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.

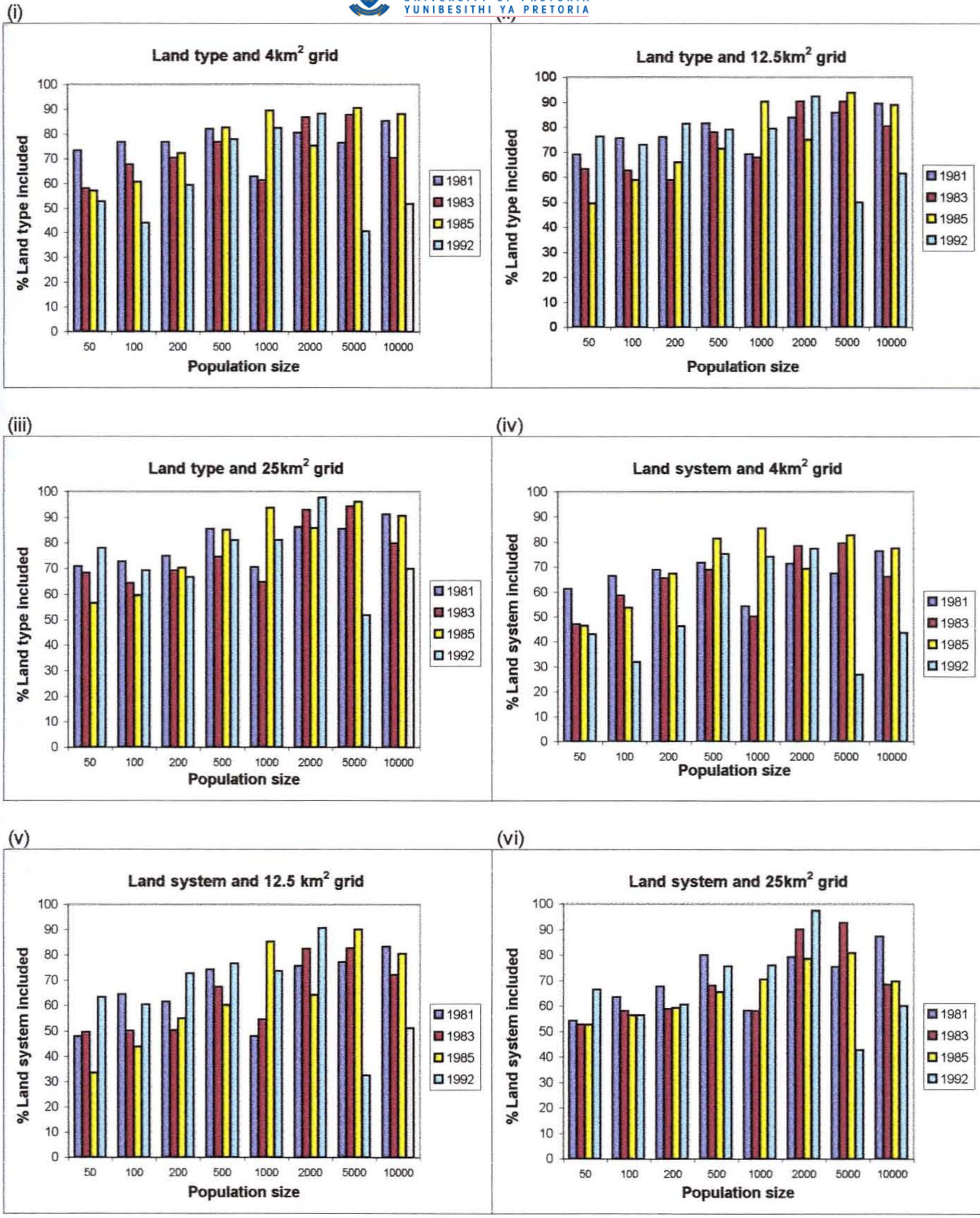
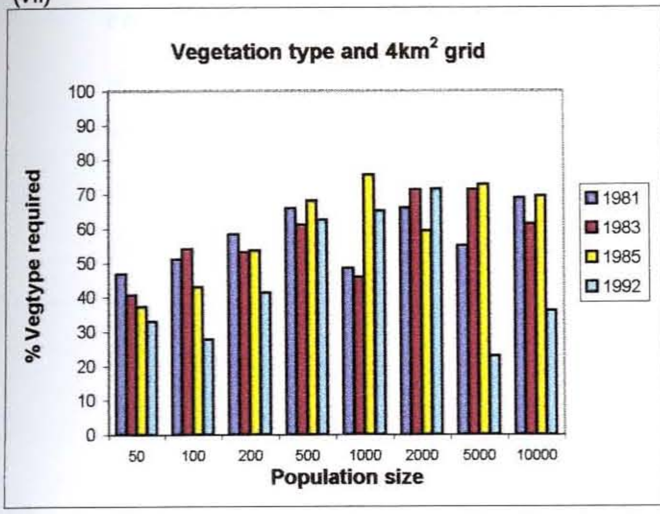
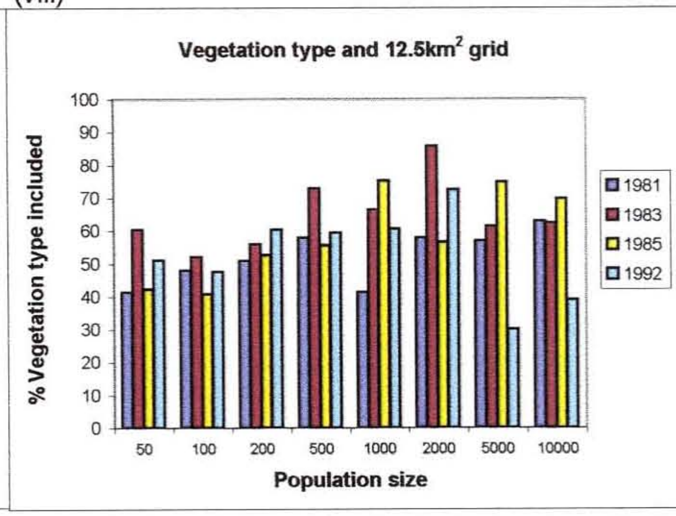


Figure 2: A summary of the area requirements for conserving 12 herbivore species in the KNP, using three different grain sizes (4, 12.5, 25km^2) and four land classification systems (land type, land system, vegetation type and landscape).

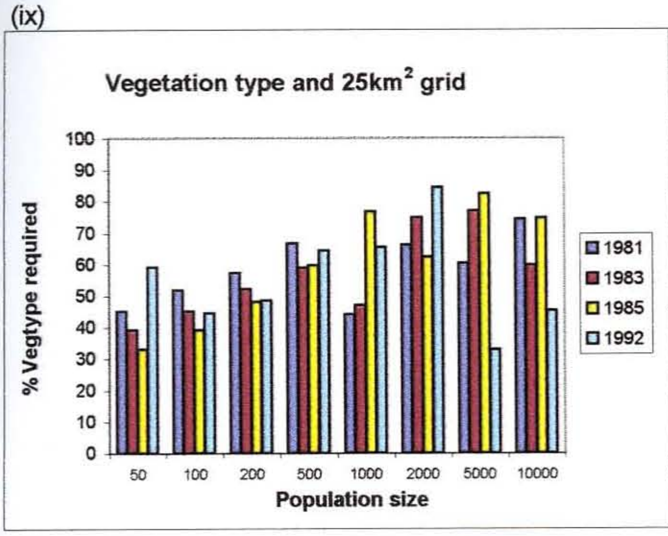
(vii)



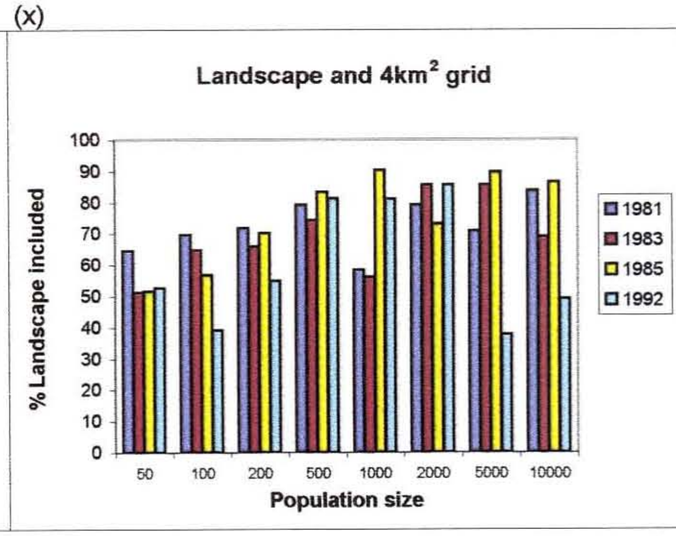
(viii)



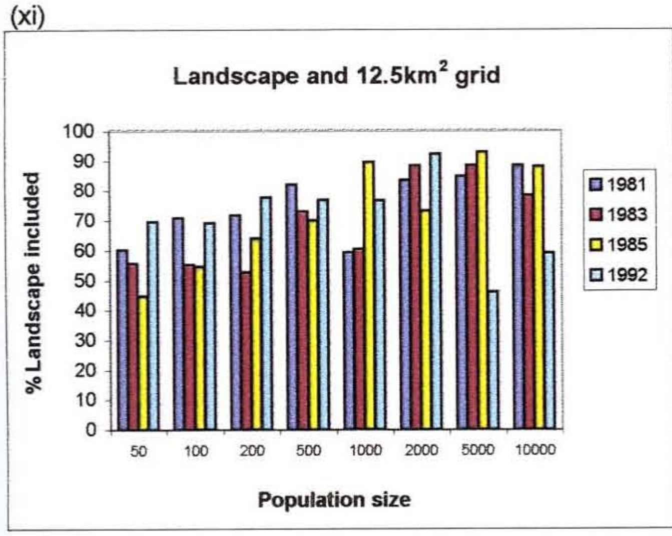
(ix)



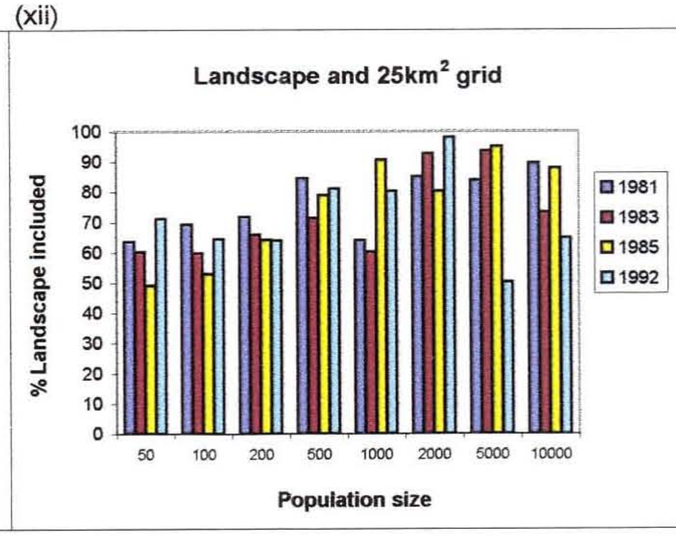
(x)



(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).

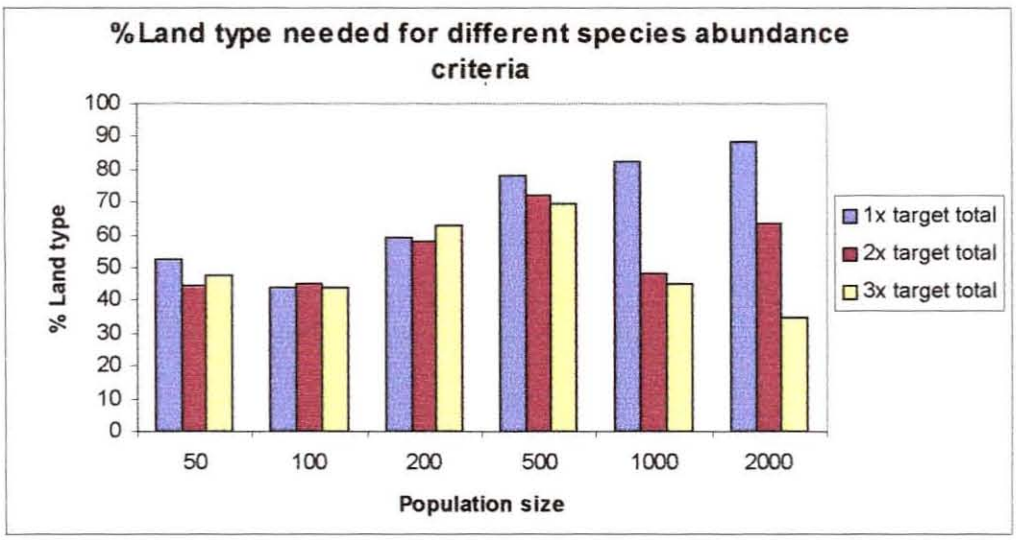


Figure 3: Percentage land area required for three different minimum population abundance selection criteria.

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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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