Table 6. Density (km^{-2}) of large herbivores in Mkuzi Game Reserve as estimated in August 1984. Land types referred to are as per Fig. 22.

Species	Land type J_j	Cr_3	Cr_2	Pl_4	H	Mean
Bushbuck	0,44	-	-	-	1,40	0,28
Bushpig	*	*	*	*	*	1,05
Duiker/Grey	0,48	2,21	2,18	7,57	*	1,85
Duiker/Red	-	*	*	-	*	1,05
Eland	*	*	*	-	-	0,09
Giraffe	0,40	1,15	0,14	0,76	-	0,49
Hippo	-	-	*	-	*	0,09
Impala	29,31	17,41	16,17	24,22	8,08	20,60
Klipspringer	0,11	-	-	-	-	0,03
Kudu	1,17	1,22	2,50	5,68	-	1,78
Nyala	2,31	7,27	12,84	28,84	29,15	11,10
Reedbuck/Common	2,02	-	0,63	-	0,70	0,87
Reedbuck/Mountain	0,65	-	-	-	-	0,21
Rhino/Black	*	*	*	*	*	0,24
Rhino/White	-	*	*	-	-	0,10
Steenbok	0,65	0,95	0,75	-	-	0,63
Suni	*	*	*	*	-	0,87
Warthog	2,07	3,42	2,11	1,10	1,05	2,20
Waterbuck	-	-	-	-	0,21	0,02
Wildebeest	1,08	1,55	1,24	4,58	0,49	1,43
Zebra	2,46	2,48	1,52	1,01	-	1,85

- Denotes species not seen in this land type.

* Denotes data too sparce to calculate density.

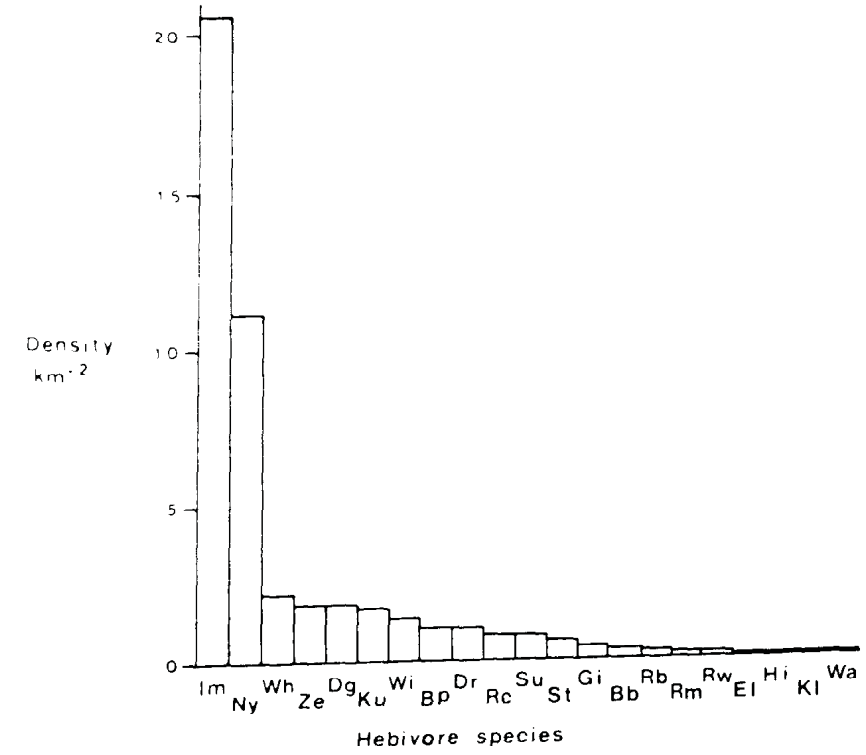


Fig. 23 Density of large herbivores in Mkuzi. Abbreviations as per Table 5.

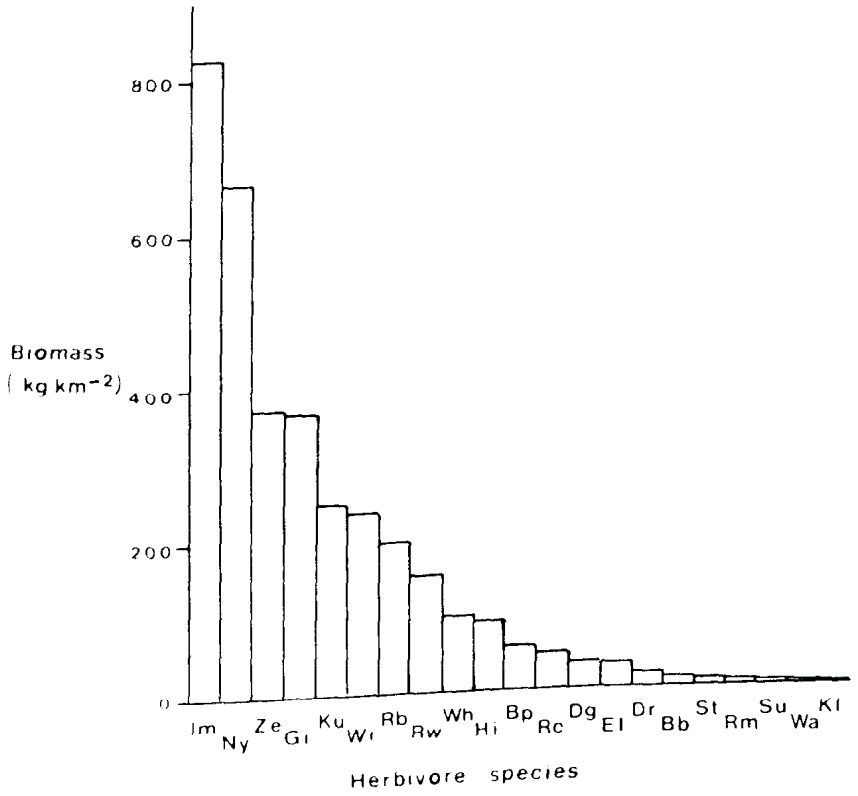


Fig 24 Biomass of large herbivores in Mkuzi. Abbreviations as per Table 5.

Table 7. Biomass (kg km^{-2}) of large herbivores in Mkuzi Game Reserve as estimated in August 1984. Land types are as for Fig. 22 and - and * denote respectively species not seen in this land type or data too sparce to calculate density.

	Land type					
Species	J_1	Cr_3	Cr_2	Pl_4	H	Mean
Bushbuck	13,2	-	-	-	42,0	8,4
Bushpig	*	*	*	*	*	56,7
Duiker/Grey	8,2	37,6	37,1	128,7	*	14,7
Duiker/Red	-	*	*	-	*	14,7
Eland	*	*	*	-	-	30,6
Giraffe	300,0	862,5	105,0	-	367,5	-
Hippo	-	-	*	-	*	90,0
Impala	1172,4	696,4	646,8	968,8	323,2	820,4
Klipspringer	1,3	-	-	-	-	0,4
Kudu	159,1	165,9	340,0	772,5	-	242,1
Nyala	138,6	436,2	770,4	1730	1749	666,0
Reedbuck/Common	101,0	-	31,5	-	35,0	43,5
Reedbuck/Mountain	18,2	-	-	-	-	5,9
Rhino/Black	*	*	*	*	*	195,8
Rhino/White	-	*	*	-	-	150,0
Steenbok	7,2	10,5	8,3	-	-	6,9
Suni	*	*	*	*	-	4,4
Warthog	93,2	153,9	95,0	49,5	47,3	99,0
Waterbuck	-	-	*	-	33,6	3,2
Wildebeest	178,2	255,8	204,6	755,7	80,9	236,0
Zebra	580,9	496,0	304,0	202,0	-	370,0
Total	2771,5	3114,8	2542,7	5177,6	2311,0	3446,6

Table 8. Relative energy consumption expressed in animal units (AU) per unit area (km^{-2}) of large herbivores in Mkuzi Game Reserve as estimated in August 1984. Land types are as for Fig. 22 and - and * denote respectively species not seen in this land type or data too sparce to calculate density.

	Land type					
Species	J_j	Cr_3	Cr_2	Pl_4	H	Mean
Bushbuck	0,06	-	-	-	0,18	0,04
Bushpig	*	*	*	*	*	0,21
Duiker/Grey	0,04	0,19	0,19	0,64	*	0,16
Duiker/Red	-	8	*	-	*	0,14
Eland	*	8	*	-	-	0,07
Giraffe	0,58	1,67	0,02	1,10	-	0,71
Hippo	-	-	*	-	*	0,16
Impala	4,74	2,81	2,61	3,91	1,31	3,33
Klipspringer	0,01	-	-	-	-	small
Kudu	0,47	0,49	1,01	2,30	-	0,72
Nyala	0,51	1,59	2,81	6,31	6,38	2,43
Reedbuck/Common	0,39	-	0,12	-	0,13	0,17
Reedbuck/Mountain	0,08	-	-	-	-	0,03
Rhino/Black	*	*	*	*	*	0,37
Rhino/White	-	*	*	-	-	0,24
Steenbok	0,04	0,06	0,05	-	-	0,04
Suni	*	*	*	*	-	0,03
Warthog	0,37	0,60	0,37	0,19	0,18	0,39
Waterbuck	-	-	-	-	0,10	0,01
Wildebeest	0,05	0,72	0,58	2,14	0,23	0,67
Zebra	1,33	1,34	0,82	0,55	-	1,85
Total	9,12	9,47	8,76	17,14	8,51	11,77

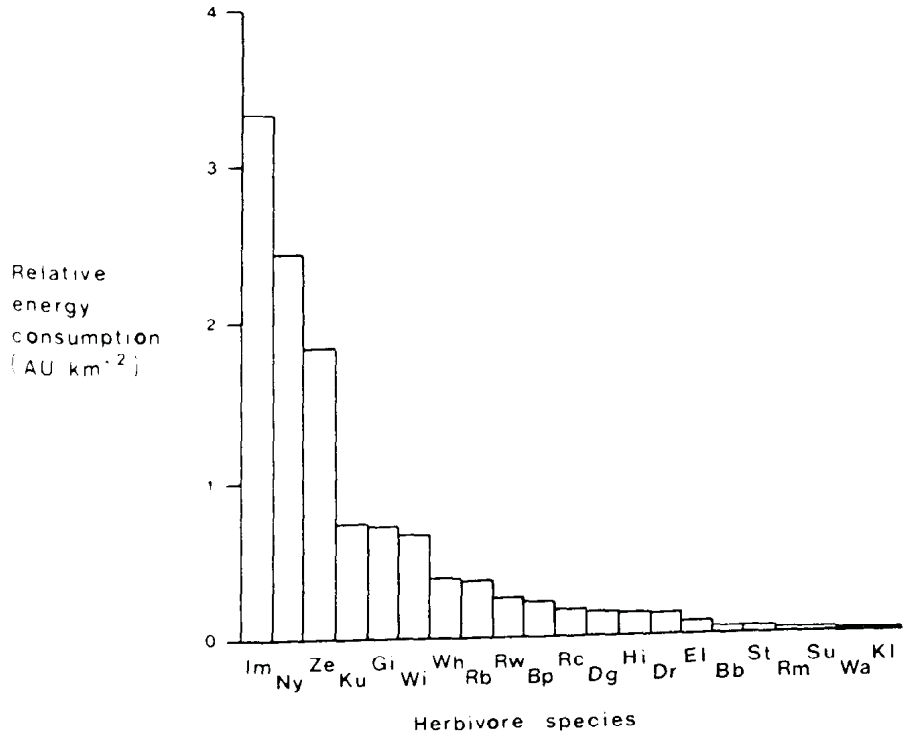


Fig.25 Relative energy consumption by large herbivores in Mkuzi. Abbreviations as per Table 5.

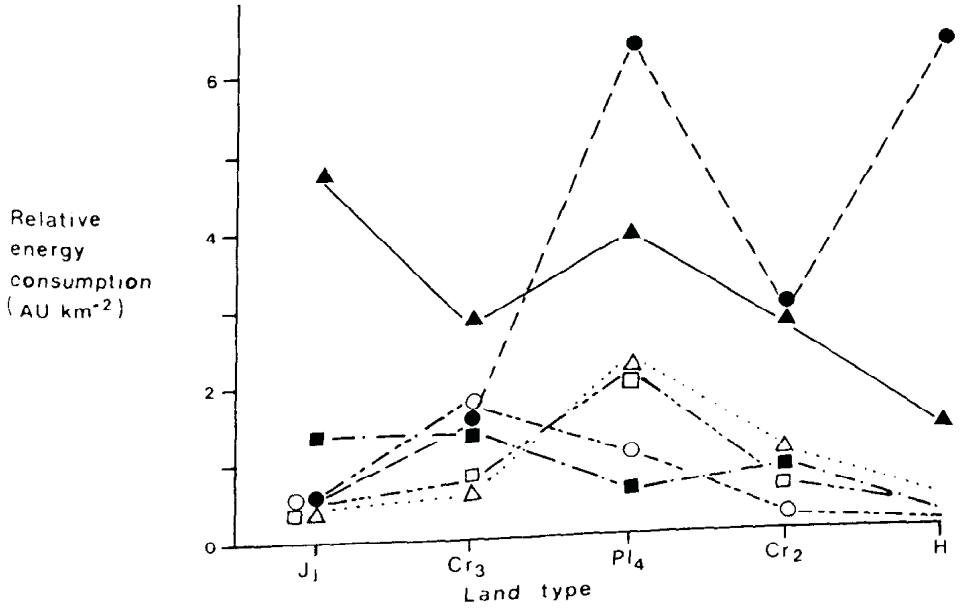


Fig.26 Relative energy consumption of the six most important large herbivore species namely: impala – ▲, nyala – ●, zebra – ■, kudu – △, giraffe – ○, and wildebeest – □, in each land type (see Fig.22 for land type abbreviations). Land types are arranged to represent a west to east cross section through the reserve.

Relative energy consumption was greatest for impala (3,33 AU km^{-2}) followed by nyala (2,43 AU km^{-2}) and zebra (1,85 AU km^{-2}). In all, these three species accounted for 65% of the energy consumed (Table 8 and Fig. 25). The next three most important species, kudu (0,72 AU km^{-2}), giraffe (0,71 AU km^{-2}) and wildebeest (0,67 AU km^{-2}) accounted for a further 18% of the energy consumed (Table 8 and Fig. 25). Warthog (0,39 AU km^{-2}) and black rhino (0,37 AU km^{-2}) accounted for 6%, with the final 11% being accounted for by the remaining 13 species.

Impala were the most important consumers in the woodlands and wooded grasslands of the Lebombo and Lower Cretaceous land types (Table 8, Fig. 26). In the denser vegetation of the remaining three land types nyala assumed the role of the most important consumer with impala ranking second (Table 8, Fig. 26). Zebra were the second most important consumer in the Lebombo land type, but achieved lower rankings in all other areas. Giraffe were the second most important consumers in the wooded grasslands of the Lower Cretaceous land type, assuming lower rankings in hilly areas (Lebombo land type) or areas with denser woody cover (all other land types) (Table 8, Fig. 26). Kudu rank fairly low as consumers in all land types except the Upper Cretaceous and Pleistocene dune areas where they rank third, and finally, wildebeest ranked consistently low in all land types (Table 8, Fig. 26).

4.3.3 Graze to browse ratio

The relative amount of energy derived from graminaceous and non-graminaceous food sources was estimated as 7,5 (64%) and 4,3 (36%) AU km^{-2} respectively. This represents a 1,74 : 1 graze to browse ratio which does not seem unduly high especially since woody plants dominate the plant biomass over at least a third of the reserves area.

4.3.4 Historical perspective and recent population dynamics 1800 - 1950

Prior to 1850 northern Zululand (of which the present Mkuzi reserve forms a small part) was said to contain an abundance of indigenous large herbivores (Drummond, 1875). Up until this period it is surmised that local hunter gatherer and pastoral peoples had little direct effect on this fauna. Between approximately 1820 and 1870,

sport, ivory and venison hunters intensified the destruction of game and buffalo, eland, elephant and hippopotomus were reduced to extremely low numbers. By 1870, the golden age of hunting was said to be over and the remaining game continued to be decimated by concession hunters (Bruton, Smith and Taylor, 1980). No relative abundance records of large herbivores are available from this era but according to Drummond (1875), eland, kudu, buffalo, bushbuck, nyala, zebra, wildebeest, waterbuck, hippopotamus and impala were abundant while elephant and black rhinoceros were said to be common.

The rinderpest epidemics from 1895 to 1904 caused great mortality in both game and cattle (Ellis, 1975). Among the wild herbivores, buffalo, bushbuck, bushpig, eland, kudu and warthog were rated as highly susceptable, while elephant, hippopotomus, impala, black rhinoceros and waterbuck were not or only slightly susceptable to rinderpest (Ford, 1971). Stevenson-Hamilton (1912) also found wildebeest to be less affected. Associated with the increase in game after the rinderpest was an increase in tsetse fly and the periodic resurgence of nagana. This triggered the game extermination programmes both in and outside the reserves which ceased in 1950 with the final eradiction of the tsetse fly using D.D.T.

During the last game eradication campaign (1943 - 1950) records were kept of the numbers of each species destroyed in the Mkuzi area (Table 9). These provide a valuable baseline of proportional species composition (Table 9, Fig. 27) at this time. It is apparent that by the time of the game eradication campaign had commenced, species that were either absent or present in extremely low numbers included buffalo, eland, elephant, hippo, klipspringer (probably still present on inaccessible mountain ridges) white rhino and waterbuck. Proportional species composition at this time is estimated by converting the number of animals shot to AU's in which case the importance of species with high intrinsic rates of increase (the smaller herbivores e.g. grey and red duiker, steenbok and suni) will be exaggerated relative to those species with lower rates of increase (the larger herbivore e.g. black rhino, zebra, wildebeest and kudu). Nevertheless, wildebeest (39%) and impala (34%) were the two most important energy consumers (Table 9, Fig. 27). Together, these two

species accounted for 73% of the energy consumption. The next two most important species were nyala (12%) and grey duiker (8%) followed by common reedbuck (2%), bushpig (1%), kudu (1%) and warthog (1%). The remaining 2% of the energy consumption was accounted for by seven species which included bushbuck, red duiker, mountain reedbuck, black rhino, steenbok, suni and zebra (Table 9, Fig. 27).

Table 9. Summary of the numbers, relative (AU) and proportional energy consumption (%) shot in and around Mkuzi during the second game eradication campaign (March 1943 to February 1950).

Species	Number	Relative energy consumption (AU)	Proportional energy consumption(%)
Bushbuck	84	10,94	0,14
Bushpig	496	100,20	1,25
Duiker/Grey	7436	631,78	7,91
Duiker/Red	436	32,04	0,40
Impala	17060	2756,06	34,50
Kudu	243	98,38	1,23
Nyala	4385	959,52	12,01
Reedbuck/Com	696	132,82	1,66
Reedbuck/Mtn	19	2,35	0,03
Rhino/Black	2	3,08	0,04
Steenbok	527	32,31	0,40
Suni	90	3,05	0,04
Warthog	364	64,20	0,80
Wildebeest	6726	3142,99	39,34
Zebra	35	18,92	0,24

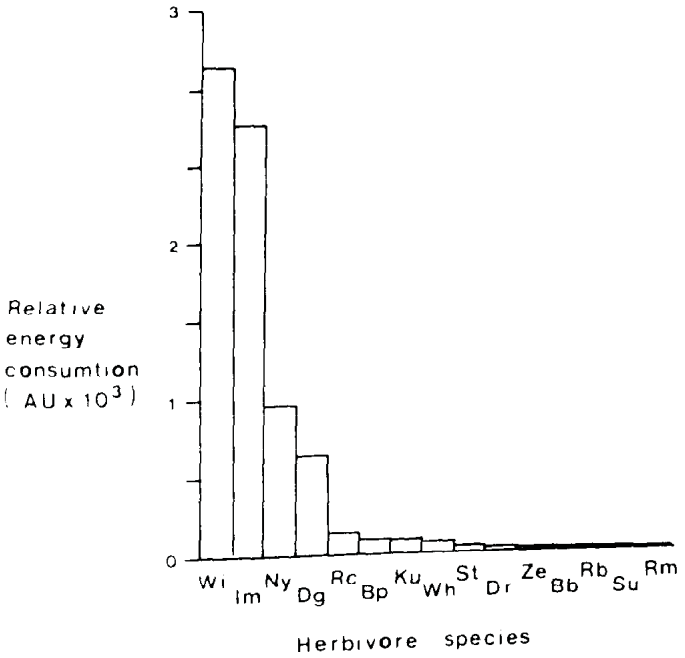


Fig. 27 Relative energy consumption values of large herbivore species culled in and around Mkuzi during the last nagana campaign (1943 - 1950). Key to species given in Table 5.

Population trends from 1951 - 1984

Reliable density estimates of even the most commmon large herbivores since 1950 are scarce. However large herbivore populations are assumed to have been extremely low immediately after the nagana hunting had ceased. In the absence of any meaningful predation pressure, populations increased rapidly. By 1963 the populations of impala were reported to be extremely high and the first attempts to estimate their density were made by Stewart and Stewart (1966) using a change in sex ratio method. The extremely high density of impala (c. 82,6 km^{-2}, Fig. 28a) and the scarcity of utilizable vegetation at this time, prompted managers to implement a population reduction programme which has continued to date (Fig. 28b). Due to the continued absence of major predators, the curtailment of dispersal from the reserve and the maintenance of artificial water points in the reserve, the present policy aims to maintain the impala population density at c. 20 km^{-2}.

The wildebeest population suffered a similar fate to that of impala with the difference that fewer estimates of density were made (Fig. 29a). However, before the first recorded subjective estimate of 2500 (density 10,3 km^{-2}) was made in 1963, wildebeest were already being culled at a rate of between 0,8 and 1,6 km^{-2} per year (Fig. 29b). Since 1976, wildebeest have for the same reasons as those given above for impala, been culled continuously in an effort to reduce and maintain the population at an estimated density of 3,5 km^{-2} (Fig. 29b).

The warthog population was estimated to have achieved a density of 6,2 km^{-2} in 1965 (Fig. 30a). Until then no serious efforts had been made to control this population (Fig. 30b). Between 1965 and 1975 no further reliable density estimates of this population were made, but population control continued on the basis of trends obtained from aerial counts. In 1976 the population density was estimated to be 3,9 km^{-2}. It was decided at this juncture to attempt to reduce and maintain this population at a density of approximately 2 km^{-2}. Despite this however, the warthog population continued to increase to a peak in 1982 (9,8 km^{-2}). Following the severe drought in 1983 this population crashed to an estimated density of 1,7 km^{-2} (Fig. 30a).

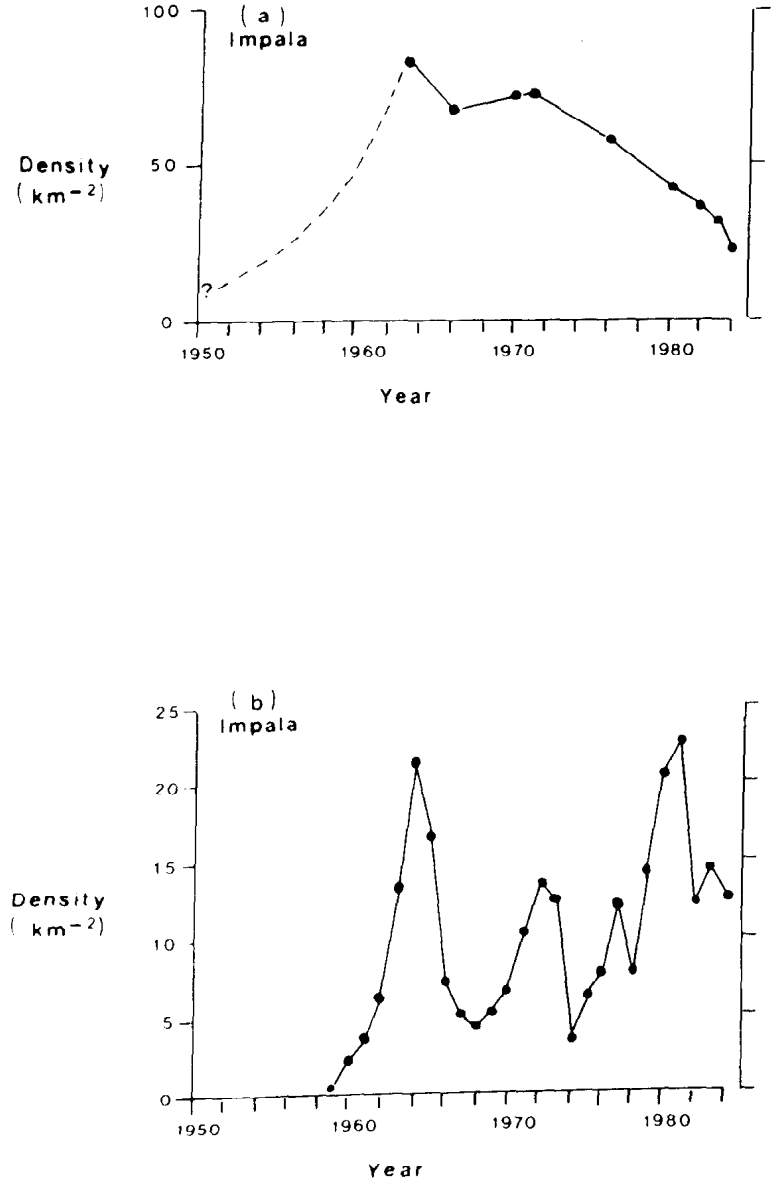


Fig 28 (a) Estimated densities of impala and (b) densities of impala removed from Mkuzi between 1950 and 1984.

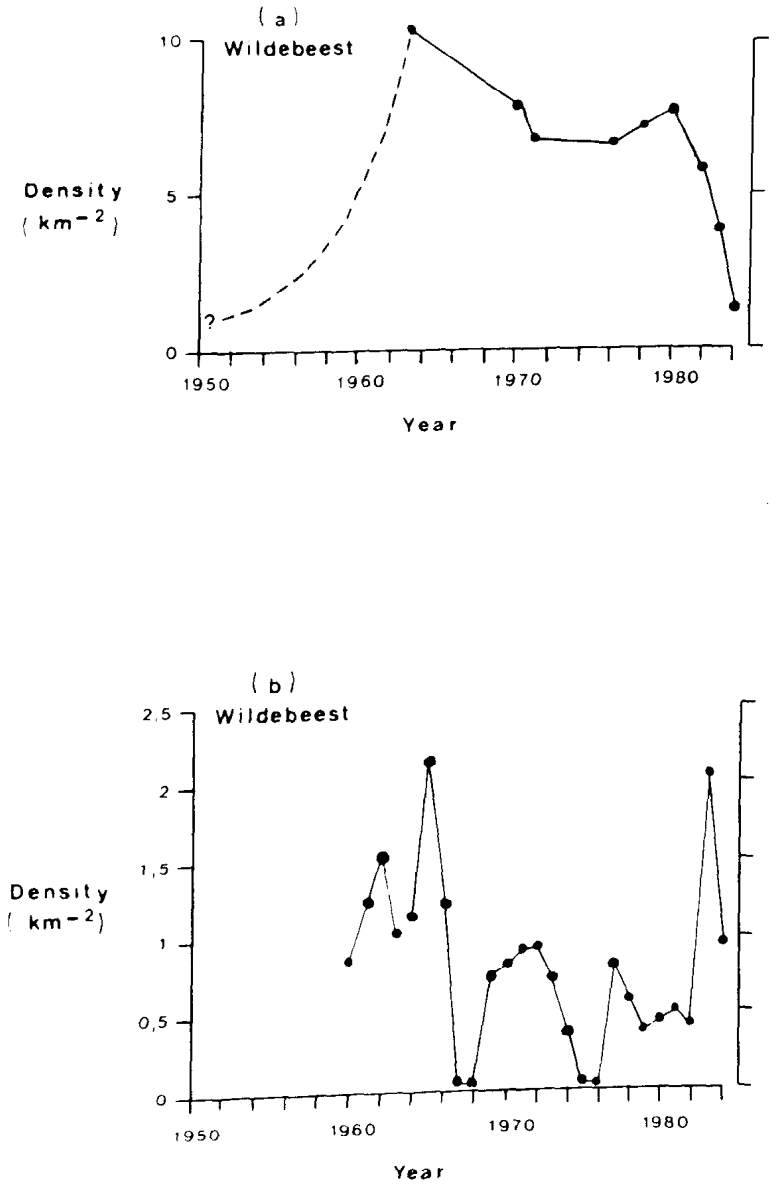
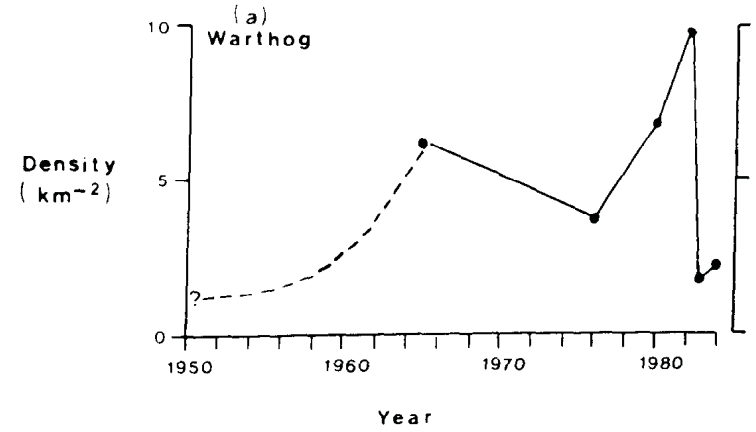


Fig. 29 (a) Estimated densities of wildebeest and (b) densities of wildebeest removed from Mkuzi between 1950 and 1984.



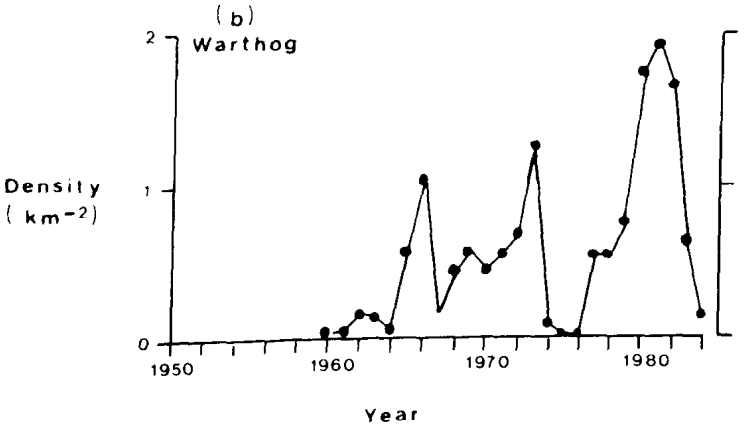


Fig. 30 (a) Estimated densities of warthog and (b) densities of warthog removed from Mkuzi between 1950 and 1984

Zebra and kudu population densities have both shown increases in recent times (Fig. 31a and b). The populations of giraffe and white rhinoceros have both increased in an approximately exponential fashion since their introduction (Fig. 32a and b), with the giraffe population now being artificially stabilized at approximately 0,5 km^{-2}. The density of nyala was first estimated in 1980 as 8,7 km^{-2} and despite the removal of an average 2,1 nyala $km^{-2}annum^{-1}$ the population had increased to a density of 11,8km^{-2} by 1984.

For the remaining large herbivores, hippo have gradually increased from six in 1960 to 27 in 1984. Otherwise few data are available on the long term trends of other species. Density estimates of grey duiker and steenbok from 1980 to 1984 have tended to indicate that these populations have remained relatively stable during this period.

4.5 DISCUSSION

At present impala followed by nyala dominate the large herbivore community in Mkuzi by being both the most dense and by accounting for the highest proportion of energy consumed by large herbivores in the reserve. Both these species are mixed feeders taking readily to both mono- and dicotyledonous foods. Impala dominate and consume the greatest amount of energy in the more sparcely wooded areas in the west of the reserve, while nyala dominate and consume greatest energy in the more heavily wooded vegetation found on sand and alluvial soils.

Prior to 1960, wildebeest then impala accounted for the highest proportion of the energy consumption. Management subsequent to 1960 has reduced the wildebeest to the sixth most important herbivore in terms of energy consumption.

Historically the large herbivore populations in Mkuzi have suffered several major perturbation events.

1) Exploitation hunting between 1820 and 1870 reduced many of the dominant species including buffalo, eland, elephant and hippopotamus to extremely low levels.

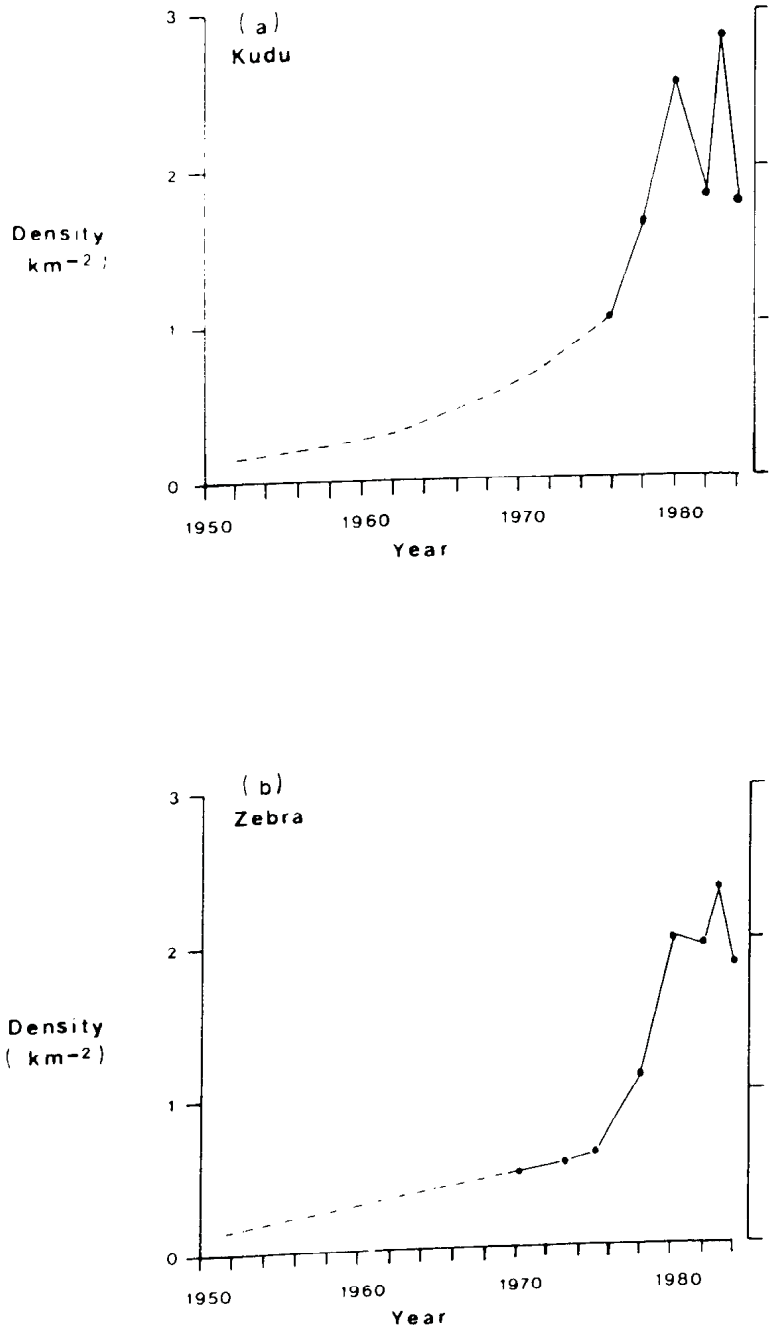
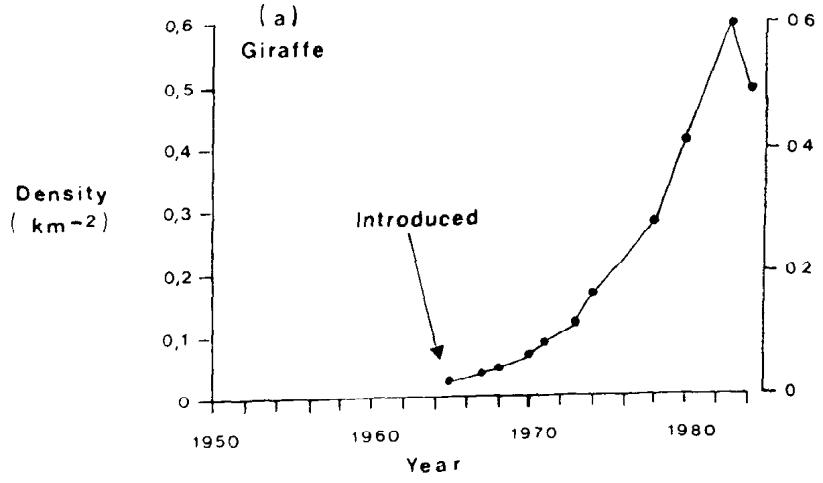


Fig. 31 Estimated densities of (a) kudu and (b) zebra in Mkuzi between 1950 and 1984



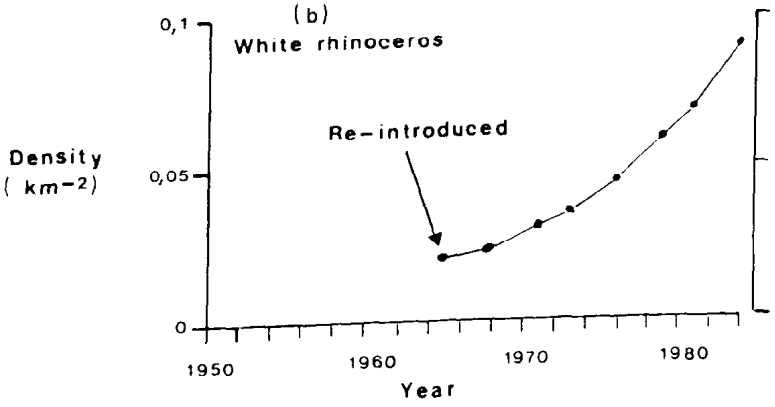


Fig. 32 Estimated densities of (a) giraffe and (b) white rhinoceros in Mkuzi between 1950 and 1984.

2) The rinderpest epidemic between 1895 and 1904 resulted in high mortalities of the remaining large herbivores in particular buffalo and kudu, but probably also bushbuck, bushpig, eland, and warthog.

3) Between 1918 and 1950, sporadic attempts were made to eradicate all game from the region under the false belief that this would curb the spread of *Trypanosomyasis*.

By 1950 when the eradication campaign finally ceased, large herbivore species richness had been reduced to 73% of what it had been prior to 1820. Depletion of buffalo, eland, elephant and white rhino had been so severe and widespread that re-invasion of the area could not take place since no remnant populations were left. In instances where populations did occur recovery has been slow (e.g. hippopotamus and waterbuck) or extremely rapid, e.g. impala and wildebeest. In addition the differential mortality amongst large herbivores caused by rinderpest might explain the dominance of wildebeest and impala at the beginning of the last nagana campaign because these two species are less susceptible than others to this disease.

The dominance diversity curve of large herbivores derived from data obtained during the nagana eradication campaign appears to conform closely to the geometric series (Fig. 33). It is possible that this could have resulted from niche pre-emption subsequent to the major perturbations enumerated above, especially since the two dominant species, wildebeest and impala, are able to exploit all major vegetation types in Mkuzi.

The relative rates of large herbivore species recovery since 1950 were probably influenced by the size of the starting populations, the lack of effective predation (e.g. lion and wild dog were by then absent from the area), resource competition with other herbivores and the water supplementation policy implemented by managers at the time. An indication of the relative rates of recovery may be gained from the dates when managers thought it necessary to start controlling each individual species population. The order was wildebeest (1960), impala (1963), warthog (1965) and nyala (1977), with population control continuing and forming one of the major influences in the dynamics of these populations to the present day.

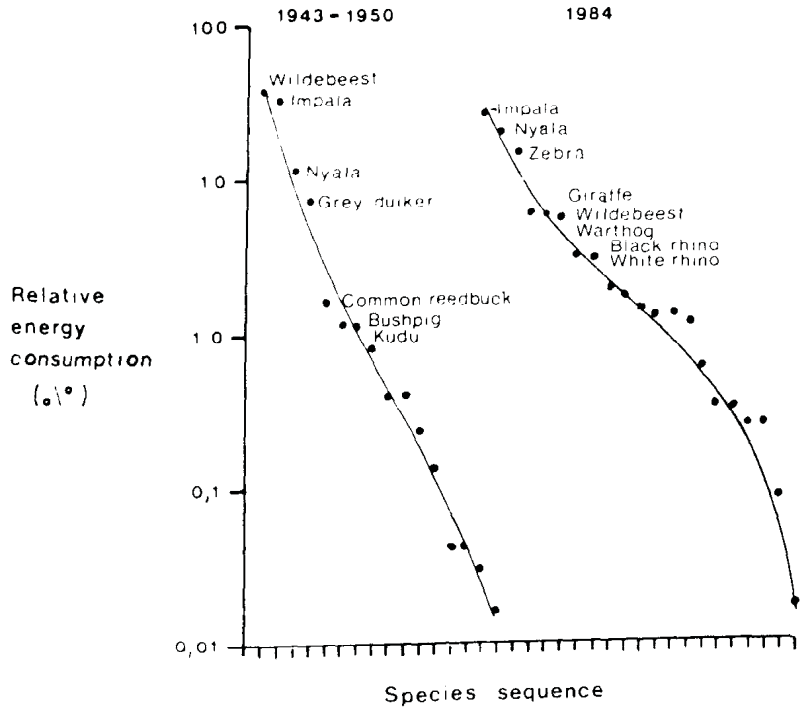


Fig. 33 Dominance diversity curves for large herbivores in Mkuzi and derived from hunting success data (1943 – 1950) during the nagana eradication campaign and the results of a large herbivore census (1984).

Other species have only begun increasing relatively recently. Two of these, giraffe and white rhinoceros were introduced in low numbers in the mid-sixties and so will continue increasing for some time. Of the smaller species, the populations of grey duiker and steenbok appear to have remained relatively stable, and it is suspected that other species for example bushbuck, bushpig, red duiker, common and mountain reedbuck, black rhino and suni have achieved ecological carrying capacity as well.

Although it is suspected that the smaller species might be at equilibrium with their environment there is little doubt that this does not apply to the dominant species. Several major perturbations over the last 150 years, some of which continue to the present day will ensure that the herbivore community is in a state of disequilibrium for some years to come.

The dominance diversity curve of large herbivores derived from the 1984 census data appears to approach the lognormal distribution (Fig. 33). As stated by May (1975, 1976), the lognormal distribution arises from the products of random variables operating on heterogeneous groups of individuals or alternatively as soon as several factors become significant in the dynamics of communities. This is indeed the case in Mkuzi where the most significant forces affecting the herbivore community are a) randomly varying climate which acts on the resource base affecting interspecific competition, b) management related stresses such as fire, culling, and the distribution of permanent water and c) predation.

CHAPTER 5. A REVIEW AND DISCUSSION OF HYPOTHESES REGARDING DIVERSITY IN ECOLOGICAL COMMUNITIES

5.1 INTRODUCTION

The literature dealing with ecological diversity and its measurement is extensive and has been summarized at intervals by Whittaker (1965, 1972 & 1977), Goodman (1975), Pielou (1975), Grassle, Patil, Smith and Taillie (1979), Huston (1979) and Patil and Taillie (1982). This review is not intended to be exhaustive but aims only to:

a) clarify the meaning of the term ecological diversity and standardise the terminology to be used in the rest of this study,
b) summarize and present the most important general hypotheses regarding ecological diversity and
c) identify and discuss the most appropriate measures of diversity to be used.

Later chapters will attempt to test some of the hypotheses summarised below.

5.2 WHAT IS ECOLOGICAL DIVERSITY?

The concept of diversity involves the apportionment of objects or entities into defined categories. In ecology, the entities of interest are typically biological in nature. The level of categorization can vary depending on the study purpose. For example plant matter from a herbivore viewpoint may be perceived at a subspecies, species, palatability, structural, habitat-type, community or regional level of subdivision.

Diversity is primarily the state of variety among members of a predefined collection. In this context, Pielou (1975) has likened the relationship that variance bears to quantitative measurements, to the relationship between diversity and qualitative observations. The diversity of a community has also been related to the probability of

encountering the same species twice. In a diverse community this probability is small, in other words even the most common species are relatively rare. Consequently, Patil and Taillie (1982) proposed that diversity should be defined as the average rarity of individuals of the same category (e.g. species) in a collection (e.g. community).

Whittaker (1965, 1972) perceived species diversity at three levels; alpha diversity, referring to the diversity of species within a community or habitat; beta diversity, which is a measure of the extent and rate of species change along an environmental gradient and gamma diversity, a measure of the species richness in a landscape or geographical area. Gamma diversity is a consequence of the alpha diversity of the communities and the range of difference between them i.e. the beta diversity. These forms of species diversity are however not always easily distinguished since many alpha diversity measurements are influenced by habitat variation and could just as well be interpreted as beta diversity.

The species-diversity concept of Whittaker is applicable to other levels of categorization. For example, one might be interested in the diversity of height classes or vegetation types in an area. In the latter instance, this diversity could be referred to as the vegetation type diversity in a landscape or 'alpha diversity of vegetation types'.

The notion of alpha diversity has been explored in greater depth than that of beta and gamma diversity and three components of diversity at the alpha level are current namely, (1) the number of species or separate entities in a collection, termed richness, (2) equitability which considers the evenness in abundance or importance of members in the collection and (3) heterogeneity, a synthetic characteristic combining both richness and equitability (Whittaker, 1972 and 1977, Peet, 1974).

The definitions of diversity discussed thus far do not recognise that some categories within a collection may be more dissimilar than others. For example a collection of herbivore species containing two pure grazers, two mixed feeders and one a pure browser is more diverse than a collection containing five grazing species only. Consequently Pielou (1975) introduced the concept of hierarchical diversity to take cognisance of differences between members of a collection which can be

arranged hierarchically. Her assumption was that position in the hierarchy is an expression of relative difference between entities.

To summarise, ecological diversity is seen to be a complex notion, so much so that some authors have suggested that it has become a nonconcept (Hurlbert, 1971). The concepts of diversity are applicable at almost any trophic level and scale, and encompass richness, equitability, species turnover rate and the difference between entities as expressed by the hierarchical relationships between them.

5.3 SOME HYPOTHESES REGARDING ECOLOGICAL DIVERSITY

The concept of diversity has captured the interest of some ecologists primarily because it is thought to be related to various other ecosystem properties and processes e.g. productivity, stability, evolution, niche structure, competition and succession. The central problem that has attracted the attention of many ecologists however, is the isolation of the determinants of species diversity. Pielou (1975) summarised the question of the latter group by asking, how have "species come to share the same habitat", "how do they maintain themselves and interact with one another" and "what determines the number of species that can live together, and their relative proportions?"

Perhaps the most intensively researched and debated topic in the range of diversity problems is the relation between diversity and stability. It is the subject of a large literature stimulated by the apparent divergence in results and opinion. Initially it was suggested that increased ecosystem complexity enhanced stability (MacArthur, 1955; Margalef, 1968). Later theoretical studies (May, 1973) and reviews (Goodman, 1975) suggested either that diversity decreased stability or that no simple relationship exists between the two in nature. At about this time Pielou (1975) suggested that the chain of cause and effect was in the opposite direction and that high environmental constancy gave rise to high community stability which in turn permitted but was not caused by high diversity. In addition she raised the possibility that high diversity might reduce community stability and hence have the opposite effect to, but not overriding the effect of, environmental stability. She suggested that this

weakening of environmental control might not take place if (1) the interaction coefficients between species are within certain limits and (2) if spatial heterogeneity reduces the number of effective interactions among species.

After investigating the relation between stability and diversity in an old field succession and a grazing exclusion study, McNaughton (1977) concluded that plant community diversity did stabilize the functional properties of the experimental communities to environmental perturbations. He found that the adjustments in species abundances in the more diverse community, while resulting in greater diversity changes, actually mediated functional stability. McNaughton stressed that the stability of community functional properties was a consequence of adaptive properties of its constituent individuals and that diversity stabilized function, not diversity.

Allen and Starr (1982) concluded that because diversity and its measurement took no account of the connectedness of the whole system or of the degree of connectedness of new individuals or species to a system, diversity had little to do with stability. They suggested that the important conclusions of May's (1973) work was not that systems with high diversity are less stable, but rather that connections are nonrandom (May's models assumed random connectedness between species). Allen and Starr (op. cit.) concluded that an increase in diversity might have opposite effects depending on whether the added individuals became a part of an already over or underconnected system. The addition of a new individual increases diversity. Depending on whether this individual is itself connected or not, will determine whether it is either a stabilizing or destabilizing force to the system. "Adding a strongly connected individual to an already overconnected system" it is suggested "will tend to destabilize the system by further increasing the total system connectedness" (Allen and Starr, 1982).

In a criticism of Zaret's (1982) paper in which he attempted to empirically test the stability/diversity hypothesis, Kimmerer (1984) stated that no general conclusions about the effect of diversity on community stability could be drawn from Zaret's findings. Kimmerer further suggested that the "putative diversity-stability relationship" was an unproductive avenue for investigation and that it should be

dropped in favour of "hypotheses that are both theoretically sound and experimentally tractable".

In the best rationalization of the complexity/stability debate to date, Pimm (1984) stated that confusion has arisen because of the many different meanings of 'complexity' and 'stability'. He proceeded to identify the components of complexity (species richness, connectance, interaction strength and evenness), stability (stable systems, resilience, persistence and resistance) and other variables of interest (viz. individual species abundances, species composition and trophic level abundance (eg. biomass or productivity)). Pimm then summarized the results of theoretical and field studies in a matrix defining the various combinations of measures of complexity, measures of stability and variables of interest. Using this approach he found that different complexity-stability questions yielded different answers. The fact that various authors had addressed different questions explains some of the earlier controversy due to conflicting results. Pimm also observed that most of the possible questions about the relationship between stability and complexity have not been asked. He concluded with the following statements:

1) The more species that are present in a community;
   a) the less connected it should be to be stable,
   b) the less resilient will be its populations,
   c) the greater will be the change in composition and biomass when a species is removed and
   d) the longer the persistence of species composition in the absence of species removal.
2) The more connected a community;
   a) the fewer species it must have in order for it to be stable,
   b) the more likely it is to lose other species if one is removed,
   c) the more resilient will be its populations,
   d) the more persistent will be its composition and
   e) the more resistant will be its biomass if a species is removed.

Closely tied to the complexity/stability arguments are those associated with the relation between disturbance and diversity. Grime

(1973, 1985), presented the hump-backed model as an explanation of species density in plants. In this model the effects on species density of environmental stress were essentially similar to those of disturbance. Under conditions of low environmental stress and/or disturbance, competitive species predominate and species density is low due to competitive exclusion. With increased environmental stress and/or disturbance, species with high competitive indices loose vigour and are suppressed allowing species of a lower competitive ability to co-exist and consequently species density is higher. At the extremes of stress and/or disturbance, species density declines as a result of the scarcity of species tolerant of the specific conditions limiting productivity and/or the specific impact of disturbance.

Connell (1978) argued that because of the influence of disturbance, few if any communities found in nature achieve a competitive equilibrium. Disturbance, (which may include herbivory and predation) acts as a source of mortality for some species and consequently a source of establishment and survival for others. Competitively inferior (fugitive) species are allowed to survive in a community by the colonization of disturbed patches and for this reason disturbance has in many instances been shown to increase diversity. Generally stated, this hypothesis predicts that an intermediate rate of disturbance will produce the highest diversity, if diversity is measured by one of the heterogeneity indices (Horn, 1985; Connell, 1978).

Huston (1979) has developed a general hypothesis of diversity on the assumption that most natural communities exist in a state of nonequilibrium. He suggested that patterns of species diversity are explained by the different rates at which populations of competing species approach competitive equilibrium. When competitive equilibrium is prevented, a stable level of diversity results if a dynamic balance is established between the rate of competitive displacement, and the frequency of population reduction (or disturbance). Huston's model predicts that at low to intermediate frequencies of population reduction, low growth rates allow the maintenance of diversity by slowing the approach to competitive equilibrium. Conditions in which the availability of essential resources is low (e.g. basic nutrients) result in a reduced growth

rate of competing organisms and therefore a higher diversity than in similar situations with high resource availability. Thus, unless diversity is low because of a high disturbance rate or a nutrient deficiency, this model would predict that increasing the nutrient availability of any environment would tend to reduce diversity. Furthermore, he suggests that since low productivity (and density) is often the result of low population growth rates, communities with low productivities (or densities) should have higher diversity than similar communities with higher productivity. From his model results, Huston argues that neither competition, predation or productivity control diversity, but that rather all of these contribute to the same basic mechanism.

Denslow (1980), has extended the hypotheses of Connell (1978) and Huston (1979) by considering the community as a "mosaic of patches colonized by species regeneration under different environmental conditions". Denslow (1980) suggested that competitive equilibrium occurs only in an environment in which the size/frequency distribution of disturbance is that under which the component species have evolved. As a result, time since disturbance (i.e. succession) and the rate of competitive replacement are de-emphasised in accounting for species diversity, in favour of whether or not the disturbance regime approximates that which was historically experienced. Consequently species diversity should be highest at the historic rate of disturbance since regeneration conditions for most species would be met under these patterns of mortality and generation of establishment sites. Denslow's model is useful in that it gives a means for predicting the 'intermediate level of disturbance' at which diversity should be highest for a particular community and offers an evolutionary reason for why 'intermediate levels' of disturbance may be different between communities.

Still further developments of the "intermediate disturbance hypothesis" emphasize the temporal rate or phasing of disturbance (Abugov, 1982) and both size and frequency of disturbance (Miller, 1982). Although Abugov's model supported the intermediate disturbance hypothesis, the phasing of this disturbance could either serve to increase or decrease diversity. Where the increase in phasing resulted in an increase in species diversity, the competitive dominant

was the most common species. Conversely where an increase in disturbance phasing showed a decrease in diversity, fugitive species were more common.

Miller's (1982) model assumed a peak in diversity at intermediate rates of disturbance for large and small disturbance regimes over a gradient of disturbance rates. His model predicted different effects of disturbance size on species diversity. At low disturbance rates, large disturbances generated a higher diversity than small disturbances. Large disturbances did not favour competitive species but allowed the persistence of colonizing species thus increasing species diversity. At high disturbance rates, small disturbances generated higher diversity. Small disturbances increased the persistance of competitive species thus accounting for higher diversity.

Like Connell (1978) and Huston (1979), Tilman (1982) modelling communities of sessile organisms also predicts maximum species diversity at moderately low disturbance rates. However, Tilman does not hold the view that the effect of disturbance is to periodically interrupt competition. He considers "disturbance to be a process that influences the relative supply rates of the resources for which competition occurs". For example, in terrestrial plant communities in which disturbance indirectly makes light and possibly nutrients available, Tilman suggests that the effect of disturbance on diversity results from changes in resource richness and resource ratios and not from the alteration of competitive effects.

Tilman's (1982) approach used information on the resource requirements of species, to predict the equilibrium outcome of these competing species. He shows that although plants have similar resource requirements this does not in theory limit the species diversity of communities at equilibrium. He shows that differences in the optimal ratio of nutrients required by plants can account for diverse, stable communities. This is in contrast to the generalizations of Connell (1978), and Huston (1979). From his models, Tilman makes several interesting predictions regarding diversity, two of which are important to this summary. Firstly, species richness should be greatest in relatively resource poor habitats. In fact he shows the curve of this relationship to be

skewed with peak diversities occurring toward the lower end of the resource axis. Secondly, he suggests that for a given level of resource richness, increased spatial heterogeneity should increase species richness, the effect being more marked in resource poor habitats.

Tilman was able to find much support for his first prediction from the general literature. In addition the decreases in diversity following enrichment of both terrestrial and aquatic plant communities provided further support for his model.

An important factor in Tilman's models is the emphasis he places on spatial heterogeneity and its effect on allowing co-existence amongst species. Although Tilman was concerned with sessile organisms and spatial heterogeneity at the microhabitat level, the hypothesis that diversity is a function of (normally positively correlated with) environmental complexity (Pielou, 1975; McNaughton and Wolf, 1973; Krebs, 1978) could be considered appropriate at almost any scale.

Pielou (1975) sees spatial heterogeneity as having two possible effects on diversity. The first of these, namely the "substrate - patchiness effect", suggests that species specializing for resources within a certain patch would avoid competition with species specializing for slightly different resources in other patch types and by so doing are able to co-exist in close proximity to one another. It is also possible that this effect may filter up through several trophic levels, leading Pielou to suggest that patchiness is possibly always hierarchical in nature.

Probably the first example of the effect of spatial heterogeneity on diversity is that of MacArthur and MacArthur (1961) in which bird-species diversity was more strongly correlated with foliage - height diversity (a measure of stratification and evenness in the vertical distribution of vegetation) than with plant species diversity. Further examples cited by Pielou (1975), MacNaughton and Wolf (1973) and Krebs (1978), support the hypothesis that environmental complexity has an important positive influence on species diversity.

The second influence of environmental complexity on species diversity has been called the 'nook - and - cranny effect' by Pielou (1975). In this instance the different patches occurring within a

spatially heterogeneous habitat act as refugia from the effects of predation. Each patch differs in the amount of protection it affords the prey species. Prey species are guaranteed survival in the refugia where populations build up to the extent that "surplus" individuals are forced out into the more hostile patches. Predators congregate in these hostile patches where hunting is easiest, and skim off the surplus individuals. In this model co-existence is mediated because prey maintain their populations within the refugia. However, if shelter from predation is defined as a resource, the "substrate - patchiness" and nook - and - cranny" effects of Pielou become one because prey species, which have the same food requirements, could co-exist by having different anti-predator strategies and thus have different habitat patches serving as their predator refugia.

More recently, Shmida and Wilson (1985) have proposed four major biological mechanisms which determine species diversity. These are: niche relations, habitat diversity, mass effects and ecological equivalency. They and Auerbach and Shmida (1987) de-emphasise the determanistic, equilibrium based explanations for the trends in species rechiness in favour of mechanisms based on stochastic processes, patch dynamics and non-equilibrium states. Finally, these latter authors suggest that the relative intensity of each determinant varies with spatial scale with niche relations being most important at within-community scales, habitat diversity most important at both with-community and landscape scales, and ecological equivalency most important at regional scales.

This section has introduced some of the more common hypotheses regarding species diversity and its possible determinants.

5.4 THE MEASUREMENT OF DIVERSITY

The measurement of diversity has been the subject of much controversy over the last one and a half decades. This controversy has lead to several reviews of the subject, the most notable being by Whittaker (1972 and 1977), Hill (1973), Peet (1974), Pielou (1975), May (1975), Kempton and Taylor (1976), Routledge (1979) and Patil and Taillie (1982). The intention of this section is to detail the methods by which diversity will be quantified in this study.

One of the most unambiguous measures of alpha diversity is simply the number of entities in a collection, which for species in a sample is termed species richness. The limitations of richness as a measure of diversity are: i) it is sample-size dependant and ii) there is no real basis for using richness as the only index of comparison unless one can assume that the underlying entity - importance relationships are similar between collections. Richness will therefore be used as one measure of alpha diversity in this study (denoted as No after Hill, 1973) and to overcome sample size dependance, the latter is standardized for comparative purposes.

The characterization of the heterogeneity component of alpha diversity has stimulated much discussion, the objective being to derive an index in which one accounts for both the number of entities and the relative quantities of each. Some authors (for example May, 1975) have expressed doubt as to the value of such single parameter measures of diversity because when the number of entities is small they tend not to distinguish between the different abundance distributions, and loss of information regarding the relation between diversity patterns and community process results.

Initially the choice of an index of heterogeneity lies with whether it should be parametric or non-parametric. Parametric indices, in particular the log series distribution, have received some attention (Taylor, Kempton and Wooiwood, 1976; Southwood, 1978). However, since communities in different developmental stages are likely to be characterised by differing species abundance curves (Whittaker, 1972; May, 1975), a single model is unlikely to describe these curves equally well.

The plethora of non-parametric diversity indices which may be found in the literature has been rationalized by Hill (1973), Pielou (1975) and Patil and Taillie (1982). Hill, and Patil and Taillie developed essentially similar series of indices with a similar notation and both Peet (1974) and Routledge (1979) have recommended the use of indices from these series. Routledge (op. cit.) has suggested that to avoid confusion with interpretation as few indices as possible should be used, but finds no single index in Hill's series universally superior. In effect each measure provides an estimate of the effective number of species, but differs in its sensitivity to