The relative performance of surrogate measures for viable populations

by

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ABSTRACT

Preservation of the total variety of the earth's biomes is necessary for the preservation of all extant species. Without sufficient quantities of their natural habitats, species will become extinct in the wild. Conservation area assessment techniques have concentrated on reserve placement, with less attention being afforded to reserve design principles such as population viability. The incorporation of viable populations of all species into conservation areas, to secure their long-term persistence, has not been explicitly accomplished to date. This study aims to explore the basis for including population viability into conservation area selection procedures. Due to the lack of spatially explicit abundance data for most species, reserve planning concentrates on representing all species in a given region a specified number of times, the current debate being about how best to achieve this goal and not about the inclusion of viable populations. The Kruger National Park annual herbivore census represents a spatially explicit data set that can be used to establish the spatial consequences of jointly incorporating viable populations of 12 large herbivore species (acting as umbrella species) into conservation area selection procedures. This was achieved by selecting for viable populations and quantifying the land surface area in which they occur, and which is subsequently needed to sustain these populations, ranging in size from 50 - 10 000 individuals per species. The outcome was that nearly 50% of each land classification unit in a region is needed to represent these individuals - irrespective of the size of the "viable population" specified. Furthermore, it was established that selecting a fixed percentage of each classification unit is not cost-effective in terms of land-use, and that this approach should be replaced with a system differentially concentrating on areas with higher conservation potential (e.g. source areas). Since conservation actions are only as good as the quality of the data on which they are based, it is imperative that biodiversity surveys be invested in.

Similarly, when selecting for increasing percentages of all the units within a land classification system, the number of individuals fortuitously included through this selection process was quantified. Also, the number of species for which viable populations was selected was deduced, for viable populations comprising either 100 or 500 individuals. Only at a 40% surrogate selection level were viable populations of all species included. Collectively, these results suggest that the most cost-effective MVP's can only be selected once the abundance-related stratification of species across a landscape is known, or if the location of source populations can be established.

In 1992 a recommendation by the IUCN that each country should strive to protect 10% of each of its biomes was made. It was implied that this target would be sufficient to conserve biodiversity world-wide. In the present study we propose that this figure is far from adequate in offering long-term protection and ensuring the survival of constituent species. These results accentuate the need for the concept of population viability to be included into conservation area selection procedures, where species representation seems to be the primary conservation goal, and long-term survival of species is not afforded adequate consideration.

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DISCALIMER

This M.Sc. dissertation consists of chapters and appendices that have been prepared for submission to, or publication in, a range of scientific journals. As a result, the chapter and appendix formats may contain some inconsistencies and overlap may occur to secure publishable entities.

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CHAPTER 1

General Introduction

> *"The worst thing that can happen - will happen ...- is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes would be for us, they can be repaired within a few generations. The one process ongoing that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats.. This is the folly our descendants are least likely to forgive us."*
>
> *- E. O. Wilson, 1985*

Biological diversity or "Biodiversity" is an umbrella term for the total degree of variety found in nature (McNeely *et al.*, 1990), and encompasses diversity at all levels of the biological hierarchy, from genes to species to ecosystems, and including the ecological processes that they are part of. The implied value that conservation biologists place on biodiversity may not be as obvious to many laypeople. In the words of Thomas E. Lovejoy: "Conservation is sometimes perceived as stopping everything cold, as holding whooping cranes in higher esteem than people. It is up to science to spread the understanding that the choice is not between wild places or people. Rather, it is between a rich or an impoverished existence for man". Subsequently, it is necessary for the conservation biologists to be able to fully explain and clarify this value to the broad public, since they are the people who's support is needed in conservation issues. Biological diversity adds abundant value to society, amongst others the goods derived from nature used for human consumption and in the medical industry, services like pollination and recycling, as well as the wealth of information that can be used in the fields of genetic engineering and applied biology (Meffe and Carroll, 1994). In addition, biodiversity has aesthetical, ethical as well as intrinsic value.

Since the beginning of the last decade, conservation biologists have been providing evidence that we are in the opening phase of a mass extinction (Ehrlich and Ehrlich, 1981; Wilson, 1992), where, if unchecked by appropriate conservation action could surpass in extent any of the prehistoric past mass extinction episodes. This will lead to genetic and species loss with accompanying loss of ecosystem diversity and irreparable damage will be done to the wealth of our planet's resources – to the detriment of our own species.

The establishment of national parks and other nature reserves, as a conservation strategy, are often conceived as being adequate for the protection of our biological resources. However, protected areas, managed exclusively for biological conservation comprise an area of only around 3% of the terrestrial land base world-wide (McNeely, 1994). The fact that land-use intensification is increasingly irreversibly depleting the world's biological heritage, accentuates the growing demand and urgency for extending the currently extant conservation area networks. Heightening this urgency is the growing competition that exists between alternative land uses, which is further limiting future opportunities to extend these conservation networks (Flather *et al.*, 1997). It is therefore imperative that the correct choice be made when setting aside additional conservation areas, in such a way as to guarantee extensive and complementary protection of every region's biota, i.e. trying to incorporate all elements of biodiversity, with special emphasis on those elements not presently under protection. How to best allocate limited conservation resources available has not been adequately resolved, but has been the main focus of many studies over the past decade (see Davis *et al.*, 1990; Vane-Wright *et al.*, 1991; Bedward *et al.*, 1992; Church *et al.*, 1996; Faith and Walker, 1996a, b; Csuti *et al.*, 1997; Flather *et al.*, 1997). One of the main factors hindering the identification of priority sites for conservation is the lack of robust data on species', as well as ecosystem distributions (Davis *et al.*,1990, Lombard, 1995; Balmford *et al.*, 1996a, b). Nevertheless, pressures from land transformation rates demand that existing biodiversity data, albeit not sound, be used as effectively and as soon as possible in conservation area decision making.

One possible way to address this problem, and one that has been investigated numerous times in the past, is the use of surrogate measures for biodiversity when conducting reserve selection (Balmford *et al.*, 1996a; Faith and Walker, 1996a, b;

Van Jaarsveld *et al.*, 1998; Wessels *et al.*, 1999). When making use of a surrogate, one has to identify a scale of surrogacy within which suitable indirect measures can be identified that will reflect species richness and species complementarity. For this reason we made use of an array of scales in the present study to establish the best possible scale for the four surrogates used here. A surrogate must be able to predict diversity (Humphries *et al.*, 1995) so that one can exploit a predictive relationship between the surrogate variable and the target variable to reduce costs and maximise the possibility of including as many elements of the biodiversity estate as possible. The study area comprises the Kruger National Park, South Africa (Figure 1), where we made use of vegetation types (Low and Rebelo, 1996), landscapes (Gertenbach, 1983), land types (Venter, 1990) and land systems (Venter, 1990) as possible surrogates for viable populations of 12 large herbivore species in the Kruger National Park. Environmental surrogates are frequently a more appropriate option than indicator groups or higher taxon richness since information on physical variables is already available for many areas, and is relatively easy and inexpensive to acquire for other areas. Furthermore, these surrogates integrate more of the functional processes important for maintaining ecosystem viability and species (Williams and Humphries, 1996). Vegetation types have been identified in previous studies as being a predictive measure of biodiversity (Woinarski *et al*, 1988; Hull, 1999). Furthermore, it has been shown that mammal diversity (as measured by species richness) is positively correlated with vegetation type diversity (Turpie and Crowe, 1994), and that using vegetation types as the primary factor influencing distribution and diversity patterns in mammals, can be justified as being "...the most meaningful ecological summary of the influences of soil, climate, topography and other static and dynamic environmental factors" (Davis, 1962). Likewise landscapes, land types and land systems were developed on the basis of a variety of environmental variables and should be able to predict diversity accurately.

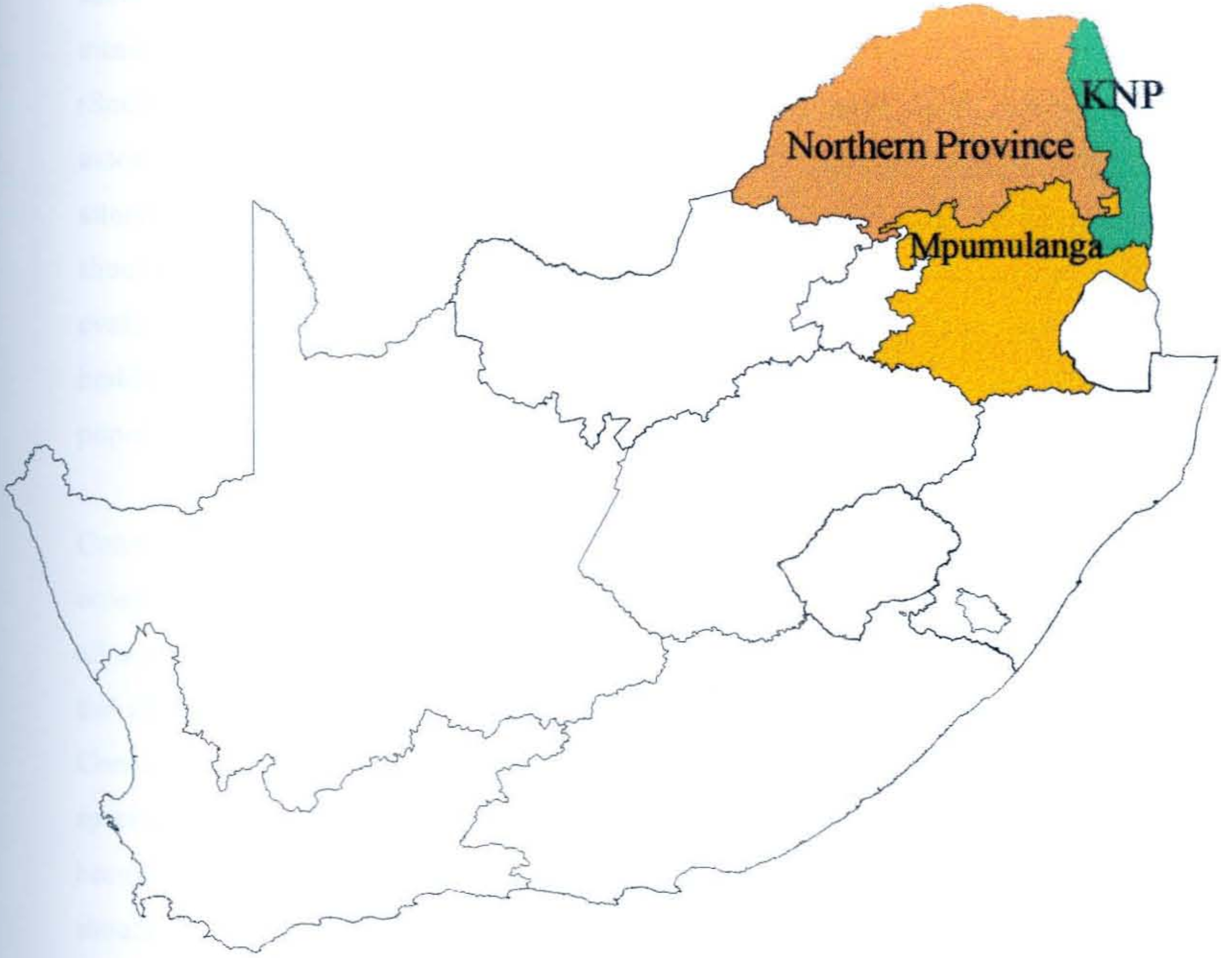


Figure 1: A map of South Africa showing the study area, the Kruger National Park (KNP), situated in the Northern and Mpumalanga Provinces

Planning for conservation includes planning for the long-term persistence and survival of all species within conservation areas. It is important to realise that any minimum viable population (MVP) will need a minimum area in which to survive (Soulé and Simberloff, 1986) and that national parks and reserves do not automatically protect the species within them (Grumbine, 1990). MVP theory attempts to determine threshold levels for species survival over the long term, and should inevitably be included in conservation planning. In the present study, we evaluate the land area needed to sustain combined viable populations of 12 large herbivore species, and we quantify the number of species for which viable populations are included at different degrees of surrogate selection.

Conservation should ideally aim at conserving ecosystems, not species, since the ecosystem approach is a much more rigorous and effective way to do conservation. If all ecosystems within all ecoregions can be successfully represented and maintained, the majority of species would be saved (David Olson (WWF) in Schmidt, 1996). Conserving the total variety of the earth's biomes is necessary to conserve all extant species. Without sufficient quantities of their natural habitats, species are bound to become extinct in the wild (Orions, 1994). But what area of each ecoregion (or biome) should be afforded protection if viable populations of all resident species are to be included?

In Chapter 2, we selected for viable populations of each of 12 large unmanaged herbivore species in the Kruger National Park using an iterative algorithm. Viable population sizes ranged from 50 to 10 000 individuals per species. The areas needed to jointly sustain these populations were quantified for each of the four land classification systems respectively, and at three grain sizes. Furthermore, differences in the distribution pattern of species in relation to changes in habitat quality was established.

Chapter 3 focuses on establishing whether viable populations are included when 10% of each land classification unit is selected. A total of 10% of the study area is thus selected, using an iterative reserve selection algorithm. Here we selected10% and up to

50% of each classification unit at different scales, and quantified the number of individuals per species fortuitously included through this selection process. This number was used to establish the number of species for which viable populations were captured in the given land surface area.

Chapter 4 explores the usefulness of setting aside a fixed area for nature conservation. We verify whether it is cost-effective to dedicate equal areas of all classification systems to nature conservation. We set up a model to determine the effectiveness of representing viable populations when setting aside a fixed percentage (ranging from 10% – 50%) of each land classification unit within a land classification system.

A detailed explanation of each of the four surrogates is given in Appendix 1, providing the area in the Kruger Park occupied by each classification unit within each classification system.

In Appendix 2, a related article on the land classification systems in the Kruger National Park, emanating from this study, is presented.

REFERENCES

Balmford, A., Green, M.B.J. & Murray, M.G. 1996a. Using higher-taxon richness as a surrogate for species richness: I. Regional tests. *Proc. R. Soc., Lond. B.* **263**, 1267-1274.

Balmford, A., Jayasuriya, A.H.M. & Green, M.J.B. 1996b. Using higher-taxon richness as a surrogate for species richness: II. Local applications. *Proc. R. Soc., Lond. B.* **263**, 1571-1575.

Bedward, M., Pressey, R.L. & Keith, D.A. 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol. Conserv.* **62,** 115-125.

Csuti, B., Polasky, S., Williams, P.H., Pressey, R.L., Camm, J.D., Kershaw, M., Kiester, A.R., Downs, B., Hamilton, R., Huso, M. & Sahr, K. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biol. Conserv.* **80**, 83-97.

Church, R.L., Stoms, D.M. & Davis, F.W. 1996. Reserve selection as a maximal covering location problem. *Biol. Conserv.* **76**, 105-112.

Davis, D.H.S. 1962. Distribution patterns of southern Africa Muridae, with notes on some of their fossil antecedents. *Ann. Cape Prov. Mus.* **2**, 56-76.

Davis, F.W., Stoms, D.M., Estes, J.E., Scepan, J. & Scott, J.M. 1990. An information systems approach to the preservation of biological diversity. *Int. J. G.I.S.* **4**(1), 55-78.

Ehrlich, P.R. and Ehrlich, A.H. 1981. *Extinction: The causes and consequences of the disappearance of species.* Random House, New York.

Faith, D.P. and Walker, P.A. 1996a. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv.* **5**, 399-415.

Faith, D.P. and Walker, P.A. 1996b. Integrating conservation and development: incorporating vulnerability into biodiversity-assessment of areas. *Biodiv. Conserv.* **5**, 417-429.

Flather, C.H., Wilson, K.R., Dean, D.J. & McComb, W.C. 1997. Identifying gaps in conservation networks: Of indicators and uncertainty in geographic-based analyses. *Ecol. Appl.* **7**(2), 531-542.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* **26,** 9-121.

Grumbine, R.E. 1990. Viable populations, reserve size, and federal lands management: A critique. *Conserv. Biol.* **4**(2), 127-134.

Hull, H.E. 1999. *The identification and distribution of Buprestidae (Coleoptera) priority conservation areas in South Africa and Namibia*. M.Sc. Thesis, University of Pretoria, Pretoria.

Humphries, C.J., Williams, P.H. & Vane-Wright, R.I. 1995. Measuring biodiversity value for conservation. *Ann. Rev. Ecol. Syst.* **26**, 93-111.

Lombard, A.T. 1995. The problem with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S.Afr.J.Zool.* **30**(3), 145-163.

Lovejoy, T.E. 1980. A projection of species extinctions. In council on Environmental Quality. *The Global 2000 Report to the President: Entering the Twenty-First Century.* U.S. Government Printing Office, Washington D.C.

Low, A.B. and Rebelo, A.G. (eds.) 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Dept Environmental Affairs & Tourism, Pretoria.

McNeely, J.A., Miller, K.R., Reid, W.V., Mittermeier, R.A. & Werner, T.B. 1990. *Conserving the world's biodiversity*. Washington, DC: IUCN, CI, WWF and World Bank.

McNeely, J.A. 1994. Protected areas for the 21st century: working to provide benefits to society. *Biodiv. Conserv.* **3**, 390-405.

Meffe, G.K. and Carroll, C.R. 1994. *Principles of conservation biology*. Inauer Associates, Inc., Sunderland, Massachusetts.

Schmidt, K. 1996. Rare habitats vie protection. *Science.* **274**, 917-918.

Soulé, M.E. and Simberloff, D. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biol. Conserv.* **35**, 19-40.

Turpie, J.K. and Crowe, T.M. 1994. Patterns of distribution, diversity and endemism of larger African mammals. *S. Afr. J. Zool.* **29**(1), 19-31.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. 1991. What to protect? Systematics and the agony of choice. *Biol. Conserv.* **55**, 235-254.

Van Jaarsveld, A.S., Freitag, S., Chown, S.L., Muller, C., Koch, S.O., Hull, H.E., Bellamy, C., Krüger, M., Endrödy-Younga, S., Mansell, M.W. & Scholts, C.H. 1998. Biodiversity assessment and conservation strategies. *Science.* **279**, 2106-2108.

Venter, F.J. 1990. *A classification of land for management planning in the Kruger National Park*. PhD Thesis. University of South Africa, South Africa.

Wessels, K.J., Freitag, S. & Van Jaarsveld, A.S. 1999. The use of land facets as biodiversity surrogates during reserve selection procedures at a local scale. *Biol. Conserv.* **89**, 21-38.

Williams, P.H. and Humphries, C.J. 1996. Comparing character diversity among biotas. In: *Biodiversity.* K.J. Gaston (ed.) pp. 54-76. Oxford: Blackwell Science.

Wilson, E.O. 1985. The biological diversity crisis: A challenge to science. *Issues Sci. Tech.* **2**, 20-25.

Wilson, E.O. 1992. *The diversity of life.* Penguin Books, England.

Woinarski, J.C.Z., Tidemann, S.C. & Kerin, S. 1988. Birds in a tropical mosaic: The distribution of bird species in relation to vegetation patterns. *Austr.J. Wildl. Res.* **15**, 171-196.

CHAPTER 2

The spatial implications of incorporating viable populations into conservation area selection procedures

The spatial implications of incorporating viable populations into conservation area selection procedures

1. INTRODUCTION

Although there is broad agreement about the need to conserve as much biodiversity as soon as possible, the most appropriate mechanism for achieving this objective has a protracted history. Meyers (1990) and Reid (1998) suggested that the conservation of hotspots (areas high in species richness, containing numerous endemic species or vulnerable species) would conserve the most species in the smallest area. These components are also frequently evaluated independently from one another (Gaston & Davis, 1994; Lombard, 1995; Mittermeier *et al.*,1998; Reid, 1998). In contrast, Margules *et al.* (1988) argued that in order to preserve maximum biological diversity in a given area, every possible species should be included in conservation area networks. They suggested that the goal of biodiversity representation can best be achieved by employing iterative algorithms that aim to represent all natural features using the principle of complementarity (Nicholls & Margules, 1993; Pressey *et al.*, 1993). Williams *et al* (1996) effectively demonstrated how the complementarity approach was significantly more land-use efficient at sampling regional features (species) than richness hotspots or rarity hotspots.

Binary data (presence/absence) form the platform for most iterative studies aimed at identifying representative conservation area networks (Nicholls & Margules, 1993; Sætersdal *et al.*, 1993; Williams *et al.*, 1996; Howard *et al.*, 1998; Van Jaarsveld *et al.*, 1998). Since abundance data are generally unavailable for most species (Davis *et al.*, 1990), the focus in conservation area network design is frequently to include at least one, or possibly more, representations per species. Freitag and Van Jaarsveld (1995) used a criterion of 3-5 records per species, whereas Williams *et al.* (1996) pursued at least 6 representations per species. More recent studies have aimed at incorporating notions of viable populations by selecting increasing numbers of individuals using abundance data (Nicholls,

1998) or by adding the criterion of viability indirectly into area-selection methods (Williams, 1998). For example, at the preselection step, one possible measure of viability - albeit very crude - is to only include records with evidence of breeding (breeding birds - Wessels *et al.,* 1999). Furthermore, niche-based modelling of the local habitat suitability can be used to exclude records for certain species from all areas where they have a poor viability prognosis. Probability models can be used to seek out "viability centres" for required species by interpolating the expected distribution of relatively well-known species and relatively widespread species where spatial information is used to model some aspects of "niche space". In this manner expected distributions and the potential viability of species can be predicted for unsampled areas (Williams, 1998).

In the present study we aim to examine the spatial implications of selecting viable populations of large herbivore species (acting as umbrella species) using the Kruger National Park annual aerial census data. These census data were collected in a spatially explicit manner (Joubert, 1983; Viljoen, 1989; Viljoen and Retief, 1994; Viljoen, 1996). The aims of the study are (1) to quantify the spatial implications of jointly selecting viable populations of 12 large herbivore species as opposed to single species representations, (2) to evaluate the impact of habitat quality, and (3) the impact of varying species densities on the distribution patterns and spatial requirements of viable populations.

2. METHODS

a) Study area

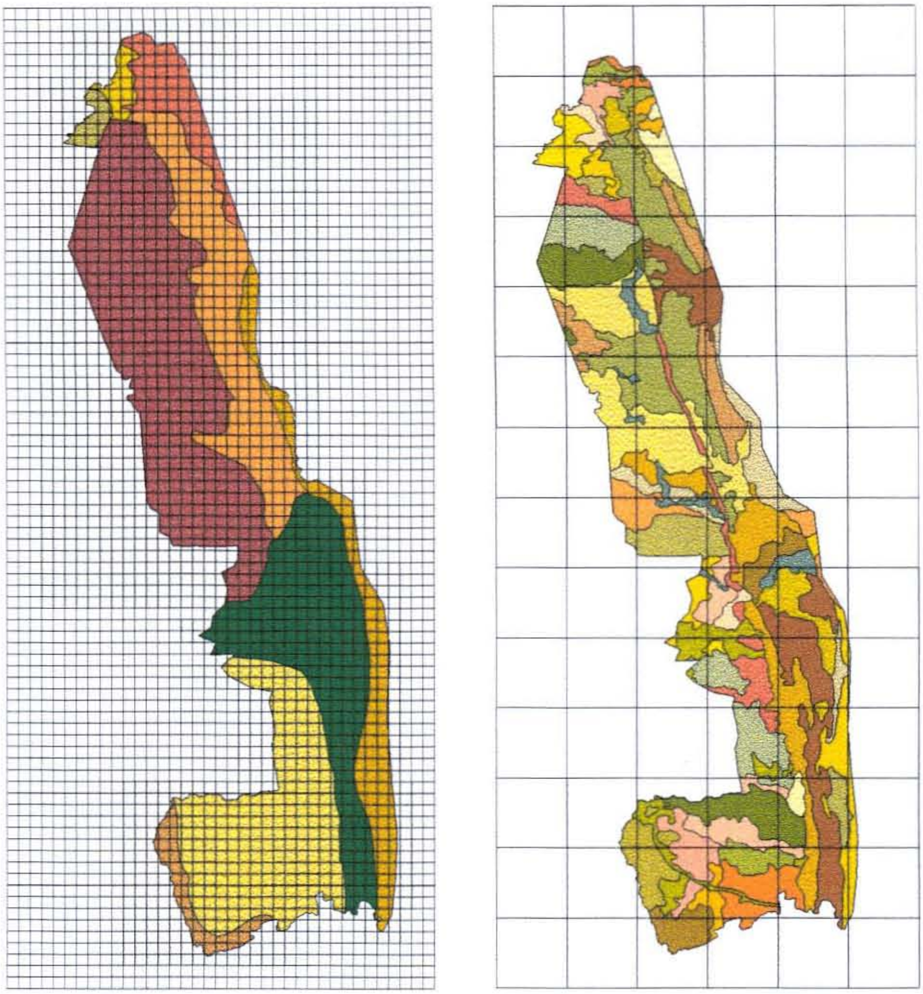
The study area comprises the Kruger National Park (KNP) situated in the Northern and Mpumalanga Provinces of South Africa, encompassing an area of roughly 20 000km^2. It is situated in the Savanna biome of South Africa, and consists of seven different Savanna vegetation types (Low and Rebelo, 1996). The mean annual rainfall for this area, measured over a period of 73 years (1919/20 – 1992/93), is 534mm. Long-term mean temperatures in the Park range between 15.8°C and 29.7 $^{\circ}$C over the same period of time (Zambatis and Biggs, 1995).

b) Animal abundance and distribution data

The present study investigates the spatial implications of selecting and incorporating large herbivore populations into conservation area planning. Point data obtained from the annual ecological aerial census for 12 unmanaged large herbivore populations in the KNP, that were obtained for the period 1981-1992, were reclassified into grid cell networks of 4km^2, 12.5km^2 and 25km^2 respectively. The twelve large, unmanaged herbivore species occurring in the KNP used in the study, are impala *(Aepyceros melampus)*, blue wildebeest *(Connochaetes taurinus)*, zebra (*Equus burchelli)*, white rhinoceros *(Ceratotherium simum)*, giraffe *(Giraffa camelopardalis)*, kudu *(Tragelaphus strepsiceros)*, sable antelope *(Hippotragus niger)*, eland *(Taurotragus oryx)*, warthog *(Phacochoerus aethiopicus)*, waterbuck *(Kobus ellipsiprymnus)*, tsessebe *(Damaliscus lunatus)* and the roan antelope *(Hippotragus equinus)*.

c) Land classification systems

Within the KNP a variety of differently scaled land classification systems have been developed, namely: land systems (Venter, 1990), land types (Venter, 1990) and landscapes (Gertenbach, 1983). These classifications, together with vegetation types (Low and Rebelo, 1996), were employed to explore the spatial consequences of conserving viable populations of large herbivores (Figure 1). The land system classification (Venter, 1990), comprising 11 land systems was developed on the basis of geology, geomorphology and broad climatic attributes. These land systems were further classified according to soil type, vegetation type and landform into 56 land types (Venter, 1990), with the land types nesting naturally within the borders of the land systems. Each land system comprises of between one and 12 land types. Thirty-five landscapes (Gertenbach, 1983) were identified according to specific geomorphology, climate, soil, vegetation pattern and associated fauna. Vegetation types (Low and Rebelo, 1996) are defined as those units that have a similar vegetation structure, sharing important plant species and having similar ecological processes.

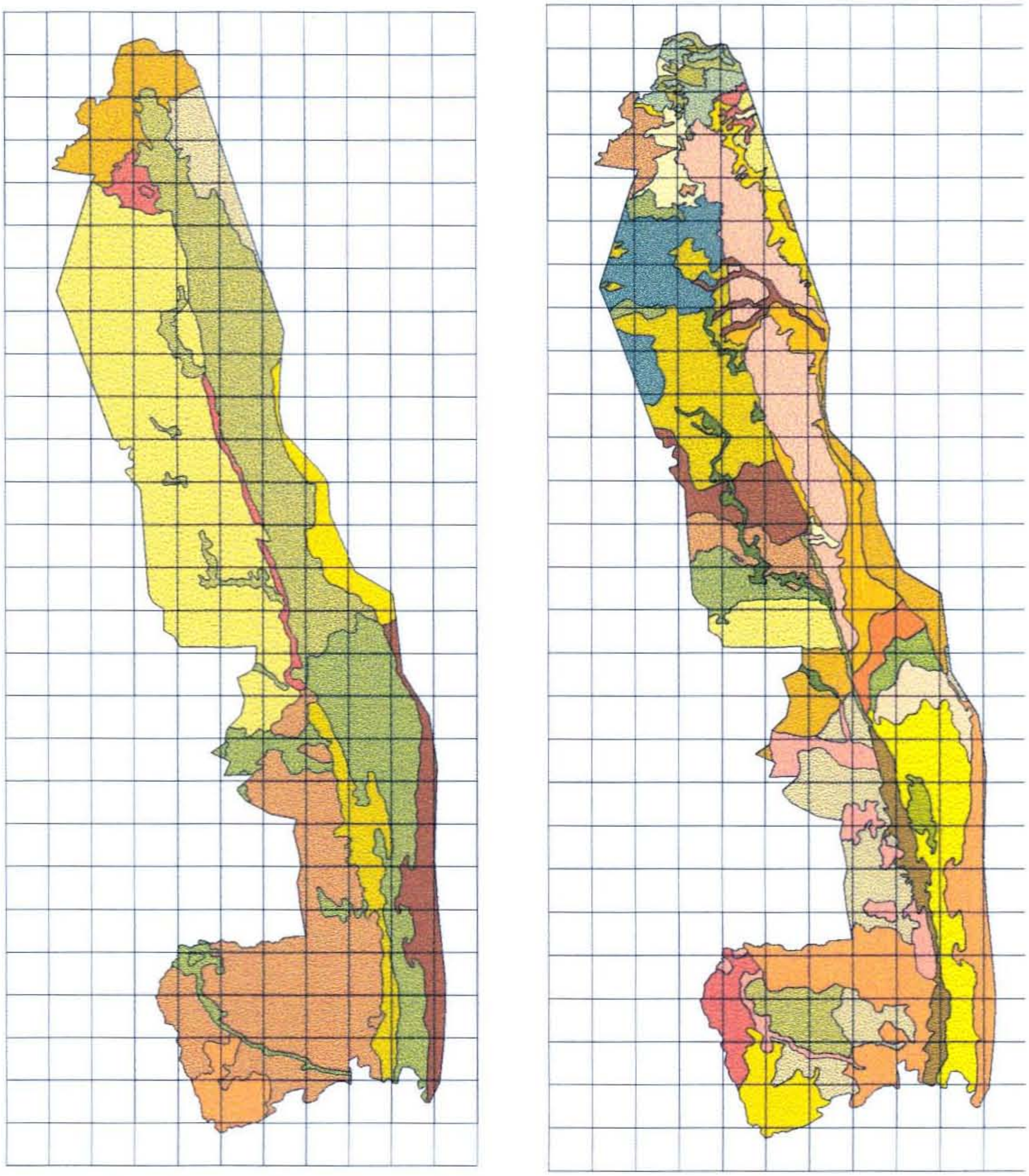


i)

ii)

Figure 1: i) The broadest scaled land classification system, vegetation types, intersected with the $4km^2$ grid cell network, and

ii) the finest scale land classification system, land types, intersected with the $25km^2$ grid cell network.



iii)

iv)

Figure 1: iii) Land systems, an intermediate scaled land classification system, intersected with the 12.5km^2 grid cell network.

iv) Landscape classification intersected with the 12.5km^2 grid cell network.

d) Scaling

In the present study fine, intermediate and broad scale grains were used (Wiens, 1989), namely: a 4km^2, a 12.5km^2 and a 25km^2 grid cell network. These grids cell networks were intersected with each of the four land classification systems respectively, using ArcInfo® GIS (ESRI, Inc., Redlands, California, USA). This resulted in 12 scale combinations (Table 1), and for each of these, information on the area of every land classification unit within a particular grid cell.

Table 1: A summary of the scale combinations used.

Land type	Land system
Land type and 4km^2 grid	Land system and 4km^2 grid
Land type and 12.5km^2 grid	Land system and 12.5km^2 grid
Land type and 25km^2 grid	Land system and 25km^2 grid
Vegetation type	Landscape
Vegetation type and 4km^2 grid	Landscape and 4km^2 grid
Vegetation type and 12.5km^2 grid	Landscape and 12.5km^2 grid
Vegetation type and 25km^2 grid	Landscape and 25km^2 grid

e) Population selection

An algorithm was coded that selects increasing target population sizes of all herbivore species, and then quantifies the area of each land classification unit fortuitously included by the selection of these target populations (see Appendix 1 for selection rules). The numbers of individuals selected are related to the grid cells in which they occur, and these grid cells, in turn, are related to the area of each classification unit within the chosen grid cells. The study was not restricted to one possible MVP size, but extended to incorporate a spectrum of possible population sizes. This was done in order to quantify the impact of increasing population sizes on conservation area selection procedures. Population sizes of 50, 100, 200, 500, 1000, 2000, 5000 and 10000 individuals were used successively. Each algorithm was run 500 times for each of the 12 scale combinations, and for each of the four years, in order to evaluate the outcomes statistically.

f) Habitat quality

Ecological aerial census data from four years were used. Two years had an above average rainfall recorded (1981, 1985; $\bar{x}$ = 774mm) and two years had a below average rainfall (1983, 1992; $\bar{x}$ = 267mm). This was to determine the possible spatial effects of varying habitat quality on the spatial distribution patterns of these herbivore species.

To determine whether changes in habitat quality affect the spatial distribution of individuals across the study area, we tested for significant differences between the data derived from the four years. As habitat quality and species density in one year influences following years, these data are not independent. Kendall's Coefficient of Concordance (Zar, 1996) was therefore used.

$$W=\frac{\sum Ri^2-[\sum(Ri)^2]/n}{[M^2(n^3-n)]/12}$$

Correlation, or association, between more than two variables can be measured nonparametrically by Kendall's coefficient of concordance. Ranks for each of the variables have to determined from frequency distributions, and these distribution data ranked according to Kendall's method to obtain *Ri* values, where *Ri* is the sums of ranks, *M* is the number of variables being correlated and *n* is the number of data points (number of classes in frequency distribution) per variable. A W-value close to one indicates high concordance (association) between the different data sets, and the closer this value gets to 0, the less association exists between the data sets.

g) Species abundance

In order to establish the possible effect that differences in species abundance may have on the area required to sustain viable populations, three different minimum population abundance criteria were set prior to analyses. First, a species had to have at least as many individuals as the target total that was being selected for in a particular run, else it was omitted (excluded) from that specific analysis. Secondly, a species had to have at least twice as many individuals as the target total selected for in each run, and thirdly, all species with less than three times the target total were omitted. Only target totals of up to 2000 were used, since too few species are included in the analyses targeting higher levels. Since these data are not independent, simple tests of significance between groups could not be performed. Thus it was necessary to calculate frequency distributions of the selected land classification unit area classes within each data set, and to rank these. Kendall's Coefficient of Concordance was then used to determine whether significant differences existed between areas included at varying population density selections.

3. RESULTS

The output of the algorithm, selecting for the specified target totals of individuals (ranging from 50 to 10 000) obtained for each of the 12 scale combinations individually, yielded percentage areas of each land classification unit fortuitously included through this selection process, i.e. all areas that area occupied by the selected number of individuals. The average percentage area values and standard deviations for all units selected in successive runs (n = 500) in every land classification system were calculated. An average value, indicating the area needed to sustain a specific population size, was obtained for each classification unit. These results are summarised in Figure 2 (i – xii), where every graph represents one of the 12 scale combinations used in the analyses. Data for all four years analysed are provided in each graph.

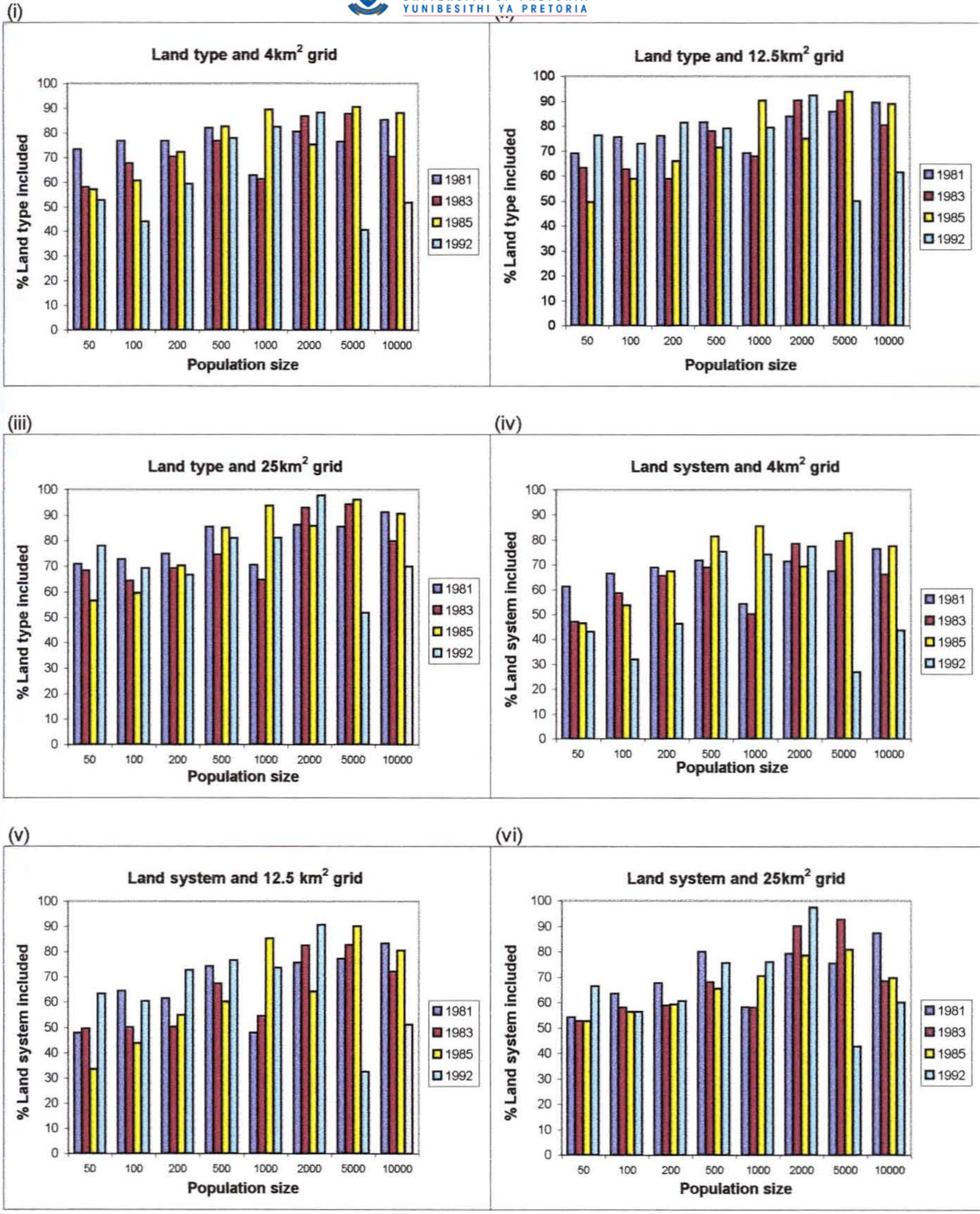
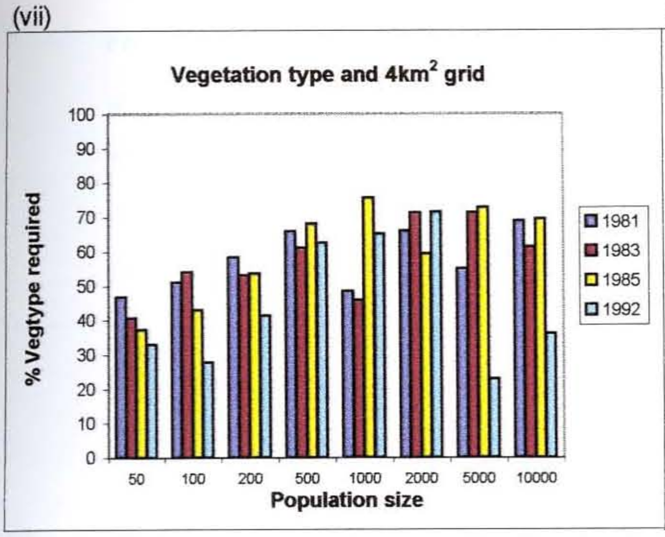
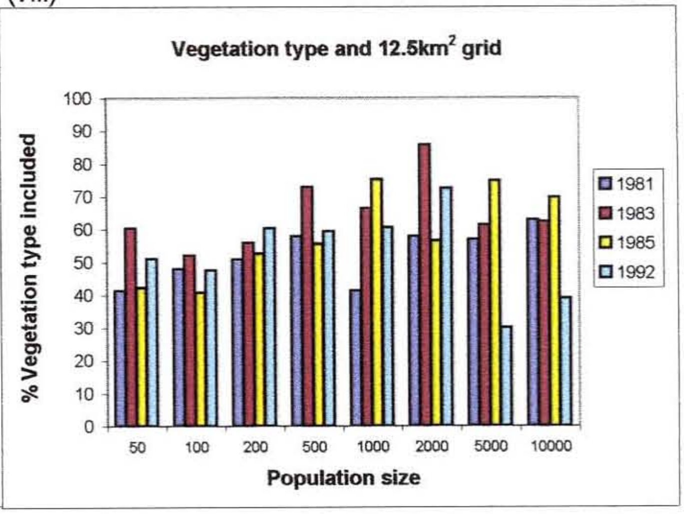


Figure 2: A summary of the area requirements for conserving 12 herbivore species in the KNP, using three different grain sizes (4, 12.5, 25km^2) and four land classification systems (land type, land system, vegetation type and landscape).

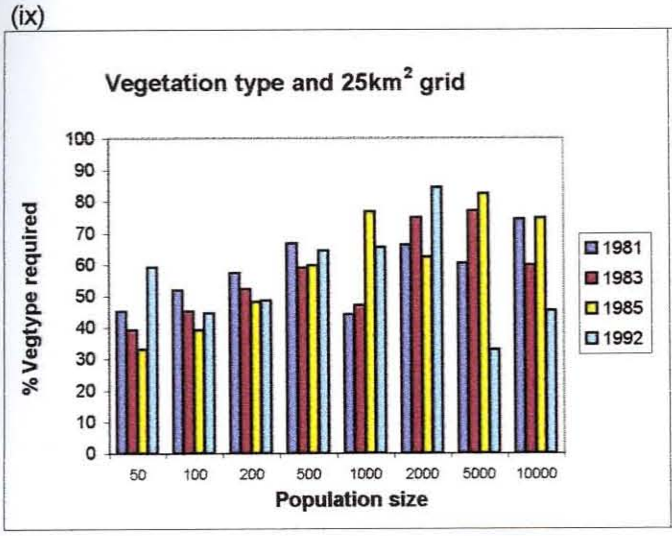
(vii)



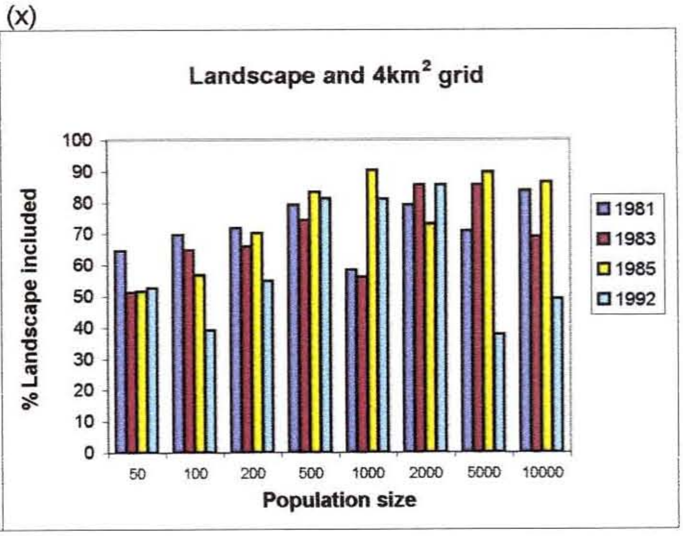
(viii)



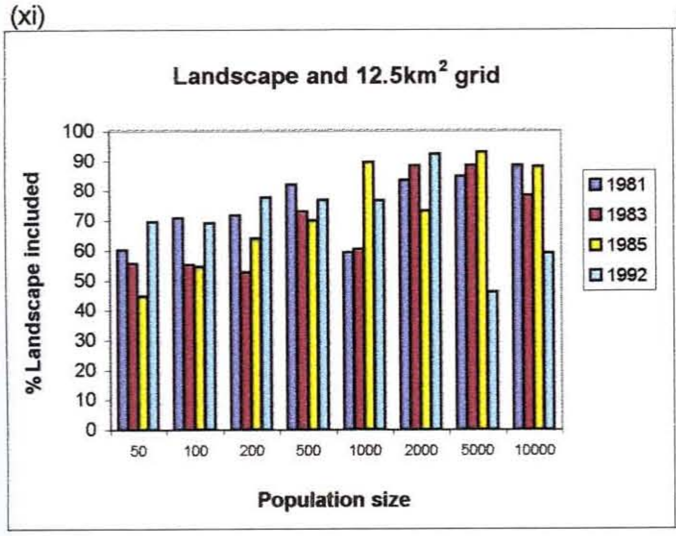
(ix)



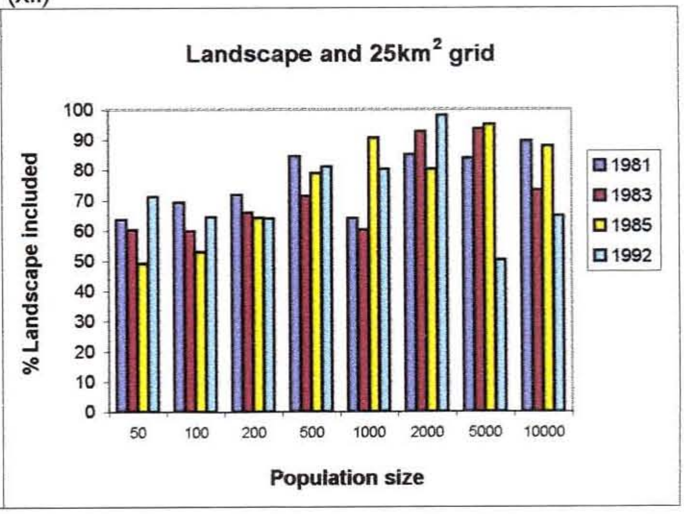
(x)



(xi)



(xii)



From Figure 2 (i to iii) it can be seen that an average of at least 50% of the KNP is needed to represent the different population targets, except in Figure 2 (i), where 45% and 40% is required for population sizes of 100 and 5000 respectively in 1992. This can be ascribed to the fact that different species are omitted from the analyses due to their population sizes being smaller than the specified target totals. In 1992, which was a particularly dry year, Roan antelope was omitted from the analyses at the 100 selection level and Kudu was omitted at the 5000 selection level, causing the areas required to be reduced. This is because the algorithm does not have to then proceed until the specified target total of these low density species is obtained, the area consequently required is much smaller than when these species are included.

Figure 2 (iv to vi) summarises the results obtained for the land system classification. For the 4km^2 and 12.5 km^2 grids, seven and five data sets respectively required less than 50% of the area of the KNP. For the vegetation type classification 11 of the 32 data sets for all three grid sizes require less than 50% of the area (Figure 2 vii to ix).

For the landscape classification in Figure 2 (x to xii), population size targets of 100 and 5000 needed less area for the 1992 data. This is as Roan and Kudu were excluded respectively from these analyses, since their population sizes were smaller than the specified target totals (see above).

To determine if changes in habitat quality affect the spatial distribution of individuals across the study area, we tested for significant differences between the four years' data. However, habitat quality and species density from one year will have an influence on that of subsequent years, thus these data are not independent of one another. Therefore, each of the 96 data sets were ranked, and Kendall's coefficient of concordance used to determine whether the fairly high observed association (Figure 2: i - xii) between different years can be statistically substantiated (Table 2: i to xii).

Table2: The degree of concordance between percentage area requirements for viable populations from the four years for each of the 12 scale combinations.

(i)

		Land type and 4km^2					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	291016	10758400	268960	85280	0.25863	<0.41050	40.3501
100	295897	10758400	268960	85280	0.31587	<0.12539	49.2831
200	317606	10758400	268960	85280	0.57043	<0.00001	88.9908
500	322389	10758400	268960	85280	0.62651	<0.00000	97.7452
1000	312041.5	10758400	268960	85280	0.50518	<0.00016	79.0431
2000	324283.5	10758400	268960	85280	0.64873	<0.00000	101.3656
5000	293736.5	10758400	268960	85280	0.29053	<0.22162	45.4422
10000	311483.5	10758400	268960	85280	0.49863	<0.00022	77.8435

(ii)

		Land type and 12.5km^2					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	295699	10758400	268960	85280	0.31354	<0.13291	48.9151
100	314109.5	10758400	268960	85280	0.52943	<0.00006	82.6002
200	305705.5	10758400	268960	85280	0.43088	<0.00332	67.2458
500	318988.5	10758400	268960	85280	0.58664	<0.00000	91.6079
1000	318090.5	10758400	268960	85280	0.57611	<0.00001	89.8940
2000	312944	10758400	268960	85280	0.51576	<0.0010	80.8587
5000	308669.5	10758400	268960	85280	0.46564	<0.00025	77.4200
10000	318962.5	10758400	268960	85280	0.58633	<0.00000	91.6292

(iii)

		Land type and 25km^2					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	320353.5	10758400	268960	85280	0.60264	<0.00000	94.0632
100	328139.5	10758400	268960	85280	0.69394	<0.00000	108.2933
200	324315	10758400	268960	85280	0.64910	<0.00000	101.3114
500	332938.5	10758400	268960	85280	0.75022	<0.00000	117.1295
1000	324235.5	10758400	268960	85280	0.64816	<0.00000	101.6645
2000	329762	10758400	268960	85280	0.71297	<0.00000	118.4455
5000	312351	10758400	268960	85280	0.50881	<0.00002	86.1108
10000	328370	10758400	268960	85280	0.69665	<0.00000	110.7283

(iv)

		Land system and $4km^2$					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3-n)}{12}$	W	p	χ^2
50	292027	10758400	268960	85280	0.2705	<0.33399	42.2026
100	294703	10758400	268960	85280	0.3019	<0.17499	47.1063
200	299718	10758400	268960	85280	0.3607	<0.03589	56.3241
500	318898	10758400	268960	85280	0.5856	<0.00000	91.9582
1000	295569	10758400	268960	85280	0.3120	<0.09777	50.8054
2000	311010	10758400	268960	85280	0.4931	<0.00022	77.8648
5000	288402	10758400	268960	85280	0.2280	<0.53962	37.4725
10000	299529.5	10758400	268960	85280	0.3585	<0.03397	56.6048

(v)

		Land system and $12.5km^2$					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3-n)}{12}$	W	p	χ^2
50	294217.5	10758400	268960	85280	0.2962	<0.19883	46.2212
100	296939.5	10758400	268960	85280	0.3281	<0.09133	51.2096
200	306051.5	10758400	268960	85280	0.4349	<0.00275	68.0242
500	315739	10758400	268960	85280	0.5485	<0.00002	86.9643
1000	296779.5	10758400	268960	85280	0.3262	<0.08442	51.6697
2000	308923.5	10758400	268960	85280	0.4686	<0.00009	81.1484
5000	292891	10758400	268960	85280	0.2806	<0.05696	53.8831
10000	303839	10758400	268960	85280	0.4090	<0.00611	64.6368

(vi)

		Land system and $25km^2$					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3-n)}{12}$	W	p	χ^2
50	292466.5	10758400	268960	85280	0.2756	<0.29059	43.3679
100	304217.5	10758400	268960	85280	0.4134	<0.00470	65.7726
200	314069	10758400	268960	85280	0.5290	<0.00004	84.2553
500	312084	10758400	268960	85280	0.5057	<0.00005	83.2839
1000	302011.5	10758400	268960	85280	0.3876	<0.00999	62.4595
2000	302093.5	10758400	268960	85280	0.3885	<0.00026	77.2689
5000	291855.5	10758400	268960	85280	0.2685	<0.08893	51.3662
10000	307712	10758400	268960	85280	0.4544	<0.00027	77.0202

(vii)

		Vegetation type and 4km^2					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	288936	10758400	268960	85280	0.23424	<0.57975	36.6024
100	292793	10758400	268960	85280	0.27947	<0.28004	43.6635
200	308691.5	10758400	268960	85280	0.46589	<0.00073	73.3036
500	310978.5	10758400	268960	85280	0.49271	<0.00018	78.5242
1000	305991.5	10758400	268960	85280	0.43423	<0.00170	69.9944
2000	313305.5	10758400	268960	85280	0.52000	<0.00003	85.0659
5000	282769.5	10758400	268960	85280	0.16193	<0.91676	27.4732
10000	296735	10758400	268960	85280	0.32569	<0.07107	52.6553

(viii)

		Vegetation type and 12.5km^2					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	293143.5	10758400	268960	85280	0.28358	<0.25689	44.3369
100	292463	10758400	268960	85280	0.27560	<0.29523	43.2397
200	300948.5	10758400	268960	85280	0.37510	<0.01948	59.3521
500	304358	10758400	268960	85280	0.41508	<0.00352	66.9896
1000	295228	10758400	268960	85280	0.30802	<0.10053	50.6390
2000	305684	10758400	268960	85280	0.43063	<0.00079	73.0006
5000	291839	10758400	268960	85280	0.26828	<0.014600	48.3111
10000	297943.5	10758400	268960	85280	0.33986	<0.03740	56.1124

(ix)

		Vegetation type and 25km^2					
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	298678.5	10758400	268960	85280	0.34848	<0.04704	54.9130
100	303414.5	10758400	268960	85280	0.40402	<0.00641	64.4287
200	313499.5	10758400	268960	85280	0.52227	<0.00004	83.8826
500	325719.5	10758400	268960	85280	0.66557	<0.00000	110.8640
1000	302793	10758400	268960	85280	0.39673	<0.00437	66.0768
2000	314466	10758400	268960	85280	0.53361	<0.00000	106.2174
5000	289391.5	10758400	268960	85280	0.23958	<0.16923	47.3331
10000	308932	10758400	268960	85280	0.46871	<0.00011	80.3168

(x)

			Landscape and 4km^2				
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	306275.5	10758400	268960	85280	0.4376	<0.00258	68.28088
100	298339.5	10758400	268960	85280	0.3445	<0.05821	53.76442
200	307431.5	10758400	268960	85280	0.4511	<0.00154	70.39451
500	325169.5	10758400	268960	85280	0.6591	<0.00000	103.0688
1000	297992.5	10758400	268960	85280	0.3404	<0.04767	54.84198
2000	316945.5	10758400	268960	85280	0.5627	<0.00001	44.77475
5000	293294.5	10758400	268960	85280	0.2853	<0.24251	44.77475
10000	305412	10758400	268960	85280	0.4274	<0.00352	66.99946

(xi)

			Landscape and 12.5km^2				
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	302338	10758400	268960	85280	0.3914	<0.01353	61.06878
100	297610.5	10758400	268960	85280	0.3360	<0.07410	52.41928
200	302549.5	10758400	268960	85280	0.3939	<0.01241	61.46727
500	315674	10758400	268960	85280	0.5478	<0.00003	85.53268
1000	307150.5	10758400	268960	85280	0.4478	<0.00174	69.9033
2000	316247	10758400	268960	85280	0.5545	<0.00002	87.13615
5000	300294	10758400	268960	85280	0.3674	<0.00785	63.53468
10000	320883	10758400	268960	85280	0.6089	<0.00000	95.0993

(xii)

			Landscape and 25km^2				
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
50	320883.5	10758400	268960	85280	0.6089	<0.00000	95.01543
100	322979.5	10758400	268960	85280	0.6334	<0.00000	98.87413
200	332835	10758400	268960	85280	0.7490	<0.00000	116.9048
500	331736	10758400	268960	85280	0.7361	<0.00000	115.5059
1000	327576.5	10758400	268960	85280	0.6873	<0.00000	107.495
2000	325635	10758400	268960	85280	0.6646	<0.00000	115.5333
5000	310674	10758400	268960	85280	0.4891	<0.00004	84.05518
10000	331333	10758400	268960	85280	0.7314	<0.00000	115.9626

If a W value close to 1 is obtained, and this value is shown to be statistically significant at the 5% level (i.e. $p < 0.05$), one can deduct that a high concordance exists between the four data sets. This would indicate that habitat quality has no, or little, effect on the observable spatial distribution patterns of large herbivore species across the employed land classification systems. If, however, a significantly high concordance is not obtained, it would suggest that there are differences either in the distribution pattern of species or in the density at which the species occur under different environmental conditions. From Table 2 (i to xii) it can be seen that none of the values denote a strong significant concordance between these data sets. All the W-values in these tables range between 0.16 and 0.75, being unsatisfactory as an indication of potential association between the data for the four years. When $p > 0.05$, no significant concordance exists between the data and we can assume that there is no association between the four data sets, and that environmental change indeed influences the distribution pattern of large herbivore species. On the other hand, where p is significant ($p<0.05$), it can be deduced that the concordance is significant, though not high in any of these investigations.

The effects of selecting specified target totals of individuals when species occur at different abundance levels on the amount of land required was assessed (Figure 3).

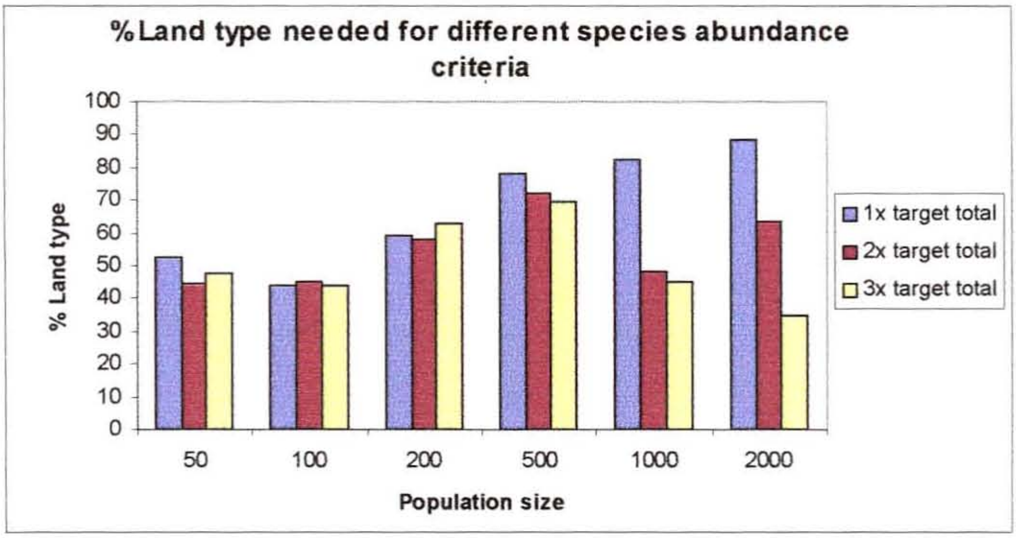


Figure 3: Percentage land area required for three different minimum population abundance selection criteria.

For population sizes up to 500 individuals a close association between the three minimum abundance criteria is evident. This apparent association is statistically confirmed by the high coefficients of concordance (W) as well as the statistically significant p-values, indicating significance, for these population sizes (Table 3).

Table 3: Coefficient of Concordance and p-values for different population sizes

Population size	Coefficient of Concordance (W)	p-value
50 individuals	$W = 0.6675$	$p < 0.0002$
100 individuals	$W = 0.9669$	$p < 0.0000$
200 individuals	$W = 0.8737$	$p < 0.0000$
500 individuals	$W = 0.7594$	$p < 0.0001$
1000 individuals	$W = 0.4280$	$p < 0.1098$
2000 individuals	$W = 0.3329$	$p < 0.4703$

From Figure 3, there does not seem to be concordance between the three abundance criteria for population sizes of 1000 and 2000. This low concordance is reflected in the W-values, which are not statistically significant. Thus, up to certain population sizes (smaller than 2000 individuals) population density will not have an influence on the amount of land included, thereafter population density will increasingly become a determining factor when selecting for viable populations of large herbivore species.

4. DISCUSSION

Holling (1992) concluded that the spatial grain at which a landscape is sampled by animals is largely a function of body size. Thus, the larger the body size, the larger the home range of the animal. It can thus be accepted that as an umbrella component of regional biodiversity, any selection procedure that effectively selects viable populations of large herbivores, with associated larger home ranges, will likely enhance the probability that viable populations of most other biodiversity components are included into a conservation area network.

Since different ecological patterns will arise at different scales of investigation in any environment, it is necessary to work at an array of scales within a study area. Therefore, the 12 scale combinations were employed in the present study. In 1989 Wiens introduced the concepts "extent" and "grain" –two components of scaling that work together to define the scale-dependency in a system. Extent can be defined as the total area encompassed by a study – in this case the Kruger National Park. Grain, on the other hand, is the size of the individual observation units (grid cells).

The changes in area required for the different scale combinations is due to the manner in which the areas included are calculated. When the conservation area selection algorithm targets a specified number of individuals of all species, it finds those species in certain grid cells. All the grid cells needed to represent these individuals are written to an output file. This file is used to identify the area of each classification unit that is fortuitously included through this selection procedure. Consequently, it may happen that species A is found in classification unit 2, but that the grid cell selected includes, for example, classification units 2, 4, 6, and 8 (see Figure 1). Areas included for these other three classifications will therefore also increase, despite the absence of relevant individuals occurring in these areas. The scale combination where this added effect will be minimised, is when the 4km^2 grid cell network is intersected with the vegetation type classification (Figure 1 i), since the probability that additional broad scale vegetation types will be included in a small grid cell are minimised. Moreover, this effect will be maximised when the 25km^2 grid cell network is intersected with the finest scale land classification, namely land types (Figure 1 ii).

A number of important findings, crucial to our understanding of the spatial requirements of viable populations of large herbivore species, emerged from these analyses. First, and perhaps most important, is that irrespective of the spatial or temporal scales employed in this study, in general, more than 50% of each land classification unit is needed to jointly sustain viable populations of the large herbivores in the KNP. This general trend seems unaffected by defining viable populations as comprising of 50, 500 or even 5000 individuals. These results are consistent with those from other studies in different parts of the world, focussing mainly on the representaion of all plant species or habitat types in a specific region (Soulé and Sanjayan, 1998). The estimates of minimum areas required to protect biodiversity according to these and other studies are listed in Table 4.

Table 4: A comparison of the percentage area needed to conserve all species or habitat types within a specific region.

Study goal	Region	Technique	% Area	Reference
To include all plant species (1 to 5 times)	Macleay Valley Floodplains, Australia	Iterative algorithm	44.9%	Margules *et al.*, 1988
To include all wetland types & all plant species	Macleay Valley Floodplains, Australia	Iterative algorithm	75.3%	Margules *et al.*, 1988
To protect all plant species	Deciduous forests in Norway	Non-heuristic algorithms	75%	Sætersdal *et al.*, 1993
Include all plant species	Transvaal region, South Africa	Iterative algorithm	60%	Unpublished
Represent eight taxa of fauna and flora	Transvaal region, South Africa	Iterative algorithm	74%	Unpublished
Represent all ecosystems	Oregon Coast Range	-	49%	Noss (In: Soulé & Sanjayan, 1998)
Preserve habitats essential for rare and declining species	Florida	-	33.3%	Cox *et al.* (In: Soulé& Sanjayan, 1998)

Secondly, differences in the distribution of individuals between years with high rainfall and years with low rainfall were found. These differences were significantly higher than that found when testing independently between the two years with above average rainfall and between the two years with below average rainfall figures (Table 5). These results suggest that there is a difference in the spatial distribution pattern of herbivore species in response to habitat quality changes at the scales investigated here. In a study correlating animal distribution patterns to the availability of water, it was found that patterns differed between years with a high rainfall figure and years with comparatively low rainfall figures (Redfern, pers. comm.). In the light of this, we can deduce that, although the correlation found between animal distribution for the four years used in the present study is significant, this association (based on W values) is too small in most cases to be biologically meaningful. Hence, although environmental variation influences distribution patterns of large herbivore species, it still does not affect the considerable amount of land needed to effectively conserve these species.

Table 6: The degree of concordance between percentage area requirements for viable populations for those population sizes were significant concordance was found between four years

(i)

	Land type and 4km^2 ; 1981&1985 (Two wet years)						
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
200	85230	268960	67240	21320	0.84381	<0.0183	65.8171
500	82329	268960	67240	21320	0.70774	<0.0043	55.2037
1000	81755	268960	67240	21320	0.68082	<0.3311	53.1037
2000	83967	268960	67240	21320	0.78457	<0.0191	61.1963
10000	84586.5	268960	67240	21320	0.81363	<0.0064	63.4628

(ii)

	Land type and 4km^2 ; 1983&1992 (Two dry years)						
Population size	ΣRi^2	$(\Sigma Ri)^2$	$(\Sigma Ri)^2/n$	$\frac{M^2(n^3 - n)}{12}$	W	p	χ^2
200	80270	268960	67240	21320	0.61116	<0.0183	47.6707
500	85721	268960	67240	21320	0.86684	<0.0099	67.6134
1000	82154	268960	67240	21320	0.69953	<0.0741	54.5634
2000	82379.5	268960	67240	21320	0.71011	<0.0481	55.3884
10000	78841	268960	67240	21320	0.54414	<0.5111	42.4427

Thirdly, when selecting for different target numbers of individuals, the dominant land unit appears to be unspecific, suggesting that a specific classification unit is not exclusively selected for. Thus, it appears that individuals from species are not actively selecting for or against specific classification units within surrogate types.

Using Kendall's coefficient of concordance, a close association between the three different minimum abundance criteria data sets can be observed for population sizes up to 500 individuals (Figure 3, Table 3).

Furthermore, the Kendall's coefficients for population sizes ranging from 50 to 500 individuals are highly significant ($p < 0.01$, Table 2), whereas no significance can be attached to the coefficients for population sizes exceeding 500 individuals. Thus it appears that population density, and therefore population size, becomes a significant determining factor in the area required at some selection level.

What are the conservation implications of these results?
At the Convention on Biological Diversity in November 1990 (which was signed by different governments at the Rio Earth Summit in June 1992) it was decided that 10-12% of each of the world's biomes should be protected. This is a very novel idea, and should this campaign work, it would double or triple the land area currently under protection. However, subsequent literature has suggested that this target may not be adequate for the protection of biodiversity. The conclusions drawn from an island biogeography perspective, is that as much as 50% of wildlands is required to represent and protect most elements of biodiversity (Soulé and Sanjayan, 1998), and that 10% is far from adequate to achieve this goal.

Similarly, the present study found that from a population viability perspective, some 50% of land may be required to conserve viable populations of umbrella species. Therefore the 10-12% figure should be regarded as the absolute minimum amount of land that a country needs to protect - and *not* the upper limit. The conservation targets set will differ for each country, but the 10% target appears to be ineffective for the adequate protection of a given country's biodiversity.

In conclusion, given the fact that conserving 10% of each biome appears inadequate for conserving viable populations of large herbivores, that conserving single representations per species is not ideal, and conserving 50 - 80% of each biome is likely to be inconceivable in terms of land use and land availability, stratified conservation objectives that represent different degrees of protection might have to be pursued - an objective similar to that proposed by the biosphere concept (World Resources Institute, 1994).

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REFERENCES

Davis, F.W., Stoms, D.M., Estes, J.E., Scepan, J. & Scott, J.M. 1990. An information systems approach to the preservation of biological diversity. *Int. J. GIS.* **4**, 55-78.

Freitag, S. and Van Jaarsveld, A.S. 1995. Towards conserving regional mammalian species diversity: a case study and data critique. *S. Afr. J. Zool.* **30**(3), 136-144.

Gaston, K.J. and Davis, R. 1994. Hotspots across Europe. *Biodiv. Letters.* **2**, 108-116.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* **26**, 9-121.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* **62**(4), 447-502.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. & Balmford, A. 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature*, **394**, 472-475.

Joubert, S.C.J. 1983. A monitoring programme for an extensive national park. Pp. 201 - 212. In: Owen-Smith, N. (ed). *Management of large mammals in African conservation areas.* Pretoria: Haum.

Lombard, A.T. 1995. The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* **30**(3), 145-163.

Low, A.B. and Rebelo, A.G. (eds.) 1996. *Vegetation of South Africa, Lesotho and Swaziland.* Dept Environmental Affairs & Tourism, Pretoria.

Margules, C.R., Nicholls, A.O. & Pressey, R.L. 1988. Selecting networks of reserves to maximise biological diversity. *Biol. Conserv.* **43**, 63-76.

Mittermeier, R.A., Myers, N, Thomsen, J.B., Da Fonseca, G.A.B. & Olivieri, S. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. *Conserv. Biol.* **12**(3), 516-520.

Myers, N. 1990. The biodiversity challenge: Expanded hot-spots analysis. *The Environmentalist.* **10**(4), 243-256.

Nicholls, A.O. (1998) Integrating population abundance, dynamics and distribution into broad-scale priority setting. (pp. 241-272) In: *Conservation in a changing world.* G.M. Mace, A. Balmford & J.R. Ginsberg. (eds). Cambridge University Press, Cambridge.

Nicholls, A.O and Margules, C.R. 1993. An upgraded reserve selection algorithm. *Biol. Conserv.* **64**, 165-169.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. 1993. Beyond opportunism: Key principles for systematic reserve selection. *TREE*, **8**(4), 124-128.

Reid, W.V. 1998. Biodiversity hotspots. *TREE.* **13**(7), 275-280.

Sætersdal, M., Line, J.M. & Birks, H.J.B. 1993. How to maximise biological diversity in nature reserve selection: Vascular plants and breeding birds in deciduous woodlands, Western Norway. *Biol. Conserv.* **66**, 131-138.

Soulé, M.E. and Sanjayan, M.A. 1998. Conservation targets: Do they help? *Science.* **279**, 2060-2061.

Van Jaarsveld, A.S., Gaston, K.J., Chown, S.L. & Freitag, S. 1998. Throwing biodiversity out with the binary data? *S.Afr.J.Sci.* **94**, 210-214.

Venter, F.J. 1990. *A classification of land for management planning in the Kruger National Park*. PhD Thesis. University of South Africa, South Africa.

Viljoen, P.C. 1989. Ecological aerial surveys in the Kruger National Park: Objectives and methods. Unpublished mimeograph, National Parks Board, Skukuza.

Viljoen, P.C. 1996. Ecological aerial surveys in the Kruger National Park: Summary of methodology. Unpublished mimeograph, National Parks Board, Skukuza.

Viljoen, P.C. and Retief, P.F. 1994. The use of the global positioning system for real-time data collecting during ecological aerial surveys in the Kruger National Park. *Koedoe* **37**, 149-157.

Wessels, K.J., Freitag, S. & Van Jaarsveld, A.S. 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biol. Conserv.* **89**, 21-38.

Wiens, J.A. 1989. Spatial scaling in ecology. *Funct. Ecol.* **3,** 385-397.

Williams, P.H. (1998) Key sites for conservation: area-selection methods for biodiversity. In: *Conservation in a changing world.* G.M. Mace, A. Balmford & J.R. Ginsberg. (eds). Cambridge University Press, Cambridge.

Williams, P.H., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R, 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conserv. Biol.* **10**(1), 155-174.

World Resources Institute. 1994. *World Resources 1994-1995*. Oxford University Press, New York, pp. 152-153.

Zambatis, N. and Biggs, H.C. 1995. Rainfall and temperatures during the 1991/92 drought in the Kruger National Park. *Koedoe* **38**(1), 1-16.

Zar, J.H. 1996. Biostatistical analysis. (3^{rd} ed). Prentice-Hall International, Inc. USA. pp. 407-445.

Appendix A

Viable population selection algorithm.

Written by Gründlingh Enslin and Mariaan Solomon (1998).

Selection rules are as follows:

1. Determine the target total of individuals that are being selected for.
2. Exclude all species with fewer individuals than the target total from the analyses.
3. Choose a grid cell at random.
4. If there are no individuals in that grid, choose another one at random, until a grid cell is found with individuals present. Write this grid cell number to a file (GridNumbers).
5. Count the number of individuals of all species present and write the numbers to an output file (NumberOfIndivs).
6. Check to see whether the target total of any given species has been reached. If the target total for a species has been reached, exclude that species form further selections.
7. Choose a grid cell as close as possible to the current cell containing individuals of unrepresented or underrepresented species. Write grid cell number to GridNumbers file. Count the number of individuals of all species present and write the numbers to NumberOfIndivs.
8. Check to see whether the target total of any given species has been reached. If the target total for a species has been reached, exclude that species form further selections.
9. Repeat this procedure until the target total for all species have been reached.
10. Use GridNumbers file and set a relation to a file containing the area of each classification unit that occurs in each grid cell. Calculate the total area of each unit needed to sustain the selected individuals.
11. Repeat the above procedures a total of 500 times.

This algorithm is run for all eight population sizes (50, 100, 200, 500, 1000, 2000, 5000 and 1000 individuals

CHAPTER 3

Using broad-scale environmental surrogate measures for selecting viable populations of "umbrella species" and regional biodiversity

Using broad-scale environmental surrogate measures for selecting viable populations of "umbrella species" and regional biodiversity

1. INTRODUCTION

Nature conservation has only recently become recognised as a legitimate form of land use (Margules and Usher, 1981), competing for limited land resources with agriculture and forestry, as well as urban and industrial development. Conservation areas play an indispensable and vital role in the protection of natural ecosystems (regional biodiversity). However, more biodiversity exists in agricultural, pastoral, forestry and other human-dominated ecosystems, that cover about 80 percent of the world's terrestrial environment, than in protected areas (World Resources Institute, 1993). A central issue in conservation biology is the importance of conserving maximum biological diversity in the limited land surfaces available to nature conservation (Freitag *et al.,* 1996). Critical decisions regarding the permanent location of protected areas are presently being made, thus emphasising the need for reserve networks to be as representative of biodiversity as possible, i.e. containing as many elements of biodiversity as possible (Pressey *et al.*, 1993).

Identifying areas with high conservation values, which are both representative of biodiversity and complements the current reserve network, requires extensive species distribution information (Pressey *et al.*, 1993). Since adequate databases on the distribution of species seldom exist (Nicholls, 1989; Belbin, 1993; Haila and Margules, 1996), the use of surrogate measures for biodiversity has to be relied on in systematic conservation area selection procedures. In the present study we aim to establish if viable populations of large herbivore species can be incorporated into conservation area selection procedures by using broad-scale surrogates and to ascertain how efficient these surrogates are at including finer scale elements of the biodiversity estate. The aims are (1) to evaluate the manner in which the selection of varying degrees of surrogate variables incorporates viable populations of the large herbivore species in the Kruger National Park (KNP) and (2) to determine whether vegetation type as a broad scale surrogate represents unsurveyed species by evaluating the species representation of this surrogate at a broader scale (Savanna biome) using existing presence/absence data on seven other taxa (mammals, birds, butterflies, termites, antlions, buprestid beetles and scarab beetles). These specific taxa were used because they have previously been used in conservation area selection procedures where a species-based approach was used and the insect groups are representative of four insect orders with diverse habitat requirements.

The concept of biological diversity first appeared in the ecological literature towards the middle of the 1980s (Ghilarov, 1996), usually in the context of concerns over the loss of the natural environment and its contents (Gaston, 1996). Various definitions for biodiversity have been proffered, all broad ranging, imprecise and providing a poor foundation for its practical measurement (Gaston, 1994). The practicalities of conserving maximum biological diversity will greatly depend on whether or not we can find effective units of measurement for biodiversity itself for the purposes of conservation planning (Soulé, 1989; Vane-Wright *et al.* 1991; Pressey *et al.*, 1993).

A wide variety of different possible measures of biodiversity have been suggested, applied and discussed (e.g. Vane-Wright *et al.,* 1991; Gaston, 1994; Gaston,1996). One possible solution to this problem of biodiversity-measurement is to find appropriate indicators for these measures. Indicators are measurable surrogates for biodiversity or other environmental endpoints (Noss, 1990). Such surrogates should be quantities that are more easily determined and which correlate strongly with those measures of biodiversity which are ultimately targeted (Gaston and Blackburn, 1995). According to Gaston and Blackburn (1995), three groups of surrogates have been suggested in the past: (i) species richness of an indicator group, (ii) the numbers of higher taxa and (iii) the diversity of various broad environmental parameters.

Broad scale environmental parameters

Systematically selecting regional conservation areas in order to represent all surrogate classes - and consequently the region's entire range of environmental variation - assumes that these areas contain all the species found in that region (Belbin, 1993; Nicholls and Margules, 1993; Faith and Walker, 1996). Through a pattern-based approach such as this, species variation is linked to environmental variation as summarised in an environmental pattern. Wessels *et al.* (1999) reviewed this rationale, and found that the environmental representativeness of reserve networks have been assessed using a variety of surrogate measures, including climatic attributes (Austin and Nix, 1978), climatic and edaphic variables (Belbin, 1993), landscapes (Pressey and Nicholls, 1989), landform-vegetation classes (Awimbo *et al.*, 1996), land systems (Pressey and Nicholls, 1989), landscape ecosystems (Lapin and Barnes, 1995), environmental groups (Mackey *et al.*, 1989), environments (Margules *et al.*, 1994) and environmental domains (Bedward *et al.*, 1992).

The highly controversial issue of population viability is one that will unlikely be resolved in the immediate future. There are two aspects associated with minimum viable population size: genetics and population dynamics. Two possible estimates for the size of populations that would be needed to conserve the genetic variance within the population is offered by Franklin (1980) - the much quoted 50/500 controversy. Animal production studies indicate that inbreeding is kept to a tolerable level if the population consists of 50 individuals. In natural populations, on the other hand, the lower limit of 500 individuals is suggested by Franklin (1980). Since this is an effective population size, the actual size of the population would be three to four times larger in order to score $N_e = 500$. Caughley (1994) argues that Franklin's 500 relates to the amount of genetic variance one might wish to retain - 500 indicating the amount of genetic variance that is equal to the amount of environmental variance expressed in the phenotype of a totally homozygous population. In a study on Drosophila it was shown that this variance would be retained by a genetically effective population of 500.

If a population conforms to the minimum conditions for the long-term persistence and adaptation in a given location, it can be termed a viable population. Long-term persistence can be defined in this context as the capacity of the group to maintain itself without significant demographic or genetic manipulation for the foreseeable ecological future (usually centuries) with a certain degree of certitude, say 95%. The probabilistic qualification is necessary, because it would be impossible to absolutely guarantee the survival of a group, no matter what the size. The long-term viability of a group does not depend solely on size and population dynamics - factors like environmental variation and stochasticity, genetics, catastrophes as well as metapopulation structure and fragmentation play a vital role in the persistence of a group. A minimum viable population (MVP) can thus be thought of as a set of estimates that are the product of a systematic process (a population viability analysis) for estimating species-, location- and time-specific criteria for persistence and survival (Soulé, 1989). Thus, no single value or magic number exists that has universal validity. The subjective choice of an acceptable level of risk will determine the numbers, densities and distribution in space of a MVP, because every situation or population is unique.

McNab (1963 *loc. cit* Holling, 1992.) found that the home ranges of mammals scaled in the classic allometric relation to body mass. Similarly, Holling (1992) concludes that the spatial grain at which a landscape is sampled by animals is largely independent of both the landscape and the animal's trophic status, but it is a function of body size, and presumably, of body form. Thus, the larger the body size, the larger the home range of the animal. It can thus be accepted that as an umbrella component of regional biodiversity, any surrogate procedure which effectively selects viable populations of large herbivores, with associated large home ranges, will maximise the probability that most other biodiversity components are sufficiently included into a reserve network, since smaller species generally require smaller ranges. This notion will be tested at a local scale, namely for the Savanna biome, by using available data on the distribution of seven other taxa.

2. METHODS

a) Study area

The study area comprises the Kruger National Park (KNP) located in the Northern and Mpumalanga Provinces of South Africa, encompassing an area of roughly 20 000km^2. It is situated in the Savanna biome of South Africa, and consists of seven different Savanna vegetation types (Low and Rebelo, 1996). The mean annual rainfall in the Park, measured over a period of 73 years (1919/20 – 1992/93), is 534mm. Long-term mean temperatures for this area range between 15.8^{O}C and 29.7 ^{O}C over the same period of time (Zambatis and Biggs, 1995).

b) Animal abundance and distribution data

Point data for the period 1981-1992 obtained from the Kruger National Park annual ecological aerial census for 12 large herbivore populations were reclassified into 4km^2, 12.5km^2 as well as 25km^2 grid square cell layers respectively. The twelve large, unmanaged herbivore species occurring in the KNP used in the study, are impala *(Aepyceros melampus)*, blue wildebeest *(Connochaetes taurinus)*, zebra (*Equus burchelli)*, white rhinoceros *(Ceratotherium simum)*, giraffe *(Giraffa camelopardalis)*, kudu *(Tragelaphus strepsiceros)*, sable antelope *(Hippotragus niger)*, eland *(Taurotragus oryx)*, warthog *(Phacochoerus aethiopicus)*, waterbuck *(Kobus ellipsiprymnus)*, tsessebe *(Damaliscus lunatus)* and the roan antelope *(Hippotragus equinus)*.

Data from four years were used to assess whether differences in habitat quality will influence the inclusion of viable populations. Two of the years had an above average rainfall, with $\bar{x}$ = 774mm/annum (1981 and 1985) and for two years (1983 and 1992) a below average rainfall figure was recorded ($\bar{x}$ = 267mm/annum).

c) Environmental surrogates

Within the KNP a variety of different scaled land classification systems have been developed, namely: land systems (Venter, 1990), land types (Venter, 1990) and landscapes (Gertenbach, 1983). These classifications, together with vegetation types (Low and Rebelo, 1996) were used as broad-scale surrogates in the present study. Environmental data can be used to assess the relative biodiversity of an area, because if the environmental variation (or habitat/ecosystem variation) is measured correctly, it should be a good indication of species diversity (Faith and Walker, 1996). These four different land classification systems were employed to explore the consequences of using environmental surrogate measures for conserving viable populations of large herbivores. Using ArcInfo® GIS, Version 7.1.2 (ESRI, Inc., Redlands, California, USA) each of these four land classification systems were intersected with each of the three grid cell layers respectively, resulting in 12 scale combinations used in the present study (Table 1). Through these intersections, the proportion of each unit in a classification system occupying all grid cells in a layer was obtained.

Table 1: A summary of the scale combinations used

Land type (Venter, 1990)	Land system (Venter, 1990)
Land type and 4km^2 grid	Land system and 4km^2 grid
Land type and 12.5km^2 grid	Land system and 12.5km^2 grid
Land type and 25km^2 grid	Land system and 25km^2 grid
Vegetation type (Low & Rebelo, 1996)	Landscape (Gertenbach, 1983)
Vegetation type and 4km^2 grid	Landscape and 4km^2 grid
Vegetation type and 12.5km^2 grid	Landscape and 12.5km^2 grid
Vegetation type and 25km^2 grid	Landscape and 25km^2 grid

The land system classification (Venter, 1990), comprising 11 land systems, was developed on the basis of geology, geomorphology and broad climatic attributes. These land systems were further classified according to soil type, vegetation type and landform into 56 land types (Venter, 1990). Thirty-five landscapes (Gertenbach, 1983) were identified according to specific geomorphology, climate, soil, vegetation pattern and associated fauna. Vegetation types (Low and Rebelo, 1996) are defined as those units that have a similar vegetation structure, sharing important plant species and having similar ecological processes.

d) Surrogate selection

An algorithm was applied to randomly select a fixed percentage of each of the land classification units of each surrogate, and the number of individuals of each species occurring in the selected areas was quantified. This was to see how, and if, viable populations of the large herbivore species are included in the selected areas. This analysis was performed on each of the four data sets (1981, 1983, 1985, 1992) and at each of the 12 scale combinations (Table 1). Thus a total of 48 different data sets were assessed using the Percentage Area Representation algorithm (Wessels *et al.*, 1999).

Although this algorithm (hereafter referred to as PAR) is land-use efficient, it provides an invariable result with the same outcome at each run, considering that the starting point is always the grid cell containing the largest area of the smallest land unit. Therefore, an algorithm that will perform a specified number of iterations at each representation level (e.g. 10%, 20% ...50% of each vegetation type), in order to generate alternative networks of grid cells, was coded. The PAR algorithm was modified, resulting in an algorithm where multiple iterations are possible, and which requires a randomly arranged list of each land type and a pre-specified random initiation grid cell. This algorithm (PARI) was used only for the land type classification, to determine whether changing the starting point and subsequent selection rules, will have any influence on the results. Average percentages of individuals included through the land type selection were calculated. The selection rules of both these algorithms are provided in Appendices A and B respectively.

e) Habitat quality

Provided that differences exist between the results obtained for the four years in the previous analyses, it would be an indication that rainfall, and hence habitat quality, influences species abundance. To deduce whether changes in habitat quality indeed affect included population sizes and the consequent spatial distribution of individuals across the study area, we tested for significant differences between the data derived from the four years. As habitat quality and species density in one year influences following years, these data are not independent. Kendall's Coefficient of Concordance (Zar, 1996) was therefore used.

$$W = \frac{\sum R^2 i - [\sum (Ri)^2] / n}{[M^2 (n^3 - n)] / 12}$$

Correlation, or association, between more than two variables can be measured nonparametrically by Kendall's coefficient of concordance. Ranks for each of the variables have to determined from frequency distributions, and these distribution data ranked according to Kendall's method to obtain *Ri* values, where *Ri* is the sums of ranks, *M* is the number of variables being correlated and *n* is the number of data per variable. A W-value close to one indicates high concordance (association) between the different data sets, and the closer this value gets to 0, the less association exists between data sets.

f) Percentage viable populations

Ultimately, the objective is to determine the number of species for which viable populations are included at various degrees of broad scale surrogate selection. Using the PARI algorithm, the mean number of individuals and percentages of species included in repeated analyses was determined. Population sizes of both 100 and 500 individuals were chosen as being possible minimum viable population sizes. Species with fewer than 100 and 500 individuals respectively, were excluded from these analyses. Therefore, for comparative purposes the percentage of species for which viable populations were included are given, and not the number of species. This percentage is calculated as the number of species that reached 100 (or 500) individuals in a given selected area divided by the number of species consisting of at least 100 (or 500) individuals. Considering the fact that the same linear trend is exhibited at all three grain sizes and across all four land classification systems, these analyses were limited to six of the 12 scale combinations - the finest and broadest grain sizes, intersected respectively with the vegetation type, landscape and land type classification systems. Only these results are displayed and discussed.

g) Effectiveness of surrogates for sampling regional biodiversity

It has also been argued that the predictive relationship between surrogates and the target elements (e.g. species) should preferably be demonstrated, and not just assumed (Pressey, 1994; Williams and Humphries, 1996). Thus the question arises as to whether different taxa show similar patterns in relation to broad-scale surrogates, i.e., whether different broad scale surrogates systematically differ in their ability to represent unsurveyed species. The data for the Kruger Park had to be extrapolated to the rest of the Savanna biome where species representation of various surrogates at a broader scale using existing presence/absence data of 7 taxa (mammals, birds, butterflies, termites, antlions, buprestid beetles and scarab beetles) was evaluated. Since these binary data are only available at a quarter degree grid square scale, and the landscape, land type and land system data only exists for the KNP, these analyses were just performed for the 25km^2 grid square cell layer intersected with the vegetation type data. Only grid cells for the Savanna biome of South Africa were used, since the KNP lies in this biome, and a true reflection would not be obtained if data were to be extrapolated to the whole country, encompassing all other biomes. All grid cells covering the Savanna biome were extracted from a database for the entire country, and these were used to select for increasing percentages of the biome. All areas currently protected were preselected, and areas were systematically added to this existing reserve network using the PAR algorithm with preselection (selection rules in Appendix C). The numbers of unique species per taxon included at each percentage vegetation type selection were calculated as well as the percentage that this number comprise of the total number of species per taxon found in the Savanna biome.

3. RESULTS

The PAR algorithm, that selects a specified percentage of a surrogate, generated outputs that can be spatially interpreted. For each spatial configuration of grid cells generated by the PAR algorithm, the number of individuals per species occurring in these grid cells was determined.

Number of individuals

When selecting for increasing percentages of a land classification system, a perceptible, but not statistical, linear relationship between the percentage land classification (surrogate) and the number of individuals occurring in that area was found. This held true for all species, at all three grain sizes, across all four land classification scales and across all four years examined (e.g. Figure 1 (i - iv)). Figure 1 illustrates this pattern for 1992 for species ranging from low density, rare species (Roan antelope) to species occurring at very high densities (Impala) in the KNP. It can be seen that population size does not considerably influence the observed linearity. The PARI algorithm was applied on the land type classification to establish whether changing the starting point of the algorithm and subsequent selection rules will have an influence on this apparent linearity that exists between the percentage surrogate selected and number of individuals occurring in these areas. No difference was found between the results obtained from the PAR and PARI algorithms.

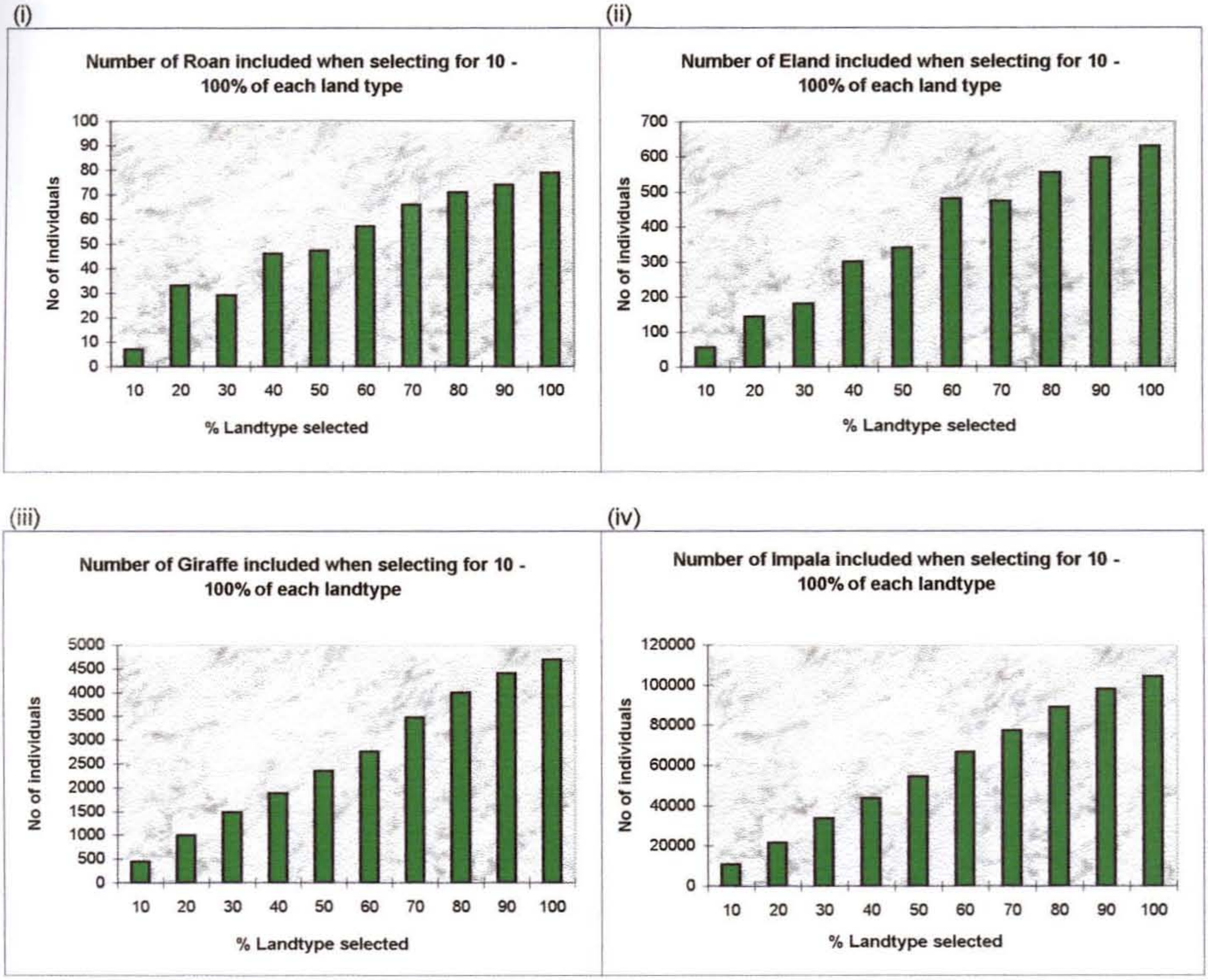
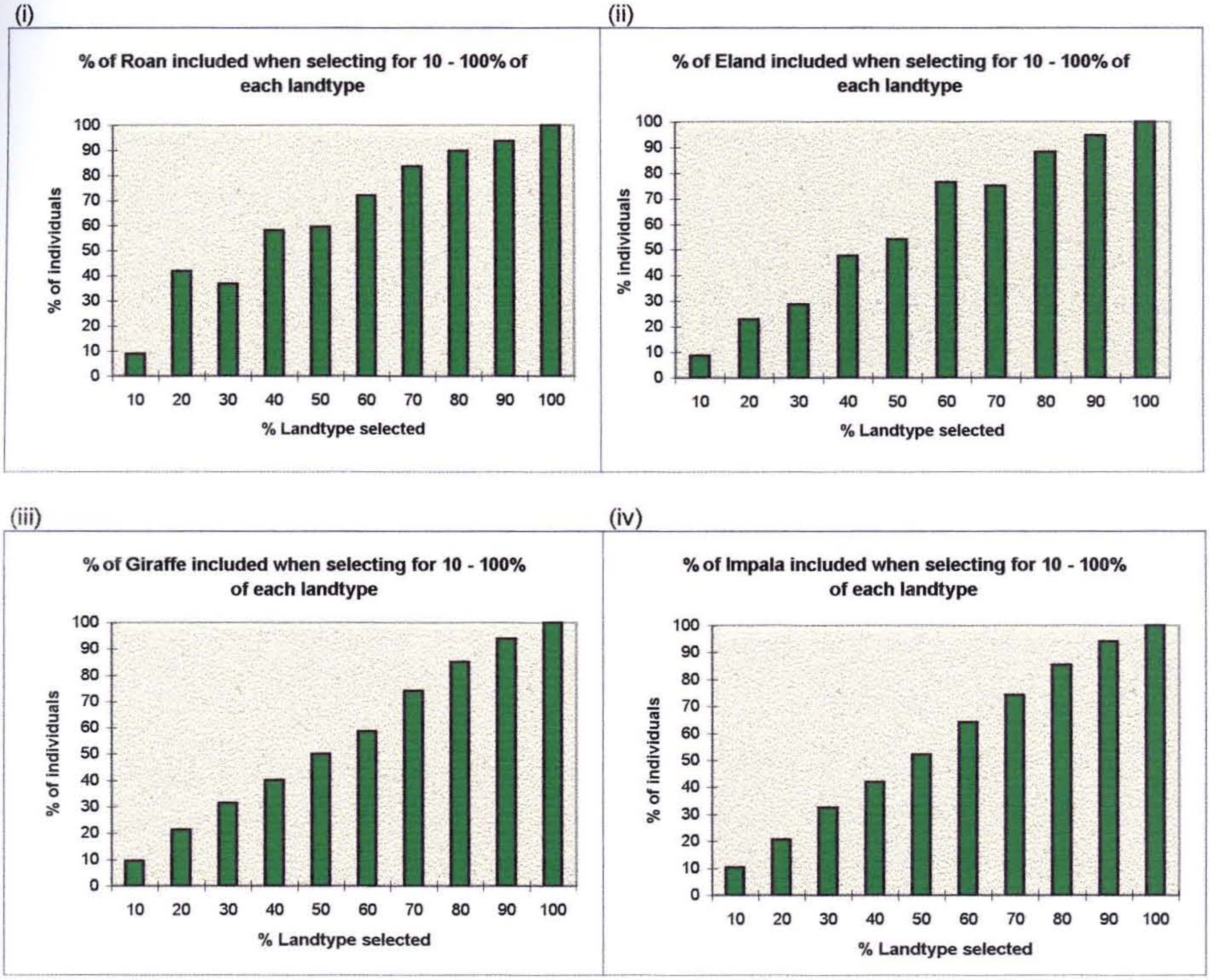


Figure 1: Number of individuals included at different degrees of land type selection for four species (1992 data) Species densities range from 79 individuals (Roan) to 104 300 (Impala).

Percentage individuals

Since species occur at different densities across the landscape, the proportion of total individuals sampled (percentage of individuals) was also assessed. Again, the same linear trend was evident. Consequently, to conserve, for example, 50% of a given species, 50% of the area of each land type is needed (Figure 2 (i - iv)). Combined data for all 12 species are provided for each of the four years (Figure 3) for the land type classification system intersected with the 4km^2 grid cell layer (finest spatial configuration).


(i) % of Roan included when selecting for 10 - 100% of each landtype

(ii) % of Eland included when selecting for 10 - 100% of each landtype

(iii) % of Giraffe included when selecting for 10 - 100% of each landtype

(iv) % of Impala included when selecting for 10 - 100% of each landtype

Figure 2: Percentage individuals included at different degrees of land type selection for four sepcies (1992 data Species densities range from 79 individuals (Roan) to 104 300 (Impala)

Kendall's coefficient of variation was used to establish whether the small difference observed between the data sets is statistically significant, since this will indicate whether environmental variation (measured by rainfall) influences species distribution patterns. If a strong significant association is found between the four data sets, it will be an indication that the influence of environmental variation upon species abundance and distribution patterns is negligible - there will be little difference in the number of individuals selected in all four years and these figures will be statistically correlated.

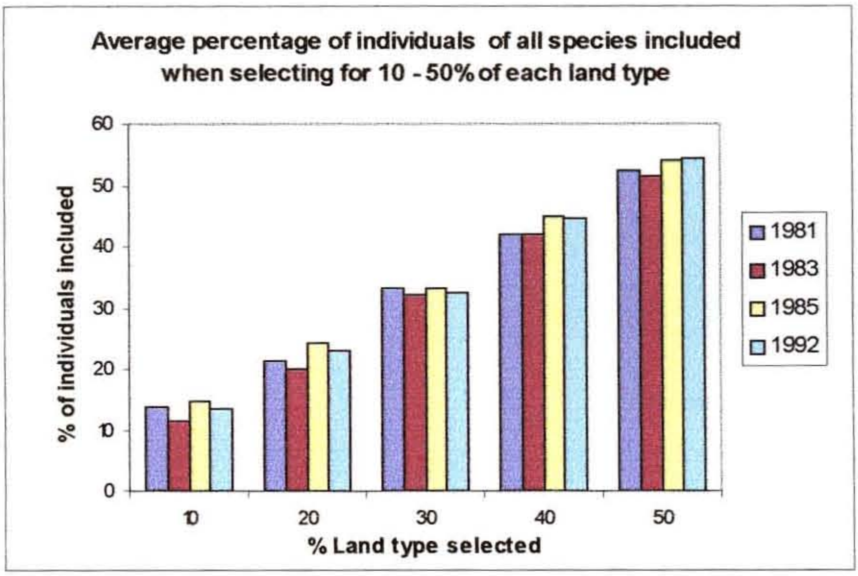


Figure 3: The average percentage of individuals of all 12 species combined, included at increasing percentages land type selection

If, however, a strong significant concordance is not obtained, it would suggest that differences exists in either the distribution patterns of the species or in the densities at which they occur across the landscape under different environmental conditions. The concordance between the data sets in Figure 3 was found to be significant, though not strong with $p < 0.05$ and W-values ranging between 0.6 and 0.75. This indicates that the concordance might be unsatisfactory as an indication of potential association between the four years.

Percentage viable populations

The mean number of individuals and percentages of species included in repeated analyses was determined. Population sizes of both 100 (Figure 4 (i - iv)) and 500 (Figure 5 (i - iv)) individuals were chosen as being possible minimum viable population sizes. Results for six of the 12 scale combinations are displayed in Figures 4 and 5.

From Figure 4 it can be seen that irrespective of the scale combination used, at 40% surrogate selection all species have viable populations being conserved, where a viable population consists of 100 individuals, except for the 1992 data set in Figure 4 (i). This

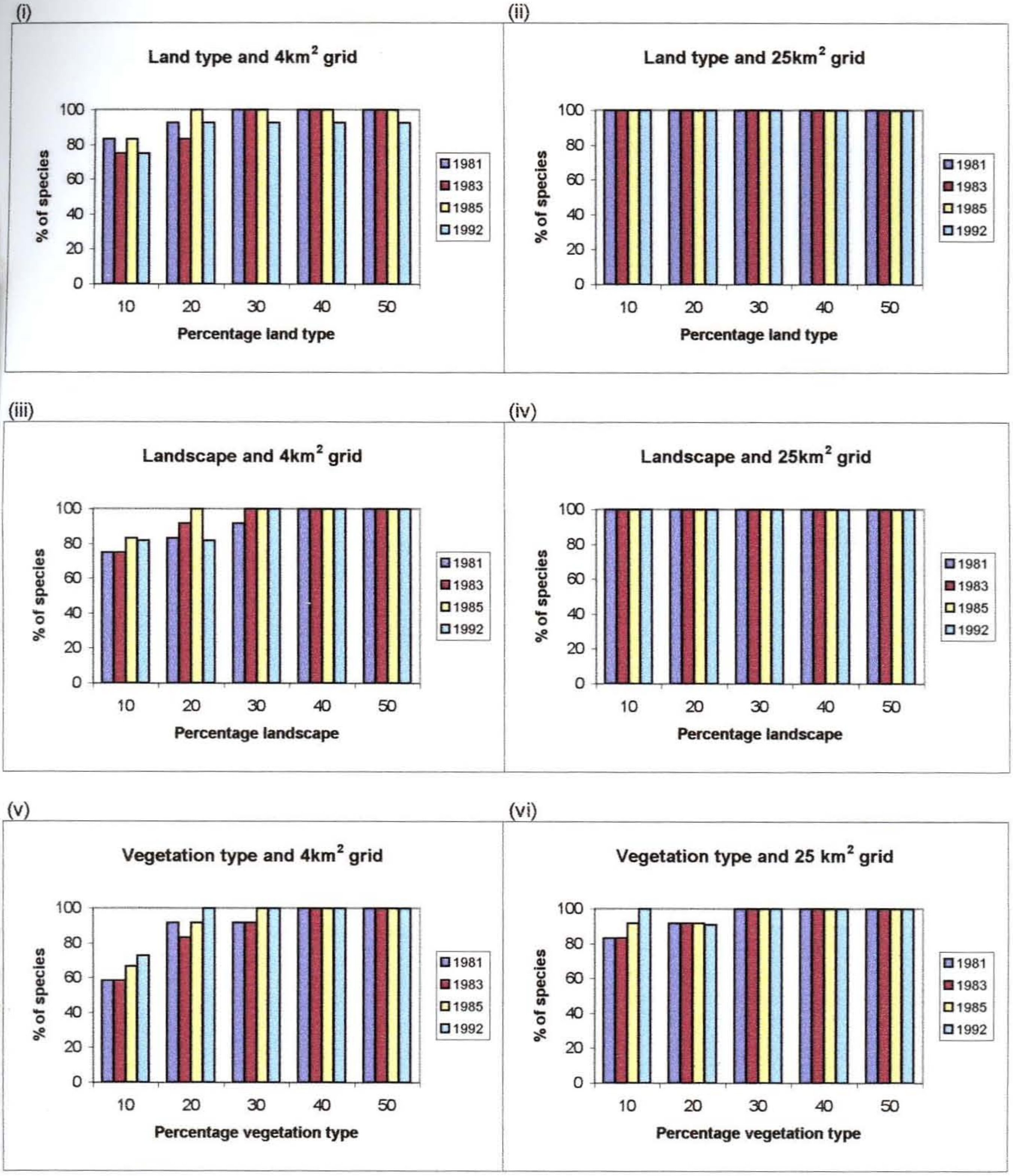


Figure 4: Percentage of species for which viable populations (100 individuals) are included at different degrees of broad scale surrogate selection

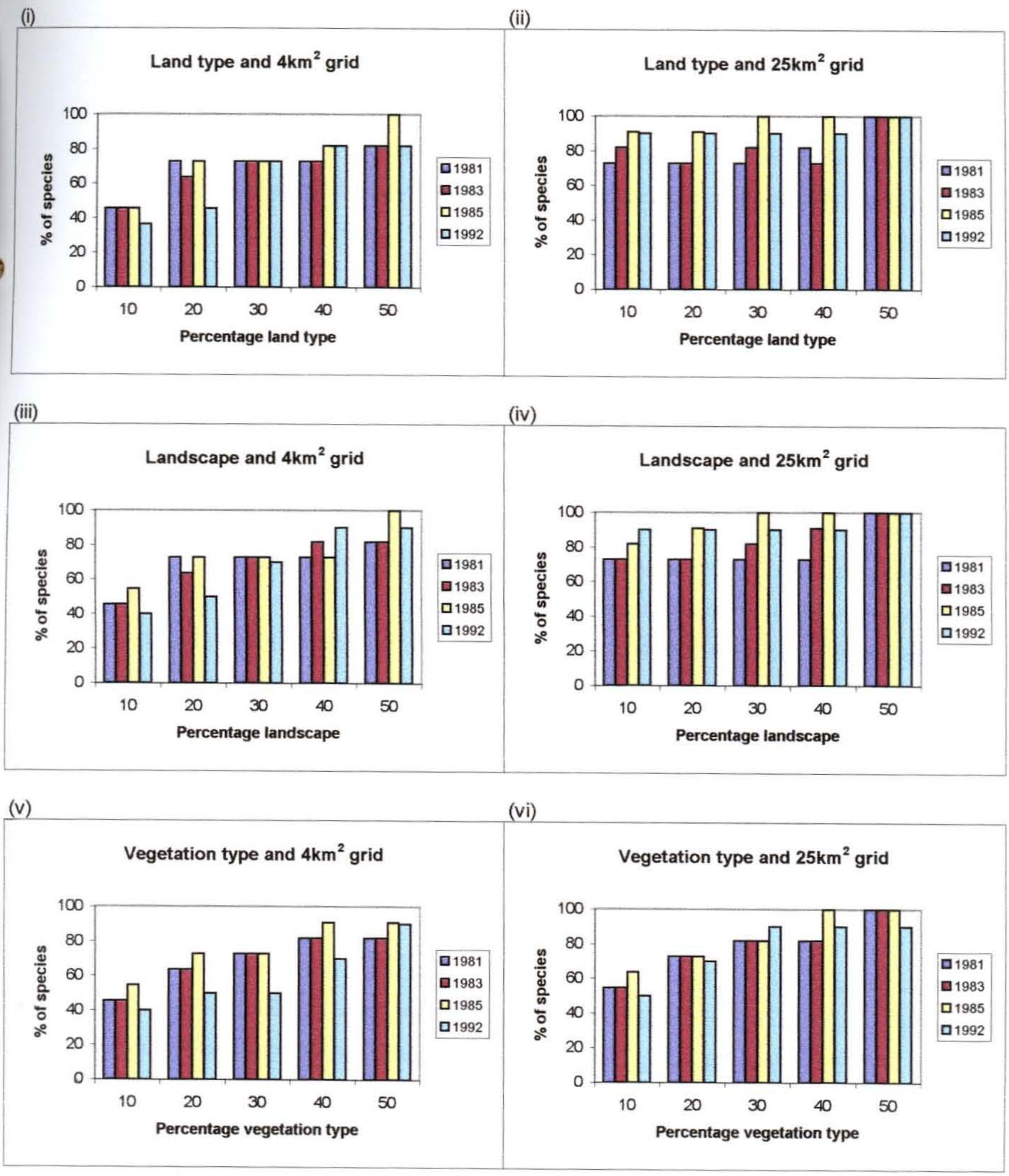


Figure 5: Percentage of species for which viable populations (500 individuals) are included at different degrees of broad scale surrogate selection

can be ascribed to the fact that the rainfall of the 1991/92 climatic year is the lowest in the recorded history of the KNP (Zambatis & Biggs, 1995), and species numbers and densities were therefore very low during the 1992 census. The results obtained when the $25km^2$ grid cell network is intersected with the land type and landscape classification systems respectively (Figure 4 (ii) and (iv)) can be expected due to the way in which the area-selection algorithm works: the larger $25km^2$ grid cells increases incidental over-representation of smaller scaled land classification units, since these cells are large relative to the total size of the study area (only 50 $25km^2$ grid cells in the KNP) and therefore the selected cells often contain untargeted replication of classification units. Consequently, when the algorithm selects for the specified percentage of each classification unit, a much larger area is thus actually selected and therefore larger numbers of individuals are fortuitously included in these over-represented areas than would be otherwise expected. This effect is less prominent when the vegetation type classification is used (Figure 4 (vi)), since this is a much broader scaled classification system (seven vegetation types vs. 35 landscapes and 56 land types) and the vegetation types fit into the large grid cells with less areas of unselected vegetation types being selected and therefore fewer individuals are incidentally included. When the $4km^2$ grid cell network is used, fewer individuals are included because the smaller classification units fit more neatly into these cells and incidental overrepresentation of units are minimised. The smallest number of species are adequately represented in Figure 4 (v), due the above mentioned factors.

A much lower percentage of the species under consideration will have viable populations conserved in the selected areas when a criterion of 500 individuals per species is used to define a viable population (Figure 5 (i – vi)). Once again when the $25km^2$ grid cell network is used, over-representation of species can be observed in Figure 5 (ii) and (v) when this network is intersected with the land type and landscape classification respectively. This effect is less profound when the vegetation type classification is intersected with these larger $25km^2$ grid cells (Figure 5 (vi)). In Figure 5 (i - iii) it can be seen that fewer species achieve viable population numbers in the selected areas, when land types, landscapes and vegetation types are intersected with the $4km^2$ grid cell network. This can be expected, since the classification units fit more neatly into these smaller grid cells and little overrepresentation of land area will occur. Consequently fewer individuals will be over-represented. From Figure 4 and 5, it can thus be seen that scale indeed influences the results obtained in the present study, and that the right choice of scale is exceedingly important when conducting biodiversity surveys.

Vegetation type as a surrogate of Savanna biodiversity

The percentages of unique species per taxon included through the selection of increasing percentages of vegetation types in the Savanna biome are displayed in Table 2. The numbers of species represented through the percentages are given in brackets. From these numbers it is clear that the invertebrate databases comprise very little species - especially the databases for antlions and termites.

Table 2: The percentage (and number) of unique species per taxon, occurring in the Savanna biome, at each percentage vegetation type selection.

% Veg type	Antlions	Birds	Buprestid beetles	Butterflies	Mammals	Scarab beetles	Termites
10	17.9 (5)	85.5 (603)	52.5 (53)	59.4 (285)	66.5 (169)	42.1 (158)	69.6 (16)
20	46.4 (13)	86.3 (607)	55.5 (56)	58.5 (281)	72.1 (183)	42.1 (158)	87.0 (20)
30	57.1 (16)	89.9 (632)	65.4 (66)	75.6 (363)	82.3 (209)	67.2 (252)	91.3 (21)
40	71.4 (20)	90.9 (639)	69.3 (70)	76.7 (368)	83.9 (213)	71.7 (269)	87.0 (20)
50	75 (21)	91.3 (642)	71.3 (72)	79.0 (379)	85.8 (218)	77.6 (291)	87.0 (20)

From Table 2 it can be seen that the antlion and termite databases comprise very few species, but that considerable percentages of these species are included through the vegetation type selection, except for antlions at the 10% selection level where only 5 species (17.9%) are represented. Generally, substantial proportions of all species are represented in the selected areas - even at the 10% level.

4. DISCUSSION

Mathematically, the linear relationship between the area selected and the number (or percentage) of individuals occurring in that area will be expected when dealing with an area where individuals are either homogeneously (as in the KNP) or randomly distributed. According to Bayes theorem (Martin, 1967; Hartigan, 1983), when any number of individuals are randomly distributed across a landscape, and an area is randomly selected, (though a fixed percentage is selected each time) the relationship between area and number of individuals will always be linear. See Chapter 4 for further discussion and explanation of the concept of fixed percentage surrogate selection, and the implications that this has in terms of number of individuals selected. It is important to note here that if the conservation issue is about representing all species, a fixed percentage rule might be considered. If, however, one would want to conserve viable populations, and thereby secure the species' future, the fixed percentage rule appears to be inappropriate.

Slight differences in the distribution of individuals between years with high rainfall and years with low rainfall were found. These results suggest that there is a difference in the spatial distribution pattern of herbivore species in response to habitat quality changes at the scales investigated here. In a study correlating animal distribution patterns to the availability of water, it was found that patterns differed between years with a high rainfall figure and years with comparatively low rainfall figures (Redfern, pers. comm.). Furthermore, when we tested for significant differences in species numbers across the four years (Chapter 2) it was found that environmental variation influences the distribution patterns of the large herbivore species investigated here. In the light of this, we can deduce that these data sets are statistically significantly correlated, but that this association (based on W values) is too small to be biologically meaningful at the scales used in this study. Hence, we can conclude that environmental variation marginally influences the distribution patterns of these large herbivore species when the number of individuals occurring in certain areas are compared between four different years. This does, however, not affect the linear relationship between percentage surrogate selection and number and percentage of individuals included, nor does it affect the considerable amount of land needed to fully conserve these species at these scales.

Presence/absence data were used to determine the success of vegetation types as a surrogate for seven different taxa in the Savanna biome of South Africa. These taxa included well-studied taxa such as mammals (Mammalia), birds (Aves) and butterflies (Hesperioidae and Papilionidae) that have been frequently used in the past as biodiversity indicators (Woinarski *et al.*, 1988; Sætersdal *et al.*, 1993, Howard *et al.*, 1998), as well as less well-known taxa, including antlions (Myrmeleontidae), buprestid beetles (Buprestidae), scarabaeoid beetles (Scarabaeoidae) and termites (Isoptera). It has to be noted that all these invertebrate databases are highly subjected to collector bias, low collection effort and taxonomic limitations (Hull *et al.*, 1998) and that the quality of the databases are generally surprisingly and alarmingly poor (Koch *et al.*, in press). The only available data for termites came from an incomplete set of published data from a systematic survey, and only about 20% of antlion species are included in this database (Freitag and Mansell, 1997). The mammal database is fairly complete in the Savanna biome with consistent sampling effort covering most of the area under consideration. The birds, on the other hand, have been surveyed in all grid cells and all species are included (Van Jaarsveld *et al.*, 1998).

According to the World Conservation Union some 10% of each of the world's major biomes should be afforded formal protection by the year 2000 (WRI, 1994; Soulé and Sanjayan, 1998). It was suggested that this should be adequate in protecting most elements of biodiversity. If only 10% of the Earth's ecosystems are protected it will endanger at least half of all terrestrial species and make them vulnerable to anthropogenic extinction in the near future (Soulé and Sanjayan, 1998). Using the Savanna biome of South Africa to evaluate this assertion, we found that at 10% vegetation type selection on average only 55% of all species across the 7 taxa occurring in the Savanna biome are represented in the selected area (Figure 6). When moving on to the 50% selection level, more than 80% of all species are represented at least once. From these analyses it would seem that the vegetation type classification is not a successful surrogate at the scale of investigation, since only little more than half of the total number of species are represented, and this number is not a sufficient conservation effort.

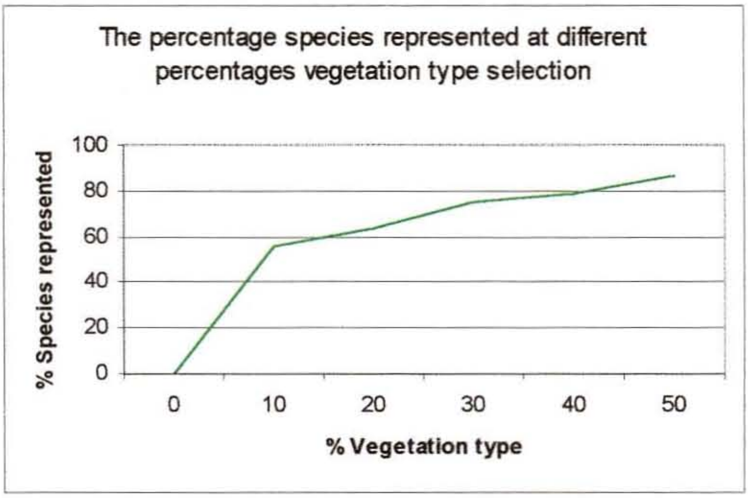


Figure 6: The percentage of 7 faunal species included at increasing percentages vegetation type selection

Furthermore, the concern should not just be to represent all species, but to actually conserve viable populations of species – and thereby secure their future. It was found in the present study that to conserve viable populations of the large herbivore species, 10% of the area is far from adequate, and nearly 50% of each land classification unit is needed to achieve this conservation goal.

REFERENCES

Austin, M.P. & Nix, H.A. 1978. *Regional classification of climate and its relation to Australian rangelands*. In Studies of Australian Arid Zone. III. Water in rangelands. K.M.W. Howse (ed.) pp9-17, Melbourne:CSIRO.

Awimbo, J.A., Norton, D.A. & Overmars, F.B. 1996. An evaluation of representativeness for nature conservation, Hokitika ecological district, New Zealand. *Biol. Conserv*. **75**, 177-186.

Bedward, M., Pressey, R.L. & Keith, D.A. 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol. Conserv*. **62,** 115-125.

Belbin, L. 1993. Environmental representativeness: Regional partitioning and reserve selection. *Biol. Conserv*. **66**, 223-230.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol*. **63**, 215-244.

Faith, D.P. and Walker, P.A. 1996. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv*. **5**, 399-415.

Franklin, I.R. 1980. *Evolutionary changes in small populations*. Pp. 135-149. In: Conservation Biology. An Evolutionary-Ecological perspective. Soulé, M.E. and Wilcox, B.A. (eds). Sinauer Associates, Sunderland, Massachucettes.

Freitag, S., Nicholls, A.O. & Van Jaarsveld, A.S. 1996. Nature reserve selection in the Transvaal, South Africa: what data should we be using? *Biodiv. Conserv*. **5,** 685-698.

Freitag, S. and Mansell, M.W. 1997. The distribution and protection status of selected antlion species (Neuroptera: Myrmeleontidae) in South Africa. *Afr. Ento.* **5**(2), 205-216.

Gaston, K.J. 1994. Biodiversity-measurement. *Progr. Phys. Geog.* **18**, 565-574.

Gaston, K.J. 1996. Species richness: measure and measurement. In: *Biodiversity. A biology of numbers and difference*. Gaston, K.J. (ed.) Blackwell Science, Oxford.

Gaston, K.J. and Blackburn, T.M. 1995. Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proc. R. Soc., Lond. B.* **262**, 335-341.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* **26,** 9-121.

Ghilarov, A. 1996. What does biodiversity mean - scientific problem or convenient myth? *TREE.* **11**(7), 304-306.

Haila, Y. & Margules, C.R. 1996. Survey research in conservation biology. *Ecography.* **19,** 323-331.

Hartigan. J.A. 1983. *Bayes Theory*. Springer-Verlag, New York, U.S.A.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* **62**(4), 447-502.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. & Balmford, A. 1998.Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**, 472-475.

Hull. H.E., Freitag, S., Chown, S.L. & Bellamy, C.L. 1998. Identification and evaluation of priority conservation areas for Buprestidae (Coleoptera) in South Africa, Lesotho, Swaziland and Namibia. *Afr. Ent.* **6**(2), 265-274.

Koch, S.O., Chown, S.L., Davis, A.L.V., Endrödy-Younga, S. & van Jaarsveld, A.S. Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa. *J. Insect Conserv.* In press.

Lapin, M. and Barnes, B.V. 1995. Using the landscape ecosystem approach to assess species and ecosystem diversity. *Conserv. Biol.* **9**(5), 1148-1158.

Low, A.B. and Rebelo, A.G. (eds.) 1996. *Vegetation of South Africa, Lesotho and Swaziland.* Dept Environmental Affairs & Tourism, Pretoria.

Mackey, B.G., Nix, H.A., Stein, J.A., Cork, S.E. & Bullen, F.T. 1989. Assessing representativeness of the wet tropics of Queensland World Heritage Property. *Biol. Conserv.* **50**, 279-303.

Margules, C.R., Cresswell, I.D. & Nicholls, A.O. 1994. *A scientific basis for establishing networks of protected areas. In Systematics and Conservation Evaluation.* P.I. Forey, C.J. Humphries & R.I. Vane-Wright (ed.) pp. 327-350. Oxford:Clarendon Press.

Margules, C.R. and Usher, M.B. 1981. Criteria used in assessing wildlife conservation potential: a review. *Biol. Conserv.* **43**, 63-76.

Martin, J.J. 1967. *Bayesian decision problems and Markov chains.* John Wiley and Sons, Inc., New York.

McNab, B.K. 1963. Bioenergetics and the determination of home range size. *Am. Nat.* **97**, 133-140.

Nicholls, A.O. 1989. How to make biological surveys go further with generakised linear models. *Biol. Conserv.* **50**, 51-75.

Nicholls, A.O and Margules, C.R. 1993. An upgraded reserve selection algorithm. *Biol. Conserv.* **64**, 165-169.

Noss, R.F. 1990. Indicators for managing biodiversity: A hierarchical approach. *Conserv. Biol.* **4**(4), 355-364.

Pressey, R.L. & Nicholls, A.O. 1989. Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. *Biol. Conserv.* **50**, 263-278.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. 1993. Beyond opportunism: Key principles for systematic reserve selection. *TREE.* **8**(4), 124-128.

Pressey, R.L. 1994. Land classifications are necessary for conservation planning but what do they tell us about fauna? In: *Future of the fauna of western New South Wales*. Lunney, D., Hand, S., Reed, P. & Butcher, D. (eds.) pp. 33-41. Mosman: Royal Society of NSW.

Sætersdal, M., Line, J.M. & Birks, H.J.B. 1993. How to maximise biological diversity in nature reserve selection: Vascular plants and breeding birds in deciduous woodlands, Western Norway. *Biol. Conserv.* **66**, 131-138.

Soulé, M.E. 1989. Chapter 1: Introduction. In: *Viable populations for conservation*. Soulé, M.E. (ed.) Cambridge University Press, Cambridge.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. 1991. What to protect? Systematics and the agony of choice. *Biol. Conserv.* **55**, 235-254.

Van Jaarsveld, A.S., Freitag, S., Chown, S.L., Muller, C., Koch, S., Hull, H., Bellamy, C., Krüger, M., Endrödy-Younga, S., Mansell, M.W. & Scholtz, C.H. 1998. Biodiversity assessment and conservation strategies. *Science.* **279**, 2106-2108.

Venter, F.J. 1990. *A classification of land for management planning in the Kruger National Park*. PhD Thesis. University of South Africa, South Africa.

Wessels, K.J., Freitag, S. & Van Jaarsveld, A.S. 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biol. Conserv.* **89**, 21-38.

Williams, P.H. and Humphries, C.J. 1996. Comparing character diversity among biotas. In Biodiversity. (ed.) K.J. Gaston. pp 54-76. Blackwell Science, Oxford.

Woinarski, J.C.Z., Tidemann, S.C. & Kerin, S. 1988. Birds in a tropical mosaic: the distribution of bird species in relation to vegetation patterns. *Aust. Wildl. Res.* **15**, 171-196.

World Resources Institute (WRI) 1993. World Resources Report 1993. Washington DC: World Resources Institute.

World Resources Institute. 1994. *World Resources 1994-1995*. Oxford University Press, New York, pp. 152-153.

Zambatis, N. and Biggs, H.C. 1995. Rainfall and temperatures during the 1991/92 drought in the Kruger National Park. *Koedoe* **38**(1), 1-16.

Zar, J.H. 1996. Biostatistical analysis. (3rd ed). Prentice-Hall International, Inc. USA. pp. 407-445.

Appendix A

Percentage Area Representation (PAR) algorithm (Wessels *et al.* 1999).

Written by Stefanie Freitag (1996).

Selection rules are as follows:

1. Choose a grid cell containing an occurrence of the smallest (in terms of area) vegetation type. If more than one type is equally small, choose the one which is also "database rarest" (i.e. there are the fewest polygons (records) of that type).
2. If there is a choice of grid cells to represent this type, choose the one containing the biggest area of the type required to bring the representation of the type to the required level, i.e. the site which contains either the smallest percentage area necessary to achieve the required representation, or the one that contributes the largest percentage area of that type - if no one site will achieve the representation target.
3. If there is a choice, select the grid cell that is nearest in space to one that is already selected (adjacency constraint).
4. If there is still a choice, select the grid cell that also contributes the largest area of the next smallest under-represented type.
5. If there is still a choice, select the grid cell that will add the biggest number of under-represented types.
6. If there is still a choice, select the first in the list of types.

Appendix B

Percentage Area Representation algorithm for iterative selections (PARI).
This algorithm was modified, using the previous algorithm (PAR), (Wessels *et al.* 1999), by Heath Hull (1998).
Selection rules are as follows:

1. Select a grid cell at random.
2. If there is only one vegetation type present in the grid cell, select further grids until the required target level is reached - using the methods described for "rule 2" in Appendix A. If there is more than one vegetation type in the grid cell, select all vegetation types present in that grid (one at a time, but in no specific order) by adding further grids until all target levels for these vegetation types are met, using the methods described in Appendix A (rules 2 - 6).
3. Go to the top of the file containing a list of all vegetation types (randomly arranged). Select the vegetation type to be fully represented next by choosing the type occurring at the top of the list.
4. Select all types using the rules described in Appendix A (rules 2 - 6). Each time that a type is fully represented, the next to be represented is the one occurring at the top of the vegetation type list.

All areas of vegetation types that are present in the grid cell chosen, other than the type for which the algorithm was selecting, are subtracted from the areas required to fully represent them, i.e. added to the area represented for these types as well.

Appendix C

Percentage Area Representation algorithm with preselection.

Written by Stefanie Freitag (1996), and modified by Heath Hull (1999).

Selection rules are as follows:

1. Preselect all grid cells currently under protection.
2. Remove these girds form the input database, and store them in the Gridsel file.
3. Determine the size of all vegetation types in the database.
4. Choose a grid cell containing an occurrence of the smallest (in terms of area) vegetation type. If more than one type is equally small, choose the one which is also "database rarest" (i.e. there are the fewest polygons (records) of that type).
5. If there is a choice of grid cells to represent this type, choose the one containing the biggest area of the type required to bring the representation of the type to the required level, i.e. the site which contains either the smallest percentage area necessary to achieve the required representation, or the one that contributes the largest percentage area of that type - if no one site will achieve the representation target.
6. If there is a choice, select the grid cell that is nearest in space to one that is already selected (adjacency constraint).
7. If there is still a choice, select the grid cell that also contributes the largest area of the next smallest under-represented type.
8. If there is still a choice, select the grid cell that will add the biggest number of under-represented types.
9. If there is still a choice, select the first in the list of types.

CHAPTER 4

Is geographical zone surrogacy effective for selection of representative biodiversity, or is the fixed percentage rule counterproductive? *

*Ms. submitted: M. Solomon and H.C. Biggs. Is geographical zone surrogacy effective for selection of representative biodiversity, or is the fixed percentage rule counter-productive? *Animal Conservation.*

Is geographical zone surrogacy effective for selection of representative biodiversity, or is the fixed percentage rule counterproductive?

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Conserving representative biodiversity has become a common goal among scientists and conservation planners alike. The question is how to achieve this goal effectively, both in terms of costs and land-use. Since very little accurate abundance data exists, the heuristic and iterative algorithms which are frequently employed, rely on presence/absence data as input, and the resultant output is less than ideal. The only alternative proposed thus far, is to conserve a fixed percentage of each biome in a country. Here, the practical conservation implications of this rule are contemplated, analysed and discussed. We conclude that the fixed percentage rule is counterproductive in conserving biodiversity, and that the most cost-effective way to conserve species across a landscape is to base analyses on thoroughly sampled data.

Introduction and background

A common approach towards the selection of representing biodiversity in a region is to select say 10% of the area of every class in a particular classification system (e.g. vegetation types). Indeed, this is recommended by the Rio Convention (IUCN,1992). During a recent study conducted in the Kruger National Park (KNP), examining how successful randomly selecting a fixed percentage of each of the classes of different classification systems (e.g. landscape, geological area, vegetation type) might be including Minimum Viable Populations (MVP) of 12 large herbivores in the KNP, a seemingly paradoxical result emerged. Instead of one classification system giving more efficient results than another (i.e. combined MVP's of all 12 species in a smaller area), all seemed to perform similarly. The graphs relating the number of individuals per species to the surface area selected, appeared linear (Figure 1), implying that the species might be evenly spread across the Park at the scale of our examination.

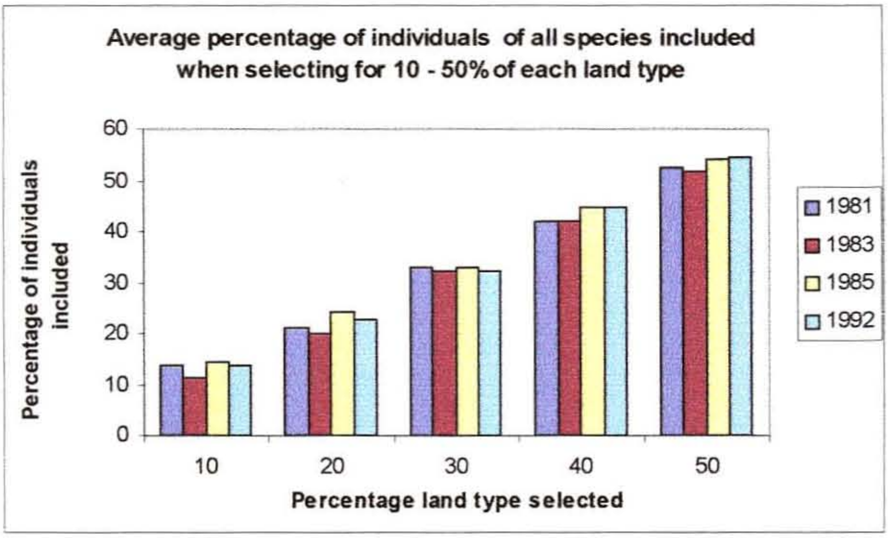
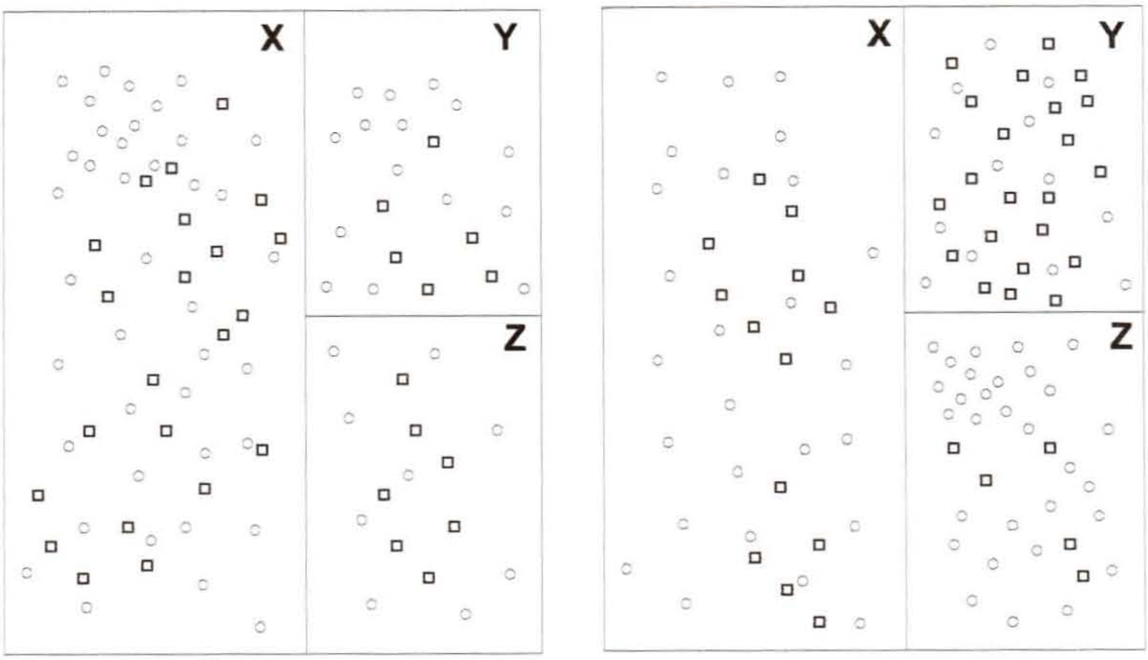


Figure 1: The average percentage of individuals included when 10 - 50% of each land type is selected in the KNP.

Methods

This question led us to set up a simple model to determine the driving factor behind the linear relationship between number of individuals and size of area. In this model one can distribute an alterable/changeable number of individuals of different species in different ways across a hypothetical reserve, consisting of a variable number of zones.

In the model, population sizes of the hypothetical species could be varied to test the influence of varying levels of population densities in different classes. The species were invariably distributed unevenly across the zones, but randomly within them with different degrees of overlap between classes (Figure 2).



(a) (b)

Figure 2: The distribution of two hypothetical species distributed at varying densities across a landscape comprising of three hypothetical zones.

The number of zones as well as the zone sizes could also be altered. The only constant was that a uniform percentage of each zone was always selected for that particular run, in accordance with the Rio convention recommendation. An algorithm was coded where the user has to specify a fixed percentage of each zone that has to be selected. The algorithm always starts out at a random point, and proceeds to find the next grid cell of the first, randomly selected zone, or of a zone that is still underrepresented. It continues until the specified percentage of each zone has been reached, and the numbers of individuals fortuitously included through this selection is then quantified.

The objective of this paper is to quantitatively evaluate the use of the fixed percentage rule using the model described above. In developing the model, we recognised a number of potential shortcomings and extended the model to incorporate these. These emergent themes will become clear as the argument develops.

Results

Regardless of how each variable was changed and in what combination it was used with other variables, the model continued to generate linear responses (Figure 3). This seemingly trivial result, similar to the observed system in Figure 1, is seen to be due to the "random" species distribution within each polygon and the fact that a fixed percentage of each surrogacy zone was chosen. Varying the number of polygons, and thereby changing the scale of the classification system, had no significant influence on the results. The final test result sought (combined area selected to give MVP's of all species) differed only in that this total percentage was reached as soon as (usually) the MVP for the rarest species was reached.

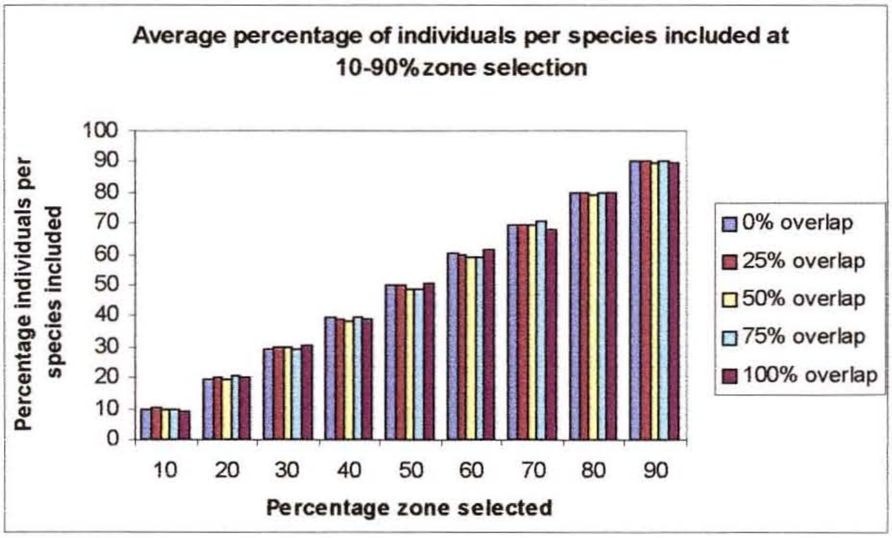


Figure 3: The average number of individuals of all species fortuitously included through the fixed percentage zone selection.

Assuming that this hypothetical system consists of three polygons when a single land classification system is used, and with individuals of a species being distributed across the polygons as shown in Figure 4 (a). Irrespective of where the selection process starts, selecting 10% of each of these polygons will obviously only result in a single outcome in terms of proportional zone sizes associated with that selection process, and the percentage individuals will be proportional to that specified area.

Now, assume another land classification system used with polygon boundaries as shown in Figure 4 (b), where the distribution of individuals in space remains the same. We can now either proceed with surrogacy selection on the three polygons, and the starting point will determine whether a larger or smaller (or perhaps similar density) population is included for that zone. If the starting point happens to be in a high density cluster, a larger number of individuals will be included when a fixed percentage of each polygon is selected. If the selection started in a medium density cluster, the outcome will be very similar to the outcome in Figure 4 (a). If, however, the selection process started in a low density cluster, fewer individuals will be included through the selection process. Presumably the formalisers of the "Rio concept" were assuming, at least implicitly, that each species is randomly distributed at different densities in each polygon or biome (the different species in these polygons are not necessarily distributed at the same densities). If they were not assuming this, they were certainly running the risk of the starting and/or subsequent follow-up points severely influencing the result in a positive or negative way as outlined above.

Alternatively, we can re-define the system. When turning the areas of species richness hotspots into homogenous polygons (Figure 4 (c)), and adding this to the data set as a new type, i.e. when delimiting the areas containing the clusters and making those new polygons of a new type - if this is feasible - the two arguments converge. Now, when selecting 10% of each type under these conditions, one will still only select 10% of each population, since these clusters containing most individuals are now a new type, and selecting 10% of this type will include 10% of the individuals.

Optimally we would want to be able to select individuals disproportionately to area (i.e. pick out those areas which will give us efficient selection - more "value for money" in terms of area selected).

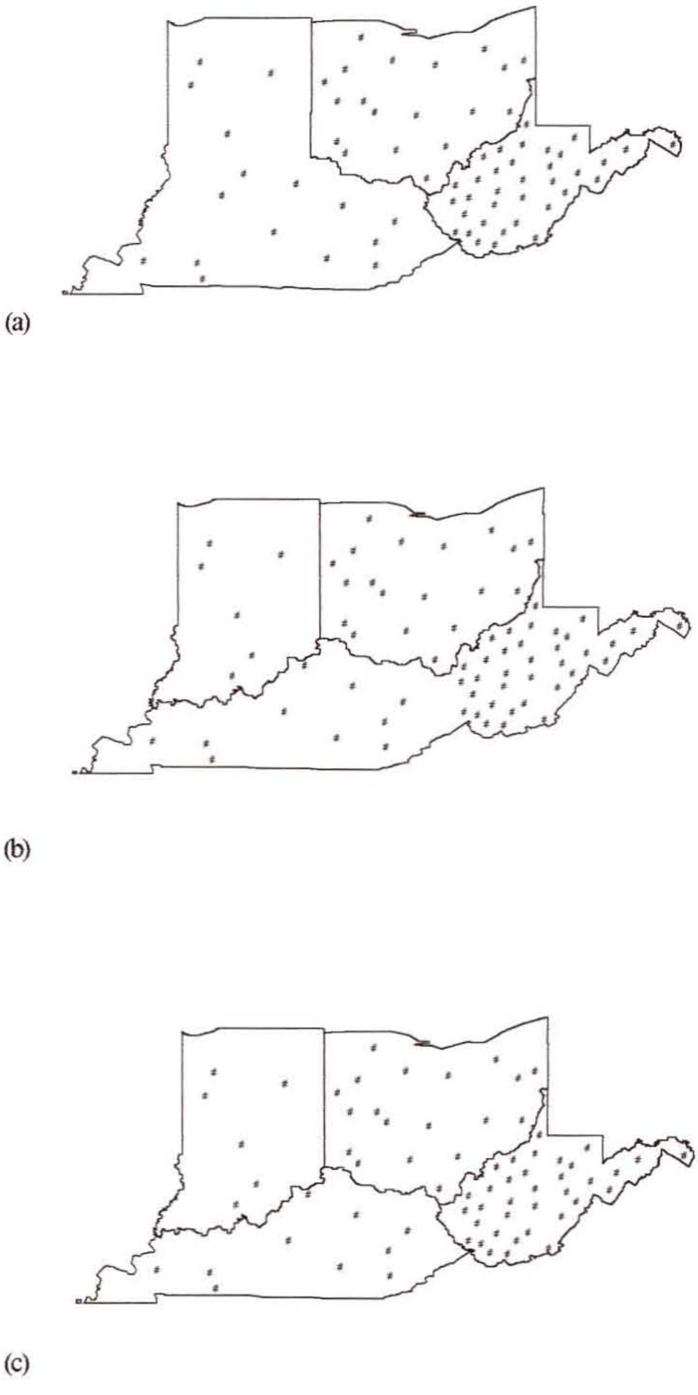


Figure 4: A reclassification of zones across the landscape with species distributions remaining constant.

Discussion

Under these circumstances a major corollary which is obvious, is that it will not help to use one broad-scale classification system rather than another (as long as they meet the two assumptions), since varying the number and sizes of zones did not change the results (Figure 1). The assumptions are that a uniform percentage is selected in each run, and that there is a relatively homogenous distribution of each species within each area.

Note that under the fixed percentage rule, there is no way to increase the efficiency of selection of the smallest amount of land to encompass a MVP. We also examined the influence of scale (pixel size) within the extent of the study area and found it to be negligible.

A re-projection of any clustered system thus appears to be able to be conceptualised as a system with more polygons, each one now with a homogeneously-spaced population within itself. In doing this, we no longer have the original classes of the classification system, but rather a new pseudo-class of homogenous density. Richness-based algorithms (Nicholls & Margules 1993; Pressey *et al.* 1996; 1997) usually do not start with a known classification system, but by selecting the richest cells or cells containing the rarest biota. In order to increase the efficiency of selection, i.e. include more individuals than a number proportional to the percentage area selected, one can either try to influence the starting point and subsequent rules to select clusters of high species density in a polygon (Figure 4 (b)) or select higher percentages of the high-density polygons in Figure 4 (c). The difference here is that the fixed percentage rule is not applied in the first step of identifying the homogenous high density areas, i.e. species rich spots are selected out of proportion to moderately low or species poor spots. This disproportional selection of areas in polygons is the only solution to move away from the linear relationship between percentage area selected and the percentage of individuals fortuitously incorporated through this area selection. According to the source-sink argument (Pulliam, 1988) there exist areas where the within-habitat reproduction is insufficient to balance local mortality (referred to as "sink" areas), and these areas only subsist because they are being locally maintained by continued immigration from more-productive "source" areas nearby. If these source areas can be captured through a selection process, rather than sink areas, a positive deviation from linearity will be obtained.

Conclusion

These are the results of a theoretically linear system with homogenous species distributions within each land class, and there appears to be no way to improve the effectiveness of a fixed percentage land area surrogacy system. All combinations of density and distribution, and the scale of the selection process, appear to make no significant difference. Although the formalism we have illustrated is straightforward and obvious once demonstrated, we believe it to be somewhat counter-intuitive. It seems attractive to believe that a fixed percentage (say 10%) of the world's surface may protect all species, but if the assumptions laid out in this paper are explicitly (or more usually inadvertently) made, whether or not this is true will depend on whether that fixed percentage may be including MVP's of the rarest species. In practice, this percentage turns out to be far higher than the 10% recommended (IUCN, 1992). The minimum percentage area required for adequate conservation will simply turn out, under these rules, to be the percentage area needed to yield a MVP of the rarest species.

We conclude that geographical surrogacy is, at least when argued in these terms, thus almost a non-concept, with the area required to support an MVP of the rarest species requiring conservation, actually becoming the deciding factor. We consequently suggest that the fixed percentage rule be seriously reconsidered, possibly to be replaced with a system differentially concentrating on areas with higher conservation potential (source areas). Even knowing all the difficulties associated with richness and rarity based algorithms, it seems that there is no practical, cost effective alternative to selecting higher percentages of areas which carry higher biodiversity. Since conservation actions are only as good as the quality of the data on which they are based (Koch, 1999), it is imperative that biodiversity surveys be invested in. Although compiling biodiversity inventories is very costly in terms of time and money, it has been shown by Balmford and Gaston (1999) that using well-sampled data, obtained from detailed surveys, results in the requirement of smaller representative reserve networks than when incomplete data are used. Furthermore, since conservation actions are only as good as the quality of the data on which they are based, it is imperative that biodiversity surveys be invested in. It is believed that only once the abundance-related stratification of species across a landscape is known, or if the location of source populations can be established, that the most cost-effective MVP's can be selected.

The argument in this paper rests on the number of individuals per species, aiming at viable populations. Even if the goal of conservation planning and conservation area selection procedures is only to represent as many species as possible in the limited land surface areas available to conservation possible (ignoring viability), the 10% proposed by the World Conservation Union (WRI, 1994) is an encouraging target but not adequate if these areas are indeed the only areas where populations or subpopulations are being conserved. In a study in South Africa evaluating the use of vegetation types as a possible surrogate for biodiversity using presence/absence data for 7 faunal taxa, it was found that at 10% vegetation type selection 56.2% of all species in the database were represented, and this figure increased to 87% species representation at a 50% vegetation type selection level (Figure 5).

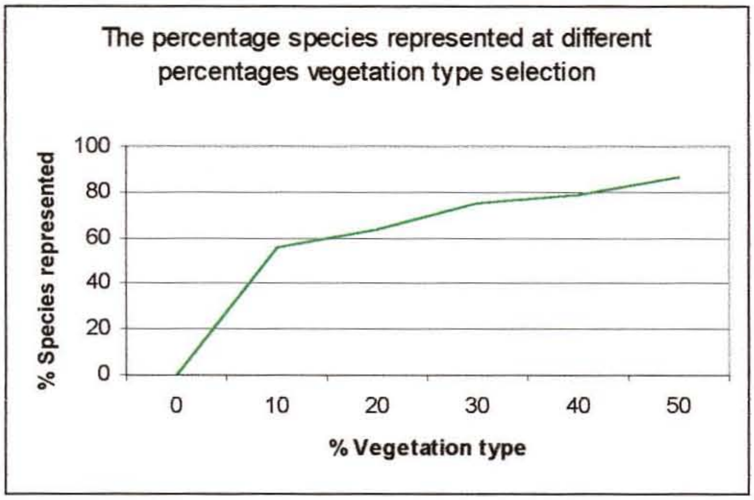


Figure 5: The percentage of 7 faunal species included at increasing percentages vegetation type selection

Similar results were obtained by Soulé and Sanjayan (1998) where they found that if only 10 - 12% of the Earth's ecosystems are afforded protection, more than half of all terrestrial species will be vulnerable to extinction in the near future.

Moreover, if national and international conservation goals are to conserve viable populations of all species, thereby securing all species' long-term persistence and survival, the fixed percentage rule appears ineffective and should be reconsidered.

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References

Balmford, A. and Gaston, K.J.C. (1999). Why biodiversity surveys are good value. *Nature.* **398:** 204-205.

Koch, S.O. (1999). *The distribution of selected Scarabaeoid (Coleoptera) taxa in South Africa and Namibia: Prospects for their conservation.* M.Sc.Thesis, University of Pretoria, Pretoria.

Nicholls, A.O and Margules, C.R. (1993). An upgraded reserve selection algorithm. *Biol. Conserv.* **64:** 165-169.

Pressey, R.L., Possingham, H.P. & Margules, C.R. (1996). Optimality in reserve selection algorithms: When does it matter and how much? *Biol. Conserv.* **76:** 259-267.

Pressey, R.L., Possingham, H.P. & Day, J.R. (1997). Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol. Conserv.* **80:** 207-219.

Pulliam, H.R. (1988). Sources, sinks, and population regulation. *Am. Nat.* **132:** 652-661.

World Conservation Union (IUCN). (1992). *IUCN Bull.* **43 :** 10.

World Resources Institute (1994). *World Resources, 1994-1995.* Oxford University Press, New York, pp. 152-153.

CHAPTER 5

General Conclusion

A number of important findings, crucial to our understanding of the spatial requirements of viable populations of large herbivore species, emerged from this dissertation. The following points constitute the main findings and conclusions drawn:

- The correct choice of scale used is exceedingly important when conducting biodiversity surveys and analysing environmental data (Nicholls and Margules, 1993; Wessels, 1999). In the present study, the percentage of the total area ultimately selected to include viable populations is largely influenced by the scale at which the land classification units are defined, the number of classification units in a classification system as well as the size of the grid cells.

- Irrespective of the spatial or temporal scales employed, in general, more than 50% of each land classification unit is needed to jointly sustain viable populations of the large herbivore species in the Kruger National Park. This general trend seems unaffected by defining viable populations as comprising of 50, 500 or even 10 000 individuals. These results are consistent with those from other studies in different parts of the world, focussing mainly on the representation of all plant species or habitat types in a specific region (Soulé and Sanjayan, 1998).

- Differences in the distribution pattern of individuals between years with high rainfall and years with low rainfall figures were found. These results suggest that there is a marginal difference in the abundance and spatial distribution patterns of herbivore species in response to habitat quality changes at the scales investigated here. In a study correlating animal distribution patterns to the availability of water, it was found that patterns differed between years with a high rainfall figure and years with comparatively low rainfall figures (Redfern, pers. comm.). Hence, although environmental variation influences distribution patterns of large herbivore species, it still does not affect the considerable amount of land needed to effectively conserve these species.

- The linear relationship between the area selected and the number (and percentage) of individuals occurring in that area is mathematically expected when dealing with an area where individuals are either homogeneously (as in the KNP) or randomly distributed. According to Bayes theorem (Martin, 1967; Hartigan, 1983), when any number of individuals are randomly distributed across a landscape, and an area is randomly selected, (though a fixed percentage is selected each time) the relationship between area and number of individuals will always be linear.

- The vegetation types of the Savanna biome in South Africa does not appear to be successful as a surrogate for seven faunal taxa at the scale of our investigation. These taxa included well-studied taxa such as mammals (Mammalia), birds (Aves) and butterflies (Hesperioidae and Papilionidae) that have been frequently used in the past as biodiversity indicators (Sætersdal *et al.* 1993, Howard *et al.*, 1998), as well as less well-known taxa, including antlions (Myrmeleontidae), buprestid beetles (Buprestidae), scarabaeoid beetles (Scarabaeoidae) and termites (Isoptera). At 10% vegetation type selection on average only 56.8% of all species (of the 7 taxa mentioned above) occurring in the Savanna biome are represented in the selected area. Moving on to the 50% selection level, some 80% of all species are represented at least once.

- What are the conservation implications of the results of the present study? At the Rio Convention on Biological Diversity in November 1990 (which was signed by different governments at the Rio Earth Summit in June 1992) (IUCN, 1992) it was decided that 10-12% of each of the world's major biomes should be protected. However, subsequent literature has suggested that this target is not adequate for the protection of biodiversity. The conclusions drawn from an island biogeography perspective, is that as much as 50% of wildlands is required to represent and protect most elements of biodiversity (Soulé and Sanjayan, 1998), and that 10% is far from adequate to achieve this goal. Similarly, the present study found that from a population viability perspective, some 50% of land may be required to conserve viable populations of umbrella species. Therefore the 10-12% figure should be regarded as the absolute minimum amount of land that a country needs to protect - and *not* the upper limit. The conservation targets set will differ for each country, but the 10% target appears to be ineffective for the adequate protection of a given country's biodiversity.

- Another major problem regarding the protection of biodiversity, is the size of protected areas (World Resources Institute, 1993). The concern is that protected areas might be too small to hold viable populations of large carnivores and herbivores. With this study we have established that at approximately half of the study area (□10 000km^2) is required if the species under consideration are to be offered long-term protection.

In conclusion, given the fact that conserving 10% of each biome appears inadequate for conserving viable populations, that conserving single representations per species is not ideal, and conserving 50 - 80% of each biome is just not possible in terms of land use and land availability, stratified conservation objectives that represent different degrees of protection may have to be pursued - an objective similar to that proposed by the biosphere concept (World Resources Institute, 1994). We furthermore suggest that the fixed percentage rule be seriously reconsidered, possibly to be replaced with a system differentially concentrating on areas with higher conservation potential (e.g. source areas). Since conservation actions are only as good as the quality of the data on which they are based (Koch, in press), it is imperative that biodiversity surveys be invested in. Although compiling biodiversity inventories is very costly in terms of time and money, it has been shown by Balmford and Gaston (1999) that using well-sampled data, obtained from detailed surveys, results in the requirement of smaller representative reserve networks than when incomplete data are used. It is believed that only once the abundance-related stratification of species across a landscape is known, or if the location of source populations can be established, that the most cost-effective Minimum Viable Populations can be selected.

REFERENCES

Balmford, A. and Gaston, K.J.C. (1999). Why biodiversity surveys are good value. *Nature.* **398:** 204-205.

Hartigan. J.A. 1983. *Bayes Theory.* Springer-Verlag, New York, U.S.A.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. & Balmford, A. 1998.Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**, 472-475.

Koch, S.O., Chown, S.L., Davis, A.L.V., Endrödy-Younga, S. & van Jaarsveld, A.S. Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa. *Journal of Insect Conservation.* In press.

Martin, J.J. 1967. *Bayesian decision problems and Markov chains.* John Wiley and Sons, Inc., New York.

Nicholls, A.O and Margules, C.R. 1993. An upgraded reserve selection algorithm. *Biol. Conserv.* **64**, 165-169.

Sætersdal, M., Line, J.M. & Birks, H.J.B. 1993. How to maximise biological diversity in nature reserve selection: Vascular plants and breeding birds in deciduous woodlands, Western Norway. *Biol. Conserv.* **66**, 131-138.

Soulé, M.E. and Sanjayan, M.A. 1998. Conservation targets: Do they help? *Science.* **279**, 2060-2061.

Wessels, K.J., Freitag, S. & Van Jaarsveld, A.S. 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biol. Conserv.* **89**, 21-38.

World Conservation Union (IUCN). 1992. *IUCN Bull.* **43 :** 10.

World Resources Institute (WRI). 1993. *World Resources Report 1993.* Washington DC: World Resources Institute.

World Resources Institute (WRI). 1994. *World Resources, 1994-1995.* Oxford University Press, New York, pp. 152-153.

APPENDIX 1

A description of the four land classification systems

Appendix 1

The area (ha) occupied by each of the land systems and land types in the Kruger National Park. Because these two classifications nest naturally within each other, their areas are given in one table to indicate the specific land types comprising each land system.

LAND SYSTEM	LAND TYPE ID	LAND TYPE	AREA (ha)	% of KNP
Malelane			41 326	7.1
	Ma 1	Malelane	30 468	
	Ma2	Stolsnek	10 858	
Skukuza			382 043	19.6
	Sk1	Pretoriuskop	47 267	
	Sk2	Napi	39 473	
	Sk3	Randspruit	23 697	
	Sk4	Lwakhale	51 290	
	Sk5	Makuthwanini	15 840	
	Sk6	Renosterkoppies	37 173	
	Sk7	Skukuza	57 422	
	Sk8	Nhlanguleni	63 508	
	Sk9	Muzandzeni	35 067	
	Sk10	Rabelais	8 112	
	Sk11	Timbavati	3 194	
Phalaborwa			507 726	26.6
	Ph1	Houtboschrand	19 801	
	Ph2	Shidyanamani	13 286	
	Ph3	Tsheri	51 289	
	Ph4	Phalaborwa	30 020	
	Ph5	Shivhulani	18 204	
	Ph6	Malopeni	24 399	
	Ph7	Mahlangeni	138 476	
	Ph8	Tsende	66 109	
	Ph9	Nalatsi	21 334	
	Ph10	Bububu	53 014	
	Ph11	Mphongolo	50 907	
	Ph12	Dothole	20 887	
Vutome			78 819	4.1
	Vu1	Vutome	78 819	
Bulweni			32 384	1.7
	Bu1	Bulweni	9 417	
	Bu2	Marithenga	12 966	
	Bu3	Tsotsi	10 000	

LAND SYSTEM	LAND TYPE ID	LAND TYPE	AREA (ha)	% of KNP
Satara			275 867	14.2
	Sa1	Satara	130 811	
	Sa2	Mavumbye	38 451	
	Sa3	Bangu	14 819	
	Sa4	Balule	25 103	
	Sa5	Orpen	58 124	
	Sa6	Salitje	8 559	
Letaba			356 664	18.3
	Le1	Olifants	38 068	
	Le2	Letaba	29 509	
	Le3	Mooiplaas	147 163	
	Le4	Manyeleti	53 270	
	Le5	Shingwedzi	45 222	
	Le6	Mashikiri	15 648	
	Le7	Shilawuri	27 784	
Sabiepoort			84 122	4.3
	Sp1	Sabiepoort	52 312	
	Sp2	Rietpan	16 033	
	Sp3	Pumbe	2 875	
	Sp4	Nwanetsi	12 902	
Klipkoppies			45 733	2.4
	Kl1	Gorge	6 835	
	Kl2	Klipkoppies	38 898	
Pafuri			92 423	4.7
	Pa1	Punda	28 104	
	Pa2	Madzaringwe	12 646	
	Pa3	Lanner Gorge	10 539	
	Pa4	Boabab Hill	23 505	
	Pa5	Pafuri	9 198	
	Pa6	Malonga	8 431	
Nwambiya			40 879	2.1
	Nw1	Nwambiya	20 056	
	Nw2	Masokosa	20 823	

The landscape classification system with the areas (ha) of each unit found in the Kruger National Park.

LANDSCAPE NUMBER	**LANDSCAPE NAME**	**AREA (ha)**	**% of KNP**
1	Lowveld Sour Bushveld of Pretoriuskop	53000	2.8
2	Malelane Mountain Bushveld	47000	2.4
3	*Combretum* Woodland	54000	2.8
4	Thickets of the Sabie & Crocodile Rivers	124200	6.2
5	*Combretum* spp./*Terminalia sericia* Woodland	157800	8.1
6	*Combretum/Colophospermum* Woodland	46930	2.4
7	Olifants River Rugged Veld	36000	1.8
8	Phalaborwa Sandveld	39600	2.0
9	*Colophospermum mopane* Savanna on Basic Soils	54600	2.8
10	Letaba River Rugged Veld	70000	3.6
11	Tsende Sandveld	115600	5.9
12	*Colophospermum/Acacia nigrescens* Savanna	104200	5.5
13	*Acacia welwitschii* Thickets on Karoo Sediments	52000	2.7
14	Kumana Sandveld	16400	0.8
15	*Colophospermum mopane* Forest	18000	0.9
16	Punda Maria Sandveld on Cave Sandstone	11700	0.6
17	*Sclerocarya caffra/Acacia nigriscens* Savanna	141100	7.2
18	Dwarf *Acacia nigriscens* Savanna	35600	1.8
19	Thornveld on Gabbro	68500	3.5
20	Bangu Rugged Veld	20400	1.0
21	*Combretum/Acacia* Rugged Veld	27000	1.4
22	*Combretum/Colophospermum* Rugged Veld	89400	4.6
23	*Colophospermum mopane* Shrubveld on Basalt	199300	10.3
24	*Colophospermum mopane* Shrubveld on Gabbro	28400	1.5
25	*Adansonia digitata/Colophospermum* Rugged Veld	28400	1.5
26	*Colophospermum mopane* Shrubveld on Calcrete	11700	0.6
27	Mixed *Combretum/Colophospermum* Woodland	32900	1.9

28	Limpopo/Levubu Floodplains	28400	1.5
29	Lebombo South	76500	4.8
30	Pumbe Sandveld	17700	0.1
31	Lebombo North	48000	2.9
32	Nwambia Sandveld	13900	0.8
33	*Pterocarpus rotundifoilius/Combretum* Woodland	18000	0.9
34	Punda Maria Sandveld on Waterberg Sandstone	29700	1.7
35	*Salvadora angustifolia* Floodplains	13300	0.7

The seven vegetation types found in the Kruger National Park.

VEGETATION TYPE NUMBER	VEGETATION TYPE NAME	AREA (ha)	% of KNP
9	Mopane Shrubveld	2618.3	13.9
10	Mopane Bushveld	6597.8	34.9
11	Soutpansberg Arid Mountain Bushveld	217.7	1.2
13	Lebombo Arid Mountain Bushveld	1651.5	8.7
19	Mixed Lowveld Bushveld	3680.5	19.5
20	Sweet Lowveld Bushveld	3496.6	18.5
21	Sour Lowveld Bushveld	636.7	3.4

APPENDIX 2

Classifications commonly used as templates for management, scientific and GIS work in the Kruger National Park*

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*Ms. In Press: M. Solomon, N. Zambatis, H.C. Biggs & N. Maré. Classifications commonly used as templates for management, scientific and GIS work in the Kruger National Park. *Koedoe* 42(2).

News and Views

Comparison of classifications commonly used as templates for management, scientific and GIS work in the Kruger National Park

M. SOLOMON, N. ZAMBATIS, H.C. BIGGS and N. MARÉ

Solomon, M., N. Zambatis, H.C. Biggs and N. Maré. 1999. Comparison of classifications commonly used as templates for management, scientific and GIS work in the Kruger National Park. *Koedoe* 42(2): 131–142. Pretoria. ISSN 0075–6458.

The two major land classification systems used in the Kruger National Park are discussed with respect to their development, sub-classification, scale, as well as current and potential usages. Their relatedness to one another, as well as to six other broad scale vegetation classifications is investigated and major similarities and differences are pointed out.

Key words: land classification, Kruger National Park, landscape, land type, land system, vegetation type, geology, GIS.

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Introduction

During the last decade, two methods of natural classification of land have been commonly used in the Kruger National Park (KNP). Confusion often exists as to which of the classification systems should be used for specific management, decision making and scientific purposes, and at which scale.

New researchers and managers often need a combined and clear explanation of these two systems to be able to carry out their own work. Therefore, the aim of this paper is to give a brief overview of the two different systems, now each developed into scaled hierarchies, and to define all terms used in these hierarchies as well as in other, similar data sets currently in use in the KNP. Furthermore, we aim to clarify the differences between the data sets by dealing with how, and for which purposes, they were developed and to make recommendations on how each one should be applied for particular situations. Figure 1 illustrates the main sub-classifications of the Venter (1990) and Gertenbach (1983) land classification systems in a hierarchical manner.

The "Venter-based land classification hierarchy"

In 1990 Venter proposed a classification of land for management planning in the Kruger National Park, with the main focus of the study being the soils of the KNP. The general objective of his study was to classify, map and quantitatively describe land in the KNP with special reference to morphological properties such as the soil, landform and woody vegetation of the study area.

The role of soil properties in plant and animal ecology decreases in extremely wet and dry climates. However, in areas with moderate climates such as the KNP, it is of vital

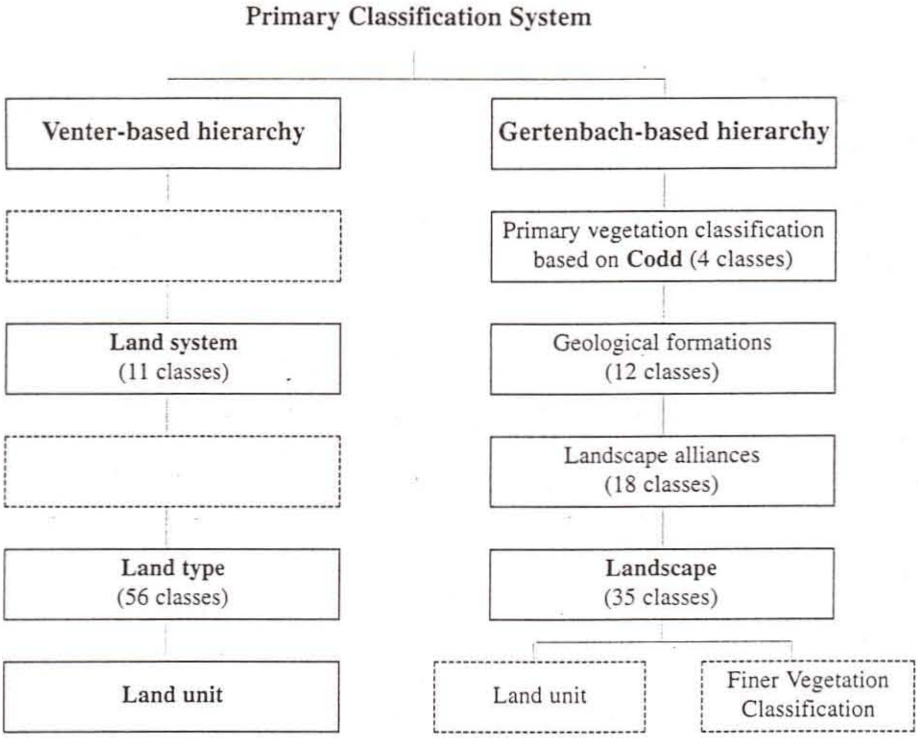

Fig. 1: The main sub-classifications of the Venter (1990) and Gertenbach (1983) land classification systems.

importance (Venter 1986) and soil characteristics, such as soil depth, texture and structure, play a decisive role in determining the availability of water and nutrients to plants. Clearly, abiotic components form an integral and complex part of the ecology in the KNP, and it can thus rightly be assumed that soil and soil properties will determine an area's biotic potential. Any classification system based on abiotic factors, rather than biotic factors, will tend to be more informative at a basic level, since resultant vegetation patterns are likely to be highly correlated with the former.

Venter recognised, mapped and described 11 land systems, consisting of a total of 56 land types. An individual land system consists of between one and 12 different land types.

A land system can be defined as an area, or group of areas in close proximity, which is associated with a specific geological formation and/or geomorphological phenomenon and/or climatic regime. Each of these land systems is described in detail with regards to its geology, geomorphology and rainfall. Furthermore, the land type(s) comprising each land system are mentioned and a broad overview of the differences between these land types is given. A land type is defined as an area, or group of areas, throughout which a recurring pattern of distinctive land units, each with its own characteristic landform and unique soil and vegetation assemblages can be recognised. Next, each land type is described in detail with respect to its morphometric features, its soils and dominant woody vegetation. Lastly, for each land type

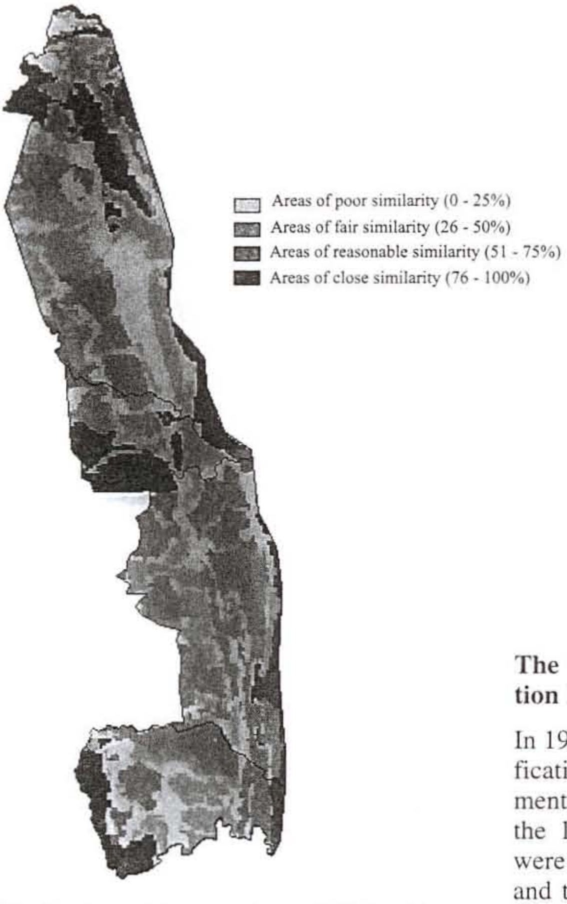

Fig. 2: A spatial comparison of 56 land types (Venter) and 35 landscapes (Gertenbach)

a hillslope profile sketch is presented, dividing land types into land units.

A land unit is a specific section of a hillslope profile with its own distinctive natural attributes, including its morphology (curvature and slope), drainage and position. Each land unit also has a distinct assemblage of soils and plants, which differ from those of other units. These differences are strikingly evident in certain areas, while in other areas they are much more subtle. Land units nest naturally into land types, are primarily based on catenal position and are mapped at a very fine scale.

The polygons formed by the landform classification do not necessarily overlap with those of the previously mentioned three classifications, but landforms were used in conjunction with soil (point data) and vegetation (point data) in classifying land types. A landform is defined as an area with distinctive morphological and physical surface features, including its attributes of local relief, slope classes, drainage pattern and stream frequency. There are five such distinct classes within the KNP, namely plains with low relief, slightly undulating plains, moderately undulating plains, extremely irregular plains and low mountains and hills.

The "Gertenbach - based land classification hierarchy"

In 1983 Gertenbach developed a land classification system on which future management could be based. Because of the fact that the landscapes recognised by Gertenbach were so widely referred to in the last decade and thus acted as a practical starting point, this hierarchy has been developed in a "bottom-up" sense. He attempted to divide the KNP into significant units for the purpose of practical conservation planning and management. As a result 35 landscapes were identified. A landscape can be defined as an area with a specific geomorphology, climate, soil, vegetation pattern and associated fauna. A detailed description of each landscape is given with respect to each of the five components mentioned in the definition, with considerable emphasis on the two biological components, namely vegetation and fauna.

An Environmental Education firm involved in the KNP named Jacana Education, needed a map (simpler than the Gertenbach classification) for tourist use, conveying general information with respect to animal and plant distribution, as well as the underlying abiot-

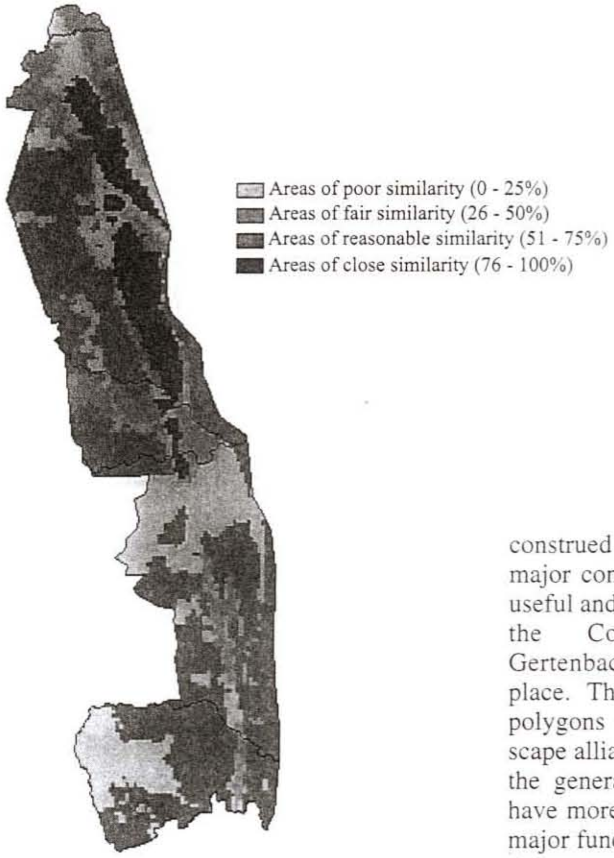

Fig. 3: A spatial comparison of 11 land systems (Venter) and 12 main geological formations (Gertenbach).

ic pattern. At that time no such map was available, and this led to an "ecozones map" being developed by Jacana Education, whereby the KNP was divided into 16 ecozones by combining certain of Gertenbach's landscapes. Although adequate and informative for the tourist, this consolidation needed some refining for technical use. Gertenbach, with the help of Zambatis, slightly modified and refined the Jacana map to come up with 18 landscape alliances (17 plus the riparian communities), which will be hereafter referred to as the landscape alliances map. Because of its ready availability, scientists and managers often use the Jacana Ecozones map, which is often adequate. However, it is important to note the refinements for certain purposes. At a level similar to the Venter land systems, the landscapes of Gertenbach can be grouped into 12 major geological formations (unpublished map).

What was originally done by Codd (1951) produced a "macro" view of vegetation in the KNP. Because so much research work aims at understanding system function, a system that has a small number of divisions—ones which can be construed as the most representative of the major conditions prevalent in the KNP—is useful and in practical terms necessary. Thus the Codd-based consolidation of Gertenbach's original classification took place. This meant that the 35 landscape polygons were aggregated (first into landscape alliances) to such a way as to preserve the general outline of Codd's system and have more accurate boundaries. However, a major functional change was made based on the presumption that macro-level differences between the basalts and granites in the northern mopanieveld of the Park exist.

For future researchers to be able to establish whether or not their study will be affected by the choice of the land classification system used, a map delineating the borders of Venter's 56 land types were compared to a similar map depicting Gertenbach's 35 landscapes to locate areas of potential high similarities and areas of high dissimilarities. Such a comparison is done by aggregating data over units of cartographic space (polygons) that are like individual locations to the extent that they provide all-inclusive, but mutually exclusive study area coverage, i.e. two data layers, conveying different information, but covering the same area in space. Using the Zonal Percentage concept as explained by Tomlin (1990), a new value is computed for each location on a map as a

Table 1
Potential usage of each land classification unit

Level	Attributes used for classification	Potential usages	Comments (strong & weak points)
Land system	Integration of macro geology, geomorphology and climate.	Macro level compartment difference in functional response (e.g. fire return period) where geomorphology/climate are decisive factors. Descriptive backdrop for abiotic classification.	Sourveld is not intuitively delineated.
Land type	Landform, broad vegetation pattern and soil.	Meso-level compartment difference, particularly where soil differences are important (catenal variation included; at this level only spatially implicit, i.e. overall percentage of each land unit within a land type is given). Differences in plant community composition and structure.	Useful because of explicit additional structure at a lower hierarchical detail level.
Land unit	Catenal subdivision of the previous classification.	Where differences within catenal variation are needed. Spatially explicit.	Currently only available for Sabie catchment within Kruger and for Northern Basaltic Plains study area.
Landform	Broad geomorphological structure, edge not contiguous with land system, land type and land unit.	Where macro physical surface structure is needed.	Only at a very broad scale.
Landscape	Geomorphology, climate, soil, vegetation, fauna.	Animal associations. Plant communities implicit.	Wide usage, but certain of these could benefit by also looking at the Venter hierarchy.

function of existing values associated with each polygon containing that location. Figure 2 was generated accordingly to indicate where and how much the two layers of the different classification systems coincide, assigning a similarity index to each region in the Kruger Park. The value assigned to each location on Figure 2 is computed as an average of the percentage of that location's land type that shares its landscape value, and the percentage of the location's landscape that shares its land type value.

From Fig. 2 areas of close similarity (75 % – 100 % similarity) between the two classification systems can be seen near Malelane, along the eastern boundary of the Park, as well as around Phalaborwa, Shingwedzi, Punda Maria, Pafuri and Nwambiya respectively. Because of the fact that there is seldom a definite and visible border between classification types (be it geology, soil or vegetation), but rather a gradual change (gradient), the boundaries of each classification unit are drawn subjectively out of necessity

Table 2

Similarities and differences between vegetation type classifications used in the Kruger National Park

		Increasing Heterogeneity						Increasing Homogeneity				
		Similarities										
		Codd (1951)	Acocks (1953)	Van der Schijff (1957)	Pienaar (1963)	Van Wyk (1972)	Coetzee (1983)	Gertenbach (1983)	Gertenbach (1998, Unpubl.) Landscapes	Gertenbach (1983, Unpubl.) Geology	Gertenbach (1983, Unpubl.) Dominant vegetation	Low & Rebelo (1998)
	Number & Type of Unit	5 Vegetation Regions	5 Veld Types	6 Communities	19 Game Habitats	19 Vegetation Units	20 Major Veg. Zones	35 Landscapes	18 Landscape Alliances	12 Major Geol. Form.	8 Dominant Woody spp.	7 Veg. Types
Differences	Codd (1951)	**± 2 025 932**	FNa; NUb	Bpa	OBa; BPa	OBa; FNb; BPa	None	None	None	FNb	None	BPa
	Acocks (1953)	OBa; FNb; BPd	**1 500 000**	OBb; FNc; BPa	BPa	BPa	None	None	None	None	FNc	BPa
	V.d. Schijff (1957)	OBp; FNc; BPd	BPd; NUa	**500 000**	OBa; BPa	OBa; BPa	None	None	None	None	FNc	BPa
	Pienaar (1963)	FNf; BPd; NUa	OBa; FNf	FNf; BPd; NUa	**± 1 450 537**	OBa; BPa; NUb	None	None	None	None	None	BPa
	Van Wyk (1972)	BPd; NUa	OBa; FNb; BPd; NUa	FNb; BPd; NUa	FNb; BPd	**250 000**	None	None	None	None	None	FNb
	Coetzee (1983)	OBc; FNe; NUa	OBc; FNe; NUa	OBc; FNe; NUa	OBc; FNe; NUa	OBc; FNe; NUa	**Unmapped**	OBc	OBc	None	OBc	OBc
	Gertenbach (1983) Landscapes	OBc;FNd; BPb,d; NUa	OBc; FNd; BPb,d; NUa	OBc;FNd; BPb,d; Nua	OBc; FNd; BPb,d; NUa	OBc; BPb,d; NUa	FNd; NUc	**250 000**	OBc; FNd; BPb,c	OBc; BPb,c	OBc; BPb,c	OBc; FNb
	Gertenbach (1998) Alliances	OBc; FNd; BPb,d; NUa	OBc; FNd; BPb,d; NUa	OBc; FNd; BPb,d; Nua	OBc; FNd; BPb,d: NUa	OBc; FNd; BPb,d; NUc	FNd; NUc	NUc	**250 000**	OBc; BPb,c	OBc; BPb,c	OBc; FNb
	Gertenbach (1983) Geology	OBc; FNa; BPb,d; NUa	OBc; FNa; BPb,d; NUa	OBc; FNb; BPb,c; Nuc	OBc; FNa; BPb,d; NUc	OBc; FNa; BPb,d; FNc	FNa; NUa	FNa; NUa	FNa; NUc	**250 000**	OBc; BPb,c	OBc; FNb
	Gertenbach (1983) Dominant woody species	OBc; FNc; BPb,d; NUa	OBc; BPb,d; NUa	OBc; BPb,d; NUa	OBc; BPb,d; NUc	OBc; BPb,d; NUc	FNc; NUc	FNc; NUa	FNc; NUc	FNc; NUc	**250 000**	OBc
	Low & Rebelo (1998)	OBc; FNb; BPd; NUa	OBc; FNb; BPd; NUc	OBc; FNb; BPd; NUc	OBc; FNb; BPd; NUc	OBc; BPd; NUc	FNb;NUa	BPd; NUc	BPd; NUc	BPd; NUc	FNb; BPd	**3880 000**

Key to the abbreviations used in Table 2

1. Objectivity (OB)	
Subjective, little or no quantitative data used	a
Semi-objective, some quantitative data used	b
Objective, scientifically based	c
2. Foundation (FN)	
Geological formations, regardless of vegetation dominants	a
Geological formation and vegetation dominants	b
Climate, geology and vegetation dominants	c
Climate and geology	d
Game habitats	e
3. Boundary position (BP)	
Approximately placed	a
Semi-accurately to accurately placed	b
Largely or completely correspond	c
Largely or completely differ	d
4. Number of units (NU)	
More than	a
Same as	b
Less than	c

to delineate a boundary. These indistinct boundaries occur both on the ground and on aerial photographs, where at a scale of 1:250 000 a one-millimetre error or shift in boundary position, represents 250 m on the ground. In these areas, a very low similarity between the two systems can thus be expected.

The same comparison was done for the 11 land systems as identified by Venter and the agglomoration of Gertenbach's landscapes into 12 main geological formations. These areas of similarity and dissimilarity are depicted in Fig. 3. Intuitively, one might expect the boundaries of these geological areas to coincide closely with the boundaries of Venter's land systems, since these two classification systems are essentially based upon the same criteria. As can be seen form Figure 3, this is however, not the case. The only areas of extremely close similarity is where Gertenbach's classification corresponds to Venter's Letaba land system. Differences between Venter (1990) and Gertenbach (1983) are primarily due to greater emphasis being placed on geology, terrain morphology and soils by Venter, whereas Gertenbach places greater emphasis on dominant woody vegetation. A further reason for differences concerns the indistinct boundaries on the ground or aerial photographs, as discussed previously.

The attributes used in developing each classification as well as potential usages and strong and weak points are given in Table 1. Only levels specifically used by Venter (1990) and Gertenbach (1983) in their respective publications are explained in this table.

Comparison of the most widely used broadscale vegetation classifications in South Africa yield a correspondence shown in Table 2. Six vegetation classifications and the Gertenbach landscapes (because of its high dependence on vegetation) are used in the first half of the table in an increasing scale of heterogeneity, i.e. from the smallest number of classes per system to the largest number of classes per classification system. In the second half of the table, three unpublished classifications identified by Gertenbach as well as the vegetation map by Low and Rebelo are compared to one another in levels of increasing homogeneity. In this table the original scale at which each system was developed is given and major similarities and differences between these systems are pointed out. In Table 3, these vegetation classifications, developed from 1951 to 1998, are explained with respect to the units used as a strategic framework for describing land in the KNP by various authors. Furthermore, the Gertenbach landscape numbers, corresponding to every individual unit in each classification system are provided for comparative purposes.

Table 3

Rationalisation of the vegetation classifications of the KNP : 1951 - 1998

	GERTENBACH (1983) Braun-Blanquet 35 LANDSCAPES
1	Moderately undulating granitic plains with *Terminalia sericea* tree savanna
2	Low granitic mountains with *Combretum apiculatum* bush savanna
3	Moderately undulating granitic plains with *Combretum zeyheri* bush savanna
4	Granitic plains with *Acacia grandicornuta* tree savanna
5	Moderately undulating granitic plains with *C. apiculatum* bush savanna
6	Slightly undulating metalava plains with *Colophospermum mopane* bush savanna
7	Irregular granitic hills with *C. mopane* tree savanna
8	Moderately undulating granitic plains with *C. mopane* bush savanna
9	Slightly undulating metalava plains with *C. mopane* tree savanna
10	Very irregular granitic plains with *C. mopane* tree savanna
11	Slightly undulating granitic plains with *C. mopane* bush savanna
12	Metalava plains with *C. mopane* tree savanna
13	Karoo sediment plains with *Acacia welwitschii* tree savanna
14	Karoo sediment plains with *T. sericea* bush savanna
15	Karoo sediment plains with *C. mopane* tree savanna
16	Very irregular Clarens sandstone hills with *T. sericea* bush savanna
17	Basaltic plains with *Sclerocarya birrea* tree savanna
18	Slightly undulating basaltic plains with *Acacia nigrescens* shrub savanna
19	Moderately undulating gabbroic plains with *A. nigrescens* bush savanna
20	Moderately undulating basaltic plains with *A. nigrescens* bush savanna
21	Irregular basaltic plains with *A. nigrescens* bush savanna
22	Irregular basaltic plains with *C. mopane* bush savanna
23	Basaltic plains with *C. mopane* shrub savanna
24	Slightly undulating gabbroic plains with *C. mopane* shrub savanna
25	Moderately undulating basaltic plains with *C. mopane* shrub savanna
26	Irregular calcitic plains with *C. mopane* shrub savanna
27	Slightly undulating basaltic plains with *C. apiculatum* bush savanna
28	Alluvial plains with *Faidherbia albida* tree savanna
29	Low rhyolitic mountains with *C. apiculatum* bush savanna
30	Recent sand plains with *T. sericea* bush savanna
31	Low rhyolitic mountains with *C. mopane* bush savanna
32	Recent sand plains with *Baphia massaiensis* bush savanna
33	Andesitic plains with *Combretum collinum* shrub savanna
34	Low Soutpansberg group mountains with *Burkea africana* tree savanna
35	Alluvial plains with *Salvadora angustifolia* tree savanna

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These landscape numbers are provided for comparative purposes in each classification system that follows.

Table 3 (continued)

CODD (1951) Subjective, coarse classification 5 VEGETATION REGIONS		ACOCKS (1953) Species abundance ranking 5 VELD TYPES		VAN DER SCHIJFF (1957) Belt transects 6 COMMUNITIES	
1. Large deciduous-leaved bush	1	9. Lowveld sour bushveld	1	1. *Dichrostachys-Terminalia Hyparrhenia* communities	1
	2		15		
	3		16	2. *Combretum* communities	2
	19		25		3
2. *Combretum* communities	4		34		4
	5	10. Lowveld	1		5
	6		2		6
	7		3		7
	8		4		11
	19		5		12
3. Knobthorn-Marula open parkland	13		17		19
	14		19		24
	15		29		29
	17	11. Arid Lowveld	6		31
	18		7		33
	20		13	3. *Acacia nigriscens-Sclerocarya birrea* associations	4
	21		14		12
	29		17		13
	30		18		14
4. Mopanieveld	9		19		17
	10		20		18
	11		21		20
	12		29		21
	15		30	5. *Colophospermum mopane* communities	6
	22	15. Mopani Veld	8		7
	23		9		8
	24		10		9
	25		11		10
	26		12		11
	27		13		12
	28		14		15
	31		15		16
	32		22		22-28
	33		23		35
	35		24	6. Mixed communities of Punda Maria Sandveld	16
5. Punda Maria Sandveld	16		25		34
	36		26	7. *Baphia massaiensis* communities of the Nwambiya sandveld	30
			27		32
			28		
			31		
			32	Unmapped communities	
			33	4. Communities of doleritic intrusions	
			35		
		18. Mixed Bushveld	16	8. Hygrophilic communities	
			18	9. Communities of rock sheets, koppies & ridges	
			25		
				10. Communities of termitaria	

Table 3 *(continued)*

Pienaar (1963) Subjective 19 Game Habitats		Van Wyk (1972) Subjective 19 Vegetation Zones		Coetzee (1983) Braun-Blanquet 20 Vegetation Zones	
1. Pumbe Sandveld	30	Area A		A. Azonal Region	
2. Deciduous shrub thickets (Nyandu bush)	32	A_1 Red bush-willow veld (granite undulations)	3 5	1. Riparian	28 35
3. Bush or forest-clad mountainous or rocky outcrops	2 16	A_2 Thorny thickets (brackish flats of granite origin)	4	B. Subhumid Regions	
4. Lebombo mountain range	25 26 29 31	Area B		2. Subhumid plains	1
5. Light montane forest and overgrown valleys	2 34	Red bush-willow/ mopani veld (granite undulation)	24 33	3. Southern subhumid hills and mountains	2
6. Riparian forest	28 35	Area C		4. Northern subhumid hills and mountains	34
7. Mopani shrub savanna of Lebombo flats	11 23 24 27	C_1 Shrub mopani veld (basalt plains)	22 23	C. Semi-Arid Regions	
8. Mopani tree savanna of Lebombo flats	23	C_2 Tree mopani veld (sandstone plains & alluvial soils)	15	5. Semi-arid grainitic plains	3 5
9. Grassland plains and dambos	23	C_3 Mixed mopani veld (basalt ridges)	25 26 27	6. Semi-arid amphibolitic and andesitic plains	33
10. Mixed Mopani - *Combretum* savanna woodland	6-12 22 24 26 33	Area D		7. Semi-arid dolerite plains	17 18 19
11. Mixed Mopani - *Combretum* tree savanna	7 8 11 12	D_1 Knobthorn/marula veld (basalt plains and dolerite intrusions)	17 18 19 20	8. Semi-arid basaltic plains	17 20
12. Mopani woodland	15	D_2 Leadwood/marula/*Albizia* veld (basalt plains)	17	9. Semi-arid Karoo sediment plains	13 14
13. Dense thorn thickets	4	Area E		10. Semi-arid sand plateau	30
14. Mixed *Combretum* savanna woodland	3 4 5 19	*Terminalia*/sicklebush veld (granite undulations)	1	11. Semi-arid hills and inselberge	31
15. Mixed *Combretum* *Acacia* tree savanna	5 13 14 19	Area F		D. Arid Regions	
16. Long grass savanna woodland and tree savanna	1	F_1 Mixed red bush-willow and mopani veld (rhyolite ridges)	29 31	12. Arid granitic plains	6 7 8 9 10 11 12 24 33
17. Dry deciduous forest	16 31 34	F_2 Lebombo ironwood forest (rhyolite ridges)	29	13. Arid dolerite plains	22 23
18. *Acacia nigriscens Sclerocarya birrea* tree savanna	17 18 20 21	Area G		14. Arid basaltic pains	22 23
19. *Acacia nigriscens Sclerocarya birrea* savanna woodland	17 18 21	Punda Maria Sandveld (Sandstone ridges)	34	15. Arid karoo sediment plains	15
		Area H		16. Southern spiny arid bushveld	4 21
		H_1 Wambija sandveld(sandy flats)	32	17. Northern spiny arid bushveld	25 26 27
		H_2 Pumbe sandveld(sandy flats)	30	18. Arid sand plateau	32
		Area I		19. Arid sandstone hills	16
		Mixed montane vegetation (granite mountains)	2	20. Arid inselberge, ridges and rhyolite range	29 31
		Area J			
		Delagoa thorn thickets (brackish flats of granite origin)	13 14		
		Area K			
		Karoo sandveld (karoo sediments)	16		
		Area L			
		Terminalia/*Commiphora*/knobthorn veld (basalt undulations)	21		
		Area M			
		Riverine forest (Alluvial soils)	28 35		

Table 3 *(continued)*

GERTENBACH (1998) Synthesis of allied landscapes 17 LANDSCAPE ALLIANCES	
1. Granitic plains with *Terminalia sericea* tree savanna	1
2. Granitic mountains with *Combretum apiculatum* bush savanna	2
3. Granitic lowlands with *Acacia grandicornuta* tree savanna	4
4. Granite plains with *Combretum zeyheri* or *C. apiculatum* bush savanna	3 5
5. Granite plains with *Colophospermum mopane* bush or tree savanna	6 7
6. Metalava with *C. mopane* tree savanna	9 10
7. Granitic plains with *C. mopane* bush savanna	8 11
8. Metalava plains with *C. mopane* tree savanna; or Andesitic plains with *Combretum collinum* shrub savanna	12 33
9. Karoo sediment plains with *Acacia welwitchii* tree savanna: or with *T. sericea* bush savanna	13 14
10. Karoo sediment plains with *C. mopane* tree savanna	15
11. Clarens sandstone hills with *T. sericea* bush savanna; or Soutpansberg group mountains with *Burkea africana* tree savanna	16 37
12. Basaltic or gabbroic plains with *S. birrea tree* savanna; or *Acacia nigriscens* bush or shrub savanna	17 18 19 20
13. Basaltic or gabbroic plains with *A. nigriscens* bush savanna; or *C. mopane* bush or shrub savanna	21 22 23 24
14. Basaltic plains or rhyolite mountains with *C. apiculatum* or *C. mopane* bush savanna	27 29 31
15. Basaltic or calcitic plains with *C. mopane* shrub savanna	25 26
16. Alluvial plains with *Faidherbia albida* or *Salvadora angustifolia* tree savanna	28 35
17. Recent sand plains with *T. sericea* bush savanna; or with *Baphia massaiensis* bush savanna	30 32

GERTENBACH (1998) Grouped according to predominant woody vegetation 8 DOMINANT WOODY SPECIES GROUPINGS	
MOPANI Tree, bush or shrub savanna on: i) Lightly, moderately, irregular or very irregular granitic plains ii) Basaltic plains, moderately undulating or irregular basaltic plains iii) Slightly undulating gabbroic plains iv) Undulating metalava plains v) Karoo sediment plains vi) Irregular calcitic plains	6 7 8 9 10 11 12 15 22 23 24 25 26 31
COMBRETUM spp. *C. apiculatum* or *C. zeyheri* bush savanna; or *C. collinum* shrub savanna on: i) Moderately undulating granitic plains or low granitic mountains ii) Slightly undulating basaltic plains iii) Andesetic plains iv) Low rhyolitic mountains	2 3 5 27 29 33
ACACIA spp. *A. nigriscens* bush or shrub savanna or *A. grandicornuta* or *A. welwitchii* tree savanna on: i) Granitic lowlands ii) Karoo sediment plains iii) Slightly, moderately or irregular basaltic plains	4 13 18 19 20 21
SCLEROCARYA BIRREA Tree savanna on basaltic plains	17
TERMINALIA SERICEA Tree or bush savanna on: i) Moderately undulating granitic plains ii) Karoo sediment iii) Recent sand plains	1 14 16 30
BURKEA AFRICANA Tree savanna on low Soutpansberg group mountains	34
ALLUVIUM *Faidherba albida* or *Salvadora angustifolia* tree savanna on alluvial plains	28 35
BAPHIA MASSAIENSIS Bush savanna on recent sand plains	32

LOW & REBELO (1998) Published classifications 7 VEGETATION TYPES	
SAVANNA BIOME	
9. Mopane shrubveld	9 22 23 27 35
10. Mopane bushveld	7 8 10 11 12 15 24 25 26 28 32 33
11. Soutpansberg arid mountain bushveld	16
13. Lebombo arid mountain bushveld	29 30 31
19. Mixed lowveld bushveld	3 4 5 13 14 19
20. Sweet lowveld bushveld	6 17 18 20 21
21. Sour lowveld bushveld	1 2 34

The question arose whether there is not a necessity for a finer vegetation based subclassification of the 35 landscapes. Raw data on the plant communities occurring in the KNP (collected by Van Rooyen (1978), Gertenbach (1978) and Coetzee (1983)) are available, and modern techniques can be implemented to reclassify these into a viable small scaled classification corresponding to the land units in the Venter-based classification. Indeed, a project on the phytosociological and syntaxonomical synthesis of the vegetation of the Kruger National Park and adjacent lowveld is currently under way. The wealth of phytosociological data that have been collected in the KNP and surroundings over the years by individual researchers for various studies (among others those mentioned above) can now be used. The objective is to prepare a comprehensive phytosociological synthesis of all available data, resulting in plant communities being identified and described at a smaller scale than was previously available. For more details on this study contact Prof. G. Bredenkamp at *gbredenk@scientia.up.ac.za.*

References

ACOCKS, J.P.H. 1975. Veld types of South Africa. *Memoirs of the botanical Survey of South Africa* 40: 1–128.

CODD, L.E.W. 1951. Trees and shrubs of the Kruger National Park. *Memoirs of the botanical Survey of South Africa* 26: 1–192.

COETZEE, B.J. 1983. Phytosociology, vegetation structure and landscapes of the Central District, Kruger National Park, South Africa. Dissertations Botanicae. FL-9490 Vaduz, Germany.

GERTENBACH, W.P.D. 1978. Plantgemeenskappe van die Gabbro-kompleks in die noordweste van die Sentrale Distrik van die Nasionale Kruger Wildtuin. M.Sc. thesis, University of Potchefstroom for CHE, Potchefstroom.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* 26: 9–121.

LOW, A.B. & A.G. REBELO (eds.). 1996. *Vegetation of South Africa, Lesotho and Swaziland.* Pretoria: Dept Environmental Affairs & Tourism.

PIENAAR, U. DE V. 1963. The large mammals of the Kruger National Park—their distribution and present day status. *Koedoe* 6: 1–37.

TOMLIN, C.D. 1990. *Geographic information systems and cartographic modeling.* New Jersey: Prentice-Hall.

VAN DER SCHIJFF, H.P. 1957. Ekologiese studie van die Flora van die Nasionale Krugerwildtuin. Deel 1. D.Sc. thesis. University of Potchefstroom for CHE, Potchefstroom.

VAN ROOYEN, N. 1978. 'n Ekologiese studie van die flora van die plantgemeenskappe van die Punda Milia-Pafuri–Wambiyagebied in die Nasionale Krugerwildtuin. M.Sc. thesis, University of Pretoria, Pretoria.

VAN WYK, P. 1972. *Trees of the Kruger National Park.* Vols. I & II. Cape Town: Purnell.

VENTER, F.J. 1986. Soil patterns associated with the major geological units of the Kruger National Park. *Koedoe* 29: 125–138.

VENTER, F.J. 1990. A classification of land for management planning in the Kruger National Park. Ph.D. thesis. University of South Africa, Pretoria.