

and P. coloratum ($t=5.16$, $p<0.001$) in the termitaria sites.

During the early-dry season again no significant difference was apparent in the white rhinos' feeding pattern between the two habitat types. In the valley savannas the palatable-tall species such as Heteropogon contortus (average 34.3%), Themeda triandra (average 14.3%), Digitaria eriantha (average 8.7%) and Hyparrhenia hirta (average 7.1%) were highly preferred. The rhinos also showed an increase in the selection for the palatable-tall species such as Heteropogon contortus, Brachyaria serrata, Digitaria eriantha, Panicum deustum and P. deustum in the secondary grasslands, termitaria or Cynodon dactylon patches and thickets.

It is interesting to note that, although the white rhinos showed a high preference for the Cynodon dactylon "lawns" (approximately 2% of the available grassland), this particular grass species was generally avoided.

Their dietary selection during the late-dry season was similar to the early-wet season and the fire period with a high preference for the palatable-tall species such as Heteropogon contortus (HC), and Digitaria eriantha (DE). However, there was an increase in the selection for both P. deustum (PD) and P. coloratum (PC) during this season as opposed to the fire and early-wet periods. In both habitats the unpalatable species were avoided while the palatable-creeper species were only slightly selected.

Thus, although the white rhinos utilized a wide range of grass species, only a third of them were highly selected throughout the year (Appendix G). During the fire period, however, most of the species represented in their diets did not differ greatly from their availability in the grasslands. The white rhinos generally selected for the palatable-tall and intermediate grass species.

Unpalatable species, such as Cymbopogon excavatus, Elyonurus argenteus and Bothriochloa insculpta, were generally avoided. However they were grazed when short (eg. during the fire and

early-wet periods) and occasionally during the early-dry season when tall stands of Bothriochloa were utilized.

Owen-Smith (1973) observed that the white rhino food selection at the Umfolozi Game Reserve was based largely on grassland type, ie. dominant species, rather than individual species. This tends to agree with the observations and analyses discussed in the previous sections on the Pilanesberg rhinos. The white rhinos at Pilanesberg showed a high preference for certain grass types (eg. palatable-tall and intermediate) irrespective of their availability. In addition, the Correspondence Analysis was able to show that both the grassland structure and grass species composition influenced herbivore feeding selection. There was also a tendency for the white rhinos to show a seasonal selection for grasslands of various heights. For example, during the fire period and most of the wet season, white rhinos concentrated their grazing on the shorter grasslands generally feeding randomly on most grass species. Most of the grasslands selected, eg. secondary grasslands, valley savannas and Cynodon "lawns", were under 15 cm tall.

As conditions became drier increasing use was made of the taller grasslands with a greater preference shown for the more palatable tall species such as Heteropogon contortus, Eragrostis superba, Panicum maximum and P. coloratum. This supports the results collected by Melton (1978), who showed that the white rhinos fed mainly on P. maximum and Themeda triandra during both seasons, although a greater variety of grass species was consumed during the drier months.

Initially the animals concentrated on the localized short patches, particularly those around termitaria, but as progressive drying and food depletion occurred a switch was made to the taller grasslands greater than 15 cm in height. The short grasslands provide food only during the growing season. To carry them through the dry season, the white rhinos are dependent on the remaining taller grasslands. The availability of this sub-maintenance forage during the drier months therefore becomes

critical.

Owen-Smith (1973) showed a similar trend with the white rhinos moving into the margins of the tall Themeda triandra stands thus expanding the extent of the short grass areas. He was able to demonstrate a seasonal movement along a catena with the animals progressively moving up as the seasons became drier. A similar situation was not found at Pilanesberg possibly for two reasons;

(i) most of the slopes are too steep and therefore inaccessible to the white rhino, and

(ii) the rhino population at Pilanesberg is at a relatively lower density than at the Umfolozi Game Reserve (0.005 animals per ha as opposed to over 3 per ha).

4.4.3.2 Dietary Selection by the Other Large Grazers

Dietary selection by the four other large grazers was only recorded during the dry season for two reasons. Firstly, because of the time restriction, greater emphasis was placed on the white rhinoceros; and secondly, because this period is believed to be most critical for grazing herbivores in terms of food limitation. Thus dietary selection and their degree of overlap would be the most important during this period.

Table 4.8 and Appendix H give the grass species composition in the diet of the other four large grazers for the early-dry and late-dry seasons. These results have been averaged for all the vegetation types. Appendix H gives the percentage contribution in the diet (PC) and the Preference Indices (PI) of the grasses consumed in each habitat type.

4.4.3.2.1 Hartebeest

Table 4.8 shows the dietary selection by hartebeest for the two parts of the dry season. Grass species such as Rhyncholetrum repens, Hyparrhenia hirta, Heteropogon contortus and Themeda triandra were highly selected during both seasons, although

Table 4.8 : Percentage Contribution in the diet (PC) and Preference Indices (PI) for grasses eaten by the other large herbivores, by habitat and season. A key to the grass species is given in Table 4.1

SEASON	HABITAT	CYDA		RHRE		HECO		THTR		ERCU		ERSU		ERRI		ERGU		HYHI		BOIN	
		PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI
Hartebeest (early dry)	SECGLD	0.0	0.0	<u>31.1</u>	<u>3.3</u>	13.1	0.9	<u>8.4</u>	<u>2.3</u>	1.0	0.2	5.4	0.6	3.7	0.6	<u>3.4</u>	<u>4.9</u>	8.2	1.0	0.0	0.0
Hartebeest (late dry)	SECGLD	0.1	0.1	<u>38.7</u>	<u>4.1</u>	0.0	0.0	<u>6.7</u>	<u>1.8</u>	0.0	0.0	<u>9.3</u>	<u>1.0</u>	3.1	0.5	<u>7.2</u>	<u>10.3</u>	<u>16.5</u>	<u>2.1</u>	0.0	0.0
	VALSAV	1.4	0.2	0.1	0.1	<u>22.1</u>	<u>1.4</u>	<u>11.2</u>	<u>2.3</u>	<u>4.7</u>	<u>2.0</u>	1.4	0.6	0.1	0.1	<u>12.0</u>	<u>30.0</u>	0.0	0.0	0.0	0.0
Wildebeest (early dry)	SECGLD	0.1	0.1	<u>24.0</u>	<u>2.5</u>	<u>28.5</u>	<u>1.9</u>	0.0	0.0	<u>7.8</u>	<u>1.9</u>	8.2	0.9	<u>10.4</u>	<u>1.8</u>	0.0	0.0	0.1	0.1	0.0	0.0
	VALSAV	0.0	0.0	0.0	0.0	<u>78.0</u>	<u>5.0</u>	0.0	0.0	<u>5.0</u>	<u>2.1</u>	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.2	0.0	0.0
	PEDGLD	0.0	0.0	0.0	0.0	<u>10.0</u>	0.7	0.0	0.0	<u>4.0</u>	<u>3.6</u>	<u>20.0</u>	<u>15.4</u>	<u>19.0</u>	<u>11.9</u>	1.0	0.2	0.0	0.0	0.0	0.0
Wildebeest (late dry)	SECGLD	3.3	0.3	<u>38.5</u>	<u>4.1</u>	4.8	0.3	<u>10.6</u>	<u>2.9</u>	0.1	0.1	0.1	0.1	6.4	1.1	0.0	0.0	0.0	0.0	0.0	0.0
	VALSAV	3.0	0.5	1.7	0.5	0.1	0.1	4.5	0.9	<u>7.0</u>	<u>2.9</u>	0.1	0.1	1.7	0.8	<u>1.7</u>	<u>4.3</u>	<u>12.3</u>	<u>2.5</u>	0.6	0.8
	PEDGLD	0.1	0.1	2.0	0.5	<u>14.4</u>	1.0	<u>10.9</u>	<u>10.9</u>	0.1	0.1	<u>14.4</u>	<u>11.1</u>	0.0	0.0	0.0	0.0	<u>14.9</u>	0.8	0.0	0.0
Zebra (early dry)	SECGLD	0.0	0.0	0.0	0.0	<u>28.1</u>	<u>1.9</u>	<u>24.5</u>	<u>6.6</u>	0.0	0.0	1.0	0.1	0.0	0.0	1.5	2.1	<u>10.7</u>	<u>2.7</u>	0.0	0.0
	VALSAV	0.0	0.0	0.1	0.1	<u>30.5</u>	<u>1.9</u>	<u>2.4</u>	<u>0.5</u>	0.0	0.0	<u>32.9</u>	<u>3.5</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zebra (late dry)	HILSAV	0.0	0.0	0.1	0.1	<u>52.9</u>	<u>1.3</u>	<u>9.1</u>	<u>1.1</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Impaia (dry)	VALSAV	<u>22.0</u>	<u>1.7</u>	0.0	0.0	1.0	0.1	0.0	0.0	<u>10.0</u>	<u>4.2</u>	0.0	0.0	<u>4.0</u>	<u>1.9</u>	0.0	0.0	0.0	0.0	0.0	0.0
	THICKET	6.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	<u>5.0</u>	<u>1.1</u>	0.0	0.0	1.0	0.5	0.0	0.0	<u>4.0</u>	<u>1.2</u>	0.0	0.0

(PAL, INT and UNP are the proportions of palatable, intermediate and unpalatable grass species, respectively).

SECGLD = Secondary grasslands
 PEDGLD = Pediment grasslands
 VALSAV = Valley savannas
 HILSAV = Hillside savannas
 THICKET = Acacia and riverine thickets

n = Number of transects

Table 4.8 : (Cont.)

SEASON	HABITAT	BRSE		URMO		LOFL		DIER		PADE		PACO		SPPY		UNPA		PAL	INT	UNP	n
		PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI				
Hartebeest (early dry)	SECGLD	<u>15.5</u>	<u>14.1</u>	2.5	0.5	0.0	0.0	<u>2.8</u>	<u>1.1</u>	0.0	0.0	1.0	1.0	0.0	0.0	0.1	0.1	45.9	54.0	0.1	9
Hartebeest (late dry)	SECGLD	0.0	0.0	3.6	0.7	0.0	0.0	<u>8.2</u>	<u>3.3</u>	0.0	0.0	<u>6.2</u>	<u>6.2</u>	0.0	0.0	0.0	0.0	25.8	74.2	0.0	4
	VALSAV	0.0	0.0	5.4	3.2	<u>2.9</u>	<u>2.6</u>	<u>22.5</u>	<u>14.1</u>	0.0	0.0	<u>9.4</u>	<u>3.8</u>	<u>2.9</u>	<u>7.3</u>	0.0	0.0	49.5	50.5	0.0	5
Wildebeest (early dry)	SECGLD	<u>2.8</u>	<u>2.5</u>	<u>5.6</u>	<u>1.1</u>	0.0	0.0	<u>11.3</u>	<u>4.5</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	45.1	54.9	0.0	5
	VALSAV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<u>15.0</u>	<u>16.7</u>	0.0	0.0	1.0	2.5	0.0	0.0	93.0	7.0	0.0	3
	PEDGLD	<u>28.0</u>	<u>20.0</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<u>19.0</u>	<u>19.0</u>	0.0	0.0	0.0	0.0	77.0	23.0	0.0	3
Wildebeest (late dry)	SECGLD	0.0	0.0	<u>14.8</u>	<u>3.0</u>	0.0	0.0	<u>3.3</u>	<u>1.3</u>	<u>12.7</u>	<u>12.7</u>	<u>4.5</u>	<u>4.5</u>	0.0	0.0	0.0	0.0	47.5	52.5	0.0	6
	VALSAV	0.0	0.0	<u>4.9</u>	<u>2.9</u>	0.0	0.0	<u>6.0</u>	<u>3.8</u>	0.0	0.0	0.0	0.0	<u>5.3</u>	<u>13.3</u>	0.0	0.0	9.6	90.4	0.0	6
	PEDGLD	<u>27.4</u>	<u>19.6</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<u>14.4</u>	<u>14.4</u>	0.0	0.0	0.0	0.0	81.5	18.5	0.0	3
Zebra (early dry)	SECGLD	<u>33.7</u>	<u>30.6</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	87.4	12.6	0.0	5
	VALSAV	<u>5.4</u>	<u>6.0</u>	0.0	0.0	<u>13.2</u>	<u>12.0</u>	<u>3.8</u>	<u>8.6</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	71.2	28.8	0.0	5
Zebra (late dry)	HILSAV	<u>12.3</u>	<u>1.2</u>	0.0	0.0	<u>9.8</u>	<u>1.0</u>	<u>6.4</u>	<u>6.4</u>	0.0	0.0	0.0	0.0	8.3	0.5	0.0	0.0	74.3	25.7	0.0	6
Impala (dry)	VALSAV	0.0	0.0	2.0	0.2	0.0	0.0	<u>22.0</u>	<u>13.8</u>	<u>22.0</u>	<u>9.0</u>	0.0	0.0	0.0	0.0	0.0	0.0	25.0	75.0	0.0	2
	THICKET	0.0	0.0	3.0	0.3	0.0	0.0	0.0	0.0	<u>68.0</u>	<u>9.3</u>	0.0	0.0	<u>16.0</u>	<u>7.3</u>	0.0	0.0	71.0	29.0	0.0	2

Eragrostis gummiflua ($t=-2.12$, $p<0.01$) and Digitaria eriantha ($t=-3.61$, $p<0.01$) significantly increased while Rhyncheletrum repens decreased ($t=3.88$, $p<0.01$).

Section 3.3.3.2 examined the habitat selection of the hartebeest, depicting a high preference for secondary grasslands with intermittent selection for valley savannas. Hence, dietary differences only occurred between these two habitats.

Palatable species such as Themeda triandra (TT), Digitaria eriantha (DE), and Panicum coloratum (PC) were highly selected in both habitats. The intermediate grass species, Rhyncheletrum repens (RR), contributed over 30% of their diet in the secondary grasslands, whereas the palatable species such as Themeda triandra (TT), Heteropogon contortus (HC), and Digitaria eriantha (DE) contributed over 50% in the valley savannas.

Although showing distinct habitat differences in their diet, the hartebeest tended to select for the more palatable to intermediate grass species (see Table 4.8).

4.4.3.2.2 Wildebeest

The wildebeests' diet was similar to that of the hartebeest, except more time was spent foraging on grass species found in the valley savannas. Very little seasonal differences (early-dry and late-dry) in their diet could be detected (see Appendix H), except that Heteropogon contortus (HC) showed a marked decrease during the latter part of the dry season ($t=6.78$, $p<0.001$).

Both Rhynchyletrum repens (RR) and Heteropogon contortus (HC) accounted for over 40% of the wildebeests' diet in the secondary grasslands. During the early part of the dry season palatable species such as Heteropogon contortus (HC) and P. deustum (PD) were highly selected, whereas the intermediate species Hyparrhenia hirc (HH) and to a lesser extent Eragrostis curvula (EC) were important during the late-dry season. In the pediment grasslands palatable species such as Heteropogon contortus (HC),

Brachyaria serrata (BS) and Panicum coloratum (PC), and the intermediate species Eragrostis superba were selected during this season.

Hence, the palatable-tall species, Rhynchetrum repens (RR), Heteropogon contortus (HC) and, to a lesser extent Themeda triandra (TT), Brachyaria serrata (BS) and Digitaria eriantha (DE), and the intermediate species, Rhyncheletrum repens form the bulk of their winter diet. Thus more palatable species were favoured in all the vegetation types. Similar results were obtained by Melton (1978) who showed that the wildebeest in the Umfolozi Game Reserve selected mainly for Digitaria macroglossa, Heteropogon contortus, Eragrostis superba, Themeda triandra, Panicum coloratum and Sporobolus smutsii during the winter months.

4.4.3.2.3 Zebra

The zebra, with their tendency to select secondary grasslands and valley savannas during the early-dry season and hillside (mainly mesocline) savannas during the late-dry season, showed preferences for grasses common in these habitats. For instance, palatable-tall species such as Heteropogon contortus (HC), Themeda triandra (TT) and Brachyaria serrata (BS), and the intermediate species Hyparrhenia hirta (HH), were favoured in the secondary grasslands, and Heteropogon contortus (HECO), Eragrostis superba (ERSU) and Loudetia flavada (LOFL) in the valley savannas. During the late-dry season Heteropogon contortus (HECO), Themeda triandra (THTR), Brachyaria serrata (BRSE), Loudetia flavada (LOFL), Digitaria eriantha (DIER) and Sporobolus pyramidalis (SPPY) contributed over 80% of their diet in the hillside savannas. By referring to Table 3.1 it is apparent that the grass species selected in this habitat are those most readily available. Hence, a high preference was made for the palatable-tall grass species especially in the secondary grasslands ($t=2.92$, $p<0.001$). The selection for the tall species confirms the results obtained in the Correspondance Analysis which depicted a close relationship between the zebra and tall

grasslands.

The grass species, Heteropogon contortus ($t=-6.04$, $p<0.001$), Themeda triandra ($t=5.66$, $p<0.001$), Brachyaria serreta ($t=-4.34$, $p<0.001$), Loudetia flavada ($t=-6.89$, $p<0.001$), and Sporobolus pyramidalis ($t=-9.38$, $p<0.001$) significantly increased, while, Eragrostis superba ($t=5.31$, $p<0.001$) and Digitaria eriantha ($t=4.68$, $p<0.001$) significantly decreased from one season to the next.

Melton (1978) found that the Umfolozi zebra mainly utilized palatable species such as Panicum maximum, Themeda triandra and Heteropogon contortus. The zebra in the Pilanesberg Game Reserve showed similar preferences in that the palatable species contributed to over 70% of their dry season diet.

4.4.3.2.4 Impala

Unfortunately, only four feeding sites were recorded for this species during the dry season, two in the valley savannas and two in the Acacia and riverine thickets. These were however, able to give some indication as to what grass species were preferred.

The palatable-tall species, Panicum deustum was highly preferred (PI of over 9.0) in both habitat types and contributed to about 50% of their diet. Palatable species such as Digitaria eriantha (DE) and Cynodon dactylon (CD), and the intermediate species Eragrostis curvula (EC) were utilized to a greater extent in the valley savannas.

Impala were observed to utilize only the highly palatable grass species during the dry season, especially in the thickets. Similar results were obtained by Melton (1978), who showed that the impala in the Umfolozi Game Reserve preferred mainly Panicum maximum in both the wet and dry seasons.

CHAPTER FIVE

HABITAT AND DIETARY OVERLAP BETWEEN THE PILANESBURG GRAZERS:

5.1 Introduction:-

The major focus in studies of community structure is the use of pattern of resource partitioning as a basis for explaining the coexistence of ecologically similar species (eg. Pulliam and Parker, 1979). Essentially ecological community theory attempts to predict the numbers and relative abundance of coexisting consumer species based on the availability of resources, and the resource utilization patterns of the species (MacArthur and Levins, 1967; MacArthur and Wilson, 1967; Levins, 1968, MacArthur, 1972; May, 1973; Pulliam, 1983). The procedure requires the calculation of firstly, carrying capacities for each species based on the availability of resources and secondly, competition coefficients for each species pair, based on the similarity of their resource utilization patterns (Pulliam, 1983).

Although the precise application and interpretation of ecological niche overlap remain a subject of debate, many ecologists nevertheless use various overlap measures to indicate degrees of ecological similarity within assemblages of species. Studies by Pianka (1975) and Cody (1974) made extensive use of niche overlap data when studying interspecific competition. Hurlbert (1978) suggested that niche overlap measures should serve "as a foundation for discussion of resource utilization strategies, competition, species packing, and so on".

The term niche has been variously defined by many authors. Elton (1927) considered the niche as the fundamental role of an organism in a community - what it does, its relationship to its

food and to its enemies. Grinnell (1924) on the other hand, referred to the niche as a subdivision of the environment occupied by a species. Hutchinson (1959) conceptualized the niche as a combination of the functional role of an organism in an ecosystem as well as its position in time and space. He therefore defined the niche of a species as an "n-dimensional hypervolume". Levins (1968) went further by stating that "niche dimensionality refers not to the number of biologically relevant factors in the environment, but to the number of factors which serve to separate species". Thus before attempting any niche study, it is important to know the species concerned and to identify those environmental factors to which they respond. Separate divisions or dimensions of the various resource types utilized by the species can then be defined. Each resource dimension is then treated as a single niche in an Euclidian space of many dimensions (Slobodchikoff and Schulz, 1980). It should be noted that these dimensions are not gradients of a resource, as is often implied (ref), but consist of discrete resource entities. For example, a herbivores diet cannot be interpreted as a gradient of grass species but rather a resource dimension consisting of a number of resource types.

Few studies on the interspecific interactions within entire large herbivore communities have been attempted in Africa (eg. Versey-Fitzgerald, 1960, 1965; Lamprey, 1960; Field, 1968; Bell, 1969; Field and Laws, 1970; Ferrar, 1973; Ferrar and Walker, 1974; Page and Walker, 1978; Attwell, 1978). Thus, the aim of this section is to analyze the nature and the relative importance of those factors which serve to separate the species, eg. white rhinos and their potential competitors in a southern African game reserve.

5.1.1 Relationships Between Overlap, Similarity, and Competition:

Before examining the various methods of estimating niche overlap, a clear understanding of the relationships and

differences between the overlap, similarity and competition coefficients, as explained by Lawlor (1980), are necessary.

Overlap measures are designed to measure the degree to which two species share a set of common resources or utilize the same parts of the environment (Lawlor, 1980). In other words, it is the region of niche space (in the sense of Hutchinson, 1958) shared by two or more contiguous niches (Colwell and Futuyma, 1971). These overlap measures are usually scaled from zero to one; zero indicating no overlap, and one indicating complete overlap. Resource use can be expressed as P_{ik} , the proportion of consumer species' (i) total utilization that is represented by each resource, k. The proportion of food type (j) depends on two factors; the consumer's electivity, and the availability of that food type in the environment. Schoener (1974) defined electivity as the consumer's relative ability (or preference) to catch and consume an item of a particular food type. If all resource types are equally abundant then their relative proportions in the diet are determined only by their relative electivities. Lechowicz (1982) referred to the electivity indices as measures of the utilization of food type (r) in relation to their abundance or availability (p) in the environment. Therefore, foods that constitute a larger proportion of the diet than of the available foods are considered to be preferred. If a particular food type is relatively scarce it may represent only a small proportion of the consumer's diet, even though the consumer has a high electivity for that food type (Lawlor, 1980).

Measures of similarity are often used in comparisons between closely related species living in different communities or environments. However, the problem with this measure is that the resources may differ in abundance between the environments thus creating two major problems. Firstly, similar species may not appear alike if living in totally different environments, and secondly, the converse situation may arise where species which are very dissimilar may appear quite similar because of the species - environment interactions (Lawlor, 1980). Consequently, conclusions about species' similarities based on their overlaps may be misleading. It is therefore important to be quite sure

whether one is interested in comparing the species themselves or the species-environment relationships. Lawlor (1980), when considering consumer similarities, concluded that they should be based on patterns of resource use rather than patterns of the resources used. Thus, the use of electivities rather than proportional utilizations should be used in any measure of similarity. This ensures that species with similar electivity patterns will appear similar even if compared in different environments with different resource abundances. Lawlor (1980) modified the Symmetric MacArthur-Levins formula (discussed later) to measure species similarities based on consumer electivities;

$$S_{ij} = \frac{\sum (a_{ik} \times a_{jk})}{\sum (a_{ik})^2 \times \sum (a_{jk})^2} \dots\dots 5.1$$

where a is the electivity of resource k by species i and j , and S is the similarity index.

The main emphasis of this chapter and the next is to incorporate competition indices, using overlap measures, to calculate stocking densities, whether at carrying capacity or at a particular maintained level of utilization. The theory of competition implies that the greater the overlap in resource use between two organisms, the greater the competition coefficient, and hence the greater the intensity of competition. By definition, competition occurs when two or more organisms interfere with or inhibit one another (Pianka, 1981). Competition can be quite direct as in the case of interspecific territoriality (eg. Brown, 1964), and is then termed "Interference Competition" (Elton and Miller, 1954; Miller, 1967). More indirect competition may also occur, such as that arising through the joint use of the same limited resources, this being termed "Exploitation Competition" (Elton and Miller, 1954; Miller, 1967). In this case, although the resource pool is

reduced in availability to the competing individuals, no direct interactions are apparent (MacNaughton and Wolf, 1973).

As mentioned earlier, the degree of resource overlap has often been used as a measure of the intensity of interspecific competition (eg. Schoener, 1968; Levins, 1968; Cody 1974, Culver 1973, 1975; May, 1975) whereby a positive relationship has been assumed between the two measures. Pianka (1972, 1974) on the otherhand, postulated an inverse relationship between the intensity of competition and the degree of niche overlap (termed the "Niche Overlap Hypothesis"). He reasoned that if resources are not in short supply, "extensive niche overlap may actually be correlated with reduced competition". "Disjunct niches on the otherhand may often indicate avoidance of competition where it could have been potentially severe". However, equating the degree of overlap to the intensity of competition can be dubious and misleading (Colwell and Futuyma, 1971). Mere overlap in resource use is no guarantee that competition is taking place. This is largely because:

- (i) the resource may not be limiting and overlap therefore does not result in competition,
- (ii) competition may be a complex function of overlap, and
- (iii) low current overlap may be the result of past competition (Colwell and Futuyma 1971, Hurlbert 1978, Petriatis 1975, Abrams 1980, Lawlor 1980, Slobodchikoff and Schultz 1980).

Hence the theory of niche overlap and competition can only be applied to systems which have limiting resources, eg. systems at, or close to carrying capacity. If one wishes to maintain a system at a level of utilization well below carrying capacity then competition is negligible - resources are not limiting hence, negligible interspecific interactions. However, if the objectives of a reserve is to allow the density of one of the species to increase while maintaining a specified level of utilization, then the species' overlap coefficients become important. Those species which depict high overlap with this

species will most likely be the ones which modify the grazing level. For example, by increasing species A, species B, which has similar requirements, must be reduced otherwise the overall grazing pressure will exceed the specified level.

Rosenzweig (1974, 1979, 1981) and Pimm and Rosenzweig (1981) have presented an interesting model with regards to habitat selection and competition. They propose that sympatric species, foraging optimally, avoid competition by utilizing different habitats, i.e. differential habitat selection reduces competition, sometimes to zero. The important point arising from this model is that although competitive interactions do not have to prevail at every possible density pair, they do have to produce an overall depression of the densities. Consequently, relating niche overlap to the degree of competition becomes meaningless, because at the stable node competition will be zero. However, Rosenzweig (1981) argued that instead of trying to relate competition to niche overlap one should rather discover whether the position of the species' equilibriums are below their carrying capacities.

The major criticism of his model is that it depends entirely on the theory of optimal foraging (Schoener, 1974; Pyke, et al, 1977), of which to date few convincing studies are available. Nevertheless, a number of important implications can be extracted from their model. They are:

- (i) there are thresholds at which one species will outcompete another.
- (ii) when at moderate densities, the increase of one species may not cause the decrease of another.

Although it seems likely that zero competition at equilibrium may exist when one or more of the resources are limiting, its importance in structuring communities seems doubtful. Rosenzweig (1975, 1981) believes, as do many others (e.g. MacArthur and Levins, 1967; MacArthur and Wilson, 1967; Levins, 1968; May, 1973; Cody, 1974; Pianka, 1975; Pulliam, 1983), that competition itself gives rise to community equilibria. In other words,

competition modifies the habitat requirements or preferences of the species, ie. competition behaves as a directive force in structuring ecosystems. They believe that continual adaptations of the components within an ecosystem occur as a result of their response to interspecific competition. An alternative explanation is proposed whereby a species' habitat selections are determined independently of each other during speciation, and thus overlap results incidentally to their past evolutionary history. Communities would therefore consist, to a large extent, of randomly assembled species. This has apparently been explained using models which randomly structure a known species assemblage and then test for significant differences between the randomly structured and the natural communities (eg. Sale 1974, Tompson and Rusterholz, 1982). If the random models are essentially similar to real communities, then one has to favour the theory that community structure is built up of a random accretion of components adapted in allopatry (ref).

Finally, it should be stressed that when concerned with estimating stocking densities or carrying capacities in multispecies systems, the processes which structured the communities in the past, eg. competition and predation, are not as important as the ecological similarities or differences presently taking place. Interest was therefore placed only on the present interactions, or the contemporary niche patterns, and not whether competition played an important role in structuring communities in the evolutionary sense. In addition, most communities, especially nature reserves, are comprised of a number of introduced and possibly alien species which have been translocated into areas which they would naturally not occur hence, unnatural processes were used to structure the community.

Thus this study was developed not to test whether competition is presently occurring between the Pilaresberg grazers, but rather to relate niche theory in estimating stocking densities in a multispecies system.

5.2 Methods:-

5.2.1 Field Data Collection:

In order to fulfil the objectives of this study it was necessary to systematically search for, and then measure and record the characteristic site attributes of each grassland site selected by the foraging herbivores. From these sites, information on both the habitat structure and dietary selection should be collected (see chapter 4).

Based on previous investigations (eg. Ferrar, 1973; Ferrar and Walker, 1974; Page and Walker, 1978; Attwell, 1978; Melton, 1978) and preliminary observations, the following dimensions were found to be important in describing the feeding niches of the five large grazers in the reserve;

(i) Habitat type, eg. whether in Secondary Grasslands, Pediment Grasslands, Valley Savannas, Mesocline Savannas, or Thickets.

(ii) dietary component, ie. grass species.

The feeding niches of the herbivores can now be described along two dimensions in terms of Hutchinson's multidimensional hyperspace (Hutchinson, 1957). A third component, the subdivisions of the herbaceous component within the major habitat types, was analyzed using a multivariate technique known as Discriminant Function Analysis. This technique essentially reduces the multidimensional herbaceous component to a few dimensions. Overlap along the habitat niche dimension could be measured in more detail.

5.2.2 Calculation of Niche Overlap

5.2.2.1 Single Dimensions

Overlap has been quantified in numerous ways (MacArthur and Levins, 1967; Schoener, 1968; Colwell and Futuyma, 1971; Pianka, 1973;). The particular overlap index used is somewhat arbitrary, since similar qualitative results are obtained with a wide array of indices. Little or no explanation is given in the literature as to why a particular overlap index was used or not. An attempt is therefore made to examine the various methods in detail, emphasising their pros and cons.

The two most widely used methods are the Symmetrical and the Asymmetrical methods. The Symmetrical method was first presented by Pianka (1973). The equation produces a symmetrical matrix of α 's so that

$$\alpha_{ij} = \alpha_{ji}$$

ie, the effect of species j on species i is equivalent to the effect of species i on species j and takes the form:

$$\alpha_{ij} = \frac{\sum (P_{ik} \times P_{jk})}{\sqrt{(\sum P_{ik}^2)(\sum P_{jk}^2)}} \quad \dots 5.2$$

Slobodchikoff and Schulz (1980) have pointed out three advantages of this method: (1) a ready geometrical interpretation, (2) the symmetrical nature of the matrix, and (3) the fact that alpha cannot exceed one.

The Asymmetrical method as proposed by Levins (1968) and MacArthur (1972) differs in that the overlap is expressed relative to only one of the species as follows:

$$\alpha_{ij} = \frac{\sum (P_{ik} \times P_{jk})}{\sum (P_{ik})^2} \dots\dots 5.3$$

ie. it measures how much a species' utilization curve overlaps that of another species curve.

According to May (1975), the alpha matrix produced by this equation is not symmetrical, ie; α_{ij} will generally not equal α_{ji} . This is because P_{ik} , the denominator, is a property of only the i th species (refer to Slobodchikoff and Schulz, 1980). In other words, pairwise overlap (α_{ij}) is calculated only with respect to species i . Values greater than one may now result depending on whether species j utilizes resource type k to a greater extent than species i , i.e. P_{ik} is greater than P_{jk} . Its major disadvantage is that one must be extremely careful to count either all individuals of species i and j , or to count the same proportion of each species (Slobodchikoff and Schulz, 1980). For example, if species j is more successful at eluding the investigator than species i , it will skew the overlap value (α_{ij}), indicating, that less competitive pressure from j is being exerted on i than it really is. However, the Asymmetrical method remains the most popular for calculating niche overlap. This is mainly because it does not assume that both species have equal effects on each other and also, because it is closely related to the competition coefficient of the Lotka - Volterra formulation of interspecific competition (MacArthur, 1968; 1972; Schoener, 1974).

The overlap measures are best explained graphically using figure 5.1. If one considers a simple system of two species, one a specialist and one a generalist, foraging along a resource gradient, then the following becomes apparent. When using Pianka's Symmetrical method, overlap is calculated irrespective of the proportional resource use of each species. In other words, one is interested only in the extent to which both share common resources, ie, the degree of similarity (represented by A in Figure 5.1).

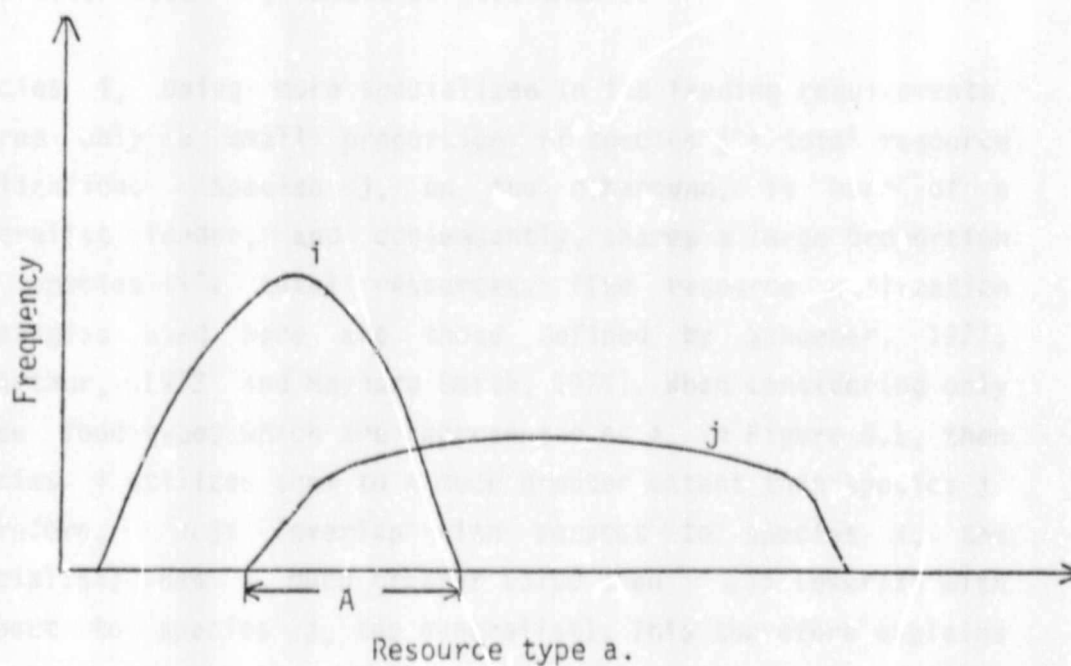


Figure 5.1 : Frequency distributions of two species, *i* and *j*, for the utilization of resource type *a*.

If interested in the niche overlap with respect to only one species, or the influence of one species on another, then the Asymmetrical method should be chosen. The measure therefore has two different values depending on whether one considers the effect of species j on species i , or vice versa. In the first instance, α_{ji} would be close to or greater than 1, whereas in the latter case α_{ji} would be less than 1.

Species i , being more specialized in its feeding requirements, shares only a small proportion of species j 's total resource utilization. Species j , on the otherhand, is more of a generalist, and consequently, shares a large proportion of species i 's total resources. (The resource utilization strategies used here are those defined by Schoener, 1977; MacArthur, 1972 and Maynard Smith, 1974). When considering only those food types which are represented as A, in Figure 5.1, then species i utilizes them to a much greater extent than species j . Therefore, α_{ji} (overlap with respect to species i , the specialist) has a much greater value than α_{ij} (overlap with respect to species j , the generalist). This therefore explains why the two overlap values differ. If for example, the two species forage on a broad range of food types then the two values will differ only slightly. This occurs because both P_{ik} and P_{jk} have similar values. The use of this method is best illustrated by referring to the following hypothetical example. The proportional use of four resources by two species is shown below;

Species	I	II	III	IV
1	0.6	0.4	0.0	0.0
2	0.2	0.3	0.4	0.1

Species 1 being more a specialist feeder consequently, utilizes resources I and II to a greater extent than species 2. This is revealed in the overlap measures using the Asymmetrical method, $\alpha_{21} = 0.80$ and $\alpha_{12} = 0.46$. Species 1, because of its greater use of resources I and II, exert a greater impact on species 2, than vice versa. Pianka's method, on the otherhand, predicts a single (mutual) overlap of 0.62.

The Asymmetrical method was therefore preferred to Pianka's method, and was subsequently used to determine the relative overlaps, along each dimension (habitat and diet) between the white rhinos and their associated grazers.

5.2.2.2 Multidimensional Overlap

Once the decision on which measure to use for estimating overlap along single resource gradients (e.g. diet or habitat) has been made, the next problem lies in assessing the combined effects of niche overlap along more than one dimension. Cody (1974) and May (1975) have both pointed out that either the Product (calculates the product of the overlap measures) or the Summation (calculates the mean of the overlap measures) methods may be used, depending on whether the resources or dimensions are dependent or independent. The Product method is generally used when resources are independent or orthogonal to each other, for example, when a grass species or prey item has an equal chance of being grazed or captured in any habitat (May, 1975). The Summation method is used for dependent resources eg. where any grass species or prey item occurs in only one particular habitat, hence, there is a direct relationship between the presence of a grass species and a habitat type (May, 1975). Thus the choice of method depends largely on the type of resources or niche dimensions that one is considering.

The Product method calculates the product of the α 's along each dimension,

$$\alpha_{ij}^P = \prod \alpha_{ij}(k) \dots\dots\dots 5.4$$

where, α_{ij}^P is the product for species i and j, and $\alpha_{ij}(k)$ is the α_{ij} for the kth resource. One simply multiplies the two overlap coefficients for each different resource dimension.

The Summation method calculates the average of the α_{ij} 's along each dimension and takes the form;

$$\alpha_{ij}^S = \frac{\sum \alpha_{ij}(k)}{n} \dots\dots 5.5$$

where α_{ij}^S is the summation for species i and j, and $\alpha_{ij}(k)$ is the α_{ij} computed for the k'th resource. This method generally overestimates true niche overlap, whereas multiplicative overall overlaps often underestimate true multidimensional overlap (Pianka, 1974). Furthermore, it is often difficult to judge whether resources are dependent or independent. Secondly, some resources may have subtle interdependence, such as use of time, use of food, and use of space (Slobodchikoff and Schulz, 1980). Thirdly, the degree of dependence or independence of particular resources may differ between the different species. The fourth problem, which was pointed out by May (1975), concerns the inaccuracy of estimating multidimensional overlap coefficients from single resource dimensions. This is best illustrated by Figure 5.2 which depicts two (continuous) resource axes a and b, eg; food and foraging height, and two - dimensional utilization functions for the two species, 1 and 2. It is clear that although the species are non-overlapping when viewed along the single resource axes and overlap is depicted. Overlap measures for multidimensional resources may therefore be overestimated.

Finally, another problem which has not been mentioned in the literature, is the complex phenomenon of electivities for a

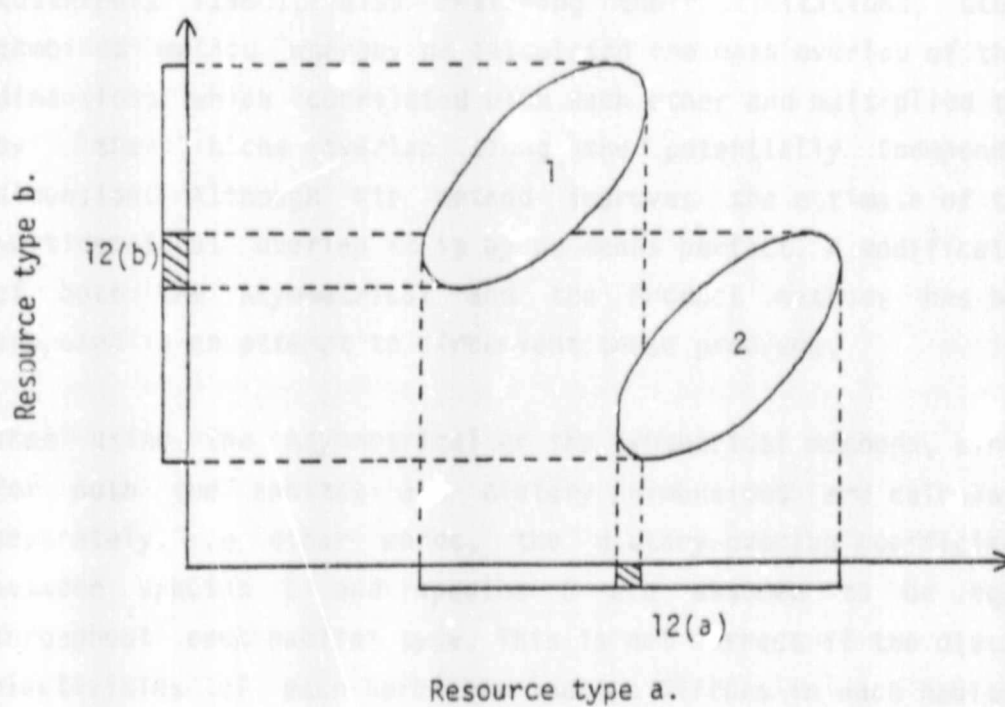


Figure 5.2 : Two non-competing species, 1 and 2, depicting overlap along the two single resource dimensions. (Adapted from May, 1975).

particular prey type differing in different habitat. For example, it has been observed that the white rhino population at Pilanesberg exhibit different dietary electivities in different habitats (refer to section 4.3.3). Consequently, the use of either the Summation or the Product methods in this case is inappropriate for determining overlap across several habitats. Rusterholz (1980), also realizing their limitations, used a combined method whereby he calculated the mean overlap of those dimensions which correlated with each other and multiplied this by the niche overlap along the potentially independent dimension. Although his method improves the estimate of true multidimensional overlap it is by no means perfect. A modification of both the Asymmetrical and the Product methods has been proposed in an attempt to circumvent these problems.

When using the Asymmetrical or the Symmetrical methods, alphas for both the habitat and dietary dimensions are calculated separately. In other words, the dietary overlap coefficients between species 1 and species 2 are assumed to be equal throughout each habitat type. This is not correct if the dietary electivities of each herbivore species differs in each habitat. The modifications must therefore first calculate the dietary overlaps within each habitat type, and then incorporate the habitat overlaps for each herbivore (consumer) species. The two-dimensional overlap equation would therefore take the form;

$$\alpha_{ij} = \sum_{n=1}^n \left[\left(\frac{\sum P_{ikH} \times P_{jkH}}{\sum (P_{ikH})^2} \right) \times \left(\frac{e_{iH} \times e_{jH}}{(e_{iH})^2} \right) \times a_H \right] \dots 55.6$$

where i, j = herbivore species,

H = habitat, $1 \dots n$,

k = plant species in diet, $1 \dots s$,

P_{ikH} = proportion of plant species k in species i 's diet in habitat H ,

e_{iH} = proportion of time that herbivore species i spent in habitat H , and

a_H = proportion of the total area made up by habitat H .

The first part of the equation calculates the dietary overlap within each habitat using the Asymmetrical method as proposed by Pianka (1973). This value is then modified or weighted, firstly by the habitat, overlap and secondly by the proportional area of that habitat. This method, termed the "Weighted Overlap" method, calculates values from 0 to 1, again 0 indicating no overlap, and 1 indicating complete overlap.

By using this approach one is incorporating the relationship between both the habitat and dietary selection. For example, species i may overlap greatly in diet with species j but, species j may spend less time in the habitat, thereby decreasing the potential overlap between them. This value is then modified by the proportional area of habitat 'H' in the reserve. Hence, the total overlap in the relatively smaller habitats are weighted less than those in the larger habitats. The new method proposed is, therefore, not so much a modification of the mathematical formulae as an alternative in the approach used to calculate resource overlap along multiple niche dimensions.

5.2.2.3 Reduced Dimensionality in the Measurement of Habitat overlap

Hutchinson's (1957) concept of the ecological niche as a n -dimensional hypervolume invites the use of multivariate statistical techniques. Rutenberry and Wiens (1980) stressed the advantage of such methods in being able to display highly correlated variables along independent axes representing what they termed, "proximate" niche dimensions. Two widely accepted techniques, namely, Principle Component Analysis (P.C.A.) and Discriminant Function Analysis (D.F.A.) have been used in niche analyses.

The major advantage of D.F.A. is that the Discriminant Functions can be used, firstly, to identify the axes of niche separation, and secondly, the dispersion of locations along these axes can be interpreted as representing niche width or specialization.

Levins (1968) initially stated that "niche dimensionality refers not to the number of biologically relevant factors on the environment,...but to the number of factors which serve to separate species". This led Cody (1968) and James (1971) to use D.F.A. to separate bird species according to habitat characteristics. However, recent applications to niche analyses appear to have been based on the papers by Green (1971, 1974) and Shugart and Patten (1972). Green (1971), used D.F.A. to identify significant ecological factors separating species in a multidimensional space. The standard deviation of discriminant scores as a measure of niche breadth, and the percent overlap of 50% probability ellipses a measure of niche overlap. Dueser and Shugart (1978, 1979), on the other hand, used the average distance of the observations for a species from the origin of discriminant space as a measure of niche exploitation or position relative to the average microhabitat available. The coefficient of variation of the distances from the discriminant origin was used as a measure of niche breadth. Indices of overlap were calculated using the planar area of overlap of concentration ellipses relative to their total area (Dueser and Shugart, 1979).

A controversial problem which arises when considering multivariate analyses of habitat use or niche space is whether to sample environmental variables at sites determined randomly, or to record the variables only where the organisms of interest were sited. Rotenberry and Wiens (1980, 1981), used the former method for generating a set of habitat vectors to be analysed by P.C.A. Cody (1968, 1978), James (1971), Green (1971, 1974), Shugart and Patten (1972), Ferrar and Walker (1974), Attwell (1975), M'Closky (1976), and Dueser and Shugart (1978, 1979), however, all used the latter method (ie, centers or singing perches within territories for birds, and successful collecting sites for molluscs and mammals) to identify locations for

habitat sampling. Green (1971), when justifying his method of recording environmental variables only where the organisms (ie, molluscs) were found, cited Hutchinson's (1968) reasoning that the "presence of a species in a sample was more informative than its absence". Presence indicates that a species could live at the site, whereas absence could arise because, either the site was unsuitable, the species had not yet colonized the area, or because the species was missed in the sample even though it was a favourable site (Hutchinson, 1968). Carey (1981) and Wiens and Rotenberry (1981), however, argued that this technique may only be meaningful for sedentary forms, or when applied on a macroscopic scale. Mobile animals may in fact be found not only in marginal habitats but also, during high densities, in completely unsuitable habitats. Presence is therefore not indicative of habitat suitability. However, the author argues that if one records the sites only where the animals are observed to forage then all the sites measured are part of the species feeding niche.

The major difference between these two sampling techniques lies in the interpretations of the canonical space. If one accepts that the origin of canonical space represents the mean of the discriminant (or factor) scores, or the mean of all sites sampled, then the niche metrics will differ for each sampling method. In the first method, the origin gives a better estimate of the average microhabitat available. The second method, however, estimates only the average of the microhabitat utilized by the species, and consequently, is influenced by their relative abundances (Carnes and Slade, 1982). Common species would contribute more to the determination of the mean than the rare species, and therefore, are more likely to be located near the origin of the canonical space.

When information is required on niche specializations or niche breadths, samples of species absence must be included. However, measurements of the sites where the organisms were present need only be recorded if interested in niche overlap. In this case one is primarily interested in the relationships between the

different species, rather than between the species and their environment.

During this study samples were measured only at the sites where the herbivores were present in order to describe the micronhabitat selection within the major habitats.

The data collected consisted of several groups (herbivore species) each comprising a number of individual sites characterized by a number of site attributes. The variables take the form of either measured (eg. grass height) estimated scores (eg. percentage herbaceous cover).

5.2.2.3.1 Discriminant Function Analysis

Discriminant Function Analysis (DFA) is a well known multivariate statistical technique originally developed by Fisher (1936) as a means of classification. The method separates populations or groups which are known to be difficult, on the basis of several characters or attributes. It is particularly useful in niche analysis because it reduces the number of criteria or dimensions used for discrimination before the interpretation of species separation is necessary (Green, 1971; Ferrar, 1973).

The first step in this analysis is the combination of F-ratios for each variable so as to identify those variables for which the ratio of between species variance to within species variance is sufficiently large to enable discrimination between herbivore species (Ferrar and Walker, 1974). Secondly, a series of latent roots (discriminant functions) and vectors are extracted from the total data set. These discriminant functions express the difference between species in terms of a few common gradients of variation instead of the gradients represented by each of the individual variables. The latent roots then give the proportion of the total variance extracted with the vector of the variable

weights indicating the degree to which each variable is associated with the discriminant function.

Discrimination between groups is therefore expressed in terms of a few common gradients which can be identified by those variable weights most strongly associated with each discriminant function (Ferrar and Walker, 1974). The next step then calculates a discriminant score for each site (feeding locality), by summing the products of the variable weights and their respective values. The mean of the discriminant scores for all sites for each species is known as the group or species centroid (Ferrar and Walker, 1974).

Discriminant Function Analysis finally provides a posteriori classification function which can be used to assess the extent of group overlap based on the site characteristics (Telford, 1982).

The program algorithm used for this analysis is that of Klecka (1975) and was performed using an S.P.S.S package (Nie, et al, 1975).

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Name of thesis Habitat Use By The White Rhinoceros In Relation To Other Grazing Ungulates In Pilanesberg Game Reserve, Bophuthatswana. 1986

PUBLISHER:

University of the Witwatersrand, Johannesburg

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