of stones in the habitat had an overall negative influence on habitat suitability.

This model can be used for the management of springbok populations in AFNP. Habitats can be sampled to develop estimates of springbok population size. A shift of springbok into unpreferred habitats can be used as an indicator of changing habitat quality and this model can therefore be used to monitor resource availability and detect possible overstocking. During the course of the study two reintroductions of springbok occurred in the southern part of AFNP where more land is being bought, and future introductions of springbok are possible. The habitat suitability model can be used to consider the suitability of the habitat for springbok before such reintroductions occur and can be used to estimate the number of springbok to be introduced given the range of habitats present. In addition to this, the model can be used to decide in which habitat (i.e. lowest GUDs and highest densities) springbok should be released into the

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park, since this should occur in the areas most suitable for springbok to reduce the stress to the animals.

This model, however, needs to be tested in order to assess its applicability and general value. This model has not been evaluated against an independent data set either from a different time series, or from another area and population. Models need to be validated using experimental testing with independent data (Cook & Irwin 1985; Johnson *et al.* 1989) to determine if they incorporate appropriate habitat variables, and to assess their predictive capabilities (Irwin & Cook 1985). To test this model, and to fully understand its behaviour, more long-term data in additional locations should be collected, covering a range of habitats and with a wider range of environmental conditions (Pearce & Ferrier 2000). Regional rather than local data should be collected to improve the reliability of this model (Irwin & Cook 1985). This may require modification to perform adequately in other areas being evaluated (Cook & Irwin 1985l O'Neil *et al.* 1988).

Isodar analysis revealed information on the mechanisms underlying preference for habitats, and can be used in conjunction with habitat suitability models to further increase our understanding of differences in habitat use. Isodar analysis implied both habitats 5 and 6 were quantitatively more suitable than habitat 7. Quantitative differences in habitat typically reflect food availability and productivity, whereas qualitative differences typically reflect risk of predation. From the habitat suitability model, the components of habitat suitability for springbok that reflect these quantitative differences between habitats 5 and 7 and habitats 6 and 7 are the percent cover of forbs and herbs, *B. albitrunca*, and *A. mellifera*.

Behaviour across the landscape
Springbok spent the majority of their time foraging. Springbok devoted more time to being vigilant and moving than to either grooming or performing other activities. Habitat did not influence the feeding and vigilance behaviour of

springbok. However, springbok spent significantly more time moving in habitat 9 than in the other habitats. This habitat had an almost equal male:female ratio.

An increase in the aerial cover of forbs and herbs results in an increase in the proportion of time feeding and moving. In contrast to this, the proportion of time feeding decreased, while the proportion of time vigilant and moving increased with an increase in the cover of *Boscia albitrunca*. Increasing the percent of boulders resulted in less time feeding. Increasing percent of sand ground cover led to a reduction in the proportion of time vigilant and moving. Both the proportion of time feeding and vigilant increased as group size increased. Springbok also moved more when in larger groups. Females spent more time feeding than males and males spent more time vigilant than females. As increasingly more females are added to a group, from territorial males to nursery herds, the more time springbok spend feeding and the less time vigilant. Finally, adults were more vigilant and moved more than subadults.

Building the environmental factors from the habitat suitability model into the behavioural model makes it possible to identify the preferred habitat of springbok as being the place where opportunities are maximised and risks minimised based on environmental and behavioural factors acting together to influence the habitat choice of springbok.

This model can be used for the management of springbok populations in AFNP in that change in foraging and movement behaviours as well as group size can be used to monitor the condition of the vegetation. Changes in vigilance can be used to assess predator abundance and distribution, since and increase in the number of predators in an area would result in more vigilance in springbok while a decrease in predator numbers would have the opposite affect.

This model, as with the habitat suitability model, requires validation in order to assess its predictive capabilities (Cook & Irwin 1985; Johnson *et al.* 1989. Also, long term data from additional locations covering a range of habitats should be collected (Pearce & Ferrier 2000), and may require modification

through experimental manipulation to perform adequately in other areas being evaluated (Cook & Irwin 1985l O'Neil *et al.* 1988).

Patch and time specific habitat use

Springbok vary their temporal and spatial utilisation so as to minimise their risk of predation and maximise their food intake. Springbok showed lower GUDs more in the open, and at night on ridges. Springbok showed lowest GUDs in habitat 9 which contradicts the conclusion drawn from the behavioural data, that habitat 9 was a safe corridor for movement to other habitats, and therefore more foraging would occur in these habitats.

Changes in behaviour related to changes in the environment can be readily assessed as differences in the giving-up densities. Note, however, in the present study, that it was not possible to strictly control potential differences in missed opportunity costs (MOC) (these would be mating opportunities, distance to water, etc.). This assumption of constant MOCs needs to be further explored. The habitat characteristics around each set of foraging trays would need to be measured in order to more directly relate the giving-up density at that patch to the characteristics of the environment. It also facilitates understanding how GUDs change in relation to changes in the habitat.

Comparison of approaches

Habitat suitability model

The measurement of the habitat variables and the estimation of springbok density were time consuming, costly, and subject to observer bias. Building the model was a lengthy and complicated process involving complex statistical techniques. There are many assumptions about the distribution of the data, such as that they are normally distributed, the error terms are independent, and there is no multicollinearity of the variables. If these assumptions are not met, transformation of the data becomes necessary. Also, habitat suitability models are based on the assumption that density is an indicator of habitat suitability, which does not always hold true, especially in systems with territorial

individuals that may result in increased density of non-territorial subordinates in sub-optimal habitats (Melton 1987).

Behaviour model

Measuring springbok behaviour using focal animal sampling required many hours in the field to locate the animals, and observe them for a sufficient length of time and a sufficient number of different individuals. While an attempt was made to standardise the definition of different behaviours, the interpretation of behaviour varies among individuals and is therefore subject to observer bias. The habitat variables that were incorporated into the model were identified from the habitat suitability model. The data used in generating the behaviour models required transformations in order to meet the assumptions of the statistical techniques used to analyse them. Analysing the behavioural data were less time consuming than building the habitat suitability model.

Giving up densities

Habituating springbok to the feeding trays required initial effort. It took many months of leaving trays with food in the field before the springbok would feed from the trays, however, once they began the springbok fed reliably from the trays. Obtaining data from the springbok then became a relatively simple task which required driving to the trays in the morning and evening to assess if foraging had occurred, and to sieve and collect the remaining food and replenish the trays with more food if they had been foraged. Generating sample sizes large enough for statistical analyses is not as time consuming as with other methods. Because paired comparisons are made, results are direct and easy to assess. Occasional transformations of the data may be required, but these are not as complex as for the other methods.

Using foraging behaviour to detect differences in habitat use is based on the assumption that an individual is foraging optimally and has the ability to instantly assess patch quality (Kotler *et al.* 1994b). These assumptions can be tested by simultaneously presenting rich and poor patches to the animal (i.e. starting with different food densities - with more food in the rich patch and less

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in the poor patch). An optimally foraging individual should leave the patches at the same quitting harvest rate, and therefore the patches should be depleted to the same giving-up density (Kotler *et al.* 1994b). This also suggests that the animal has *a priori* expectations of patch quality when starting to exploit a patch, with the estimate being updated as foraging continues (Kotler *et al*. 1994b). Note that it was beyond the scope of this study to test these assumptions.

Conclusion

The estimation of springbok density, the measurement of the habitat variables, and the assessment of springbok behaviour incorporated into the models is time consuming and subject to bias. Also, these models are based on the assumption that density is an indicator of habitat quality, which does not always hold true, especially in systems with territorial individuals (Melton 1987). Finally, analysis of these models is a lengthy and complicated process involving complex data transformations and statistical techniques. Data collection for GUDs is relatively quick and not subject to observer bias, and data analysis and interpretation is not as complicated as for the habitat suitability and behaviour models.

Opportunities for future research

Habitat suitability models and behavioural models need to be developed in other areas at other times to validate the findings here, to assess their predictive capabilities and more fully understand the behaviour of the models. These models may require modification in order to apply in a range of habitats. GUDs can be applied in a range of habitats at different locations if the same experimental design is used. This would include a standardised set of artificial food patches.

The ability to apply giving-up densities to springbok provides a range of opportunities for further research. The assumption that springbok are foraging optimally can be tested as outlined above. Also, the habitat variables at each patch can be measured in order to more directly assess the effect of habitat on

giving-up density. The functional response of springbok to changes in forage quality can be tested by adding toxins to the foraging trays or by altering the quality of food in the trays. The effect of water on the foraging behaviour of springbok can be assessed by comparing giving-up densities of springbok where water is present or absent. It may be possible to develop a 'landscape of fear' (Altendorf *et al.* 2001) for the springbok by placing a grid of trays across an area. Differences in GUDs can be plotted relative to habitat features and in this way generate a map outlining areas of equal risk.

The different approaches used to assess the preferential use of habitats (GUDs, density, group size and composition) provided snapshots into various aspects of springbok habitat selection which, if considered together, may form a composite image of the factors interacting to influence springbok ecology. These approaches need to be combined to simultaneously assess the interaction between them within habitats in order to provide a unified habitat preference approach to habitat suitability. One of the challenges will be to integrate the different scales of habitat selection. In order to do this the GUD data would need to be collected at a landscape level (at the scale of km^2 as opposed to m^2), requiring a large number of replicates of GUD trays, in order to compare the vegetation type habitats. This has not been done here since it was no within the scope of this project, however further work on this is planned.

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Appendix 1: Vegetation community description for AFNP as described by.
Buk (2004). There are 11 vegetation communities with one community sub-
division.

1. ***Schotia afra – Indigofera pechuelii* low, open woodland** (Habitat 10 in this
   study) occurs on red biotite granite gneiss, which is typically orange brown
   to reddish. The terrain varies from flat to almost vertical, but is typically
   rolling to mountainous. The dominant substrates are bedrock and large
   rocks. The diagnostic species of this community are primarily the tree
   Schotia afra and the herbs *Indigofera pechuelii* and *Hibiscus englerii*. The
   amount of available browse is below average, but its diversity is high. Of the
   available browse, *Schotia afra* contributes 28%, *Indigofera pechuelii*
   contributes 10%, and the succulent shrub *Euphorbia rectirama* contributes
   6%.This community makes up 36% of the study area.

2. ***Adenolobus garipensis – Boscia albitrunca* tall, open shrubland** (Habitat 8
   in this study) occurs on grey granite. The terrain is rolling with crests, steep
   upper slopes, canyon walls and almost horizontal foot slopes. The dominant
   substrates are a mixture of gravel, bedrock, rocks and pebbles. The
   diagnostic species of this community are the shrub *Adenolobus garipensis*,
   the small tree *Boscia albitrunca* and the succulent shrub *Ceraria
   namaquensis*. Available shade is quite limited. The available browse is
   dominated by *Adenolobus garipensis* which contributes 23%, while *Boscia
   albitrunca* contributes 9%. The herbs *Osteospermum microcarpum* and
   Monechma spartiodes contribute 18% and 9% of the available browse,
   respectively.

3. ***Euphorbia gregaria - Osteospermum microcarpum* tall, open shrubland**
   (Habitat 9 in this study) occurs exclusively on substrates with a high content
   of quartz in the form of bedrock and large rocks interspersed with gravel and
   sand. This community is typically found on the crests and slopes of the
   quartzitic outcrops that occur in any of the non-alluvial land types. This
   community is characterised by the consistently high presence of the

conspicuous succulent shrub *Euphorbia gregaria*. Shade is virtually absent in this community, and browse diversity is low, being strongly dominated by *Euphorbia gregaria* and *Monechma spartioides* which contribute 57% and 7% of the available browse, respectively.

4. ***Acacia mellifera – Euphorbia* spp. tall, open shrubland** (Habitat 4 in this study) mostly falls within the foot slopes and valley bottoms. The dominant substrate is gravel strewn with rocks and pebbles, and interrupted by outcropping bedrock and sandy drainage lines. The diagnostic species of this community are primarily the large shrub *Acacia mellifera*, the succulent shrubs *Euphorbia rectirama* and *Euphorbia gregaria* as well as the herbs *Blepharis furcata*, *Indigofera pungens*, *Hermannia spinosa* and *Trianthema triquetra*. Available shade is limited and browse availability is relatively low, but diverse. *Acacia mellifera* contributes 24%, *Indigofera pechuelii* contributes 11%, and *Schotia afra* contributes 10% of the available browse.

5.1. ***Acacia mellifera – Zygophyllum dregeanum – Euphorbia rectirama* tall, open shrubland** (Habitat 6 in this study) occurs on foot slopes, on red biotite gneiss, mostly overlain with gravel and pebbles of the same material. The gravel in this community features a structure peculiar of arid areas where the top 1-2 mm forms a relatively hard, "polished" crust over more porous, compactable material, making this substrate unfavourable for plant establishment. Outcrops of red gneiss also occur, with vegetation affiliated with community 1. The *Acacia mellifera – Zygophyllum dregeanum – Euphorbia rectirama* sub-community is primarily characterised by the high occurrence of the diagnostic species in its name. Shade availability is very low, and the availability of browse only half of the average for the study area. Browse is dominated by *Acacia mellifera* which contributes 49% and *Schotia afra* which contributes11% of the browse.

5.2. *Acacia mellifera – Zygophyllum dregeanum – Monechma spartioides* **tall, open shrubland** (Habitat 7 in this study) differs from the previous sub-community by being dominated by pebbles at the expense of gravel, bedrock and drainage lines. This results in higher total cover and browse availability as well as in the virtual absence of *Euphorbia rectirama* and much higher occurrence of *Monechma spartioides*. The sub-community is dominated by *Acacia mellifera* and *Zygophyllum dregeanum* which contribute 49% and 18% of the available browse, respectively. This sub-community makes up only 2.8 % of the study area.

6. *Acacia mellifera – Stipagrostis hochstetteriana* **tall, open shrubland** (Habitat 5 in this study) occurs on gentle slopes where the dominant substrate is an almost equal mixture of sand and gravel. This community is characterised by the combination of the species *Acacia mellifera*, *Boscia albitrunca*, *Boscia foetida*, the smallish shrub *Rhigozum trichotomum*, the shrub *Lycium bosciifolium*, and the herb *Monechma spartioides* in combination with the virtual absence other differential species. After good rains the otherwise sparse herbaceous layer becomes completely dominated by the grass *Stipagrostis hochstetteriana*. More shade is available in this than the previous communities. Browse availability is average for the study area to which *Acacia mellifera* contributes 44%, *Monechma spartiodes* contributes 10%, *Boscia spp.* contributes 8% and *Rhigozum trichotomum* contributes 5%.

7. *Sisyndite spartea - Forskaolea candida* **tall, open shrubland** (Habitat 11 in this study) occurs on wide drainage lines and plains occasionally subject to flooding. The substrate is 95% washed gravel. This community is characterised by one character species, the shrub *Sisyndite spartea*, plus by high availability of *Acacia mellifera* and *Schotia afra*. Browse is average in availability, but low in diversity, dominated by *Sisyndite spartea* (26%), *Acacia mellifera* (15%) and clumps of *Schotia afra* (45%). This community only covers 0.7% of the study area in one patch.

8. *Acacia erioloba – Schmidtia kalahariensis* short, closed woodland (Habitat 1 in this study) is found on gently sloping terrain with a high percentage of sand mixed with some gravel. This community is characterised by the predominance of the species in its name. The herbaceous layer is poorly developed except for the ubiquitous, opportunistic creeper *Tribulus cristatus* and the annual grass *Schmidtia kalahariensis*, the preponderance of which is highly dependant on summer rainfall. *Acacia erioloba* provides abundant shade but only contributes about 20% of the browse available up to 2 metres. *Acacia mellifera* and *Monechma spartiodes* contribute significant amounts of browse (10% and 7% respectively). This community covers only 0.4% of the study area.

9. *Acacia erioloba – Zygophyllum microcarpum* short, closed woodland (Habitat 2 in this study) occurs on pure gravel near large drainage lines. This community is characterised by the high availability of the species in its name. *Acacia erioloba* provides abundant shade but only contributes about 24% to the available browse. *Zygophyllum microcarpum* contributes about 20% and *Acacia mellifera* 11% of browse. The herbaceous layer is poorly developed. Only 0.1 % of the study area falls in this community.

10. *Tamarix usneoides - Gymnosporia linearis* tall, open shrubland (Habitat 12 in this study) occurs on floodplains with a dusty mixture of silt and clay. The diagnostic species of this community are the smallish tree *Tamarix usneoides*, the succulent herb *Mesembryanthemum guerichianum* and two succulent *Psicaulon* herbs. *Gymnosporia linearis* is also very conspicuous in this community. Browse availability is more than twice the average for the study area. *Tamarix usneoides*, and *Sueda fruticosa*, both make up 28% of the browse, while *Gymnosporia linearis* and *Psilocaulon absimile* contribute 13% and 12% to the available browse; respectively.The community makes up 1.0% of the study area.

**11. *Acacia karroo – Ziziphus mucronata* short, riverine forest** (Habitat 3 in this study) occupies a 5 – 30 m wide strip along the Orange River and a few tributaries, where terrain and hydrology allow soil to build up. The basic

substrate is alluvial silt-clay combination, highly enriched with humus. The diagnostic species for this community are the trees *Acacia karroo* and *Ziziphus mucronata*. Virtually the entire community is shaded. Browse availability is 13 times the average for the study area. Most abundant is climbing *Asparagus spp* (one or more species) which contributes 27% of the available browse. *Acacia karroo* and *Salix mucronata* contribute 25% and 10% of the available browse, respectively. *Ziziphus mucronata* is heavily browsed yet only contributes 8% of available browse. The herbaceous layer contributes relatively little to browse due to the abundance of woody plants. This community makes up only 1.1% of the study area.

Appendix 2: Map of AFNP showing the geographical location of the different land types (Buk 2004). Table 2.1 (Chapter 2) describes the location and geology of the four land types represented in the study area (Land Type Survey Staff 1986).
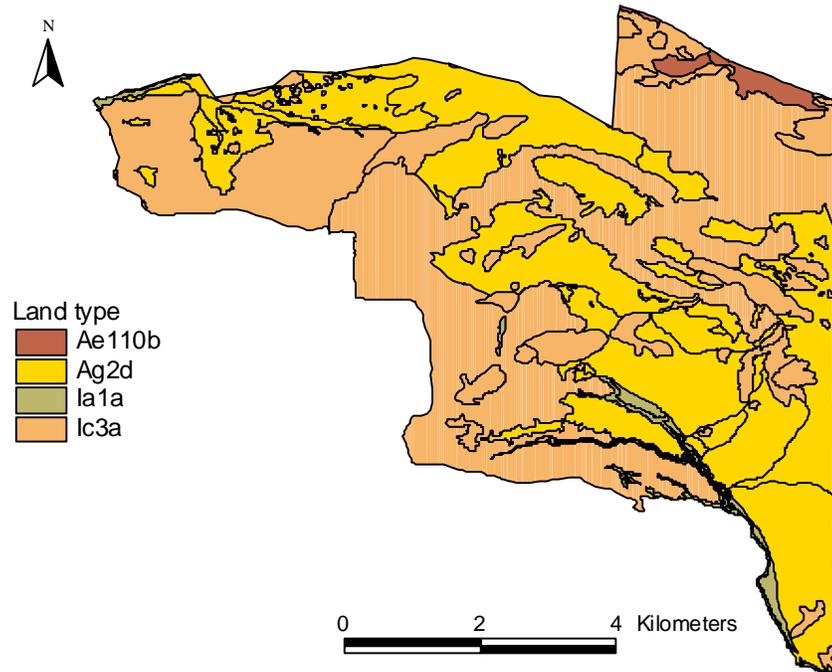
Appendix 3: Maps of AFNP showing the different habitats (Buk 2004) and the area covered by the drive transects. a) Drive transect S1 was driven a total of 13 times, b) Drive transect S2 was driven a total of 12 times, c) Drive transect M1 was driven a total of 4 times, and d) Drive transect L1 was driven in a clockwise direction a total of 19 times while Drive transect L2 (B) was driven in a counter-clockwise direction a total of 20 times.
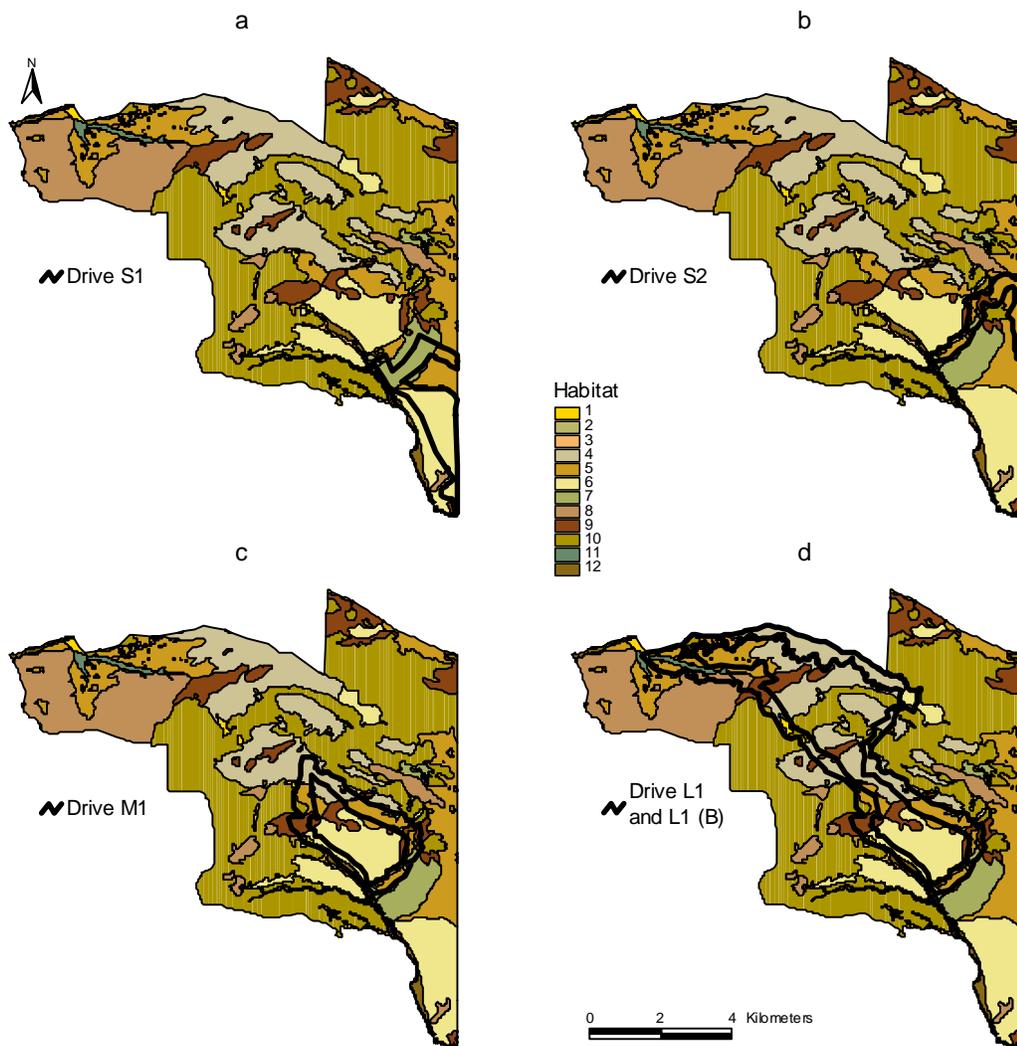
Appendix 4: The non-categorical habitat variables and their components, (Table 1), and the categorical habitat variables and their codes (Tables 2-12), measured in determining the characteristics of the habitat for the habitat suitability model.

Table 1: Non-categorical habitat variables, and their components, measured in determining the characteristics of the habitat for the habitat suitability model.

Variable	Component	
Slope		
Ground cover (%)	Boulders:	(particles >100 cm diameter)
	Rocks:	(particles 20 - 100 cm diameter)
	Stones:	(particles 5 - 20 cm diameter)
	Pebbles:	(particles 1 - 5 cm diameter)
	Grit:	(particles 0.5 - 1 cm diameter)
	Sand:	(particles 0.05 - .05 cm diameter)
	Clay	
Aerial and Basal cover (%)	Grass	
	Herbs	
	Forbs	
	Succulents	

Table 2: The codes, and their descriptions, used to define topographic position in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Top of Escarpment
2	Cliff - Scarp
3	Scree Slope at Bottom of Cliff
4	Plateau - Top of Hill
5	Upper Third of Slope
6	Middle Third of Slope
7	Lower Third of Slope
8	Bottomland
9	Upper Terrace of Alluvium
10	Lower Terrace of Alluvium
11	Edge of Drainage Line
12	Rock Outcrop
13	Dyke
14	Anthill

Table 3: The codes, and their descriptions, used to define aspect in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	N
2	NE
3	E
4	SE
5	S
6	SW
7	W
8	NW

Table 4: The codes, and their descriptions, used to define soil texture in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Clay
2	Clay Loam
3	Loam
4	Coarse Sandy Loam
5	Coarse Sandy Clay
6	Fine Sandy Loam
7	Fine Sandy Clay
8	Coarse Sand
9	Fine Sand
10	Loamy Sand
11	Silty Clay
12	Silty Clay Loam
13	Silt Loam
14	Silt

Table 5: The codes, and their descriptions, used to define moisture status in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Permanently Wet with Exposed Surface Water
2	Seasonally Flooded
3	Permanently Moist (Seep, Depression, Shaded Area, etc)
4	Seasonally Moist (Drainage Line or Seep)
5	Occasionally Moist - Mostly Dry (Depression or Bottom of Slope)
6	Dry (Top of Ridge or Mound)
7	Very Dry

Table 6: The codes, and their descriptions, used to define protection from wind in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Fully Protected
2	Partially Protected
3	Exposed

Table 7: The codes, and their descriptions, used to define shading in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	In Permanent Deep Shade
2	In Deep Shade for between 7 and 9.5 hrs in summer (½ - ¾ day)
3	In Deep Shade for between 4.5 and 7 hrs in summer (1/3 - ½ day)
4	In Deep Shade for between 4.5 and 3.5 hrs in summer (1/3 - ¼ day)
5	In Deep Shade for between 2.5 and 3.5 hrs in summer (¼ - 1/5 day)
6	In Deep Shade for < 2.5 hrs (1/5 day)
7	In Permanent Dappled Shade
8	In Dappled Shade for between 7 and 9.5 hrs in summer (½ - ¾ day)
9	In Dappled Shade for between 4.5 and 7 hrs in summer (1/3 - ½ day)
10	In Dappled Shade for between 4.5 and 3.5 hrs in summer (1/3 - ¼ day)
11	In Dappled Shade for between 2.5 and 3.5 hrs in summer (¼ - 1/5 day)
12	In Dappled Shade for < 2.5 hrs (1/5 day)
13	No Shading

Table 8: The codes, and their descriptions, used to define erosion type in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Sheet Erosion
2	Rill Erosion
3	Runnel Erosion
4	Gully Erosion
5	Wind Erosion
6	Trampling and Wash

Table 9: The codes, and their descriptions, used to define deposition type in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Wash in Depression
2	Wash on Levee
3	Obstacle

Table 10: The codes, and their descriptions, used to define herbivory type in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Parts of Leaves Removed
2	Young Leaves and Leaf Buds Removed
3	Mature Leaves Removed
4	Senescent Leaves Removed
5	Leaves and Small Twigs Removed
6	Leaves, Small Twigs and Small branches Removed
7	Leaves, Twigs, Small Branches and Large Branches Removed
8	Stem Broken
9	Plant Uprooted
10	Bark Removed
11	Flowers Removed
12	Fruit Removed

Table 11: The codes, and their descriptions, used to define the intensity of erosion, deposition and herbivory in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Light
2	Moderate
3	Intense

Table 12: The codes, and their descriptions, used to define the frequency of erosion, deposition and herbivory in determining the characteristics of the habitat for the habitat suitability model.

Code	Description
1	Weekly
2	Monthly
3	Twice Yearly
4	Annually
5	Bi-annually
6	Tri-annually
7	Every Four Years
8	Every Five Years
9	> 5 yrs
10	very infrequent

Appendix 5: The nutritional information of the pellets used in determining patch and time specific habitat use by springbok, through an assessment of giving-up densities.

Table 1 shows the nutritional information of the sheep pellets. The information is given in g/kg, and since each pellet weighed approximately 1 g, the nutritional information outlined in Table 1 may be used to represent the nutritional information for each pellet and therefore for the food patches too.

Table 1: The nutritional information of sheep pellets used in determining the giving-up density of springbok. All units are in g/kg unless otherwise stated.

Compound	g/kg
Protein	min 100
(Protein ex NPN)	max 8%
Ammonia chloride	max 5
Moisture	max 120
Fat	max 25
Fibre	max 200
Calcium	max 12
Phosphorus	max 0