HABITAT SUITABILITY ASSESSMENT FOR INDIGENOUS BROWSING UNGULATES IN THE NORTHERN CAPE

Christo Fabricius

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ABSTRACT

The small scale habitat selection of kudu and eland was investigated by quantifying habitat resources within 340 m² circular plots where the animals were present and absent respectively. By an approach of successive approximation, habitat suitability models were constructed. Several iterations of model building, testing and refining were carried out.

Suitability index curves and linear discriminant functions were calculated to discriminate between the presence and absence of the animals. Submodels for wet and dry seasons were formulated, based on plant phenophases. The discriminant functions were converted to flow charts and expert systems which made use of functional plant guilds rather than plant species as variables. This should permit the application of the models to other biogeographic regions.

During the wet and dry seasons kudu selected patches of dense vegetation with shade in close proximity. These patches contained mostly thorny trees or shrubs. Patches with thornless plants were utilized towards the late dry season as 'stepping stones' to overcome this period of food shortage.

In the wet season, eland selected patches containing dense grass and large-leaved trees or shrubs, or trees producing an abundance of pods or succulent new shoots. In the dry season they preferred shady patches which contained pods and evergreen trees with an abundance of leaves.

The models were validated by independent data. With the exception of the winter eland model, they predicted the presence or absence of kudu and eland significantly better than would be expected of random models.

The models have mostly regional applicability. The extended models might however be applied to other biogeographic regions, provided they are validated in the process.

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Master of *Science in* the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

Johannesburg, February 1989

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CHAPTER 1. INTRODUCTION

1 Aims

The aims of this study were to

1) develop and test habitat evaluation models for kudu and eland in the Northern Cape;

2) develop a rapid, objective approach to habitat suitability assessment which could be applied to a wider range of game species than the proposed study animals;

3) improve understanding of habitat selection by browsers.

To realize these aims, I sought answers to the following questions.

1) What were the quantitative and qualitative biotic and abiotic features which discriminate between the presence and absence of kudu and eland?

2) Which criteria should be used when evaluating habitat suitability for browsers in the semi-arid parts of the Cape Province, and how can those criteria be modeled for objective habitat evaluation?

3) How could those criteria developed on a specific study area be applied to other areas in the Northern Cape?

The results will be used by wildlife managers to objectively evaluate habitat suitability for browsers on private game farms in the semi-arid parts of the Cape Province, South Africa. These areas mainly consist of the Nama-Karoo and Savanna biomes (Rutherford & Westfall 1986).

2 General background and justification

The Chief Directorate of Nature and Environmental Conservation (CDNEC), Cape Provincial Administration, has recently established a game utilization advisory service. The motivation for the CDNEC's involvement in game utilization is to promote the conservation of all natural resources by the private sector. Their involvement in game farming is a means to realize this objective. The concept of game farming should therefore be advocated to farmers as a viable form of resource utilization. CDNEC's game farming extension work should produce satisfactory results from a land-owner's point of view in order to remain credible.

Up until present their recommendations were largely based on experience and knowledge of the available literature, for lack of previous research. Recommendations based on expert opinion are time saving, and often produce fair results. They do not however leave any scope for monitoring and adaptive management, and there is no basis for the comparison of their results. This project has been initiated to provide the necessary baseline information to contribute towards objective decision making.

3 Definitions of habitat

The word 'habitat' is variously used in ecological literature and discussions. It is therefore appropriate to define the term to avoid confusion. In A Dictionary of Biological Terms (Kenneth 1976) it is 'The locality or external environment in which a plant or animal lives.'. It is derived from the Latin <u>habitare</u> (to inhabit). Riney (1982) defines habitat requirements as '...the minimum requirements for the existence of that individual' while Bothma (1986) defines habitat as the area in which a plant or animal preferably occurs and where all its life-sustaining requirements are met (translated from Afrikaans). Smith (1966) calls the specific set of conditions that surround an organism its habitat. Odum (1971) simply defines habitat as '...the place where it (an organism) lives, or the place where one would go to find it.' Grinell's (1928 in Melton 1967) definition of habitat is 'the sum of the environments in which it (a species) occurs'.

For the purpose of this project habitat is defined as 'the area containing the biotic and abiotic environmental components which are required by an organism to sustain its life-supporting activities and which enables the survival of a population of that organism.'

3.1 Habitat scale and order

Whittaker, Levin & Root (1973) discuss the misuse of the term habitat and its confusion with the term niche. They suggest that the intracommunity variables which a species responds to should be termed 'niche variables'. The variables which influence a species' distribution within landscapes should then be termed 'habitat variables'. When niche and habitat variables intergrade, the term 'ecotope', which is independent of the community concept, should be used.

Carey (1981) suggests that the term habitat should be more rigorously defined to avoid confusion. He proposes that, on a large scale, habitat should be replaced by 'biotope'. Biotopes are homogeneous areas within landscapes. The biotopes contain recognizable communities. Within communities, the variables with extensive spatial components are called habitat variables. If presented graphically, their axes describe a multidimensional habitat hyperspace. Within a fraction of the habitat hyperspace a habitat hypervolume is contained. The intracommunity variables are called niche variables and define the 'microhabitat' of a species. The definitions of niche can be broken down into niche hyperspace (large scale) and niche hypervolume (small scale).

Odum (1971) and Melton (1987) distinguish 'niche' from 'habitat'. According to them, habitat is a concept concerned with distribution while niche applies to the role of a species in a community.

3.2 Habitat selection by herbivores

Johnson (1980) defines four hierarchical orders of habitat selection. The first order selection by a species is the geographical range within which it occurs. The second order selection comprises the home range of a species within its geographical range. Its third order selection is the utilization or avoidance of different habitat components within its home range. The fourth order habitat selection of the animal is defined as the actual food plants the animal selects among the third order habitat components. These selection orders may be even more finely divided.

A feature of African ungulates is their wide range of morphological diversity. This causes resource partitioning through dietary selection, and co-existence by employing different feeding strategies (Owen-Smith 1985b). Dietary selection is manifested on a small scale by selection of plant parts and plant species. On a larger scale, the selection of plant species and plant parts leads to habitat selection (French 1985; Demment & Van Soest 1985).

The time spent moving from one preferred food item to another is limited by the energy requirements of an ungulate. It therefore selects for an area with sufficient densities of its preferred food items to allow it to spend more time feeding and less time travelling (Senft, Coughenour, Bailey, Rittenhouse, Sala & Swift 1987). Diet is, however, only a part of the animals' survival requirements. Physiological adaptations allow some ungulates to tolerate heat or cold better than others, while morphological adaptations enable them to employ different predator avoidance strategies. A species of ungulate will thus frequent areas where its feeding preferences and shelter requirements are best met and where its Darwinian fitness is likely to be high.

Animal-habitat studies can be approached in several ways. First the vegetation can be floristically and structurally classified and the distribution of animals within these phytosociological units determined (Hirst 1975; Jooste 1980). When using this method to study an animal which selects habitat on a small scale, the larger units often overshadow ('mask') the actual patches selected by the animals. Hirst (op. cit.), for example, concludes that kudu have no preferred habitat in the Transvaal lowveld. Second, individual animals could be followed (Cooper 1985, Catt & Staines 1987), which is probably the most effective method. Relatively tame animals are required for this approach and the study area should be totally accessible. A third possibility is to find areas which the study animals have the opportunity to utilize, but which they seldom or never occupy. These voluntarily unutilized areas are then compared to areas of high animal density (Krausman & Leopold 1986). The models developed following this approach should have a high predictive value within the study area, particularly if they are tested by cross-validation. The possibility of omitting 'lurking variables' (Johnson 1981) is high. The approach is prone to the inclusion of overshadowing variables which, by themselves, are not indicators of habitat suitability.

4 The use of models for habitat suitability assessment

Habitat suitability models can be widely applied, among others for environmental impact assessment, motivation for new parks and reserves and land use planning. They can be a valuable tool in the management and planning

c. game farms and even nature reserves or national parks. Once a habitat suitability model has been developed for a species, certain areas can be managed towards better or worse habitat for that species, depending on the objectives for the management unit. During environmental impact analysis the models can be utilized to predict the potential of areas to support certain species of fauna.

The concept of habitat suitability modeling is new for southern Africa. A thorough search of the literature did not reveal records of habitat suitability models for any of our native fauna, with the possible exception of the multiple regression equation of Howard (1986) for common reedbuck on farmland.

In the United States, on the other hand, habitat suitability modeling seems to receive a high research priority. The United States Fish and Wildlife Service (USF & WS) initiated a Habitat Evaluation Procedures project as early as 1977, and since then habitat suitability models have been developed for a wide range of fauna, and the project is continuing. A large part of the 47th North American Wildlife and Natural Resources Conference (1982) was devoted to habitat suitability modeling, and since then a host of published and unpublished habitat suitability models have come to light. The USF & WS has gone so far as to appoint a Habitat Evaluation Procedures Group, whose main purpose it is to develop, verify and validate habitat suitability models in the field. Recently the Wildlife 2000 Conference in 1984 focused on habitat suitability models for terrestrial vertebrates (Verner, Morrison & Ralph 1986).

4.1 Fundamentals of habitat suitability modeling

The principles of Habitat Suitability Index (HSI) modeling, which is the system applied by the U.S. Fish and Wildlife Service (Farmer, Armbruster, Terrel & Schroeder 1982), are as follows.

1) Model objectives are clearly set. The acceptance levels of the models (i.e. the level of resolution at which the model is expected to function) are defined.

2) A theoretical model is constructed, based on the available literature and the opinions of experts on the particular species. Variables are subjectively identified, and subjective values are assigned to each variable. A graph is then constructed for each variable of the model, relating habitat suitability (on a scale of zero to one), to different variable values. The habitat is then scored according to a formula which weights variables according to their importance. At this stage the formula, too, is based on subjective assumptions.

3) Species authorities are once more consulted, and they judge whether the model has the potential to perform satisfactorily. If not, the model is adjusted.

4) Sometimes several models are developed independently for the same species, and then compared with one another. If different models predict similarly it is assumed that their results are reliable.

5) Some models are then evaluated. The evaluation process consists of two phases (Farmer et. al. 1982). They are i) verification, which evaluates the model's ability to match the model-builder's perceptions, and ii) validation, which determines how well the model-builder's perceptions reflect reality. Areas are first evaluated theoretically, and the predicted habitat suitability indices for each site are then compared with the relative population levels of the species within each area. A linear regression is then drawn, with predicted habitat suitability indices on one axis and observed population numbers on the other. The curve

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should be a straight line running through the intercept if the model performs satisfactorily. Lancia, Miller, Adams & Hazel (1982), Cole and Smith (1983), Bart, Petit & Linscombe (1984), Cook & Irwin (1985), and Irwin & Cook (1985) have demonstrated that most habitat suitability models are virtually useless before going through the latter process.

4.2 My approach towards habitat modeling

After literature surveys and discussions with colleagues, I undertook the study under the following philosophy.

1) A process of successive approximation should be followed in instances where the data are sparse and the problem is poorly defined, which is mostly the case with ecological models. The model should go through several iterations of building, testing and refinement, starting with a crude model with as few as possible variables.

2) Model objectives should be stated explicitly, and there should be no doubt about the desired level of resolution of the model.

3) Model assumptions should be stated. Most of the USF & WS models, for example, assume that density is an indicator of habitat quality, and many habitat suitability models do not consider interspecific interaction. These are rather crude assumptions, but they can be tested at a later stage, as separate projects.

4) Initial models should incorporate as few variables as possible. It is therefore important that careful consideration should be given to the most appropriate variables to be included. If any doubt exists about the inclusion or exclusion of a variable, a sensitivity analysis can be done by comparing the model output with the dubious variable included to output without the variable.

5) We do not need more research to develop initial habitat suitability models for most of our indigenous fauna. Wildlife managers are often overheard making statements such as 'Springbok should do well here' or 'This looks like black mamba country'. This means that they have subjected the habitat to a mental habitat assessment model, albeit crude. All that needs to be done is to put the assessment process on paper.

6) Habitat suitability models must be validated after their formulation. The many theoretical models which perform poorly have shown that the validation process can hardly be excluded.

7) Habitat suitability models, if related to animal density within the variously rated habitat units, are a step towards improving game stocking policies.

5 *Study* area

In an extensive study of this nature, the choice of study area should comply with certain criteria. 1) It should be large enough to allow for free animal movement. 2) It should have sufficient spatial variability to encompass a range of habitat types wide enough to allow the animals to manifest their preferences. 3) It should contain densities of the study animals that are high enough to allow sufficient data to be gathered within the allocated time span. 4) The habitat should be representative of the areas to which the results will be applied. 5) It should be accessible by vehicle, and should contain the necessary infrastructure.

The De Beers' farm Rooipoort complied with these criteria. It had the added advantage of having data, consistently gathered over a period of five years, available on animal numbers and distribution (M.P.S. Berry, c/o De Beers Consolidated Mining Company, Stockdale Street, 8301 Kimberley <u>in litt</u>.) as well as floristic data and results (A.A. Gubb, East London Museum, P.O. Box 11021, 5213 Southernwood in litt.).

Rooipoort is a privately owned estate of some 420 km² which is mostly used for game ranching purposes. The largest portion of the property (approximately 345 km²) is farmed for indigenous game only. The estate is situated about 52 km west of Kimberley, Cape Province. It falls within the False Orange River Broken Veld vegetation type, with patches of Kalahari Thornveld invaded by Karoo (Acocks 1975).

5.1 Vegetation and geology

The estate was divided into 11 major vegetation types by Bigalke & Leistner (1962). These range from the riverine thicket of the Vaal River to sandveld areas which have strong resemblances to the Kalahari semi-desert. Large portions of the study area consist of andesite hills with medium to high, dense Acacia mellifera and A. tortilis shrubland. The andesite is interspersed with bands of quartzite. Another wide ranging land facet consists of high Tarchonanthus camphoratus shrubland on shallow soils on a calcrete bedrock. The soils generally have a high lime and low clay content (Dept. of Agricultural Technical Services, 1987). The shrublands are interspersed with open patches on shallow soils. Some of the open patches consist of pans, i.e. shallow depressions which contain water only during high rainfall years. The largest of these, Volstruispan, is more than 1000 hectares in size. Bigalke & Leistner (1962) compiled a plant species checklist of 157 species for Rooipoort.

The environment is extremely patchy with small patches of woodland interspersing the predominantly high shrubland. The pans, many drainage lines and varying topography also contribute to the β diversity. The land facets seem to be regulated by soil depth. The patchiness can probably be attributed to pockets of deeper soil among the predominantly shallow soils. These deeper soils are a result of aeolian and alluvial deposits.

5.2 Climate

Climatic data were obtained from the meteorological office at the B.J. Vorster airport in Kimberley, approximately 60 km from the study area. Berry & Crowe (1985) found no significant differences between mean annual rainfall measured at Kimberley and at Rooipoort. They regard the rainfall regimes at Kimberley and Rooipoort as similar. Kimberley and Rooipoort fall within the same rainfall district (Weather Bureau 1986).

The mean annual rainfall for the area is 419 mm, based on 90 years' rainfall data. Most of the rain falls in late summer (January to April). During these months the average monthly rainfall is between 61 and 73 mm, with between 1,7 and 2,1 rainy days per month. Between 1894 and 1984 an average of 12,7 rainy days per year have been experienced in the area (Weather Bureau 1986). The rainfall is unpredictable, and the annual amount of rain that can be expected with a 90% probability is in the vicinity of 200 mm (Tyson 1986).

The mean minimum monthly temperature is lowest in July (2,3° C) while the average hottest month is January (32,8° C). In January, temperatures in excess of 35° C were experienced on an average of 8,5 days, while in July an average of 7,8 days with below zero temperatures were experienced for the period 1931 to 1984 (Weather Bureau op. cit.).

Mean monthly minimum and maximum temperatures during the study period ranged from 1,7° in July 1987 to 35,6° in January 1988. The highest temperature experienced during the study patchiness can probably be attributed to pockets of deeper soil among the predominantly shallow soils. These deeper soils are a result of aeolian and alluvial deposits.

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Mean monthly minimum and maximum temperatures during the study period ranged from 1,7° in July 1987 to 35,6° in January 1988. The highest temperature experienced during the study period was 40,4° C in January 1988, while the lowest temperature was -4,8 ° C in June 1987.

5.3 Status of study animals

During a game survey by helicopter in March 1987, 171 kudu and 547 eland were counted from the air. The total number of kudu in the study area is estimated at more than 300 (Berry 1987). This represents a density of about 0,87 kudu/km² for the entire study area if Berry's estimate is used. The kudu density varies enormously between landscapes. It might be as low as <0,1/km² in the sandveld areas and as high as >13/km² in the riverine thicket (my own unpublished data). The eland density is approximately 1,6/km².

Kudu are harvested mostly for trophy hunting purposes, but during 1987 and 1988 approximately 60 kudu were caught alive. Eland are harvested annually and the estate managers attempt to keep the eland population at between 500 and 600 (M.P.S. Berry <u>pers. comm.</u>).

Fifteen species of ungulate occur on the estate. Three of these are classified as browsers (kudu, giraffe, and common duiker), four as intermediate feeders (eland, springbok, impala and steenbok) and eight as grazers (plains zebra, red hartebeest, blue wildebeest, black wildebeest, blesbok, gemsbok, mountain reedbuck and sable antelope) (Hofmann & Stewart 1972; Bothma 1986). The status of the animals as obtained during the 1987 census by helicopter and their scientific names are supplied in Appendix 1.

6 Layout of thesis

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6 Layout of thesis

Models should be used as aids to define problems, organize thoughts, understand data, communicate that understanding and make predictions (Starfield & Bleloch 1986). My models were constructed by successive approximation, starting off with sparse data and a poorly defined problem. I will attempt to illustrate how the models progressed together with an increase in my understanding, how they were used to make predictions and, finally, how they were employed to communicate that understanding.

1) As a point of departure, crude provisional models for kudu and eland habitat suitability assessment were constructed. These were based on a literature survey of the habitat requirements of the study animals (chapter two).

2) A pilot study was then executed to test the initial models and the feasibility of the proposed techniques (chapter three).

3) Data were collected and new data-based models were constructed and verified (chapter four).

4) The models were validated (chapter five).

5) The models were updated and extended (chapter six).

6) The methods and results were discussed (chapter seven).

7) Conclusions about the applicability and success of the models were drawn and management recommendations were made (chapter eight).

CHAPTER 2. PROVISIONAL MODELS

1 Introduction

In this chapter provisional habitat suitability models for kudu and eland are described. The formulation of initial models had several advantages. First, the initial models were used to obtain a conceptual image of the results of the project. Second they guided me to the collection of the appropriate field data. Third, they helped me to define and understand the nature and extent of the problem I was dealing with.

2 Methods

Model objectives were clearly stated before the models were constructed. Based on the literature I selected the Habitat Suitability Index (HSI) type models (U.S. Fish & Wildlife Service 1980, 1981). I then made a thorough literature survey of the autecology of kudu and eland, with the emphasis on their food and shelter requirements. All references to habitat requirements encountered in the literature were listed and important model variables were identified accordingly.

Experts were then consulted to ascertain whether any variables had been omitted, or whether any unnecessary variables had been included.

Suitability index (SI) curves, based on my personal opinion, were then constructed for each variable. For each variable, the SI curve was shaped according to my imagined response of kudu or eland to change in the parameters of the variable. In addition, variables were subjectively weighted according to indications of their importance to kudu or eland habitat suitability. This was obtained from the literature and personal opinion.

3 Results

3.1 Literature survey

The results of a literature survey of the habitat requirements of kudu and eland are summarized in tables 1 and 2 respectively. Literature references appear in the tables and are not repeated in the text below.

3.1.1 Kudu

From table 1 it is clear that kudu are selective feeders with seasonal food preferences. They select food plants with a high protein content, but energy is the most limiting factor during the dry season. They prefer fruit, pods and flowers when these are available and favour browse plants growing on high nutrient soils. These plants contain spines and small leaves as protection against herbivory as opposed to plants on low nutrient soils, which are protected by secondary compounds (Owen-Smith 1982). It seems as though they prefer broad leaved plants to small-leaved ones if the former do not contain large amounts of secondary chemicals.

Kudu need specific food items at certain times of the year to see them through critical periods of food shortage. During the late dry season they will take otherwise neglected food, such as broad leaved browse with a high secondary chemical content, to compensate for the overall scarcity of food. They will occasionally take new green grass leaves, while a large part of their diet consists of forbs. The phenophase of woody plants plays an important part in the food selection of kudu. They will eat the new growth, fruit and flowers of plants which are otherwise neglected by them. They utilize a wide variety of plants in order to meet their nutritional requirements and frequent heterogeneous surroundings. The preferred food items of kudu do not belong to any particular genera, with the

Table 1. Literature survey of habitat requirements of kudu

PREFERENCE	*REFERENCE*
	FOOD
Water dependent	Simpson 1972
Seasonal diversity	Jarman 1974, Owen-Smith 1979, Owen-Smith & Cooper 1987d&e, Simpson 1972
No preferred habitat	Hirst 1975
New green grass	Conybeare 1975
Litter	Beardall, Joubert & Retief 1984
Large variety	Owen-Smith 1982
Hill base ecotone vegetation	Owen-Smith 1979
Plants on high nutrient soils	Underwood 1978
Heterogeneous *surroundings*	*Ferrar* & Walker 1974
Unpalatable evergreens towards end of dry season	Owen-Smith & Cooper 1987d,e
Critical plant species at certain times of the year	Owen-Smith & Cooper 1987d
Tree and shrub foliage	Hofmann & Stewart *1972, Jarman 1974*
Selective for forbs *Wide variety of dicots*	Conybeare <u>op. cit.</u>, Owen-Smith 1979, Owen-Smith Cooper & Novellie 1983 Wilson, 1965
Broad leaved trees in late dry season	Beardall et al. <u>op. cit.</u> *Conybeare* 1975, Owen-Smith 1979
High energy plant species	Owen-Smith & Cooper 1987d
Green leaves & twigs	Wilson 1965
Protein-rich foliage Pods Fruit Flowers Phosphorous rich plant species	Owen-Smith & Novellie 1982, Owen-Smith 1979, 1985a
Dry pods	Wilson 1965
Dislike chemical deterrents	Owen-Smith, Cooper & Novellie 1983, *Owen-Smith & Cooper 1987e*

Table 1 (continued)

Combretaceae, Tilliaceae, Rhamnaceae	Owen-Smith 1985a
Diospyros spp.	Jarman 1971, Owen-Smith & Cooper 1987e
Grewia spp., Olea spp.,	Funaioli & Simonetta (in Hoffman & Stewart 1972)
Combretum spp. Commiphora spp., Croton spp.	Conybeare, op. cit., Jarman 1971
Acacia spp. during growing season	Funaioli & Simonetta (in Hofmann & Stewart 1972) Conybeare op. cit., Owen-Smith 1979, Owen-Smith, Cooper & Novellie 1983
Spinescent plants Plants on high nutrient soils	Owen-Smith & Cooper 1987e
SHELTER & COVER	
Warm areas in winter	Simpson 1972
Steep slopes	Beardall, Joubert & Retief 1984,
Hills	Crowe, Schijf & Gubb 1981, Simpson 1972
Dense vegetation: riparian fringe and thickets	Underwood 1978
Open forb-rich savannas or dense mixed woodland	Owen-Smith 1985b
Broken country	Walker 1979

Table 2. Literature survey of habitat requirements of eland

PREFERENCE	REFERENCE
	FOOD
Water-independent	Western 1975, Taylor 1969
Water-dependent seasonally, Grassland to open woodland	Lamprey 1963
Plants with high water content	Taylor 1969
Wide range of altitudes, slopes and aspects	Rowe-Rowe 1983
Mixed diet Low preference for *Acacia* spp. Browse or grass, depending on availability Grass & browse leaves in dry season ca. 48% grass, 52% browse	Nge'the & Box 1976
ca. 24% grass, 76% grass	Van Zyl 1965
ca. 30% grass, 70% browse	Lamprey 1963
ca. 7% grass, 93% browse	Kerr, Wilson & Roth 1970
Green grass	Van der Schijff 1959
Unselective, diverse food items	Jarman 1974
Primarily browse, will eat grass mainly in wet season	Littlejohn 1968; Wilson 1969; Buys 1987
Will avoid dry grass if browse is available; diet varies considerably	Hofmeyr 1970 in Hofmann & Stewart 1972
Forbs	Glover, Stewart & Gwynne 1966 in Hofmann & Stewart 1972
Seeds, fruit	Eloff 1959; Leistner 1959
Grass in wet season when protein content > [illegible] Palatable deciduous browse in early dry season, evergreens in late dry season	Field 1975
	SHELTER & COVER
Dry sandveld, open or mixed savanna	Crowe, Schijf & Gubb 1981

possible exception of Acacia spp.

Kudu need warm areas for shelter in winter such as steep slopes and hills, and prefer dense vegetation such as riparian fringes and thicket. Where they are found in more open vegetation, it normally contains large amounts of their favourite food plants, such as forbs. Kudu are water dependent browsers.

3.1.2 Eland

Eland are less selective and more catholic than kudu in their feeding habits. They are regarded as mixed feeders and include between 7 and 48% grass in their diets. The bulk of the literature shows that eland will rather browse than graze if they have a choice. Grass is mostly utilized in the wet season in the form of grass leaves of which the protein content exceeds seven percent. They also feed on forbs, seeds and fruit. Eland frequent grassland and open woodland vegetation types.

Eland are largely water independent in the wet season when the water content of their food plants is high. During the dry season they will migrate in search of water.

3.2 Provisional models

Preliminary kudu and eland models are presented in figures 1 and 2 respectively.

The variables included in the kudu model, as indicated by the earlier literature study, were:

total tree density (V1),
density of large-leaved trees (V2),
density of thorny trees (V3),
density of trees bearing edible fruit (V4),
density of trees bearing edible flowers (V5),

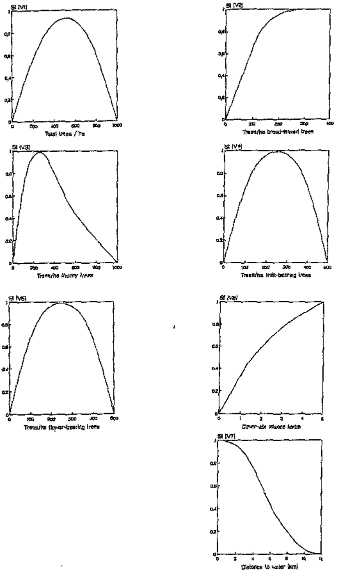

Figure 1. *Provisional* habitat suitability model for kudu. *SI* = *suitability* index. HSI = (0,5SI(V1) + 0,25SI(V2) + 0,25*SI*(V3) + 0,25SI(V4) + 0,25SI(V5) + 0,5*SI*(V6) + 0,25*SI*(V7)) / 2,25.

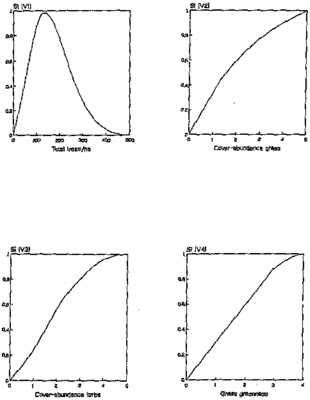

Figure 2. Provisional habitat suitability model for eland. SI = suitability index. HSI = SI(V1) + SI(V2) + SI(V3) + SI(V4) / 4.

a Braun-Blanquet cover-abundance score for forbs (V6) and
distance to available water (V7).

It was estimated that the response curves of kudu to total tree density (V1), fruit-bearing trees (V4) and flower-bearing trees (V5) would be Gaussian. Either too few or too many of these trees would have a less advantageous effect on kudu habitat suitability than moderate densities. Too few trees would mean a shortage of food, whereas too many trees of either of the above variables would compete with other, more preferred food sources such as large-leaved trees.

Large-leaved trees (V2) followed a virtual straight line up until a density of 100 trees/ha, whereafter the curve flattened. The argument used was that large-leaved trees reached 'optimal' densities at 250 trees/ha or more. Because of the preference kudu had for large-leaved trees, this variable did not influence habitat suitability negatively at high densities, which would have resulted in a Gaussian curve.

The response curve to thorny trees (V3) dipped sharply after an initial sharp rise. Thorns act as deterrents, and more than 250 of such trees per hectare would be less preferred by kudu than lower densities of thorny trees.

The literature pointed to forbs (V6) as a highly preferred food item for kudu and therefore its response curve followed a virtual straight line.

It was thought that water in closer proximity than 2 km would have made an 'optimal' contribution towards habitat suitability. Water farther than that would have had a progressively less positive effect on habitat suitability until it was farther than 10 km, when it made no positive contribution.

When weighting the variables the argument was that total trees per hectare and forb density (V1 and V6) were roughly twice *as important* habitat factors as any of the other variables. Therefore V1 and V6 received double the weighting coefficients of the other variables.

The habitat suitability index (HSI) for kudu was calculated by *weighted averaging*, i.e.
HSI = ((0,5SI(V1) + 0,25SI(V2) + 0,25SI(V3) + 0,25SI(V4) + 0,25SI(V5) + 0,5SI(V6) + 0,25SI(V7)) / 2,25).

Variables for the eland model were:

total tree density (V1),
a cover abundance score for grass (V2),
a cover-abundance score for forbs (V3) and
grass greenness on a scale of naught to four (V4).

The literature showed that eland preferred *open woodland*. Therefore the response curve of eland to total tree density (V1) dipped sharply after 150 trees/ ha, which was considered as the 'optimal' *tree density for eland*.

Eland would react positively to *an increase* in *grass* density (V2), which was why the grass curve was almost linear. The slight curve was because of the opinion that the relative *increase* in habitat suitability was sharp at low grass densities. The same argument applied to forb density (V3).

The suitability index increased linearly with grass greenness (V4) because of a perceived linear relation between the two variables.

No indication could be found from the literature that some variables contributed *more than* others to eland habitat suitability, and therefore no weighting was done. The HSI score for eland was computed by the arithmetic average of the four *variables*, *i.e.* $(SI(V1) + SI(V2) + SI(V3) + SI(V4))/4$.

4 Summary of Chapter 2

Provisional models were constructed to facilitate the collection of the appropriate *field data*. They were also used to obtain *in* advance a conceptual image of the *results* of the project and to understand the nature and extent of the problem I was dealing with.

The models were based on the *HSI procedure* proposed by the *USF & WS*, *after* a thorough literature study of the habitat requirements of kudu and eland.

The provisional models are presented in figures 1 and 2 (pages 20 and 21).

CHAPTER 3. PILOT STUDY

1 Introduction

A pilot study was carried out to evaluate the applicability of my provisional models. The pilot study was also used to determine the scale at which habitat selection should be studied and to test the feasibility of my techniques of data collection and analysis.

2 Methods

2.1 Landscape map

A preliminary vegetation map of the study area was drawn, with the boundaries of my vegetation types based on 1:50 000 scale aerial photographs. Stratified sampling of the delineated vegetation types was employed to describe the composition and structure of the vegetation.

At points 500 m apart along a pre-selected vehicle route, the three most important woody plant species were listed in order of dominance. The vegetation was evaluated from the vehicle without demarcating plots. The structure of the vegetation was then described as 'open', 'closed' or 'sparse' and 'woodland' or 'shrubland' according to the criteria proposed by Edwards (1983). The data were fed into an electronic database (dBase III plus, Ashton Tate) and by using the alphabetical index facility, indexing on first, second and third species and structure, in that order, a crude classification of sampling points was obtained.

My vegetation types were then transferred to a 1:50 000 scale topographical map. Landscape features such as hills, plains, pans, and river banks were included whereupon land facets were demarcated. The end product was a functional landscape map (Bell & McShane

1984) of the study area (figure 3, p. 30), which was verified and updated during later stages of the project.

2.2 Detailed sampling

More detailed vegetation surveys were done by the Point Center Quarter (PCQ) and Braun-Blanquet methods (Mueller-Dombois & Ellenberg 1974). The methods were used to obtain the parameters for my preliminary models along the regular game census route used by the estate managers (see next section).

One hundred and twenty 25 m² rectangular plots were laid out by stratified random placement to obtain a detailed habitat description along the census route. The stratification was based on the landscape map (figure 3 p. 30). The densities of trees used as model variables (see figures 1 and 2, pp. 20 and 21) were calculated by the PCQ method while grass and forb densities were estimated by the Braun-Blanquet method.

2.3 Data analysis

2.3.1 Use of existing data

Mark Berry (M.P.S. Berry, c/o De Beers Consolidated Mining Company, Stockdale Street, 8301 Kimberley) had done monthly game censuses along a fixed route in the study area since 1983. His data consisted of the species observed, group sizes and a location to the nearest 0,1 km from the beginning of the census route to where the observation was made.

A landscape code, based on my landscapes described earlier, was allocated to each of Berry's observations. Frequencies of observations in each landscape were tabulated and ordinated by correspondence analysis (Greenacre 1984) to explore the landscape relations of kudu and eland.

In addition, the data obtained by the more detailed vegetation surveys (see section 2.2) were assigned 'presence' or 'absence' ratings, depending on whether Berry had observed kudu or eland within 200 m of the location of the plot. The provisional models were validated by applying them to these data.

2.3.2 Correspondence analysis

Correspondence analysis (CA) (Greenacre 1984) was used to explore the landscape relations of kudu and eland after the pilot study. I also attempted to use it as a modeling aid. Its greatest advantage, however, is that it is effective as an exploratory tool to investigate the initial structure of the data (Greenacre 1984). The computer program *SIMCA (Greenacre 1986)* was used for this purpose.

Correspondence analysis is a multivariate eigenanalysis technique which is similar to principal components analysis (PCA). Instead of decomposing the variance along the principal axes, CA decomposes the chi-square statistic for row-column independence along the principal axes. CA is sometimes called reciprocal averaging (RA) (Gauch 1982) but Greenacre & Vrba (1984) note that the two techniques should not be confused. CA makes use of a geometric framework within which it displays data points in multidimensional space. RA makes use of linear regressions to scale the rows and columns of the data matrix, mostly in unidimensional space. The most useful output of CA is the graphical display of the data, which is a low dimensional summary of the relations among the row and column points of a two-way matrix.

The tabular format used was

Rows	Columns		
	Landscape 1	Landscape 2	Landscape n
Summer Kudu present	fr 1	fr 2	fr n
Winter Kudu present	"	"	"
Summer Eland present	"	"	"
Winter Eland present	"	"	"

(fr n = frequency of kudu/eland in landscape n)

2.3.3 Evaluation of provisional models

The preliminary models were applied to each of my detailed vegetation plots. Their ability to correctly predict the presence of kudu or eland was evaluated. The following procedure was followed.

The parameters for the model variables were estimated or measured and the corresponding suitability indices (SI) were read from the SI graphs (see figures 1 & 2, pp. 20 and 21). The SI values were multiplied by the provisional weighting coefficients assigned to the model variables and averaged by weighted averaging (see pp. 23 and 24) to provide a habitat suitability index (HSI). A critical HSI value, which separated plots where kudu or eland were present from those where they were absent, was determined by inspection of the data. The cut-off point was shifted until 'optimal' classification success was obtained, i.e. until as many 'presence' and 'absence' plots were correctly classified.

3 Results

3.1 Ordination of existing data

Figure 3 is a land facet map of the study area. The frequencies of occurrence of Berry's kudu and eland observations within these land facets were ordinated by correspondence analysis.

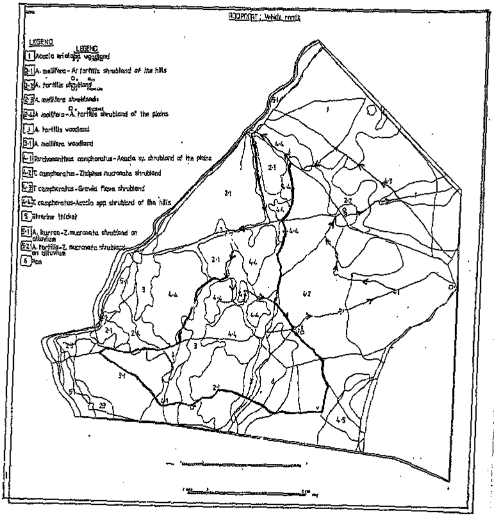

Figure 3. Land facet map of the study area with the census routes superimposed on it (dark lines). Route 1 is symbolized by arrows.

The graphical output of a correspondence analysis of Berry's census data and my preliminary vegetation surveys are presented in figure 4. The tabled output of the row and column masses, contributions and correlations can be seen in table 3.

The ordination indicates that kudu frequent Acacia karroo, Ziziphus mucronata shrubland and riverine thicket in winter and in summer. Eland prefer Acacia woodland in winter and Tarchonanthus camphoratus shrubland in summer.

Figure 4 shows a gradient of closed to open vegetation from left to right. Kudu was associated with closed and eland with open landscapes.

3.2 Model evaluation

The provisional models predicted the presence or absence of kudu or eland correctly for only 52 out of the 120 plots.

3.3 Lessons from the pilot study

After interpreting the results of this pilot ordination, it became apparent that the ordination of land facets and animal occurrences did not yield satisfactory results for predictive modeling purposes. The animals' habitat selection had to be measured at a finer scale to determine which patches within these land facets the browsers preferred, and a more appropriate method than CA had to be used to analyze my data.

The scale at which the pilot study was executed seemed to be too coarse. The use of phytosociological methods to describe animal habitat was also questionable.

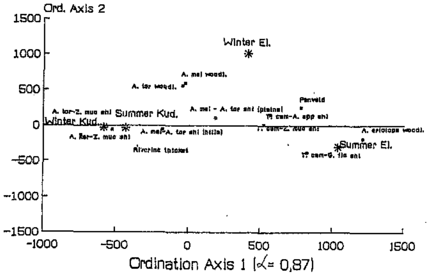

Figure 4. Correspondence analysis of winter and summer kudu and eland landscape relations. El = eland, Kud = kudu, wl = woodland, shl = shrubland, A. kar = A. karroo, A. mel = A. mellifera. A. spp = Acacia spp., A. tor = A. tortilis, G. fla = G. flava, T. cam = T. camphoratus, Z. muc = Z. mucronata

Table 3. *Masses, contributions and correlations* of landscape ordination of kudu and eland (cf. Fig. 4)

Name	Qualt.	Mass	Inr.	Axis 1	Corr.	Contr.	Axis 2	Corr.	Contr.
Row contributions									
A. erioloba woodland	998	88	26	1212	974	296	-191	24	50
A. mellifera - A. tortilis shrubland of the hills	681	86	8	-177	656	6	-35	26	2
A. mellifera - A. tortilis shrubland of the plains	573	52	9	192	438	4	106	135	9
A. tortilis woodland	994	49	34	-23	1	0	587	992	263
A. mellifera woodland	993	66	45	-23	2	0	587	992	532
T. camphoratus - Acacia spp. shrubland of the plains	1000	50	34	564	935	37	148	65	17
T. camphoratus - Z. mucronata shrubland	991	69	44	564	991	51	9	0	0
T. camphoratus - G. flava shrubland	980	78	130	823	807	121	-382	173	176
A. karoo - Z. mucronata shrubland on alluvium	1000	162	89	-522	968	102	-61	14	9
A. tortilis - Z. mucronata shrubland on alluvium	998	250	279	-738	965	313	-137	33	72
Panveld	981	50	68	781	888	70	252	92	49
Column contributions									
Winter kudu	838	83	55	-529	836	53	-30	3	1
Summer kudu	971	237	108	-472	965	121	-36	6	5
Summer eland	1000	130	301	1039	921	323	-304	79	186
Winter eland	1000	50	118	410	142	19	1007	858	791

The CA showed differences in the seasonal habitat selection of the study animals, *especially eland. Based* on that information, I decided to develop seasonal submodels. The preliminary models presented in Chapter 2 did not explain the habitat selection of kudu or eland as determined by Berry's census data. They were therefore discarded.

The provisional models did not seem appropriate for the identification of model variables either. They did, however, provide an indication of the type of data that should not be collected for modeling purposes. I had to *use my own data* to identify a posteriori the most important model variables by the inductive approach (Mentis 1988), after the main data collection phase of the project.

4 Summary of Chapter 3

A pilot study was conducted to test the feasibility of the proposed techniques for field data collection and analysis. In addition the *provisional models* ,were evaluated during this period.

A landscape map of the study area was constructed. It was based on aerial photographs and superficial floristic and structural descriptions done from a vehicle. Detailed vegetation sampling was done for the evaluation of the provisional models. The landscapes and existing census data were ordinated by CA to inspect the large scale habitat relations of kudu and eland.

CA revealed that kudu preferred A. karroo - Z. mucronata woodland and shrubland and riverine thicket. Eland preferred Acacia woodland in winter and T. camphoratus shrubland in summer.

The provisional models performed poorly and were discarded.

I learned the following from the pilot study.

1) CA was not a suitable technique for my modeling purposes.
2) The habitat had to be studied at a finer scale.
3) The inductive approach had to be followed to formulate the models.
4) I had to develop seasonal submodels.

CHAPTER 4. MODEL CONSTRUCTION

1 Introduction

This chapter deals with data-based habitat suitability models for kudu and eland. The models were formulated by applying the insight acquired following the construction of the provisional models and the execution of the pilot study.

The earlier results indicated that the habitat relations of kudu and eland had to be studied at a finer scale than that of the pilot study. I had to construct the models after the data collection phase, as the provisional models were of little practical value. The approach adopted was to measure parameters of habitat variables indicated by the literature and pilot study, at locations where the animals were present and absent respectively. If I could derive a function which discriminated between the presence and absence of the study animals, I would be able to predict suitable habitat for them.

In my new approach I assumed that patches of suitable and unsuitable habitat were interspersed. I attempted to identify patches of Johnson's (1980) third order habitat within first and second order landscape-sized units. I assumed that the size of a patch was determined by the distance at which an animal could distinguish the resources in its vicinity. If the models could identify these patches they would be useful and applicable to other areas.

As proposed by Senft, Coughenour, Bailey, Rittenhouse, Sala & Swift (1987), the selection of large scale habitat units, e.g. landscapes and communities, by herbivores (Johnson's first and second orders of habitat selection) appeared to be a consequence of their third and fourth orders of habitat selection (cf. chapter 1, p. 4).

2 Methods

2.1 Field data

2.1.1 Selection of detailed survey areas

A detailed census route had to be selected to study the small-scale habitat selection of kudu and eland. The habitat would then be described as patches where kudu or eland were present and where they were absent. The census route would be travelled by vehicle to save time and to cover *as large an area as possible in as short a* time [illegible] possible.

[illegible] on the results of the earlier pilot or[illegible] a census route 97 km in length was then selected to cover approximately equal amounts of preferred and non-preferred landscapes for each species. These landscapes were indicated by the correspondence analysis of Berry's census data (see *figure 4). Other considerations when selecting* the survey areas were representativeness of the area for which the models were intended, i.e. the arid savanna regions of the Cape Province, and accessibility, e.g. the condition of the roads.

After travelling the proposed route a few times by day and by night, I realized that it took between five and six hours to cover the entire route, without attempting any habitat surveys. *This was considered to* be impracticable and too time-consuming. Two census routes, 40 and 45 km in length respectively, were then selected to cover the proposed area (figure 3). Data from Route 1 were used to construct the habitat suitability models (considered in this chapter), while data from Route 2 were used for the validation of the models (considered in chapter 5).

2.1.2 Period of data collection

Data collection commenced in June 1987 after completion of the pilot study and continued until February 1988. Floods in the middle of February 1988 precluded field work until the end of May 1988. By that time a full year had elapsed since the beginning of data collection.

2.1.3 Animal surveys

About one half of my time was allocated to the collection of data on the distribution of kudu and eland. Censuses were done from the back of a four wheel drive vehicle.

A census seat was constructed, which consisted of a bucket-type car seat mounted inside an angle iron frame. The seat served several purposes. It increased the number of animal sightings per unit effort, because the increase in height enabled me to see over the high shrubland which predominated the study area. The seat also considerably reduced fatigue compared with standing on the back of the vehicle. In winter it offered some protection against the cold.

I attempted to maintain a constant vehicle speed of as close to 20 km/h as possible during animal censuses. The average speed was about 10 km/h due to rough terrain in places.

Animal censuses were conducted by day and by night, alternating the two routes every other census day. At night a chain was dragged to the point where an animal was observed to facilitate location of the point the following day. Exact localities where the animals were observed at night were marked by barrier tape which was fixed to the plant next to the animal or otherwise tied to a stake. In addition, a brightly coloured stake was placed in the road opposite to the point of observation to locate the point of departure of the drag marks of the chain. The purpose of marking these localities was to perform a habitat analysis at the point of observation in daylight (see next section).

Diurnal censuses were combined with the gathering of habitat data at the localities marked at night. Habitat data were gathered immediately at the localities where animals were observed during the day.

The previous use of Berry's census data and the construction of provisional models gave me some insight into the appropriate census data which should be collected. Regardless of its size, an entire group of animals was used as a unit of observation. Only one habitat analysis plot was done at a locality where an animal or group of animals was observed to ensure the independence of my data. Data on group size and composition was collected, however, as an estimate of browser density within each landscape unit. The latter data will not be used during this project.

The maximum distance at which I thought it would be possible to observe a kudu was measured by range finder to obtain an indication of the total area covered during these animal censuses (Collinson 1985).

2.1.4 Habitat surveys

i) Where the animals were present

Habitat surveys were done by a modified version of the Point Centre Quarter (PCQ) method (Mueller-Dombois & Ellenberg 1974). A chain cross was laid out at the point of observation with one of its axes perpendicular to the census route. Each plant species taller than

0,5 m which occurred within a radius of a 10 m was scored according to the number of quadrants in which it occurred. Plants smaller than 0,5 m in height were difficult to locate and were considered to be insignificant food sources. This view is supported by Owen-Smith & Cooper (1987a).

I initially experimented with nested plots to derive the most practicable and efficient plot size. *Ferrar & Walker (1974) used a circle of 5 m radius for* a similar study in the Kyle National Park, Zimbabwe, while Owen-Smith & Cooper (1987a, 1987b) considered 10 m to be the distance at which a kudu would be able to select a food item in the Nylsvley Nature Reserve, Northern Transvaal.

Total woody plant density was calculated by the PCQ method by pacing the distance to the nearest plant in each of the four quadrants. The average area per plant was calculated by squaring the average of the four nearest plant distances (Mueller-Dombois & Ellenberg 1974).

The structure of the vegetation was additionally quantified by estimating the crown:gap ratio *(Edwards* 1983) at 1,8 m above ground level between the nearest two plants not occurring in the same quadrant. The crown:gap ratio is a dimensionless measure, estimated as the ratio of the crown width (always a magnitude of one) to the number of crown diameters that could fit in the space between the crowns (figure 5). It must be noted that the crown:gap value used by Edwards, which I adopted, is strictly spoken the gap:crown value. By convention, however, the crown width is given a value of one, and the crown:gap ratio is then expressed as the value of the gap ratio (Prof. G.K. Theron, Botany Dept., University of Pretoria, 0001, pers. comm.).

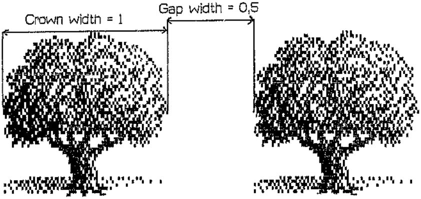

Figure 5. The crown:gap ratio as proposed by Edwards (1983). In this example the ratio is 0.5 i.e. the space between the crowns is approximately half the crown width.

I believed that estimating the crown:gap ratio would approximate the way the animals perceived their surroundings. In addition it was a time saving method if compared with actual measurements using, for example, a measuring tape.

A shade tree was defined as a tree or large shrub of which the canopy could be entered by kudu (cf. Hirst 1975). The distance to the nearest shade tree was paced if it was closer than 30 m or estimated if it was further. Initially a range finder was used for this purpose until the necessary skills to estimate the distance by eye were developed.

Grass availability was estimated as the percentage projected canopy cover. This variable was applicable to habitat selection by eland only and was not included in the kudu model, as all the literature pointed to kudu consuming very little grass.

Plots where kudu were observed were searched for sign of eland and vice versa.

ii) Independent surveys

Independent habitat surveys were done on a monthly basis to obtain an index of the availability of the various habitat components (Neu, Byers & Peek 1974). Systematic plots were placed along both routes and the entire routes were sampled with every series of plots. The position of the first plot of every series of systematic plots was determined by a random number and all subsequent plots were spaced three kilometers apart. At three km intervals a random digit was used to determine whether the plot would be situated to the left or to the right of the road. A random number between zero and 600 was then used to determine the number of paces to the centre of the plot at a right angle to the road. Both routes were sampled on a monthly basis, yielding at least 28 samples per month.

These independent plots were searched for any recent (fresher than seven days old) sign of kudu or eland. It was assumed that animal tracks and the shiny mucus layer of dung remained visible for approximately seven days, depending on weather conditions. Where no sign could be found, the plot was assigned an 'absent' rating for either or both of the species.

2.1.5 Phenology of browse plants

Data on the phenology of woody plants in the Northern Cape were not available from the literature. I therefore had to collect them as part of this study. Plant phenophase influences the feeding preferences, and hence the habitat selection, of browsers (Owen-Smith & Cooper 1987e, Robbins, Hanley, Hagerman, Hjeljord, Baker, Schwartz & Mautz 1987). It was also important to know which plants could be excluded as variables in the seasonal models due to their being deciduous.

The phenophase of the closest individual of each species to an independent habitat plot was categorized according to its leaf stage, fruit stage and flowering stage. The following categories were recognized: leaves: *'full', 'budding', 'dropping' or 'absent'*; flowers: 'full', 'buds', 'dropping' or 'absent', and fruit: 'full', 'unripe', 'dropping' or 'absent'. At least ten individuals of each plant species in the study area were sampled monthly, with the exception of locally rare species.

2.1.6 Browse class data

Plant species were placed in browse categories based on the amount of growth removed by herbivores. The purpose of this exercise was to later exclude plant species as model variables which hardly ever showed sign of browse removal. The browse class data were also used to place plant species in palatability categories.

The plant was viewed from one angle only and the outside twigs were examined for sign of being browsed. Four browse categories were recognized: '0' for no visible *browse removal*, '1' *for some but not more than* 10% of the twigs showing sign of being browsed, '2' for 10% or more but not more than 30% of the twigs showing sign of being browsed, and '3' for more than 30% of the twigs showing sign of being browsed (cf. Dickenson 1978; Frelich & Lorimer 1985).

2.1.7 Data capturing

All data were entered into a programmable Psion Organizer pocket sized computer. The computer made use of EPROM data packs to store as much as 128 Kilobytes of data at a time. Customized data storage programs were written in OPL (Organizer's Programming Language). After every field trip the field computer was interfaced using an RS232 cable to a DOS operated personal computer. The data were uploaded in ASCII format and imported by an electronic database.

2.2 Data analysis

2.2.1 *Phenograms*

Phenophases were presented in the form of column-shaped phenograms (Skarpe & Bergstrom 1986). The proportion of sampled individuals bearing leaves represented the width of the column, while the months of the year *formed the vertical* dimensions of the column. The left half of the column was reserved for mature leaves and the right half for new leaves. Fruit and flowering times were symbolized *by vertical asterisks and plus* signs respectively (figure 6, p. 52).

2.2.2 Preference for structural variables

Confidence intervals for the proportional utilization of categories were *calculated to ascertain which* structural variable categories were significantly preferred (Neu et al. 1974). These variables included the crown:gap ratio, distance to the nearest shade tree and grass density.

The formula was

$\{pu \pm z_{(1-\alpha/2k)}\sqrt{pu(1-pu)/n}\}$ where

pu = proportional utilization of the category

α = the significance level required

k = the number of categories

n = the *sample size*, i.e. the *number* of observations in all categories

The scaling down of α *by dividing it by 2k was* necessary to determine the family of confidence intervals when the number of categories exceed one. The resulting statistic is called the Bonferroni-z confidence interval as opposed to an 'ordinary' interval, because α partially depends on the number of simultaneous estimates (k, (Neu *et al.* 1974). The 90% family of confidence intervals was used.

2.2.3 Discriminant function analysis

Discriminant function analysis (DFA) (Fisher 1936) was used as a model developing tool for two reasons. First it indicated the important variables which discriminated significantly between the presence and *absence of the study animals (Ferrar & Walker 1974).* Second the end product was a linear model which could be used to classify unknown data (Krausman & Leopold 1986; Mosher, Titus & Fuller 1986 *inter alia*).

DFA is a multivariate classification technique which is based on eigen-analysis (Gauch 1982). It calculates a linear function to separate two or more groups of data as effectively as possible if the affiliation of the members of each group is known. The discriminant function consists of a series of linearly additive weighting coefficients for each input variable. Variables with high discriminating power receive larger weighting coefficients than variables with low discriminating power (Fatti, Hawkins & Raath *1982, Van Laar 1987). The unstandardized* discriminant function takes the form

$$C_i = C_{i1}V_1 + C_{i2}V_2 + C_{i3}V_3 + \ldots. + C_{ij}V_j + C_{i0}$$

where C_i is the classification score, C_{ij} is a weighting coefficient, V is the raw variable value and C_{i0} is a constant. The standardized version is equivalent to the unstandardized with the constant removed. The weighting coefficients are then transformed to compensate for the removal. The Statgraphics computer package (Statistical Graphics Corporation 1986) was used.

The discriminant function can be applied to an independent datum with unknown affiliation which can then be assigned to the group closest to its discriminant function score (cf. Fabricius, Van Hensbergen & Zucchini _in press_). DFA assumes that input variables are independent, as it makes use of the within-groups covariance matrix to calculate the discriminant function. The assumption that the *variables are uncorrelated is not strict* but should be borne in mind when interpreting the data (Prof. W. Zucchini, Dept. of Mathematical Sciences, University of Cape Town, Rondebosch 7700 pers. comm.). Another assumption is that the data are multivariate normally distributed.

2.2.4 Model construction

i) Submodels

The literature pointed to plant seasonality being an important determinant of the feeding preference of herbivores (Owen-Smith 1982; Owen-Smith & Cooper 1987e; McNaughton 1985). The CA of Berry's census data (figure 4) also showed seasonal habitat preferences by eland. I decided to construct seasonal submodels for kudu and eland, rather than a single model for the entire year.

The phenograms described earlier were used to identify *two major phenophases which* could be subdivided into four minor ones. Climatic data and the opinion of experts were also consulted before the seasons for the final submodels were decided.

During the early stages of data analysis it became apparent that I did not have enough data to construct and verify four submodels. Early and late winter submodels were then combined to form winter submodels. The same was done with the spring and summer submodels to form a summer submodel. The winter and summer submodels were based on Route 1 data only and the Route 2 data were set aside for the validation of the models.

ii) Combined species

Some plant species were infrequently encountered in the study area and could not be used as input variables. The reason for this was that, if they were identified as important variables, one would have expected many of the potential habitat plots to have been misclassified as non-habitats due to the rare species being absent from the plot. These locally rare species therefore had to be combined with other, more common species to which they were functionally related from a browser's point of view.

All plant species which were sampled more than five times during the study period were therefore incorporated in a species-by-attributes matrix. The attributes selected were those of importance to browsers, i.e. growth form, leaf size, presence of thorns or spines, chemical deterrents, seasonality and palatability (Owen-Smith 1982). The latter attribute was derived from my browse class data, personal experience and the limited available literature. A value of either one or zero was entered in the matrix, depending on whether an attribute was present or absent.

The matrix was classified by Two Way Indicator Species Analysis (TWINSPAN, Hill 1979) and Cluster Analysis (COMPCLUS, Gauch 1979). As a precaution against losing information at an early stage, only the locally rare species were assigned to combined species classes.

iii) *Index curves for structural variables*

Habitat suitability rarely responds linearly to an increase in the parameters of a continuous variable (U.S. Fish & Wildlife Service 1980, 1981). To objectively determine the *shape of the response curve*, an index to the preference of an animal for different categories of structural variables has to be found.

Variables were categorized and chi-square goodness-of-fit statistics were calculated for each structural variable. For the crown:gap ratio, the six categories suggested by Edwards (1983) were used, i.e. ≤0,2; >0,2-0,9; >0,9-2,0; >2,0-8,5; >8.5-30; >30. For proximity of shade, six categories were *distinguished*, i.e. ≤5 *m;* >5-10 m; >10-30 m; >30-60 m; >60-100 m; >100 m. For grass density, which was only applicable to the eland models, four categories of percentage projected canopy cover were recognized: ≤5 %; >5 % - 10 %; >10 - 20 %; >20 %. The expected frequencies of an animal's association with a category were obtained by multiplying the proportional availability of the category by the total number of observations of that animal. The null hypothesis was that the observed frequencies of observations equaled the expected frequencies of observations. Structural variables for which H_0 was rejected at the 90% confidence level, were included in the analysis.

Preference indices (p) (Petrides 1975) were calculated for each variable category by dividing the proportional utilization (pu) of a category by its proportional availability (pa) (p = pu/pa). A preference index greater than one means that the browser prefers that category, while an index of smaller than one means that the category is neglected.

The preference indices were transformed to (preference index - 1) values, i.e. neglected categories received negative values. The transformed values underwent a second transformation, this time to scale them to values between 0 and 1. The preference indices for a variable were simply divided by the largest preference index of all categories of that variable.

The categories were then plotted against their transformed preference indices to obtain suitability index curves.

iv) Sensitivity analysis

A sensitivity analysis was done on the structural variable response curves (SI curves) and floristic variables to ascertain how this would affect the model output. The SI curve shapes were manipulated several times and the model performance assessed after every iteration. The objective was to generate SI curves which were as close as possible to either positively linear, negatively linear, Gaussian or U-shaped for each variable. This was done until the best possible results were obtained within the time limitations of the project.

Two of the submodels, i.e. the summer kudu model and summer eland model, were used on an experimental basis. Inferences were made from their output after the modification of the SI curves and applied to the other submodels.

v) Weighting of variables

Linear discriminant functions (Fisher 1936) were used to discriminate between the presence and absence of the animals (Krausman & Leopold 1986) with the SI values for structural variables and presence/absence transformed floristic variables as input. For the variables depicting vegetation structure, the SI values were read from the variable response curves. For the categories received negative values. The transformed values underwent a second transformation, this time to scale them to values between 0 and 1. The preference indices for a variable were simply divided by the largest preference index of all categories of that variable.

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A habitat suitability index (HSI) was calculated by multiplying the *discriminant* function coefficients by the SI values. Only data originating from Route 1 were used for the following calculations.

Variables with low discriminant function coefficients (<0,05) were removed and new discriminant functions were calculated for the remaining variables. This was done several times for each submodel until the best classification power of the dependent data was obtained.

The correlation matrix for each discriminant function was calculated and highly correlated variables (P ≤ 0,05) were also omitted and replaced in a stepwise manner. This was done to ascertain how sensitive the model was to the omission of the correlated variables. The Statgraphics computer package (*Statistical Graphics* Corporation, 1986) was used.

vi) Decision rules

The objective when determining a cut-off point or critical value was to minimize the cost of *misclassification*. The cut-off point between the 'presence and 'absence' HSI scores was therefore shifted to a value at which the *maximum* number of observations were correctly classified, as proposed by Snedecor & Cochran (1974, p. 415). I assumed that the cost of misclassifying either a 'presence' or an 'absence' observation was equal.

2.2.5 Verification of models

The verification of the models involved subjectively scrutinizing them for inaccuracies (Farmer, Armbruster, Terrell & Schroeder 1982). The models were applied to the dependent data and the number of correctly classified presence and absence plots were counted. A chi-square test was done to determine whether the observed classification power of my models differed significantly from a random classification. The expected number of correctly classified plots were determined as 50% of the total number of plots, which is what would be expected from a random classification.

The results of the discriminant analysis, chi-square tests and Bonferroni-z confidence intervals were used to verify the inclusion or exclusion of the appropriate variables. Personal opinion also played a role in determining whether the unverified models had the potential to reflect [illegible] abstraction of the real world situation (Sta [illegible] leloch 1986). The habitat suitability index scores of the 'presence' and 'absence' data were additionally compared by the Mann-Whitney U-test to determine whether the differences between the medians were significant (cf. Fabricius *et al.* in press.)

3 Results

3.1 Phenophases

The phenograms (figure 6) of my data revealed two main phenophases: a period of food abundance (September to May) and a period of food shortage (June to August). The two major phases could be broken down into two minor phenophases each: September and October (green leaf and flower period), November to May (mature leaf period), June and July (less than 50% of the deciduous

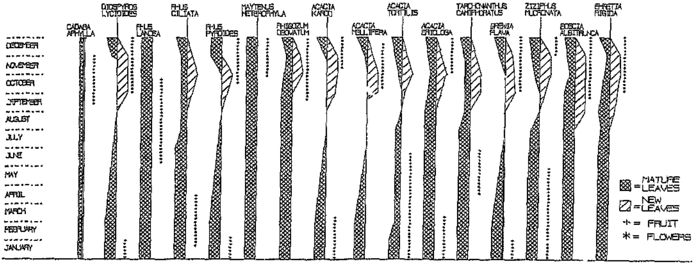

Figure 6. *Phenograms of the most important browse in the study area.*

species have lost their leaves) and August (more than 50% of the deciduous species have lost their leaves).

Based on the phenograms, I initially developed four seasonal submodels for kudu and eland respectively. Due to a shortage of data the submodels were reduced to two for each browser, i.e. a winter submodel for the period June to August and a summer submodel for the period September to May.

3.2 Utilization-availability analysis of structural variables

The results of the preference calculations for the structural variables crown:gap ratio, nearest shade tree and grass density are summarized in tables 4 and 5.

In summer, kudu utilized vegetation with a crown:gap ratio (at 1,8 m above ground level) of <0,9, significantly in excess to its availability (table 4). Vegetation with a crown:gap ratio of 0,9 – 2 was utilized more than its availability, but not significantly so, while vegetation with a crown:gap of 2 – 8,5 was utilized less than its availability, once more not significantly. Vegetation with a crown:gap >8,5 was utilized significantly less than its availability.

Summer kudu showed a significant preference for patches where the nearest shade tree was closer than 5 m. Patches where the nearest shade tree was farther than 5 m and less than 10 m away were utilized slightly more than their availability, but not significantly so. Patches where the nearest shade tree was farther than 30 m away were significantly avoided, with the exception of patches where the nearest shade was between 30 and 60 m away, which were avoided, but not significantly.

Table 4. Bonferroni-z confidence limits for utilization of structural variables by kudu

RESOURCE	Proportional utilization = Pu	Proportional availability = Pa	Bonferroni-z confidence intervals = 90%		PREFERENCE		AVOIDANCE		CHI-SQUARE
			Pu > (Lower)	Pu < (Upper)	Significant	Insignificant	Insignificant	Significant	
SUMMER KUDU									
Crown:gap ratio at 2m									212,2
c:g <0,2	0,23	0,05	0,14	0,32	X				
c:g 0,2 - 0,9	0,13	0,02	0,06	0,21	X				
c:g 0,9 - 2	0,12	0,06	0,05	0,19		X			
c:g 2 - 8,5	0,33	0,4	0,23	0,43			X		
c:g 8,5 - 30	0,17	0,31	0,09	0,24				X	
c:g >30	0,02	0,16	0	0,06				X	
Nearest shade tree									393,5
Shade < 5m	0,46	0,06	0,35	0,56	X				
Shade 5 - 10m	0,08	0,07	0,02	0,14		X			
Shade 10 - 30m	0,16	0,23	0,08	0,23				X	
Shade 30 - 60m	0,13	0,29	0,06	0,2			X		
Shade 60 - 100m	0,1	0,16	0,04	0,17				X	
Shade >100m	0,08	0,19	0,02	0,14					
WINTER KUDU									
Crown:gap ratio at 2m									86,6
c:g <0,2	0,15	0,05	0,09	0,22	X				
c:g 0,2 - 0,9	0,05	0,02	0,01	0,09		X			
c:g 0,9 - 2	0,15	0,06	0,09	0,22	X				
c:g 2 - 8,5	0,41	0,4	0,31	0,5		X			
c:g 8,5 - 30	0,21	0,31	0,13	0,29				X	
c:g >30	0,03	0,16	0	0,06				X	
Nearest shade tree									171,8
Shade < 5m	0,29	0,06	0,2	0,38	X				
Shade 5 - 10m	0,07	0,07	0,02	0,12		X	X		
Shade 10 - 30m	0,25	0,23	0,17	0,33		X			
Shade 30 - 60m	0,22	0,29	0,14	0,3			X		
Shade 60 - 100m	0,06	0,16	0,01	0,1				X	
Shade >100m	0,11	0,19	0,05	0,17				X	

Table 4. Bonferroni-z confidence limits for utilization of structural variables by kudu

RESOURCE	Proportional utilization = Pu	Proportional availability = Pa	Bonferroni-z confidence intervals = 90% Pu > (Lower)	Pu < (Upper)	PREFERENCE Significant	Insignificant	AVOIDANCE Insignificant	Significant	CHI-SQUARE
SUMMER KUDU									
Crown:gap ratio at 2m									212,2
c:g <0,2	0,23	0,05	0,14	0,32	X				
c:g 0,2 - 0,9	0,13	0,02	0,06	0,21	X				
c:g 0,9 - 2	0,12	0,06	0,05	0,19		X			
c:g 2 - 8,5	0,33	0,4	0,23	0,43			X		
c:g 8,5 - 30	0,17	0,31	0,09	0,24				X	
c:g >30	0,02	0,16	0	0,06				X	
Nearest shade tree									393,5
Shade < 5m	0,46	0,06	0,35	0,56	X				
Shade 5 - 10m	0,08	0,07	0,02	0,14		X			
Shade 10 - 30m	0,16	0,23	0,08	0,23				X	
Shade 30 - 60m	0,13	0,29	0,06	0,2			X		
Shade 60 - 100m	0,1	0,16	0,04	0,17				X	
Shade >100m	0,08	0,19	0,02	0,14					
WINTER KUDU									
Crown:gap ratio at 2m									86,6
c:g <0,2	0,15	0,05	0,09	0,22	X				
c:g 0,2 - 0,9	0,05	0,02	0,01	0,09		X			
c:g 0,9 - 2	0,15	0,06	0,09	0,22	X				
c:g 2 - 8,5	0,41	0,4	0,31	0,5		X			
c:g 8,5 - 30	0,21	0,31	0,13	0,29				X	
c:g >30	0,03	0,16	0	0,06				X	
Nearest shade tree									171,8
Shade < 5m	0,29	0,06	0,2	0,38	X				
Shade 5 - 10m	0,07	0,07	0,02	0,12		X	X		
Shade 10 - 30m	0,25	0,23	0,17	0,33		X			
Shade 30 - 60m	0,22	0,29	0,14	0,3			X		
Shade 60 - 100m	0,06	0,16	0,01	0,1				X	
Shade >100m	0,11	0,19	0,05	0,17				X	

Table 5. Bonferroni-z confidence intervals for utlization of structural variables by eland

RESOURCE	Proportional utilization = Pu	Proportional availability = Pa	Bonferroni-z confidence intervals = 90%		PREFERENCE		AVOIDANCE		CHI-SQUARE
			Pu > (Lower)	Pu < (Upper)	Significant	Insignificant	Insignificant	Significant	
SUMMER ELAND									
Crown:gap ratio at 2m									7,8
c:g <0,2	0,1	0,05	0,03	0,18		X			
c:g 0,2 - 0,9	0,02	0,02	0	0,06					
c:g 0,9 - 2	0,05	0,07	0	0,11			X		
c:g 2 - 8,5	0,38	0,4	0,26	0,5			X		
c:g 8,5 - 30	0,27	0,31	0,16	0,38			X		
c:g >30	0,18	0,16	0,08	0,27		X			
Nearest shade tree									33,9
Shade < 5m	0,19	0,06	0,09	0,28	X				
Shade 5 - 10m	0,04	0,07	0	0,09			X		
Shade 10 - 30m	0,23	0,23	0,13	0,33		X	X		
Shade 30 - 60m	0,21	0,29	0,11	0,3			X		
Shade 60 - 100m	0,19	0,16	0,09	0,28		X			
Shade >100m	0,15	0,14	0,07	0,24		X			
% Projected canopy cover									13,8
Grass < 5%	0,23	0,31	0,13	0,33			X		
Grass 5 - 10%	0,24	0,33	0,13	0,34			X		
Grass 10 - 20%	0,38	0,27	0,26	0,5		X			
Grass >20%	0,15	0,09	0,07	0,24		X			
WINTER ELAND									
Crown:gap ratio at 2m									34,2
c:g <0,2	0,11	0,05	0,05	0,16	X				
c:g 0,2 - 0,9	0,03	0,02	0	0,06		X			
c:g 0,9 - 2	0,13	0,06	0,07	0,2	X				
c:g 2 - 8,5	0,37	0,4	0,28	0,45			X		
c:g 8,5 - 30	0,27	0,31	0,19	0,35			X		
c:g >30	0,1	0,16	0,04	0,15				X	
Nearest shade tree									63,7
Shade < 5m	0,19	0,06	0,12	0,26	X				
Shade 5 - 10m	0,07	0,07	0,02	0,11		X	X		
Shade 10 - 30m	0,21	0,23	0,14	0,28			X		
Shade 30 - 60m	0,24	0,29	0,16	0,31			X		
Shade 60 - 100m	0,12	0,16	0,06	0,18			X		
Shade >100m	0,17	0,14	0,11	0,24		X			
% Projected canopy cover									2,8
Grass < 5%	0,44	0,41	0,35	0,53		X			
Grass 5 - 10%	0,26	0,24	0,19	0,34		X			
Grass 10 - 20%	0,21	0,26	0,14	0,29			X		
Grass >20%	0,08	0,1	0,03	0,13			X		

Winter kudu (table 4) significantly preferred patches with a crown:gap ratio closer than 0,2. Patches with a crown:gap ratio between 0,2 and 0,9 were preferred, but not significantly so, while they showed a significant preference for a crown:gap ratio between 0,9 and 2,0. Patches with a crown:gap > 8,5 were significantly avoided in winter.

In winter kudu significantly preferred areas where the nearest shade tree was closer than 5 m. Patches where the nearest shade was between 5 and 60 m away, were avoided, but not significantly, while patches where shade was farther than 60 m away were significantly avoided.

Eland had no significant preference for any crown:gap ratio in summer (table 5). They had a significant preference for areas where the closest shade was less than 5 m away. Patches where the closest shade tree was farther than that were neither significantly preferred nor avoided. They avoided patches where the percentage projected canopy of the grass was less than 10%, but not significantly. Patches where the grass cover was higher than 10% were insignificantly preferred. The chi-square value for grass selection was significant, however.

In winter, eland significantly preferred patches with a crown:gap ratio of closer than 0,2 (table 5). They showed an insignificant preference for a crown:gap ratio of 0,2 - 0,9 but significantly preferred patches where the crown:gap ratio was between 0,9 and 2,0. Eland avoided patches where the crown:gap ratio ranged from 2 to 30, but not significantly. They significantly avoided patches where the crown:gap ratio was greater than 30.

3.3 Combined species

Figure 7 is a two-way table based on a TWINSPAN of the most important trees and shrubs in the study area. Because of its relation to palatability, the variable pertaining to secondary chemicals was omitted from the final analysis. Morphological attributes received either 0 or 1 values, depending on whether they were absent or present.

Three combined species groups were established: the 'Palatable Evergreen' group, consisting of Rhus lancea, Maytenus heterophylla, Rhigozum obovatum, Boscia albitrunca and Cadaba aphylla; the 'Gre-pyr' group consisting of Grewia flava and Rhus pyroides and the 'Ehr-hir' group consisting of Ehrethia rigida and Lycium hirsitum.

The 'Palatable Evergreen' group have a shrublike growth form, contain leaves for more than 11 months of the year and are well utilized. It was established as a result of the infrequent occurrence of R. lancea, M. heterophylla and R. obovatum.

The 'Gre-pyr' group are shrubs with broad leaves and variable palatability. This group was established due to the infrequent occurrence of R. pyroides.

The 'Ehr-hir' group consists of Ehrethia rigida and Lycium hirsitum. They are shrubs of variable palatability which are mostly palatable, and are short-deciduous, i.e. they lose their leaves for a very short period only. This group was established as a result of the low frequency of occurrence of L. hirsitum.

Several other functional species combinations could possibly have been recognized on this basis. This would have served no purpose, however, as the other species occurred in high enough abundances to allow them to be

	Large leaves	Variable palatab.	Early leaves	Short-decid.	Thorns	Palatable	Evergreen	
A. mellifera	-	-	1	-	1	-	-	0000
A. tortilis	-	-	-	1	1	-	-	0000
D. lycioides	-	-				-	-	0000
P. spinosum	-	-				-	-	0000
A. erioloba	-	1	1	1	1	-	-	0001
R. ciliata	-	1	1	1	1	-	-	0001
Z. mucronata	1	1	1	1	1	-	-	0010
G. flava	1	1	1	-	-	-	-	0011
R. pyroides	1	1	-	-	1	-	-	0011
E. rigida	-	1	1	1	-	1	-	010
L. hirsitum	1	1	-	1	1	1	-	011
T. camphoratus	1	1	-	-	-	-	1	10
A. karroo	-	-	-	-	1	1	-	1100
R. lancea	1					1	1	1101
M. heterophylla	-	-	-	-	1	1	1	1101
R. obovatum	-	-	-	-	1	1	1	1101
B. albitrunca	-	-	-	-	-	1	1	111
C. aphylla	-	-	-	-	-	1	1	111
	0	0	0	0	0	1	1	
	0	0	1	1	1	0	1	
		0	1	0	0	1		
				0	1			

Figure 7. Two-way table resulting from a TWINSPAN of the morphological attributes of the most important browse in the study area. Plant species are along the left-hand margin and morphological attributes along the top margin. Hierarchies are denoted along the right-hand and bottom margins in binary notation. As opposed to decimal notation, this facilitates visual interpretation of the classes. Horizontal lines demarcate functional plant guilds identified, and vertical lines separate attribute classes. Morphological properties received either 0 or 1 values, depending on their absence or presence

incorporated as entities in the analysis. By incorporating them as combined functional species, the dimensionality of my data would have been reduced at an early stage, with the risk of losing information.

3.4 Suitability index curves

A sensitivity analysis on the SI curves of the floristic variables revealed that the models performed better after the values were transformed. After the transformation, a floristic variable received a value of either one or zero, depending on whether the plant species was present or absent within the 10 m circle.

SI curves for the structural variables, based on the transformed preference indices of the variable categories, are shown in figures 8 and 9. A sensitivity analysis was done on the shape of the curves. It made no significant difference to the classification power of the discriminant function when the curves were simplified to linearity. There was little difference between the complex SI curves for summer and winter kudu. The simplified SI curves for the summer and winter kudu models were therefore identical.

3.5 Discriminant functions

The discriminant function coefficients for the transformed floristic variables and SI values of structural variables are shown in figures 10 and 11. The horizontal dimensions of the bars represent the relative contributions of variables to the models.

For kudu in summer, the important plant species that discriminated between the presence and absence of kudu were *A. mellifera*, *Z. mucronata*. *A. karroo* and the structural variables crown:gap and shade (figure 10 a). The function for summer kudu was

$$HSI = 0,48V1 + 0,36V2 + 0,4V3 + 0,35V4 + 0,39V5$$

where

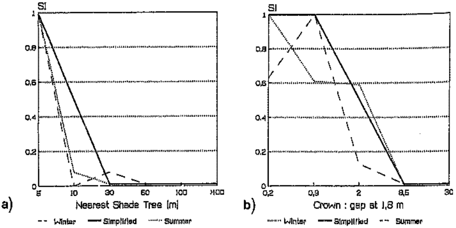

Figure 8. Suitability index curves for proximity of shade (a) and crown:gap ratio (b) applicable to the summer and winter kudu models. SI = suitability index. Simplified curves are linear versions of the more complex SI curves

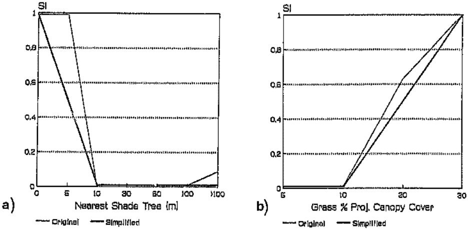

Figure 9. Suitability index curves for proximity of shade in the winter eland model (a) and percentage canopy cover of grass in the summer eland model (b)

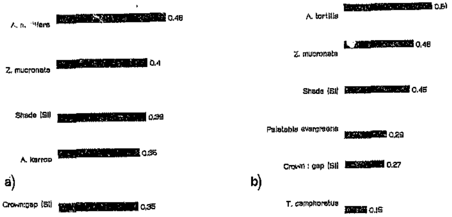

Figure 10. Functions discriminating between the presence and absence of kudu in (a) summer and b) winter. Variables pertaining to plant species were presence/absence transformed while parameters for structural variables (shade and crown:gap ratio) were obtained from SI graphs (figure 8)

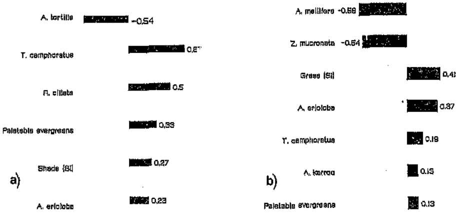

Figure 11. Functions discriminating between the presence and absence of eland in a) summer and b) winter

HSI = habitat suitability index
V1 = presence of *A. mellifera*
V2 = presence of *A. karroo*
V3 = presence of *Z. mucronata*
V4 = SI for crown:gap ratio (from fig. 8b, p. 60)
V5 = SI for proximity of shade (from fig. 8a p. 60)

For kudu in winter, *A. tortilis*, *Z. mucronata*, 'Palatable evergreens', *T. camphoratus*, crown:gap (SI) and shade (SI) discriminated between the presence and absence of kudu (figure 10 b).

The function for winter kudu was

$\text{HSI} = 0{,}61V1 + 0{,}15V2 + 0{,}48V3 + 0{,}29V4 + 0{,}27V5 + 0{,}45V6$ where

V1 = presence of *A. tortilis*
V2 = presence of *T. camphoratus*
V3 = presence of *Z. mucronata*
V4 = presence of 'palatable evergreens'
V5 = SI for crown:gap ratio (from fig. 8b p. 60)
V6 = SI for proximity of shade (from fig. 8a p. 60)

For eland in summer, variables *A. mellifera*, *A. erioloba*, *Z. mucronata*, *T. camphoratus*, 'Palatable evergreens', *A. karroo* and grass % canopy cover discriminated between the presence and absence of eland. *A. mellifera* and *Z. mucronata* made a negative contribution to the discriminant function (figure 11 a).

The function for summer eland was

$\text{HSI} = -0{,}58V1 - 0{,}54V2 + 0{,}37V3 + 0{,}13V4 + 0{,}19V5 + 0{,}13V6 + 0{,}41V7$ where

V1 = presence of *A. mellifera*
V2 = presence of *Z. mucronata*
V3 = presence of *A. erioloba*
V4 = presence of *A. karroo*
V5 = presence of *T. camphoratus*
V6 = presence of 'palatable evergreens'
V7 = SI for grass density (from fig. 9b p. 60).

HSI = habitat suitability index
V1 = presence of *A. mellifera*
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V3 = presence of *Z. mucronata*
V4 = SI for crown:gap ratio (from fig. 8b, p. 60)
V5 = SI for proximity of shade (from fig. 8a p. 60)

For kudu in winter, *A. tortilis*, *Z. mucronata*, 'Palatable evergreens', *T. camphoratus*, crown:gap (SI) and shade (SI) discriminated between the presence and absence of kudu (figure 10 b).

The function for winter kudu was

$HSI = 0,61V1 + 0,15V2 + 0,48V3 + 0,29V4 + 0,27V5 + 0,45V6$ where
V1 = presence of *A. tortilis*
V2 = presence of *T. camphoratus*
V3 = presence of *Z. mucronata*
V4 = presence of 'palatable evergreens'
V5 = SI for crown:gap ratio (from fig. 8b p. 60)
V6 = SI for proximity of shade (from fig. 8a p. 60)

For eland in summer, variables *A. mellifera*, *A. erioloba*, *Z. mucronata*, *T. camphoratus*, 'Palatable evergreens', *A. karroo* and grass % canopy cover discriminated between the presence and absence of eland. *A. mellifera* and *Z. mucronata* made a negative contribution to the discriminant function (figure 11 a).

The function for summer eland was

$HSI = -0,58V1 - 0,54V2 + 0,37V3 + 0,13V4 + 0,19V5 + 0,13V6 + 0,41V7$ where
V1 = presence of *A. mellifera*
V2 = presence of *Z. mucronata*
V3 = presence of *A. erioloba*
V4 = presence of *A. karroo*
V5 = presence of *T. camphoratus*
V6 = presence of 'palatable evergreens'
V7 = SI for grass density (from fig. 9b p. 60).

In winter, the variables A. tortilis, 'Palatable evergreens', A. erioloba, T. camphoratus, R. ciliata and shade discriminated between the presence and absence of eland. A. tortilis contributed negatively towards the discriminant function (figure 11 b).

The function for winter eland was

HSI = - 0,54V1 + 0,23V2 + 0,67V3 + 0,33V4 + 0,5V5 + 0,27V6 where

V1 = presence of A. tortilis
V2 = presence of A. erioloba
V3 = presence of T. camphoratus
V4 = presence of 'palatable evergreens'
V5 = presence of R. ciliata
V6 = HSI for proximity of shade (from fig. 9a p. 60).

The distributions of the 'present' and 'absent' HSI scores of the dependent data were explored by means of 'Box-and-Whisker' plots (Tukey 1977) (figures 12 a to d).

3.6 Verification of models

The models' ability to classify the dependent (Route 1) data was acceptable within the context of the model objectives and statistically significant.

The summer kudu model classified 62% of the 'Presence' plots (n = 74) and 82% of the 'Absence' plots (n = 73) correctly (Eigenvalue = 0,41; chi-square = 49,05; d.f. = 5; P < 0,00001). The discriminant scores of the two categories were separated with a high degree of significance ($P \approx 2 \times 10^{-10}$, Mann-Whitney U-test).

The winter kudu model was able to classify 82% of the 'Presence' data (n = 87) and 80% of the 'Absence' data (n = 56) correctly (Eigenvalue = 0,74; chi-square = 76,4; d.f. = 6; P < 0,00001). The discriminant

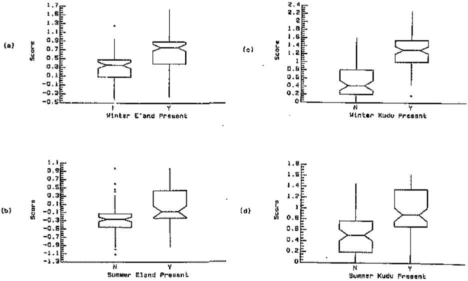

Figure 12. Distribution of 'present' (Y) and 'absent' (N) data on the discriminant function. a) eland in winter and b) in summer; c) kudu in winter, and d) in summer. The notches represent the 95% confidence intervals, while the vertical limits of the boxes represent the interquartile values of the range. The central horizontal lines represent the medians

scores of the two categories were significantly separated ($P \approx 1,8 \times 10^{-14}$).

The summer eland model could classify 64% of the 'Presence' data ($n = 56$) and 77% of the 'Absence' data ($n = 92$) correctly (Eigenvalue = 0,19 chi-square = 24,94 d.f. = 7 $P = 0,0008$). The two categories were significantly distinct ($P \approx 3 \times 10^{-7}$).

The winter eland model classified 65% of the 'Presence' data ($n = 103$) and 72% of the 'Absence' data ($n = 75$) correctly (Eigenvalue = 0,18 chi-square = 28,96 $P = 0,00006$). The categories differed significantly ($P \approx 6 \times 10^{-8}$).

4 Summary of Chapter 4

The models were constructed after the data collection phase of the project by measuring important habitat variables where the animals were present and where they were absent.

Two census routes were selected: one to collect data for the formulation of the models and another for their validation. Kudu and eland were censused by day and by night and data were collected within a 10 m radius circle where animals were spotted. Independent samples were also randomly taken along the census routes, which were searched for fresh sign of kudu or eland. If no sign of either of the species was found within the circle, the sample was labeled 'absent' for that species.

Phenophase data were collected and presented in the form of phenograms. Seasonal submodels were identified based on plant phenophases, which indicated two major seasons: June to August (cold dry) and September to May (hot wet). Plants were categorized according to browse classes based on the amount of growth removed by herbivores.

Preference indices were calculated for structural variables on which SI curves were based. All variables and curves were subjected to a sensitivity analysis. This revealed that floristic variables could be presence/absence transformed and structural variable curves could be transformed to linearity.

Linear discriminant functions were calculated for kudu and eland respectively to discriminate between patches where they were present and patches where they were absent. Cut-off values were determined by shifting the critical HSI value until the cost of misclassification was minimized. Plots with HSI's above the critical value predicted the presence of the model species.

The function for summer kudu was
$HSI = 0{,}48V1 + 0{,}36V2 + 0{,}4V3 + 0{,}35V4 + 0{,}39V5$
where
HSI = habitat suitability index
V1 = presence of _A. mellifera_
V2 = presence of _A. karroo_
V3 = presence of _Z. mucronata_
V4 = SI for crown.gap ratio
V5 = SI for proximity of shade.

The function for winter kudu was
$HSI = 0{,}61V1 + 0{,}15V2 + 0{,}48V3 + 0{,}29V4 + 0{,}27V5 + 0{,}45V6$ where
V1 = presence of _A. tortilis_
V2 = presence of _T. camphoratus_
V3 = presence of _Z. mucronata_
V4 = presence of 'palatable evergreens'
V5 = SI for crown:gap ratio
V6 = SI for proximity of shade.

The function for summer eland was
$HSI = - 0{,}58V1 - 0{,}54V2 + 0{,}37V3 + 0{,}13V4 + 0{,}19V5 + 0{,}13V6 + 0{,}41V7$
where
V1 = presence of _A. mellifera_
V2 = presence of _Z. mucronata_
V3 = presence of _A. erioloba_
V4 = presence of _A. karroo_
V5 = presence of _T. camphoratus_
V6 = presence of 'palatable evergreens'
V7 = SI for grass density.

The function for winter eland was
$HSI = - 0{,}54V1 + 0{,}23V2 + 0{,}67V3 + 0{,}33V4 + 0{,}5V5 + 0{,}27V6$ where
V1 = presence of _A. tortilis_

V2 = presence of A. erioloba
V3 = presence of T. camphoratus
V4 = presence of 'palatable evergreens'
V5 = presence of R. ciliata
V6 = HSI for proximity of shade.

The models were verified by determining the percentage successfully classified dependent samples. The success of the summer kudu, winter kudu, summer eland and winter eland models were 72%, 81%, 71% and 69% respectively.

CHAPTER 5. MODEL VALIDATION

1 Introduction

In this chapter I explain the validation of the data-based habitat suitability models. This consisted of the application of the models to real but independent data (Farmer, Armbruster, Terrell & Schroeder 1982). Data from Route 2 were used to validate the models. At this stage no manipulation of the models was allowed. The discriminant functions, cut-off points and decision rules obtained from the dependent data were regarded as final.

2 Methods

The independent data were used as model parameters and the number of presence and absence plots which were correctly classified by the models were counted.

The 95% confidence limits of the proportion of correctly classified observations were calculated, to determine whether it differed significantly from 0,5. I assumed that randomly operating or chance models would correctly predict the presence or absence of the animals in 50% of the efforts. The formula used was
$p \pm z_{(1-\alpha/2)}\{\sqrt{(pq/n)}\}$ (Snedecor & Cochran 1974, p. 210)
where
p is the proportion of correctly classified observations,
q is (1-p) and
n is the total number of observations.

3 Results

The results of the models' validation by means of independent (Route 2) data are summarized in table 6.

Table 8. Results of model verifications by independent data

MODEL		RECORDS CORRECTLY CLASSIFIED	RECORDS WRONGLY CLASSIFIED	% SUCCESS	95% CONFID. LIMITS
Summer Kudu	PRESENT (n=53)	42	11	79,2	
	ABSENT (n=57)	38	19	66,7	
	COMBINED (n=110)			72,7	± 8,8 %
Winter Kudu	PRESENT (n=68)	49	19	72,1	
	ABSENT (n=34)	20	14	58,8	
	COMBINED (n=102)			67,6	± 9,6 %
Summer Eland	PRESENT (n=41)	27	14	65,9	
	ABSENT (n=67)	40	27	59,7	
	COMBINED (n=108)			62,0	± 9,6 %
Winter Eland	PRESENT (n=75)	43	32		
	ABSENT**	** **	** **		
	COMBINED (n=75)			57,3	± 11,9 %

** Not tested

In general, the models had an overall success ratio of between 57,3 and 79,2 percent. The summer kudu, winter kudu, summer eland and winter eland models achieved 73, 68, 62 and 57 percent success ratios respectively. If the models classified at random, one would have expected a 50% success ratio. With the exception of the winter eland model, the 95% confidence limits of the proportional classification success of the models did not fall below 50%. The overall ('Presence' and 'Absence' combined) predictive capabilities of the models were, with the exception of the winter eland model, statistically significant.

4 Summary of Chapter 5

The models were validated by independent data from the same study area which were collected along a different route.

With the exception of the winter eland model, the 95% confidence interval of the proportion of correctly classified data were above 0,5. The models were able to classify the independent data significantly better than would be expected of random models, with one exception, the winter eland model.

CHAPTER 6. EXTENDING THE MODELS

1 Introduction

The extension and refinement of the validated models are explained in this chapter. The models were modified to increase their geographical range of application. The extension of the models should not be regarded as the last step in the modeling process. The refined models described in this section have not been tested, which would be the logical next step in the modeling procedure.

2 Methods

2.1 Flow charts

The models were converted to flow charts to increase their ease of application and to introduce qualitative decisions to them. I made provision for the user to attach a probability to the presence of kudu or eland at a habitat patch. This was done by supplying the user with the cumulative percentage of kudu or eland which occurred at plots with similar or lower habitat suitability index (HSI) scores (figures 13 and 14).

Plant species were not used as input variables to the algorithm. Functional plant properties I deemed important, and it was that I used. Structural attributes remained unchanged.

2.2 Expert systems

The evaluated models and their flow charts were finally converted to expert system models to improve their flexibility and application to other biogeographical areas.

Expert systems are rule-based models which guide the user in making decisions. The knowledge base of the expert system consists of fundamental facts, which it uses to derive its response, by interpreting the user's answers to pertinent questions (Starfield & Louw 1986). The inference engine of the expert system is the logic structure of the program which enables it to make decisions based on IF/THEN/ELSE rules the programmer specifies. The inference engine is used to reduce the number of possible reactions to a user's response (Marcot 1986). Expert systems have been used for habitat suitability modeling by Marcot (op. cit.).

The discriminant functions were carefully examined to ascertain which variables were essential habitat components. The expert system rules were formulated to accommodate essential variables.

The expert systems require the parameters of all model variables as input so that an HSI score can be calculated. The program then prompts the user for the level of strictness or conservativeness at which he would like to evaluate the habitat. A critical value which is dependent on the strictness level the user supplies is then obtained from the knowledge base. The critical values were derived from the graphs shown in figures 13 and 14. If the HSI score falls above the critical value then the habitat is classified as suitable.

The model variables all contribute towards habitat suitability. The HSI score can be misleading in this respect, because a patch can be classified as suitable habitat when essential habitat components, such as plants which provide food at critical times of the year or shelter, are absent. A habitat patch without an essential habitat component can however be suitable if another patch containing that component is close enough to it.

Rules were built into the expert systems to issue warnings when either of the essential components was absent from a patch. If an essential habitat component was absent from a sample patch, the program cautioned the user that a suitable patch which included the absent component should have been situated nearby.

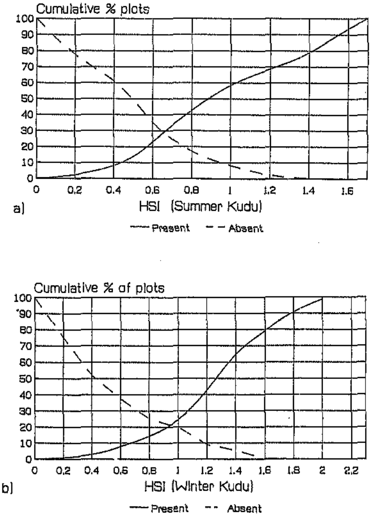

Figure 13. Plot of cumulative percentage of kudu 'present' (solid line) and 'absent' data (broken line) against habitat suitability index (HSI). a) Summer kudu and b) winter kudu

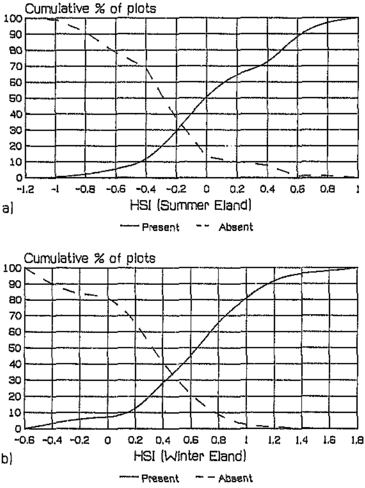

Figure 14. Plot of cumulative percentage of eland 'present' (solid line) and 'absent' data (broken line) against habitat suitability index (HSI). a) Summer eland and b) winter eland

The VP Expert shell (Paperback Software International) was used to generate the expert system. The programs were compiled by the VP Expert Runtime System following a program license agreement with Paperback Software.

3 Results

3.1 Functional plant groups

The functional plant groups identified from the discriminant function variables were as follows.

In the summer kudu model, Acacia mellifera represented any deciduous tree or shrub which bore large quantities of flowers in early spring and soft shoots and pods in early summer. A. karroo and A. mellifera were functionally similar in this regard. Ziziphus mucronata could be replaced by any broad-leaved, thorny tree or shrub which did not contain obvious chemical defenses such as oil glands.

In the winter kudu model, A. tortilis was representative of trees or shrubs which bore nutritious pods until mid-winter. Tarchonanthus camphoratus could be replaced by evergreen trees or shrubs which contained an abundance of large leaves which were generally neglected by browsers.

The palatable evergreen group was already functional and had been used as such as a model variable, after the TWINSPAN (see page 52). This group included species which showed sign of heavy browsing and were evergreen. Z mucronata was functionally similar to any tree or shrub which lost its leaves for a short period towards the end of winter only, and which did not contain obvious chemical deterrents.

In the eland models, A. mellifera and Z. mucronata could be replaced by any small- or sparse-leaved tree or shrub with hooked thorns. A. erioloba was functionally similar to any tree which produced large, nutritious pods. T. camphoratus

The VP Expert shell (Paperback Software International) was used to generate the expert system. The programs were compiled by the VP Expert Runtime System following a program license agreement with Paperback Software.

3 Results

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In the summer kudu model, *Acacia mellifera* represented any deciduous tree or shrub which bore large quantities of flowers in early spring and soft shoots and pods in early summer. *A. karroo* and *A. mellifera* were functionally similar in this regard. *Ziziphus mucronata* could be replaced by any broad-leaved, thorny tree or shrub which did not contain obvious chemical defenses such as oil glands.

In the winter kudu model, *A. tortilis* was representative of trees or shrubs which bore nutritious pods until mid-winter. *Tarchonanthus camphoratus* could be replaced by evergreen trees or shrubs which contained an abundance of large leaves which were generally neglected by browsers.

The palatable evergreen group was already functional and had been used as such as a model variable, after the TWINSPAN (see page 52). This group included species which showed sign of heavy browsing and were evergreen. *Z. mucronata* was functionally similar to any tree or shrub which lost its leaves for a short period towards the end of winter only, and which did not contain obvious chemical deterrents.

In the eland models, *A. mellifera* and *Z. mucronata* could be replaced by any small- or sparse-leaved tree or shrub with hooked thorns. *A. erioloba* was functionally similar to any tree which produced large, nutritious pods. *T. camphoratus* represented thornless trees or shrubs with an abundance of large leaves, which were not sought-after by other browsers for most of the year. 'Palatable evergreens' was a functional group by itself and remained the same. A. karroo was the functional equivalent of deciduous trees with soft new shoots and an abundance of soft young pods in early summer. A. tortilis could be replaced by any tree or shrub with hooked thorns and small or sparse leaves. R. ciliata represented aromatic evergreen shrubs without hooked thorns and with an abundance of medium sized leaves.

3.2 Flow charts

Flow charts 1 to 8 symbolize the kudu and eland models.

3.3 Expert systems

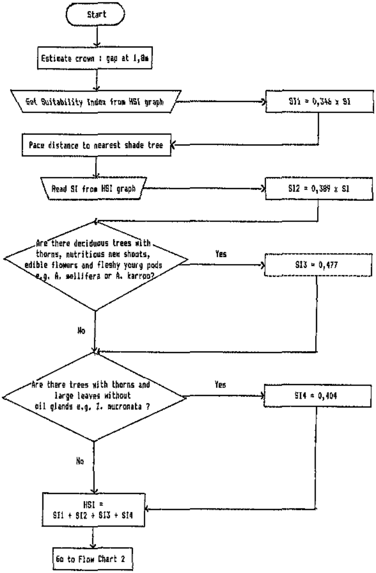
Expert systems for kudu and eland habitat suitability assessment are available on diskette attached to the back cover of the thesis.

3.3.1 Kudu

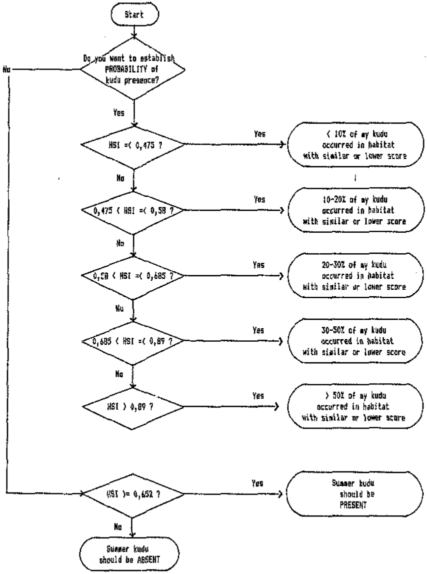
The SI models were examined and essential components and variables which compensated for the absence of one another were identified. The components of the discriminant functions are illustrated in figures 15 and 16.

The summer kudu model consisted of two basic components: food and shelter (figure 15 a). The food component consisted of A. karroo, A. mellifera and Z. mucronata, (or their functional equivalents) while the shelter component consisted of the crown:gap ratio and proximity to shade.

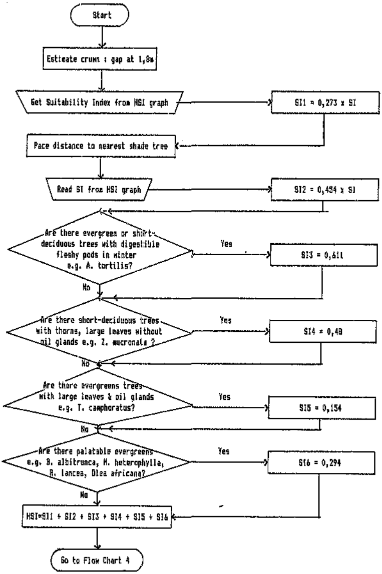
It was possible to obtain an HSI score above the cut-off value with either a food or a shelter component excluded from a sample patch. If either component was absent, the program 'told' the user that the absent component should be present at a nearby patch for the habitat to be classified as suitable.



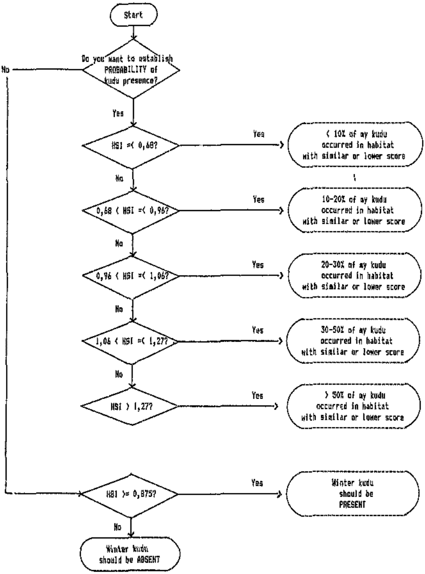
Flow chart 1. Habitat suitability assessment for summer kudu. Suitability index (SI) graphs are in figure 8, p. 60. Crown:gap ratios are illustrated in figure 5, p. 41. HSI = habitat suitability index



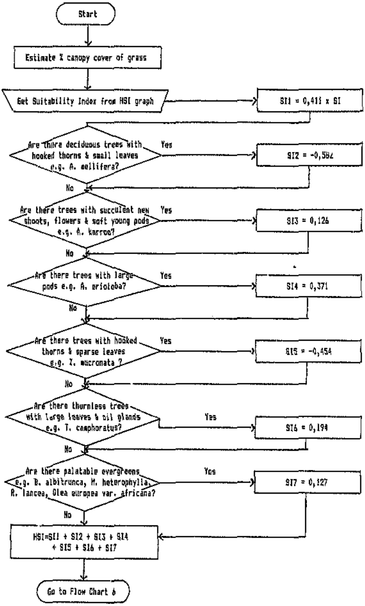
Flow chart 2. Habitat suitability assessment for summer kudu (continued). Probabilities and critical values were obtained from figure 13 (a), p. 74



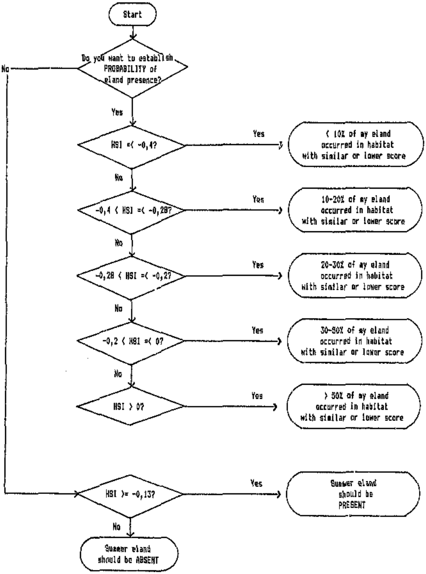
Flow chart 3. Habitat suitability assessment for winter kudu. SI graphs are in figure 8, p. 60



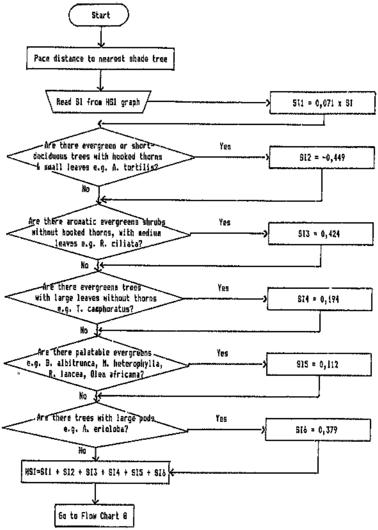
Flow chart 4. Habitat suitability assessment for winter kudu (continued). Probabilities and critical values were obtained from figure 13 (b), p. 74



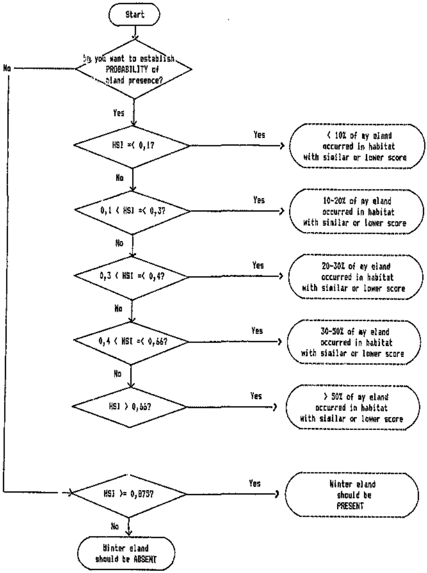
Flow chart 5. Habitat suitability assessment for summer eland. SI graphs are in figure 9, p. 60



Flow chart 6. Habitat suitability assessment for summer eland (continued). Probabilities were obtained from figure 14 (a), p. 75



Flow chart 7. Habitat suitability assessment for winter eland. SI curves are in figure 9, p. 60



Flow chart 8. Habitat suitability assessment for winter eland (continued). Probabilities and critical values were obtained from figure 14 (b), p. 75

The winter kudu model had three components: a mid-winter food component which consisted of the variables A. tortilis and Z. mucronata, a late winter or 'stepping stone' food component consisting of T. camphoratus and 'palatable evergreens', and a shelter component (figure 15 b). All floristic variables could be replaced by functional equivalents as explained earlier. The shelter component was represented by proximity of shade and the crown:gap ratio.

For a patch to be classified as suitable, the score had to be above the user-indicated critical value to predict winter kudu presence. If either of the three components was absent the program issued a cautionary message that the missing component had to be available close to the patch.

3.3.2 Eland

The expert systems for eland in winter and in summer had only one component, which consisted of food (figures 16 a and b). Sub-se sonal components were not identified because all the plant species of the winter eland model were evergreen and could be utilized throughout winter. The habitat was simply classified as suitable if the HSI score was above the critical value.

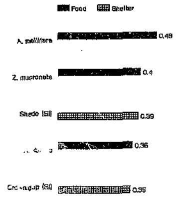


Figure 15 a. Components of the discriminant function for summer kudu habitat suitability evaluation. The function consists of two components: food and shelter. SI is the value read from the suitability index curve

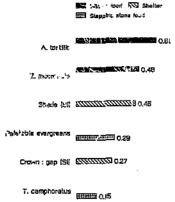


Figure 15 b. Components of the discriminant function for winter kudu habitat suitability evaluation. The function consists of three components: shelter, early to mid-winter food and late winter or 'stepping stone' food

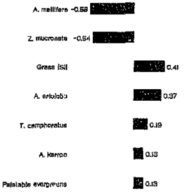


Figure 16 a. Components of the discriminant function for summer eland habitat suitability assessment. Only one component, i.e. summer food, was recognized

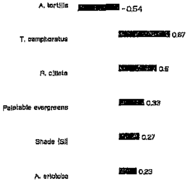
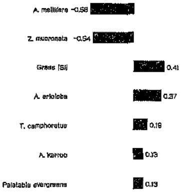


Figure 16 b. Components of the discriminant function for winter eland. Winter food is the on component



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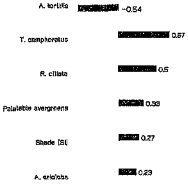

Figure 16 b. Components of the discriminant function for winter eland. Winter food is the only component

4 Summary of Chapter 6

The models were expanded to extend their geographical range and applicability. They were converted to flow charts and expert systems.

The floristic variables were converted to functional plant attributes which appeared to be important to the study animals. The discriminant functions were inspected and broken down into components consisting mostly of food and shelter.

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CHAPTER 7. DISCUSSION

The relevance of the techniques of data collection and analysis and the implications of the results of the project are discussed in this chapter. The project as a whole is considered, rather than its individual chapters and their subsections.

1 Techniques

1.1 Field data collection

The successful validation of the kudu models suggested that the field data collected for them were appropriate. There are bound to be other habitat factors which are of relevance to habitat selection by kudu. As has been shown in other habitat studies, many components of the ecosystem are interrelated. One would therefore expect factors such as soil chemistry, geology and soil moisture to be potential predictors of habitat suitability due to their correlation with plant communities (Palmer, Cooke & Lubke 1988). What I attempted to measure was the animals' perceptions of their surroundings, which was centred mainly around food and shelter (Owen-Smith 1982).

The scale at which I studied kudu habitat also seemed to be realistic, and was supported by other studies on kudu (Owen-Smith & Cooper 1987 a - e). Because kudu are territorial (Simpson 1972) with small home ranges (Kelso 1987), the probability of seeing an animal in unsuitable habitat is smaller than in the case of eland. It still remains a problem, though, particularly when dealing with a patchy environment such as my study area. The study area was interspersed with small patches or islands of potential kudu habitat within larger landscape units. Some of these landscape units, if viewed on a large enough scale, would superficially not comply with the habitat requirements of kudu.

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The eland models did not perform as well as the kudu models. This could have been due to several factors, to which measuring the wrong variables might have contributed. The most important factor to which I attributed the relatively poor performance of the eland models was the fact that eland moved around so much in search of food. In accordance with other studies, eland formed small groups of one to six individuals in winter. These groups moved around extensively. There seemed to be a rapid selection of habitat patch after habitat patch and the eland seemed to eat 'on the move' (Kelso 1987). Eland were not territorial in the true sense of the word. They did, however, occupy home ranges which varied in size between 50 km² in the case of solitary males and 200 km² in the case of breeding herds (Hillman 1979). Kelso (1987) found that eland home ranges varied between 28,5 and 69,8 km² in the Pilanesberg National Park, while Underwood (1975) in Kelso (op. cit.) found that the Loskop Dam Nature Reserve (120 km²) was too small for female eland. The probability of seeing an eland between favourite habitat patches in my study area was therefore high.

In summer, eland formed large aggregations (see also Kelso 1987, Hillman 1979). These large herds settled in an area for some time. By studying habitat in units of approximately 314 m² (the area of a circle with a radius of 10 m) I was sampling only a small proportion of what the herd was actually selecting. In some instances this might not have been representative of the larger area in which the herd occurred. The second possible reason for the relative inefficiency of the summer eland model was therefore that the resolution at which the study was carried out, was too high.

Although more quantitative field techniques such as the variable quadrant method (Coetzee & Gertenbach

1977, Ben-Shahar 1986) and traditional phytosociological methods (Jooste 1980) are available, they are time-consuming and often produce unsatisfactory results (Ben-Shahar op. cit.). The field techniques I used consisted mostly of estimates and had the advantage that they were rapidly executable. A large quantity of data could therefore be gathered quickly. This was an important consideration if the size of the study area (approximately 350 km^2) and the length of the census routes were borne in mind. Another reason for using rapid estimates rather than tedious measurements was that I attempted to imitate the decision processes of the study animals when I gathered data. This excluded measurements by quantitative devices.

1.2 Data analysis

Habitat selection by an animal is essentially a multivariate process, with several factors simultaneously influencing several options the animal has. Multivariate statistics are intuitively selected as the most appropriate method for the analysis of such data (Shugart 1981). Multivariate analysis is not without its disadvantages (Johnson 1981). One of these is that the parameter space and complexity of the data are not effectively reduced as is commonly believed. The original variables are still incorporated in the analysis and still influence the results. A second disadvantage is that the output of multivariate analysis is difficult to interpret and understand. If the results do not reflect reality, it is almost impossible to determine 'what went wrong'. A third problem is the assumption of almost all multivariate techniques that the variables are linearly related, which is mostly not the case in ecosystems. Green (1971 in Johnson, 1981) is of opinion that the linear additivity of variables apply to ecosystems, a view which is opposed by Johnson (op. cit.). This should still not deter ecologists from using multivariate statistics. It should, however, be borne in mind when interpreting the results.

I used multivariate statistics in combination with univariate analysis to enable me to understand and verify the results of the former. The two methods complemented each other, and where one failed the other generally succeeded.

1.2.1 Correspondence analysis

Correspondence analysis seemed to be suitable for exploratory data analysis when large numbers of variables were incorporated. It certainly indicated the most important associations between variables. Where the emphasis was on the identification of the numerical importance of variables and their quantitative relationships, CA failed. To use an example: I used CA to explore the plant species associated with kudu in summer. It showed that there were definite associations between kudu and _Acacia karroo_ and _Ziziphus mucronata_, but failed to indicate that _A. mellifera_ was an important habitat component. These three species were incorporated in the discriminant function, though, and _A. mellifera_ received a relatively high weighting coefficient (figure 10 a). The conflicting results were because of the abundance of _A. mellifera_ in the study area. Therefore the contrast between its presence where kudu were present and where kudu were absent was low if considered on a coarse scale. CA is efficient for low resolution studies of animal-habitat relationships, especially where the data is categorical, such as those by Beardall, Joubert & Retief (1984), Greenacre & Vrba (1984) and Ben-Shahar (1986).

1.2.2 Discriminant function analysis

Discriminant function analysis or DFA is one of the most frequently used data analysis techniques for predictive habitat suitability assessment procedures (Brennan, Block & Gutierrez 1986; Capen, Fenwick, Inkley & Boynton 1986; Krausman & Leopold 1986; Cavallaro, Menke & Williams 1981; Mosher, Titus & Fuller 1986; Christensen 1985; Klopatek & Kitchings 1985 inter alia). In this study it clearly indicated the variables of importance to the habitat selection of the study animals. It also showed which variables were relatively more important than others. I found DFA's main advantage to be its ability to classify a record with unknown group membership, which agreed with the aims of this project.

DFA assumes that the data are multivariate normally distributed, and that the covariance matrices are equal. Klecka (1975, p.435) states that 'in practice, the technique is very robust and these assumptions need not be strongly adhered to'. Johnson (1981) mentions the numerous examples where the assumptions have been violated in animal-habitat studies and concludes that DFA might be much more robust than statisticians believe.

Johnson (op. cit.) suggests that researchers should generate discriminant functions with few, well thought-over variables. I had adopted this approach since the data-collection phase of the project. My policy was to include as few as possible variables in the discriminant function without significantly affecting its discriminating power.

A disadvantage of the technique is that it is 'forced to' generate a function to discriminate between two groups which are a priori indicated by the researcher. The discriminant function almost always classifies more than 50% of the dependent data correctly (Prof. W. Zucchini, Dept. of Mathematics and Statistics, University of Cape Town, Rondebosch 7700, pers. comm.). It is therefore of the utmost importance to validate the discriminant functions by means of independent data. This may be done in several ways, e.g. by cross-validation (Capen et al. 1986) or by using data from a new study area. In this study I selected independent test data from a different part of the same study area.

Another disadvantage of the technique is the linearity of the model it generates. The fact that I transformed my floristic data to presence/absence values to some extent compensated for this demerit. The preference index curves also reduced the linear contribution of variables to habitat suitability.

The stepwise version of DFA is useful for filtering out unimportant factors when the variables are numerous. Green (1979) is of opinion that classical DFA should rather be used, but does not state why. Johnson (1981) states that stepwise DFA tempts the researcher to include numerous variables in the initial analysis. The risk of including the wrong variables in the discriminant function is then increased. I did not have access to stepwise DFA, but nevertheless was able to discard unimportant variables by going through several iterations of calculating discriminant functions. This was possible because I commenced the analysis with relatively few variables.

1.2.3 Alternative statistical techniques

Other techniques for the statistical analysis of habitat suitability assessment data are numerous. Of these, the most promising seems to be logistic regression (Capen et al. 1986, Brennan et al. 1986). This method has the advantage that, apart from generating a function which enables one to classify independent data, it also attaches a probability of group membership to the record. Prof. W. Zucchini analyzed some of my data by logistic regression and was of opinion that the method warranted investigation.

Another technique which has been used is Pattern Recognition. The technique is useful for the creation of decision support systems, and has been employed by Seitz,Farmer & Kling (1982), Flather & Hoekstra (1985) and Kirkman, Eberly, Porath & Titus (1986). Prof. M.J. Greenacre (Dept. of Statistics, University of South Africa) analyzed some of my data by CART, a pattern recognition program developed for the analysis of symptoms of medical patients. The results were no better than that of discriminant analysis, but the important variables identified by the two methods corresponded.

Multiple regression is another technique which has been used by Grue, Reid & Silvy (1981), Howard (1986) and Maurer (1986) inter alia. The method is useful when the dependent variable consists of continuous data, which was not the case in my study. The end product, like that of DFA, is a linear model which predicts animal density in most instances.

1.2.4 TWINSPAN and COMPCLUS

These techniques were used to functionally classify the important browse plants. The techniques had the advantage that the classification generated was better than a subjective one. The disadvantage was that the creation of functional groups in accordance with one's value judgement was tempting when using the Cornell Ecology programs. They were so flexible in allowing the transformation and omission of data, that the data could be manipulated almost at will from within the programs.

COMPCLUS and TWINSPAN produced compatible results, which gave me some assurance that the classes identified were valid.

1.3 Modeling techniques

The linear HSI models produced by the discriminant functions were simple and could no doubt be sophisticated. One of the shortcomings, as mentioned earlier, lay in the linearity of the models.

A second demerit was that some of the minor components of the discriminant function, i.e. those with low coefficients, might have been important habitat factors at crucial times of the year and could not have been replaced by other variables. An example: Tarchonanthus camphoratus had a low discriminant function coefficient in the winter kudu model. I nevertheless regarded it as a crucial habitat component during the late dry season when two of the other plant species in the model, Z. mucronata and A. tortilis, had lost their leaves.

It was difficult to ascertain which variables in the discriminant function were indispensable. In the case of the kudu models, for example, a patch would be classified as potential habitat if the variables shade and crown: gap ratio were optimal. This implied that the animals needed only shelter and cover in order to have been present. If the plant species composition was optimal, the patch would also have been classified as potential habitat, which implied that kudu did not need shelter. On the other hand kudu could probably survive in an area where their food requirements occur in one group of patches and their shelter requirements in another.

The expert system models could overcome this problem if the data are well understood. Marcot (1986) states that expert systems are promising modeling techniques for habitat suitability assessment. I agree with him, provided that they are thoroughly tested.

Whichever modeling technique is selected will be as good as the data on which it is based. If the correct variables are selected and enough data are available, most objective data analysis techniques are bound to produce a useful model. It is essential to validate all models in the field and preferably in different study areas.

2 Habitat preferences

I assumed that the plant species which were mostly associated with the animals also represented their preferred food items. This was supported by unpublished data of J. du Toit (Zoology Dept., University of the Witwatersrand, Johannesburg 2000). Some plant species had similar habitat requirements, however, and were therefore associated with each other. It could therefore have seemed as though the animals preferred a plant which was phytosociologically associated with a species which they actually selected.

I attempted to avoid this pitfall when analyzing the data by investigating the correlation coefficients of the variables. One of two highly correlated variables were omitted and a new discriminant function calculated based on the remaining variables. The classification power of the new discriminant function was then compared to that of the previous one. Sometimes it was impossible to avoid the inclusion of correlated variables because the classification power was severely reduced if one of them was excluded. This did, however, provide some indication that both variables were selected by the animals.

2.1 Kudu

2.1.1 Summer

The discriminant functions for kudu indicated that in summer, kudu preferred areas where A. mellifera, A. karroo and Z. mucronata were present within 10 m. They also preferred areas close to shade with small crown:gap ratios. The index curves for the latter variables indicated that small crown:gap ratios and close shade provided high suitability index values.

It was interesting that all the plant species included in the summer kudu discriminant function were spinescent. Plants on high nutrient soils are generally protected by spinescence, as opposed to plants on low nutrient soils, which are mostly chemically defended (Owen-Smith & Cooper 1987e). Spinescent plants might be an indication of the dislike of kudu for plants containing defensive secondary chemicals (Owen-Smith, Cooper & Novellie 1983) or the preference of kudu for high nutrient plants (Underwood 1978). Plants growing on high nutrient soils generally have a high nutrient content, and can act as nutrient sinks (Salisbury & Ross 1978).

A. karroo and Z. mucronata were correlated in the study area. When I omitted either one of them and calculated a new discriminant function, the classification power of the new function was reduced to such an extent that I was forced to include both variables. This indicated to me that both species were important habitat components, even though they were correlated. Kudu were observed feeding on the new shoots and pods of A. karroo, while they fed extensively on the mature leaves of Z. mucronata throughout the year (personal observations). The small mouth width of a kudu enabled it to pick out the pods and succulent shoots of the Acacia spp., as well as the flowers and flower buds. Z. mucronata had broad, but sparse leaves. The relatively narrow mouth parts of kudu allowed them to select individual leaves from between the hooked thorns.

The Acacia spp. were preferred food plants of kudu in other areas, especially during the growing season of the plants (Hoffman & Stewart 1972; Conybeare 1975; Owen-Smith 1979; Kelso 1987). The preference of kudu for Z. mucronata was corroborated by Owen-Smith (1985a).

The preference of summer and winter kudu for dense vegetation and shade was expected. Kudu are timid animals which rely on cover for predator avoidance. The cryptic coat colour of kudu and the striped pattern on the coat are indications that they rely on camouflage to avoid predators (Kelso 1987).. The small group size of kudu is also in accordance with this strategy (Jarman 1974). Shade was an important component of kudu habitat, which they utilized for camouflage purposes as well as for protection against the sweltering temperatures in summer. Summer temperatures of close to 40° C were recorded during the study period.

2.1.2 Winter

Plant species which did not provide food during winter were totally omitted from the discriminant functions for winter kudu, for obvious reasons.

In winter, kudu preferred patches where A.tortilis, T. camphoratus, Z. mucronata and 'palatable evergreens' were present. Once more, the discriminant function coefficients for the thorny species (A. tortilis and Z. mucronata) were high (figure 10 b). T. camphoratus received a very small coefficient and contributed little to the discriminant function. This was accordance with the work of Cooper (1985) who found that kudu took otherwise avoided food items during the dry season. T. camphoratus possessed aromatic oils which were easily detectable, even by humans. I regarded it as a 'stepping stone' which enabled kudu to overcome the late part of the dry season. It might therefore have been a more important habitat component at the end of winter than indicated by the discriminant function.

The preference of kudu in winter for palatable evergreen plants was obvious. What was less obvious, is why it did not form part of the summer discriminant function for kudu. Virtually all of these plants had a shrublike growth form, and were eaten by other herbivores which did not have the same ability as kudu to utilize the higher leaves of trees. Kudu might have avoided these plants in summer because they were already heavily browsed by other browsers and mixed feeders, and therefore did not contain large quantities of food. In winter, kudu utilized them because of the overall scarcity of food (figure 6).

Kudu were probably associated with A. tortilis in winter because it bore large quantities of pods until late in the dry season (figure 6). The species had extremely small leaves and I was of opinion that the leaves were not an important food source for kudu.

The same reasons for the preference of kudu for dense vegetation in summer applied to their preference for it in winter. The importance of shade for winter kudu could be explained by the shelter it provided against the cold. Trees with canopies reflect the earth's heat at night and a pocket of warmer air forms underneath them. They also form 'blankets' against frost and retain the animals' body heat under their canopies. Many of my censuses were done at night or very early in the morning. Sub-zero temperatures were more often than not measured in the study area during June, July and August. It might be argued that kudu preferred shade in winter because of the preference of forbs for shade. Forbs were the favourite food items of kudu elsewhere (Conybeare 1975; Owen-Smith 1979; Owen-Smith, Cooper & Novellie 1983; Kelso 1987). The period of study was towards the end of a major drought and the moisture content of the soil must have been low. Very few forbs were therefore encountered in the study area, and those that were seen, had been killed by frost.

The preference of kudu for dense vegetation was corroborated by the ordination of Berry's census data and my land facets (figure 4). It was also corroborated by the Bonferroni-z confidence interval tests (tables 4 and 5).

2.2 Habitat preferences of eland

2.2.1 Summer

The discriminant function for summer eland showed that they preferred patches where A. erioloba, A. karroo, T. camphoratus, 'palatable evergreens' and good grass cover were present. They avoided patches where Z. mucronata and A. mellifera were present.

Eland are larger than kudu, and have larger mouth parts. As a consequence, they found it difficult to select individual leaves from trees. They rather stripped whole branches of their leaves and sometimes consumed woody material in the process (personal observation). Eland should also have been able to digest forage with a high fibre content due to their large size (Hanley & Hanley 1982).

It is difficult to explain the preference of eland for A. karroo, bearing the above in mind. The species grew along watercourses in the study area, and I could only assume that they were selecting it for its high more often than not measured in the study area during June, July and August. It might be argued that kudu preferred shade in winter because of the preference of forbs for shade. Forbs were the favourite food items of kudu elsewhere (Conybeare 1975; Owen-Smith 1979; Owen-Smith, Cooper & Novellie 1983; Kelso 1987). The period of study was towards the end of a major drought and the moisture content of the soil must have been low. Very few forbs were therefore encountered in the study area, and those that were seen, had been killed by frost.

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It is difficult to explain the preference of eland for A. karroo, bearing the above in mind. The species grew along watercourses in the study area, and I could only assume that they were selecting it for its high water content. This is corroborated by Taylor (1969). Eland are adapted to semi-desert conditions and one of these adaptations is to get moisture from their food. Artificially applied water was freely available in the study area, but I expected the animals to instinctively select high moisture plants nevertheless.

The preference of eland for *A. erioloba* was probably due to the large pods these trees produced. The species is normally a tall tree with very few branches within feeding reach of the animals. I doubted it strongly that eland fed on the foliage. The pods are large and fibrous and the seed have a high nutritional value (Coates Palgrave 1977). They are dropped to the ground where they are picked up by the animals. *A. erioloba* is restricted to deep sandy soils (Leistner 1967). These soils are characterized by good grass cover and a rapid recovery of the grass layer after rain (A.A. Gubb, East London Museum, P.O. Box 11021, Southernwood 5213, South Africa, unpublished data). It might therefore have been that eland were associated with the good grass cover on the sandy soils, where *A. erioloba* was found.

T. camphoratus was preferred in summer because of its abundance of large leaves. As mentioned earlier, the leaves contained aromatic oils. Eland should be less susceptible to secondary chemical plant defences than kudu. Animals which do not regularly browse are normally less sensitive than true browsers to chemical defence mechanisms of plants (Owen-Smith 1982).

The preference of eland for 'palatable evergreens' in summer was difficult to explain. The only explanation was that they utilized these plants because they were generally thornless with possibly a high protein content. It was unlikely that these plants could have been a major food source of eland, as their leaves were generally sparse and they did not contain an abundance of food. In the absence of other herbivores, palatable evergreens could have formed a large part of the eland diet. The coefficient of 0,13 did not contribute much to the discriminant function, however.

The high discriminant function coefficient for grass cover was in accordance with studies elsewhere, where a large proportions of the diet of eland consisted of grass in summer (Nge'the & Box 1976; Lamprey 1963; Kelso 1987).

The large negative contributions of Z. mucronata and A. mellifera to the discriminant function could have had several explanations. Both possessed very efficient hooked thorns. A. mellifera had a relatively small compound leaf on a short rachis. Such leaves would have been difficult to select by eland, and the hooked thorns would have deterred them from stripping the branches. Kelso ([illegible] that A. caffra, which possessed hooked stipules [illegible] the preferred food of eland in the Pilanesberg National Park. This species had a large compound leaf on a tall rachis. The leaves were abundant and eland would have been able to economically remove individual leaves from the plant. It should also be borne in mind that stipules are not as formidable as thorns in defending plants, as they break off more easily. In addition, the stipules of A. caffra were small and sparsely distributed.

Z. mucronata had large but sparse leaves. Eland would not have been able to economically select individual leaves of this species without stripping the branches.

It could of course be that the hook-thorned species, which grew on high nutrient soils, were associated with [illegible] grass cover. The grass was kept short by selective grazers such as wildebeest and red an abundance of food. In the absence of other herbivores, palatable evergreens could have formed a large part of the eland diet. The coefficient of 0,13 did not contribute much to the discriminant function, however.

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Z. mucronata had large but sparse leaves. Eland would not have been able to economically select individual leaves of this species without stripping the branches.

It could of course be that the hook-thorned species, which grew on high nutrient soils, were associated with poor grass cover. The grass was kept short by selective grazers such as wildebeest and red hartebeest, which were numerous in the study area. There was however no significant negative correlation between any of the hook-thorned species and grass cover.

I used a 2 x 2 table to test the null hypothesis that eland were present in equal proportions where the hook-thorned species, i.e. *A. tortilis*, *A. mellifera* and *Z. mucronata* were present, compared to patches where these species were absent. The null hypothesis was rejected with a high confidence level ($P \ll 0{,}001$).

Eland did not seem to prefer any cover or shelter, as the coefficients for shade and crown:gap ratio were small (below 0,05). The coat colour and social structure of eland indicated that they did not rely on camouflage for predator avoidance (Geist 1974). The adaptations of eland to semi-desert conditions (Taylor 1969) allowed them to tolerate heat, which was probably why they did not need shade.

2.2.2 Winter eland

In winter, eland preferred areas where *A. erioloba*, *T. camphoratus*, 'palatable evergreens' and *Rhus ciliata* were found and where shade was nearby. They avoided patches where *A. tortilis* occurred (figure 11 b).

Once more only evergreen or short deciduous species were included in the discriminant function. The avoidance of plants with small leaves and hooked thorns was again evident from the negative contribution of *A. tortilis* to the discriminant function.

The preference of eland for *A. erioloba* was once more as a result of the pods found under this species throughout the year. Eland were regularly observed picking up pods under *A. erioloba* trees, and at night eland were often heard chewing A. erioloba pods, especially in winter.

Eland preferred T. camphoratus in winter for the same reasons they did so in summer (see previous section). The high contribution of the species to the discriminant function indicated that they relied more heavily on it in winter. Virtually all fresh eland dung found in winter had a distinctive camphor smell, which could only have originated from the leaves of T. camphoratus. Kelso (1987) also recorded a preference of eland for T. camphoratus in winter.

The preference of eland for 'palatable evergreens' was probably during the late dry season, when food was scarce. I suspected that these plants did not form an important part of the eland diet throughout winter. As explained earlier, plants belonging to this group generally had small, sparse leaves. They were eaten by many other browsers and mixed feeders (cf. the winter kudu model) and eland would have had to compete with other herbivores for this food source. I observed eland stripping the bark of R. lancea and Boscia albitrunca in winter.

The inclusion of R. ciliata in the discriminant function was probably because of its relatively large leaves and the abundance of the shrub in localized areas. The species was a short shrub which generally occurred in large, homogeneous stands of up to 500 m^2. It was seldom eaten by other herbivores and had a characteristic acidic smell when the leaves were crushed. The species was possibly defended by secondary chemicals. It had relatively 'blunt' spines which were far apart and which should not have deterred eland. The large contribution of R. ciliata to the discriminant function once more corroborated that eland were not very susceptible to secondary plant chemicals and preferred plants with an abundance of food which were readily available.

The preference of eland for shade in winter was probably due to a secondary effect. Eland were less susceptible to cold than kudu because of their large body size, and I doubted whether eland were using the shade for shelter against the cold. The preference of eland for shade could have been due to their selection for pods in winter. Eland could also have selected shade for the dry forbs which grew under the trees. The moisture content of the soil was possibly higher under trees, and in winter green grass was still found there (personal observation). Kelso (1987) found that eland were associated with thorny thickets along drainage lines in winter.

2.3 Resource partitioning between kudu and eland

Although this was not one of the aims of the project, resource partitioning between the two browsers was so obvious that I had to briefly consider the topic.

Structurally, kudu preferred dense vegetation with small crown:gap ratios. They also preferred patches of vegetation where shade trees were in close proximity. Eland, on the other hand, had no preference for any crown:gap ratios. In summer they were independent of shade, while they preferred shade in winter mainly for the higher moisture content of the food found there. Kudu and eland frequented different structural vegetation types. Kudu tended to occur in closed woodland or high shrubland and eland in open woodland or shrubland (see figure 4).

Kudu were associated with spinescent plants in winter and in summer, and used thornless plants mainly as 'stepping stones' towards the end of winter. Eland, on the other hand, preferred thornless plants and preferred plants with an abundance of food which were readily available.

The preference of eland for shade in winter was probably due to a secondary effect. Eland were less susceptible to cold than kudu because of their large body size, and I doubted whether eland were using the shade for shelter against the cold. The preference of eland for shade could have been due to their selection for pods in winter. Eland could also have selected shade for the dry forbs which grew under the trees. The moisture content of the soil was possibly higher under trees, and in winter green grass was still found there (personal observation). Kelso (1987) found that eland were associated with thorny thickets along drainage lines in winter.

2.3 Resource partitioning between kudu and eland

Although this was not one of the aims of the project, resource partitioning between the two browsers was so obvious that I had to briefly consider the topic.

Structurally, kudu preferred dense vegetation with small crown:gap ratios. They also preferred patches of vegetation where shade trees were in close proximity. Eland, on the other hand, had no preference for any crown:gap ratios. In summer they were independent of shade, while they preferred shade in winter mainly for the higher moisture content of the food found there. Kudu and eland frequented different structural vegetation types. Kudu tended to occur in closed woodland or high shrubland and eland in open woodland or shrubland (see figure 4).

Kudu were associated with spinescent plants in winter and in summer, and used thornless plants mainly as 'stepping stones' towards the end of winter. Eland, on the other hand, preferred thornless plants and avoided areas where spinescent plants were present, especially if these had small leaves and hooked thorns.

The habitat components that kudu and eland had in common, were 'palatable evergreens' and _T. camphoratus_ in winter. The latter species made a small contribution to the kudu model and a large contribution to the eland model.

The above accorded with what optimal foraging theory predicted (Demment & Van Soest 1985, Owen-Smith & Novellie 1982). Social behaviour hypotheses (Geist 1974) also predicted that eland should have been independent of cover for hiding and kudu dependent on it.

Kelso (1987) found that kudu and eland shared several resources in the Pilanesberg Nature reserve. These included the large-leafed _A. caffra_ and forbs. The two species of browser nevertheless selected different areas in the Park. She concluded that potential competition between kudu and eland was greatest in the dry season.

3 Scale of habitat study

Contrary to the earlier definitions of habitat, which recognize only macro- and microhabitat, ecologists are now realizing that habitat can be described at different scales or orders (Johnson 1980; Melton 1987; Senft, Coughenour, Bailey, Rittenhouse, Sala & Swift 1987). So, for instance, a CA of the landscape relations of the animals (figure 4) represented their second order habitat selection, while the 314 m^2 circles I used as my scale, represented the third order habitat. The actual plant species the animals would select within these circles, would be their fourth order habitat as studied by Cooper (1985).

If the landscape relations of kudu and eland as analyzed by correspondence analysis are compared to the discriminant functions, the similarity is remarkable. Bear in mind that the correspondence analysis was based on Berry's census data, and the discriminant functions on my own. The association of winter and summer kudu with Ziziphus mucronata was indicated by both methods. The association of winter kudu with A. tortilis was indicated by both methods, as well as the association of summer kudu with A. karroo. A. mellifera was also closely associated with summer kud in the second and third order habitat analysis. The importance of T. camphoratus and 'palatable evergreens' was overlooked by the CA of the second order habitat analysis. The reason for this was that T. camphoratus was too frequently encountered, and 'palatable evergreens' were not abundant enough to include in the nomenclature of my landscape descriptions. The preference of summer and winter kudu for shade and shelter was evident in figure 4, where riverine thicket was associated with kudu. These two components were also indicated by the discriminant functions.

Summer eland's preference for T. camphoratus and A. erioloba was obvious from both the second and third order analysis. The preference of eland for dense grass in summer was indicated by the third order analysis and could be inferred from the second order analysis, as A. erioloba woodland was normally associated with good grass cover. The summer preference of eland for A. karroo and 'palatable evergreens' was not indicated by the second order analysis, but was part of the third order discriminant function.

The third order habitat selection of winter eland did not compare with their second order habitat selection at all. Figure 4 indicated that eland preferred the second order habitat A. mellifera and A. tortilis woodland in winter. Kelso (1987) also found that the second order habitat of eland in the dry season consisted of thorny thickets along drainage lines.

My discriminant functions, however, indicated that the third order habitat selected by eland in winter consisted of T. camphoratus, R.ciliata, 'palatable evergreens', A. erioloba, and shade trees. The discriminant functions indicated that A. tortilis contributed negatively to the third order habitat selection of eland, and the phenograms showed that A. mellifera lost its leaves and pods early in winter. It could therefore not have contributed to the winter habitat of eland. Why this discrepancy? Eland were extremely nomadic in winter and were indeed often found in A. mellifera and A. tortilis woodland. These landscapes contained shade, which was part of the third order discriminant function. 'Palatable evergreens', particularly Boscia albitrunca and Cadaba aphylla were frequently encountered in these woodlands as well as fair quantities of T. camphoratus. These components were all part of the third order habitat of eland in winter. They occurred in localized patches in the woodland which were overlooked when the landscapes were classified.

It seemed as though the second and third order habitat selection of territorial animals, such as kudu, compared favourably. This did not seem to be the case with nomadic animals such as eland.

The lower down the hierarchy one moves in studies of the habitat relations of animals, i.e. the lower the resolution of the study becomes, the more scope there is for the omission of 'lurking variables'. The overshadowing effect also becomes greater as one moves down the hierarchy, i.e. small patches of seemingly unimportant habitat are overshadowed by larger ones. Senft et al. (1987) propose that animals interact most with their resources at a patch and community scale and that their resource selection at landscape and regional scales could be a coincidental result of the small-scale selections. Laymon & Reid (1986) found that a four-fold decrease in grid cell size dramatically increased the efficiency of a habitat suitability model for spotted owl. They concluded that small pockets of highly suitable habitat, which formed the core areas of the owls' home range, were being masked by larger scale habitat ratings.

Laymon & Barret (1986) conclude that the geographic scale at which models are developed should reflect the home range size and the degree of habitat specialization by the animal. They also state that a heterogeneous landscape calls for a higher resolution of study. They suggest that, as a rule of thumb, the plot size by which habitat should be measured should be about one quarter of the home range size of the animal in reasonably homogeneous surroundings.

My 314 m^2 plots measured the habitat preferences of kudu and eland at a much higher resolution than what Laymon & Barret (op. cit.) proposed. The CA, again, was done at a much lower resolution. It is perhaps unfair to compare the performance of two different techniques which are employed at different scales of study and then conclude about the efficiency of the scale of study only. In my experience CA was more efficient than DFA in low resolution studies and vice versa. I justified the use of two different statistical techniques on that basis.

4 Appraisal of my models

Of the numerous published and unpublished habitat suitability models, few have been tested. Among the tested models, many have proved to be inefficient and most required some adjustment (Berry 1986).

When validating a model, it is firstly difficult to decide which level of precision or predictability is acceptable (Starfield & Bleloch 1986; Mentis 1988). Secondly, it is difficult to decide on a strategy of model validation (Schamberger & O'Neil 1986). Buchman & Shifley (1983 in Brand, Shifley & Ohmann 1986) identified three criteria for the evaluation of a habitat model. 1) The ease of application of the model. 2) The model's predictive capabilities and 3) the model design, i.e. its biological realism and flexibility. The most important criterion when evaluating a habitat preference model, is how closely the model resembles habitat selection by the modeled species (Lancia, Miller, Adams & Hazel 1982). This cannot be done statistically, however. The most obvious method by which a model's efficiency is judged but which is not mentioned by any of quoted authors, is 4) whether the modeling objectives had been met.

Using the criteria proposed by Buchman & Shifley (op. cit.), my models performed as follows.

1) Ease of application. The models are easy to apply, as the variables incorporated in them are easily measurable. The expert systems and flow charts are 'user friendly' and can be mastered with very little training.

2) Predictive capabilities. The models could predict the presence or absence of kudu and summer eland significantly better than what would be expected of random models.

3) Resemblance to the 'real world' situation. The resemblance of the models to real habitat selection by the animals was difficult to evaluate. First, the relatively small number of variables with which I attempted to simulate the decision processes of the

animals, should be borne in mind. There were undoubtedly a vast array of interlinking factors which ultimately influenced habitat selection but to incorporate all of them and correctly quantify their interrelations in a mathematical model, was impossible. I am of opinion that the models represent a compromise between an oversimplified version of real habitat selection and a too complex one with the risk of being impracticable. Second, I could justify all the variables included in the discriminant functions by results of other studies. Third, the scale I used to develop the kudu models seemed to reflect the perceptions of kudu of their surroundings. I am not sure whether the same is true of the eland models. Fourth the use of seasonal submodels was an important feature which added to the realism of the models.

4) Flexibility. I am of opinion that my models are flexible. They can be readily updated and expanded as new data becomes available and the user is not bound by rigid rules. The flow charts afford the user the opportunity of attaching a probability to the presence of kudu or eland, but he ultimately makes his own decision. The variables incorporated in the flow charts and expert systems are functional plant groups rather than plant species. This feature allows the application of the model to other biogeographical areas with different floristic attributes.

5) Meeting of objectives. Referring to chapters one and three, I set two model objectives. Firstly I wanted the models to improve our understanding of habitat selection by browsers, and secondly I wanted them to predict the presence and absence of kudu and eland based on habitat suitability.

The models definitely contributed to my understanding of habitat selection by browsers. They provided a conceptual framework for the combined deduction and induction of new hypotheses. The first model objective had therefore been met.

Could the models predict the presence or absence of kudu and eland? The empirical answer is that they did so significantly better than 50% of the time, with one exception. One would then conclude that they were better than random models. But what about the other 21 to 43% incorrectly classified data? It is difficult to decide whether these records were classified incorrectly because of intrinsic shortcomings of the models, or for other reasons mentioned in section 1.1 of this chapter.

In my opinion the kudu models are adequate and can be used in the field. The incorrectly classified data could easily be due to animals being observed in movement from one favourite habitat patch to another. Such an observation would receive a 'present' rating, even though the patch did not represent suitable habitat. 'Absent' records could also have been incorrectly classified, due to the animals being absent from potentially suitable habitat patches.

The eland models are not entirely useless, but I would hesitate to recommend their immediate implementation by management. If one considers the diverse regions where eland occur, it does not make much sense to include variables such as plant species in the eland model. These regions range from coastal vegetation types to the Natal Drakensberg and from the grassland plains of the Orange Free State to the Kalahari semi-desert savanna. Perhaps other low resolution variables are determinants of eland presence. These could be annual rainfall for the region, or the presence of heart-water disease, or the average number of frosty days per year for the region. If these low resolution variables are combined with medium resolution, qualitative variables which apply to communities, the presence of eland would probably be better accounted for. The latter could be questions such as 'is the percentage projected canopy cover of the grass layer greater than 10%?' for a summer model and 'are there more than 10 individuals per hectare of thornless, large leafed evergreen trees?' for the winter model.

Both models can be refined while they are being implemented by management. Considering the violation of the assumptions of DFA and the short study period, I contend that the models should be applied on an experimental and exploratory basis. More data for their refinement can be gathered during the period of application.

5 Comparison with other models

Habitat suitability modelers have diverse objectives, assumptions, approaches and employ different techniques. It is therefore difficult to compare the efficiency of models constructed by different people. I here discuss only models with similar objectives to mine which were deemed successful by their authors.

Krausman & Leopold (1986) developed a discriminant function to predict the presence or absence of desert sheep. An important difference between their study and mine is that they previously selected areas where sheep often occurred, and then compared them to an adjacent area which was uninhabited by sheep. They then described the two habitat types by 2,59 km^2 plots. They set aside a random 50% of their data from the same localities to validate the discriminant functions with. They found that 88% of their plots were correctly classified by the discriminant function and concluded that their model 'excellently' differentiated the two areas they studied. Brennan et al. (1986) compared the percentage of correctly classified habitats in two groups, i.e. 'available' and 'used' habitat. They did not attempt to discriminate between used and unused habitat and state that their 'available' habitat could also have been potential habitat. Between 73 and 81% of their independent data were correctly classified. Numerous other models (Cole & Smith 1983; Cook & Irwin 1985; Lancia, Miller, Adams & Hazel 1982; Lancia, Adams & Lunk 1986) found a significant correlation between habitat suitability score and density or frequency of use.

CHAPTER 8. CONCLUSIONS

The models developed, tested and refined in this study were mostly suitable for regional application. With the exception of the winter eland model, they showed better than random predictive capabilities.

The eland models should be experimentally applied in practice and improved while they are being implemented. The kudu models performed well enough , in my opinion, to be applied and tested in other biogeographic areas. They can also be used as baselines for further research.

The model and project objectives had been reached, being that knowledge and understanding of habitat selection had been increased and practicable models had been developed. An approach towards the formulation of habitat suitability models had been developed. This approach can be applied to the construction of habitat models for other browsers.

FINAL SUMMARY

The aims of the study were to

1) develop and test habitat evaluation models for kudu and eland in the Northern Cape;

2) develop an approach towards habitat suitability which can be applied to a wider range of game species;

3) improve understanding of habitat selection by browsers.

The project was initiated to improve the standard of management advice by conservation officials to game ranchers.

The approach adopted in this study was to commence with crude provisional habitat suitability models and to then test and update them by several iterations. The preliminary models were tested during a pilot study, reconstructed, retested, updated and extended. The provisional models had no predictive values and had to be discarded. New models were formulated by the inductive approach, i.e. they were based on analyzed data.

The habitat selection of kudu and eland were studied at a fine scale by making use of 314 m^2 circular plots. Food and shelter resources were measured at plots where the animals were observed and at random localities. Discriminant function analysis was used to calculate linear functions to discriminate between the presence and absence of kudu and eland respectively.

The phenophases of the most important browse plants in the study area were analyzed by phenograms. The phenograms indicated a period of food shortage, i.e. June to August (winter) and a period of food abundance, September to May (summer). Based on phenology, winter and summer submodels were constructed for each species by means of discriminant functions and suitability index

(SI) curves. The curves were simplified after a sensitivity analysis.

Locally rare plant species were combined into functional groups based on a TWINSPAN of morphological characteristics.

In summer, kudu preferred patches where *Acacia mellifera*, *A. karroo* or *Ziziphus mucronata* were present. Structurally, the crown:gap ratios in these patches were small and shade was in close proximity. Kudu in winter selected patches where *A. tortilis*, *Z. mucronata*, 'palatable evergreen' plants or *Tarchonanthus camphoratus* were present. These patches also had small crown:gap ratios and shade nearby.

Eland in summer preferred patches where *A. erioloba*, dense grass, *T. camphoratus*, *A. karroo* or 'palatable evergreens' were present. They avoided patches where *Z. mucronata* or *A. mellifera* were present. In winter they selected patches with *T. camphoratus*, *Rhus ciliata*, 'palatable evergreens' or *A. erioloba*. They avoided patches where *A. tortilis* was present.

The function for summer kudu was
HSI = 0,48V1 + 0,36V2 + 0,4V3 + 0,35V4 + 0,39V5 where
HSI = habitat score
V1 = presence of *A. mellifera*
V2 = presence of *A. karroo*
V3 = presence of *Z. mucronata*
V4 = SI for crown:gap ratio
V5 = SI for proximity of shade.

The function for winter kudu was
HSI = 0,61V1 + 0,15V2 + 0,48V3 + 0,29V4 + 0,27V5 + 0,45V6
where
V1 = presence of *A. tortilis*
V2 = presence of *T. camphoratus*
V3 = presence of *Z. mucronata*

V4 = presence of 'palatable evergreens'
V5 = SI for crown:gap ratio
V6 = SI for proximity of shade.

The function for summer eland was

$$HSI = -0{,}58V1 - 0{,}54V2 + 0{,}37V3 + 0{,}13V4 + 0{,}19V5 + 0{,}13V6 + 0{,}41V7$$

where

V1 = presence of *A. mellifera*
V2 = presence of *Z. mucronata*
V3 = presence of *A. erioloba*
V4 = presence of *A. karroo*
V5 = presence of *T. camphoratus*
V6 = presence of 'palatable evergreens'
V7 = SI for grass density.

The function for winter eland was

$$HSI = -0{,}54V1 + 0{,}23V2 + 0{,}67V3 + 0{,}33V4 + 0{,}5V5 + 0{,}27V6$$

where

V1 = presence of *A. tortilis*
V2 = presence of *A. erioloba*
V3 = presence of *T. camphoratus*
V4 = presence of 'palatable evergreens'
V5 = presence of *R. ciliata*
V6 = SI for proximity of shade.

The models were verified by determining the percentage successfully classified dependent samples. The success of the summer kudu, winter kudu, summer eland and winter eland models were 72%, 81%, 71% and 69% respectively. They were then validated by independent data from the same study area which were collected along a different route.

With the exception of the winter eland model, the 95% confidence intervals of the proportion of correctly classified data were above 0,5. The models were able to classify the independent data significantly better than would be expected of random models, with one exception, the winter eland model. After validation the HSI models were converted to flow charts and expert systems.

In general, kudu preferred dense, shady patches where thorny plants without chemical defence mechanisms were present. Eland, on the other hand, preferred patches where plants with a high biomass of readily available leaves were present. They avoided patches with thorny trees or shrubs, especially if these contained hooked thorns. Eland were not averse to patches which contained plants with chemical defences such as aromatic oils.

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Appendix 1. Scientific names and status of ungulates occurring in the study area

Common name	Scientific name	Numbers
Black wildebeest	*Connochaetes gnou* (Zimmerman, 1780)	228
Blesbok	*Damaliscus dorcas phillipsi* Pallas 1766	120
Blue wildebeest	*Connochaetes taurinus* (Burchell, 1823)	517
Burchell's zebra	*Equus burchelli* (Gray, 1824)	67
Common duiker	*Sylvicapra grimmia* (Linnaeus 1758)	6 *
Eland	*Taurotragus oryx* (Pallas, 1766)	547
Gemsbok	*Oryx gazella* (Linnaeus, 1758)	566
Giraffe	*Giraffa camelopardalis* (Linnaeus, 1758)	36
Impala	*Aepyceros melampus* (Lichtenstein, 1812)	6
Kudu	*Tragelaphus strepsiceros* (Pallas 1766)	171
Mountain reedbuck	*Redunca fulvorufula* (Afzelius, 1815)	1 *
Red hartebeest	*Alcelaphus buselaphus* (Pallas, 1766)	782
Sable	*Hippotragus niger* (Harris 1838)	7
Springbok	*Antidorcas marsupialis* (Zimmerman, 1780	1438
Steenbok	*Raphicerus campestris* (Thunberg, 1811)	7 *

* Extreme undercount, due to small size and preferred habitat

Appendix 2. *Notes for users* of the BROWSHAB expert system

The expert system on diskette attached to the back cover of the thesis has been written in VPExpert and runs under DOS. It has been compiled by the VPExpert Runtime system under license agreement with Paperback Software International.

The program is activated by typing '*BROWSHAB*'. The highlight can be moved among options by the *arrow keys*. The user indicates his choice by the *ENTER key*, but may alter it by pressing the *DEL key*. The choice is confirmed by the END key, *whereafter* it cannot be altered.

The user can *determine* the reason why a question is being asked by typing '/W'. The program will respond with a *highlighted* message. The program can be *terminated* at any stage by typing '/Q'.

At the the final decision, any of the variable parameters may be altered by choosing the 'WHAT IF' option from the bottom menu. A list of variables will appear. Please ignore unknown variables. *The* appropriate variable should be highlighted, *entered* and altered, whereafter a new decision will be *displayed*.

Author Fabricius Christo
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