In Correspondence Analysis the principle axes are chosen so as to maximize what is termed the "Inertia". The inertia can be considered as a measure of dispersion of the points in space. Thus Beardall (1982) defined a correspondence analysis as the "identification of a subspace (cloud of points of subjects and objects) along which the inertia is a maximum (i.e. the eigenvector associated with the largest eigenvalue)". The second axis is that axis orthogonal to the first along which the inertia is also a maximum, and so on for the third and fourth axes.

To summarise, the rows and columns of a data matrix are represented by two clouds of points in a multi-dimensional space. The inertia of these clouds can be considered as a measure of dispersion or spread of these points, taking into account both their distance and their attributed masses (ie. the proportion of the contribution that a subject makes on the whole sample).

Correspondence Analysis thus provides a visual interpretation of the relative position of both these clouds in a common subspace of low dimension (Beardall, 1982). To get an idea of how close the subjects and objects are to each other, one measures the angle that the two points make to each other when joined to the origin. The smaller the angle, the closer they are related. An "Importance Index" was calculated by first dividing this angle by 180 and then subtracting from one. The values therefore range from 0 (no relatedness or avoidance) to 1 (closely related or high preference). Therefore, by measuring the angles between the points of the herbivores and the habitat factors, information can be collected on the relatedness of the two, ie. the importance of particular habitat factors on the herbivore's habitat selection.

The rows in the matrix represent the herbivore species and the columns, the habitat factors. The entries in the matrix represent the frequency of occurrence of a certain species with a particular habitat factor (see Table 4.1).

The computer program used for the analysis was written in FORTRAN by Beardall (1982).

4.4 Results and Discussion

4.4.1 Seasonal Changes in Habitat Selection

The annual cycle was divided into four seasons; Early-wet (October to December), Late-wet (January to April), Early-dry (May to July) and Late-dry (August to September).

Petrides (1956), Darling (1960), Vesey-Fitzgerald, Blankenship and Field (1972), Pienaar (1974), Ferrar and Walker (1974) and others have all identified vegetation as the all-important factor governing herbivore distributions. The seasonal changes in habitat selection were therefore analysed for all species. Figures 4.1 to 4.5 show the seasonal changes in habitat selectivity for the five major wild ungulates.

The habitats considered here are the major vegetation types defined in section 3.3.1. They were based largely on topography, tree density, successional stage and the percentage bulk contribution of the grass species.

This section attempts to identify, firstly, which habitats were preferred by the Pilanesberg grazers, and secondly, what environmental factors influenced their selection.

4.4.1.1 White Rhinoceros

Based on the data collected from the road strip transects, the white rhinos showed a marked seasonal change in habitat preference (refer to Appendix B), especially between the secondary grasslands, valley savannas, thickets and Cynodon dactylon lawns (figure 4.1). During the wetter months there was a high preference for the secondary grasslands ($p < 0.001$, Chi-square test), whereas during the drier seasons the more wooded valley savannas and thickets were selected ($p < 0.001$, Chi-square test). There were no marked seasonal differences in their selection for the pediment grasslands ($p > 0.1$, Chi-square test). Negative selection, ie. avoidance, was observed for the hillside

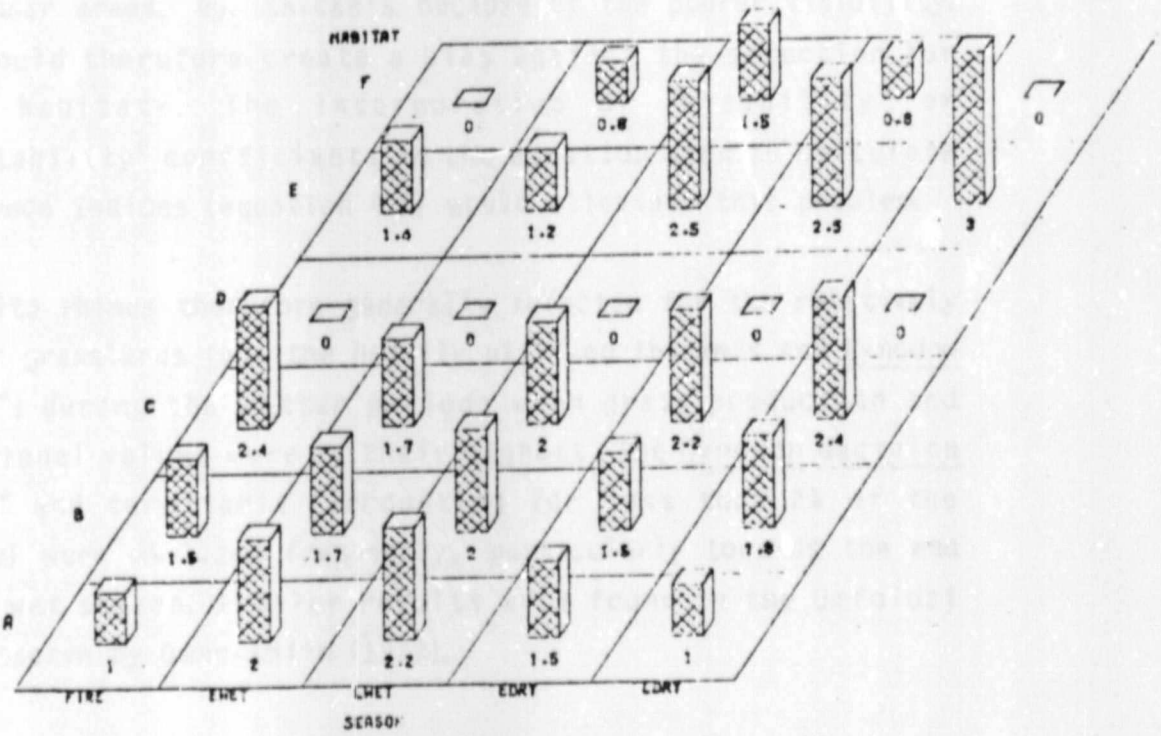

Figure 4.1 : Seasonal patterns of habitat selection by the White Rhino in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = Cynodon dactylon "lawns" and termitaria. FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

savannas. This probably results from their inaccessibly steep slopes.

As shown in Figure 4.1, selection for the thickets was prevalent throughout the entire year except for the early-wet and fire periods which showed only a slight positive selection. These results may unfortunately underestimate the rhino's selection for the denser areas, eg. thickets because of the poorer visibility. This would therefore create a bias against the selection for these habitats. The incorporation of "visibility" or "detectability" coefficients in the equation used to calculate Preference Indices (equation 4.6) would alleviate this problem.

The white rhinos therefore generally selected for the relatively shorter grasslands (eg. the heavily utilized thickets and Cynodon "lawns") during the wetter periods when grass production and nutritional values were at their highest. The Cynodon dactylon "lawns" and termitaria (accounting for less than 2% of the reserve) were utilized frequently, particularly towards the end of the wet season. Similar results were found in the Umfolozi Game Reserve by Owen-Smith (1973).

It is interesting to note how the presence of a fire affects the herbivore distribution and habitat selection. Significant differences in habitat selection occurred between the fire and the other seasons ($p<0.001$, Chi-square tests). The importance of any particular habitat tends to decrease with the presence of a green flush after a burn, ie. habitat selection tends to be more random.

These "megaherbivores" (Owen-Smith, 1981) therefore tend to behave as habitat generalists by utilizing a wide range of habitat types, both on an annual, and seasonal basis. Five out of the six habitats were positively selected for at least once during the year.

This generalistic behaviour may therefore imply one of two possibilities. Firstly, these animals may require a high habitat

diversity in order to survive in this reserve; or secondly, because of their "plastic" or generalistic foraging behavior, the white rhinos are able to survive in either one of the habitat types. The importance of either of these possibilities becomes apparent when estimating carrying capacities in the reserve. The relationship between diet and habitat selection may provide an indication as to which possibility is most likely. For instance, if dietary selection, which changes seasonally, is closely related to the habitat type then the first possibility is most likely. However, if their dietary selection differs little seasonally, but seasonality is shown in habitat selection then the latter is most likely.

4.4.1.2 Hartebeest

The hartebeest, in contrast to the white rhinoceros, behaves largely as a habitat specialist, specializing almost exclusively on the secondary and pediment grasslands and to a lesser extent valley savannas. Seasonal variation in their habitat selection was apparent for most of the habitats with marked differences between the wet and dry seasons (see Appendix B and Figure 4.2). The hartebeest also showed a high selection for the valley savannas during the early-wet season. Positive selection for both the pediment and secondary grasslands occurred throughout the entire year, although their importance does tend to drop during the drier months. The hillside savannas however, were negatively selected throughout most of the year, but showed a greater importance during the drier months. The hartebeest also tend to move up on the slopes during the early- and late-dry seasons when the selection for the secondary grasslands drops.

No selection was observed for the Cynodon dactylon "lawns" or termitaria.

4.4.1.3 Wildebeest

Significant differences in the wildebeest habitat selection was shown throughout the entire year (refer to Appendix B) again

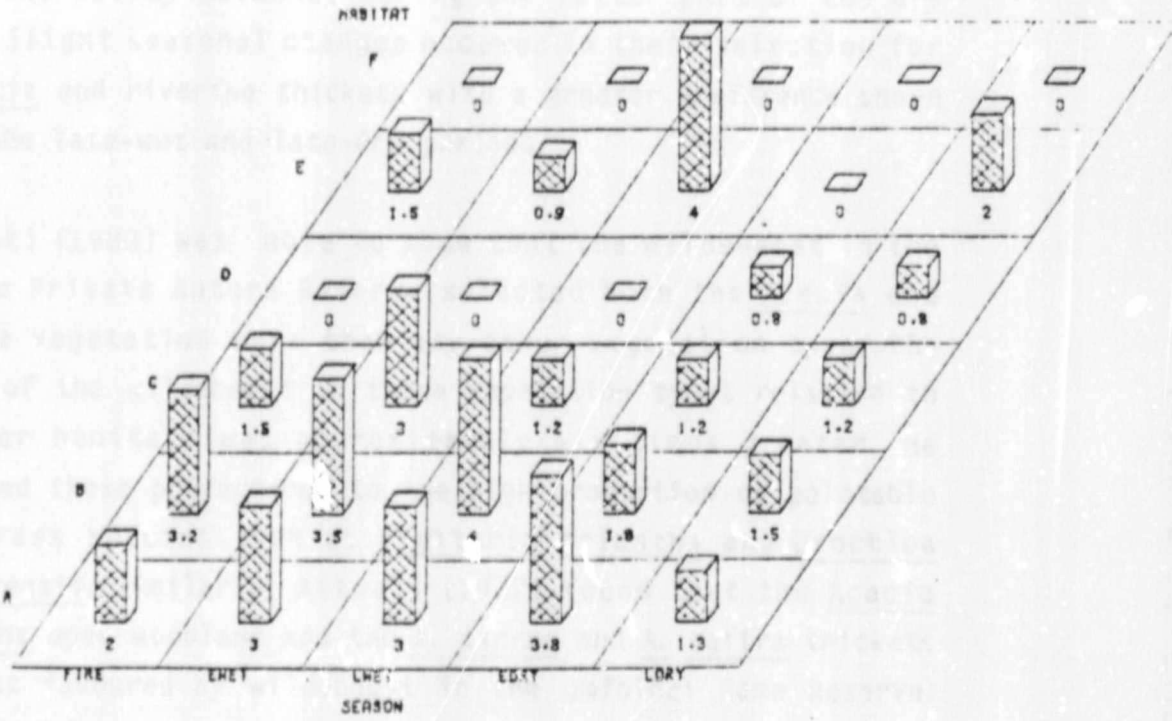

Figure 4.2 : Seasonal patterns of habitat selection by the Hartebeest in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = Cynodon dactylon "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

indicating a generalistic feeding behaviour similar to that of the white rhino. A positive selection for all habitats except the hillside savannas and Cynodon dactylon "lawns" was apparent (Figure 4.3). A high preference was shown for the secondary grasslands, valley savannas and thickets throughout the year. However, there was a greater tendency for the wildebeest to select the valley savannas during the latter part of the dry season. Slight seasonal changes occurred in their selection for the Acacia and riverine thickets with a greater preference shown during the late-wet and late-dry periods.

Witkowski (1983) was able to show that the wildebeest in the Klaserie Private Nature Reserve selected both the Acacia and riverine vegetation more than any other vegetation type. The density of the wildebeest in these vegetation types relative to the other habitats was approximately six times greater. He attributed these preferences to the high proportion of palatable short-grass species such as Digitaria eriantha and Urochloa mosambicensis. Similarly, Attwell (1977) found that the Acacia nigrescens open woodland and the A. karroo and A. caffra thickets were most favoured by wildebeest in the Umfolozi Game Reserve. These habitats were dominated by either Panicum maximum, Themeda triandra or Cyperus textilis. Hirst (1975) found that in the Timbavati reserve in the Transvaal, the wildebeest were most often associated with "open short-grass savannas". Other habitats which were frequently utilized by the Timbavati population included the "wooded short- and tall-grass savannas" and the sparsely wooded "grass / forblands".

Similar results were obtained in the Pilanesberg Game Reserve where the more palatable species such as Heteropogon contortus, Rhynchyletrum repens and Themeda triandra are present in both the secondary grasslands and valley savannas. The relationship between habitat selection and diet is discussed in section 4.3.3.

4.4.1.4 Zebra

Figure 4.4 and Appendix 3 show the seasonal changes in the

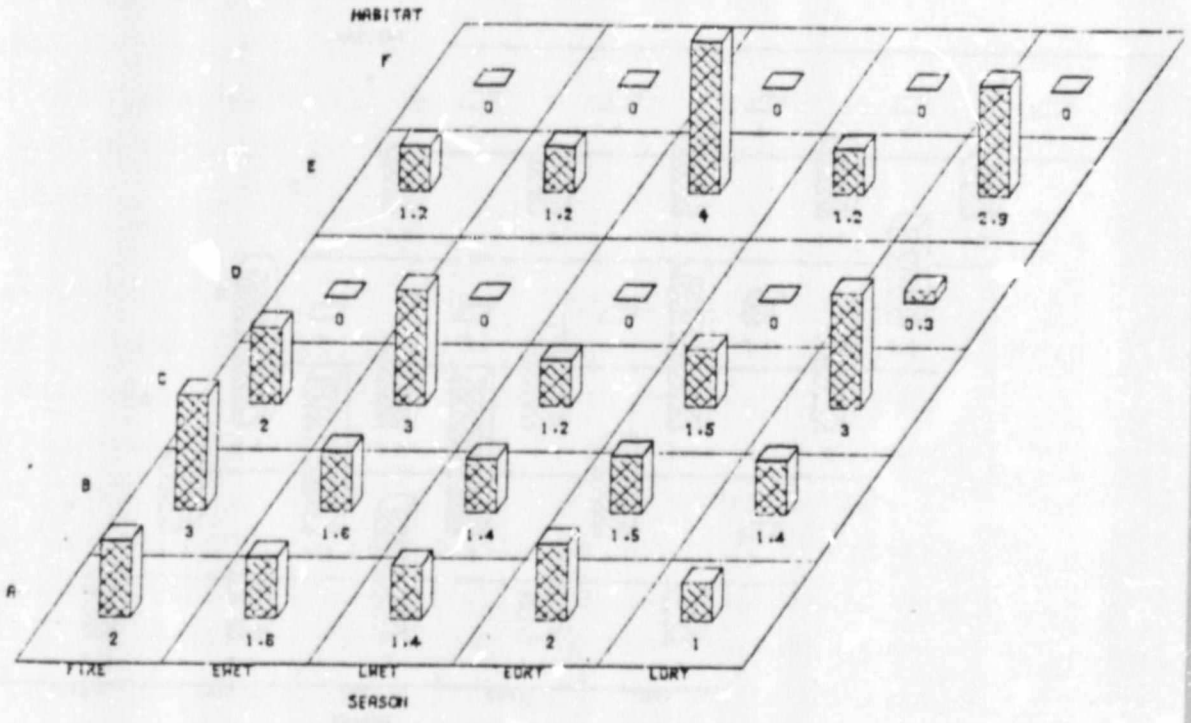

Figure 4.3 : Seasonal patterns of habitat selection by the Wildebeest in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = Cynodon dactylon "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

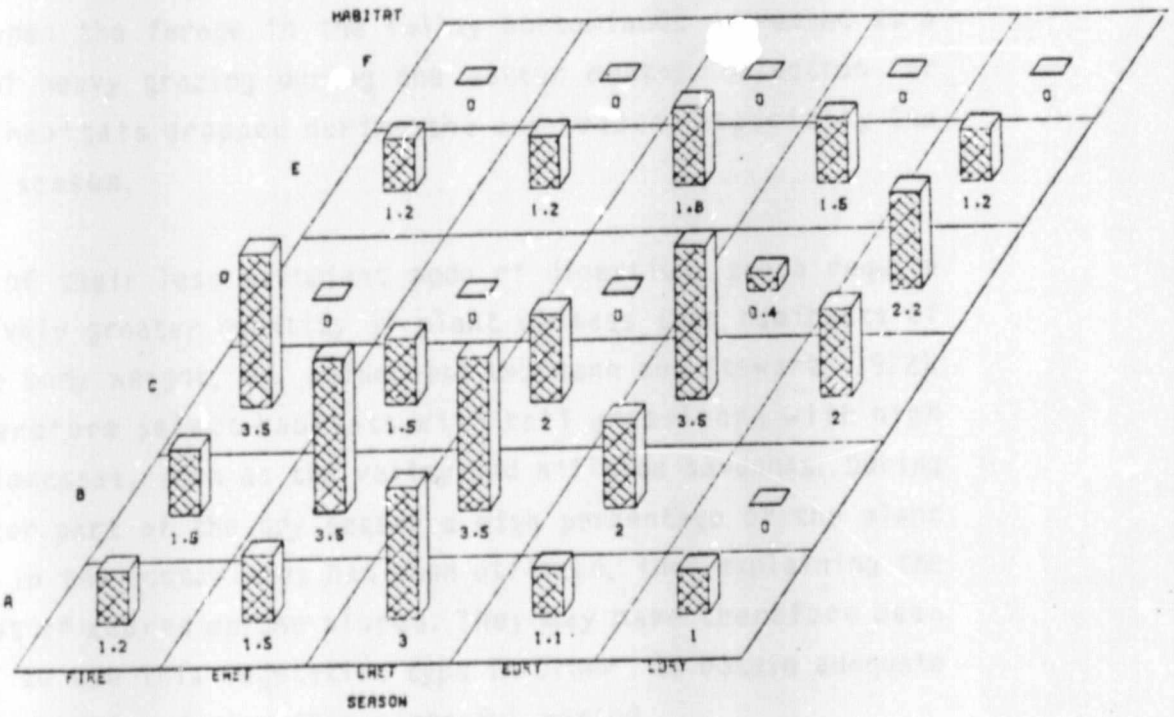

Figure 4.4 : Seasonal patterns of habitat selection by the Zebra in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = Cynodon dactylon "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

preferences for the six major habitat types by the zebra. There was generally a high positive selection for the secondary grasslands, valley savannas and pediment grasslands throughout most of the year. There was also a slight tendency for the zebra to select positively for the Acacia and riverine thickets especially during the late-wet seasons. It was also interesting to note the sudden positive selection for the hillside savannas during the late-dry season. There was thus a movement up the slopes when the forage in the valley bottomlands decreased as a result of heavy grazing during the wetter months. Selection for all the habitats dropped during the dry season, especially the late-dry season.

Because of their less efficient mode of digestion, zebra require a relatively greater quantity of plant biomass than ruminants of the same body weight, eg. wildebeest (Hofmann and Stewart, 1972). They therefore select habitats with tall grasslands with high plant biomasses, such as the valley and hillside savannas. During the latter part of the dry season a high percentage of the plant biomass in the bottomlands had been utilized, thus explaining the movement of zebras up the slopes. They may have therefore been "forced" to use this vegetation type in order to obtain adequate forage to survive during this stressful period.

4.4.1.5 Impala

The impala were included in this study for two reasons; firstly, because of their relatively high densities, and secondly, because of their ability to maintain these high densities under adverse environmental conditions (Dassman and Mossman, 1962). Although, this species is classed as an intermediate or mixed feeder, ie. it alternates from a browsing to a grazing habit, its high densities do have a heavy impact on the habitat and its condition.

Their most preferred habitats were, firstly, the Acacia and riverine thickets, and secondly, the valley savannas (Figure 4.5 and Appendix B). The impala showed a negative selection for the

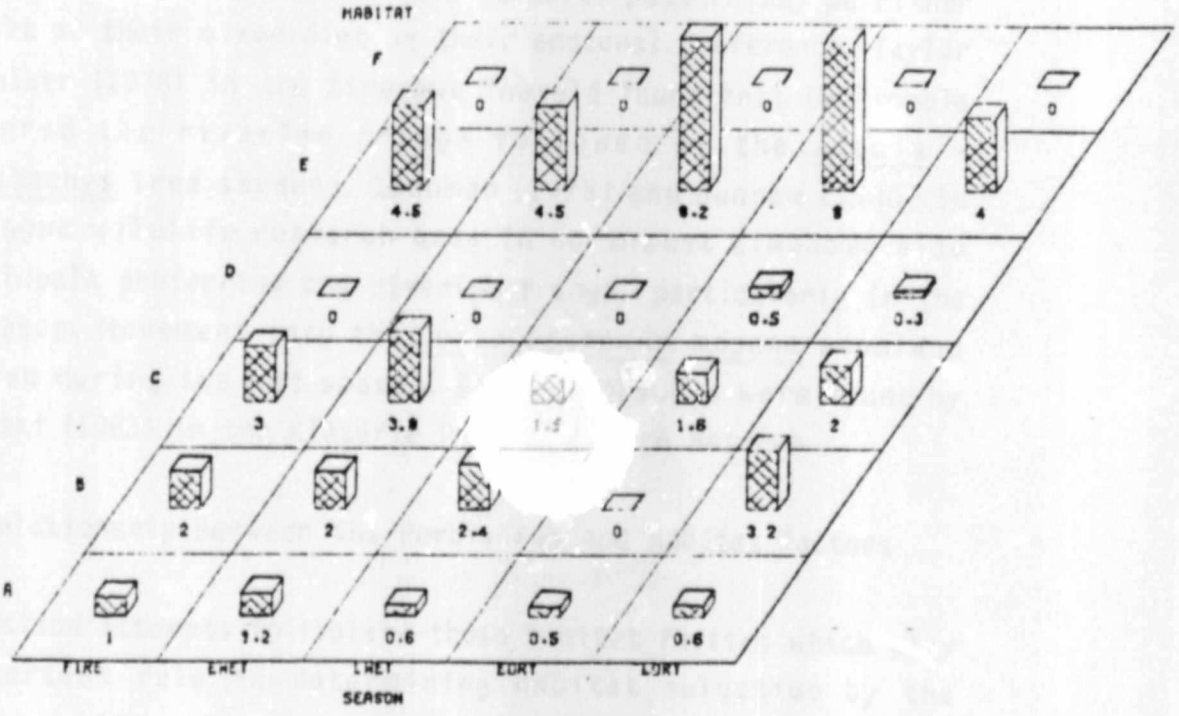

Figure 4.5 : Seasonal patterns of habitat selection by the Impala in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = Cynodon dactylon "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

hillside savannas throughout the entire year, and for pediment grasslands only during the early-dry season.

Figure 4.5 shows a slight alternate selection between the thickets and the valley savannas. The Acacia and riverine thickets were preferred during the late-wet and early-dry seasons, with higher preferences shown for the valley savannas during the early-wet seasons. This seasonal pattern may be either a result of their mixed diet or their ecotonal preference. Taylor and Walker (1978) in the Zimbabwe lowveld found that the impala preferred the riverine fringe followed by the Acacia - Spirostachys tree savanna. Goodman (1975) and Dunnam (1980) in the Sengwa wildlife research area in northwest Zimbabwe also found impala preferring the riverine fringe, particularly in the dry season. Movement into the Colophospermum mopane woodland occurred during the wet season. Similar results were found by Witkowski (1983) in the Klaserie Private Nature Reserve.

4.4.2 Relationship Between the Herbivores and Habitat Factors

This section attempts to isolate those habitat factors which play an important role in determining habitat selection by the herbivores. It has become apparent in a number of studies (eg. Ferrar and Walker, 1974; Attwell, 1977) that herbivores select for certain microhabitat factors when feeding.

In order to extract those variables influencing the herbivores' habitat selection, the frequency scores of the herbivore species for each of the 35 habitat factors were used (Table 4.2). The information output retained by the computer will be first explained, and then the results interpreted.

Table 4.3 gives the breakdown of the inertia (ie. the dispersion of the points in space) for each axis or factor. Those axes which contribute the most to the scattering have higher eigenvalues. The total inertia (I), is calculated as the sum of the moments of inertia for each axis (Beardall, 1982). Each eigenvalue is expressed as a percentage of the total inertia

Table 4.2 : Frequencies of Association of the 5 Herbivore Species with each of the 35 Habitat Factors. A key to Habitat Factors is given in Table 4.1 (n = Total number of observations).

	Canopy									Grass Height			Grass Species							
	Canopy			Lateral			Herbaceous													
SPECIES	CCA	CCB	CCC	LCA	LCB	LCC	HCA	HCB	HCC	HEA	HEB	HEC	CYDA	ARCO	RHRE	HECO	THTR	ERCU	ERSU	ERRI
White rhino:Fire	1	5	1	4	2	1	1	2	3	2	4	1	6	5	3	4	2	2	3	3
Early wet	18	6	0	21	4	0	1	7	17	8	18	0	19	10	9	19	5	13	15	17
Late wet	5	8	5	12	3	3	0	2	16	3	14	0	14	6	2	8	2	10	9	8
Early dry	12	6	5	11	9	3	1	2	20	1	17	5	20	18	12	22	10	16	8	16
Late dry	4	4	1	6	1	1	0	0	9	1	8	0	6	5	3	9	4	4	4	6
Wildebeest	11	3	2	14	2	0	1	0	15	1	10	5	14	13	9	11	4	15	7	8
Hartebeest	10	1	3	12	1	0	0	1	13	0	6	7	9	11	10	9	5	9	5	8
Zebra	2	5	5	8	0	0	0	0	8	0	6	2	2	7	5	7	6	2	3	1
Impala	1	0	3	2	2	0	0	2	2	1	3	0	3	3	0	2	1	4	1	4

Table 4.2 : (Cont.)

SPECIES	ERGU	UNPA	HYHI	BOIN	BRSE	URMO	LOFL	DIER	PADE	PACO	POSQ	SPPY	CHVI	SENI	ERCR	n
White rhino:Fire	0	2	3	0	2	0	0	2	0	0	0	0	0	0	3	9
Early wet	0	12	14	1	2	8	0	3	3	0	1	2	0	2	4	22
Late wet	0	4	4	3	1	14	0	3	11	2	0	4	5	1	5	16
Early dry	3	11	10	3	6	11	0	6	12	9	2	2	5	1	10	23
Late dry	2	5	8	0	5	4	0	3	5	4	2	0	1	0	4	10
Wildebeest	4	10	10	3	7	6	0	7	2	5	5	5	3	0	5	16
Hartebeest	5	10	11	0	7	4	1	6	0	3	6	0	1	2	5	12
Zebra	1	6	2	1	3	2	3	1	0	0	0	3	0	0	0	10
Impala	0	0	1	0	1	2	0	1	3	0	0	2	0	0	2	4

Table 4.3 : Moments of Inertia and their Percentage of the Total Inertia.

FACTOR	INERTIA (eigenvalue)	PERCENT	CUMUL. PERC.
1	0.0850	32.2	32.2
2	0.0541	20.5	52.7
3	0.0528	20.0	72.7
4	0.0227	8.6	81.3
5	0.0199	7.5	88.8
6	0.0122	4.6	93.4
7	0.0094	3.6	97.0
8	0.0080	3.0	100.0

(column PERCENT) and the cumulative percentages of inertia are listed in the column headed CUMUL. PERC.

The program then calculates the decomposition of the moments of inertia for the subjects and the objects, respectively (Tables 4.4 and 4.5). In other words, it calculates the contribution that both the subjects (herbivores) and objects (habitat factors) make on each axes' inertia (see below).

From Tables 4.4 and 4.5 the following information can be extracted, based on Beardall (1982);

(i) For each point the mass (defined as the proportion of the contribution that each subject makes on the whole sample) and inertia are given in the columns headed MASS and INR, respectively.

(ii) For each moment of inertia and corresponding principle axis the coordinate of the point on the axis (column headed F), and the relative contribution in the column headed CTR, are given.

(iii) The cosine squared of the angle that the point makes with this subspace is given in the column headed QLT. Beardall (1982) has defined this value as the quality of each point's representation in the subspace of the first three axes. It is calculated as the sum of the relative contributions of these axes.

From Table 4.3 it can be seen that 72.7 percent of the inertia is accounted for by the first 3 moments of inertia. Thus, only the first 3 axes are considered.

By analyzing Tables 4.4 and 4.5 in conjunction with the graphical display (Figure 4.6), interpretations can be made so as to relate the herbivore feeding sites to particular habitat factors. It should be noted that the axes are so orientated as to account for maximum inertia (or scattering) in the ordination space. Thus, the values under columns COR - the contribution of the axis to the inertia of the subjects or objects - and those in

Table 4.4 : Decomposition of the first 3 Moments of Inertia in terms of the Herbivore Species and Seasons (subjects).

NAME		QLT	MASS	INR	1 F	COR	CTR	2 F	COR	CTR	3 F	COR	CTR
White rhino:	Fire	997	45	78	119	31	8	-248	138	52	-164	60	23
	Early wet	998	170	154	160	107	52	-283	336	252	-347	507	391
	Late wet	996	127	152	464	684	324	53	8	7	213	144	111
	Early dry	996	208	66	57	39	8	200	475	154	80	77	26
	Late dry	996	81	51	-27	4	1	175	184	46	1	0	0
Wildebeest:	Dry	995	148	70	-231	336	80	138	152	53	-37	11	4
Hartebeest:	Dry	997	123	137	-481	790	338	107	39	27	-111	42	29
Zebra:	Dry	997	62	199	-392	183	113	-595	420	408	575	390	391
Impala:	Dry	995	31	90	455	272	77	11	0	0	207	56	26

Table 4.5 : Decomposition of the first 3 Moments of Inertia in terms of the Habitat Factors (objects). See Table 4.1.

	NAME	QLT	MASS	INR	1 F	COR	CTR	2 F	COR	CTR	3 F	COR	CTR
1	CCA	995	43	25	-86	48	4	-38	9	1	-311	632	80
2	CCB	996	25	44	217	104	14	-348	269	58	221	107	24
3	CCC	997	17	53	30	1	0	-198	48	12	764	712	189
4	LCA	996	61	18	-43	25	1	-218	623	55	-66	58	5
5	LCB	996	16	25	394	374	30	162	63	8	-23	1	0
6	LCC	997	5	27	709	384	32	367	103	14	390	116	16
7	HCA	995	2	15	105	7	0	-209	30	2	-511	180	14
8	HCB	996	10	49	606	308	47	-496	207	50	-510	219	54
9	HCC	995	70	5	-10	5	0	-17	14	0	67	205	6
10	HEA	996	11	45	641	396	56	-525	267	60	-569	313	72
11	HEB	997	58	11	182	631	23	-103	206	12	23	9	1
12	HEC	996	13	47	-827	741	110	215	49	12	89	8	2
13	CYDA	997	63	13	165	494	20	30	16	1	-129	309	20
14	ARCO	997	53	12	-158	404	16	-24	10	1	75	89	6
15	RHRE	996	36	21	-348	759	52	-75	36	4	-67	28	3
16	HECO	996	62	11	-11	2	0	-77	131	7	-36	30	2
17	THTR	996	26	22	-241	261	18	-174	137	15	235	247	28
18	ERCU	996	51	13	57	44	2	122	208	14	-59	50	3
19	ERSU	995	37	15	165	242	12	-194	342	26	-161	235	19
20	ERRI	996	41	17	101	92	5	236	510	43	19	3	0
21	ERGU	998	10	33	-810	766	79	413	199	32	31	1	0
22	UNPA	996	41	17	-275	675	37	-124	138	12	-59	31	3
23	HYHI	996	43	21	-161	202	13	19	2	0	-273	576	61
24	BOIN	996	7	17	214	73	4	115	21	2	393	248	22
25	BRSE	995	23	26	-440	653	53	127	53	7	71	16	2
26	URMO	995	34	32	350	491	50	123	60	10	168	113	19
27	LOFL	996	2	88	-1424	237	65	-1806	382	165	1755	360	160
28	DIER	995	21	11	-209	327	11	209	324	18	-54	22	1
29	PADE	997	24	72	673	579	131	396	200	71	340	148	54
30	PACO	996	15	36	-176	50	6	676	736	133	119	22	4
31	POSQ	997	10	44	-802	595	83	484	216	47	-284	75	17
32	SPPY	997	12	40	181	37	5	-245	69	14	548	342	70
33	CHVI	994	10	29	332	144	13	562	414	60	361	170	25
34	SENI	996	4	13	-70	5	0	-71	5	0	-455	230	16
35	ERCR	997	25	14	109	79	4	264	466	33	-39	10	1

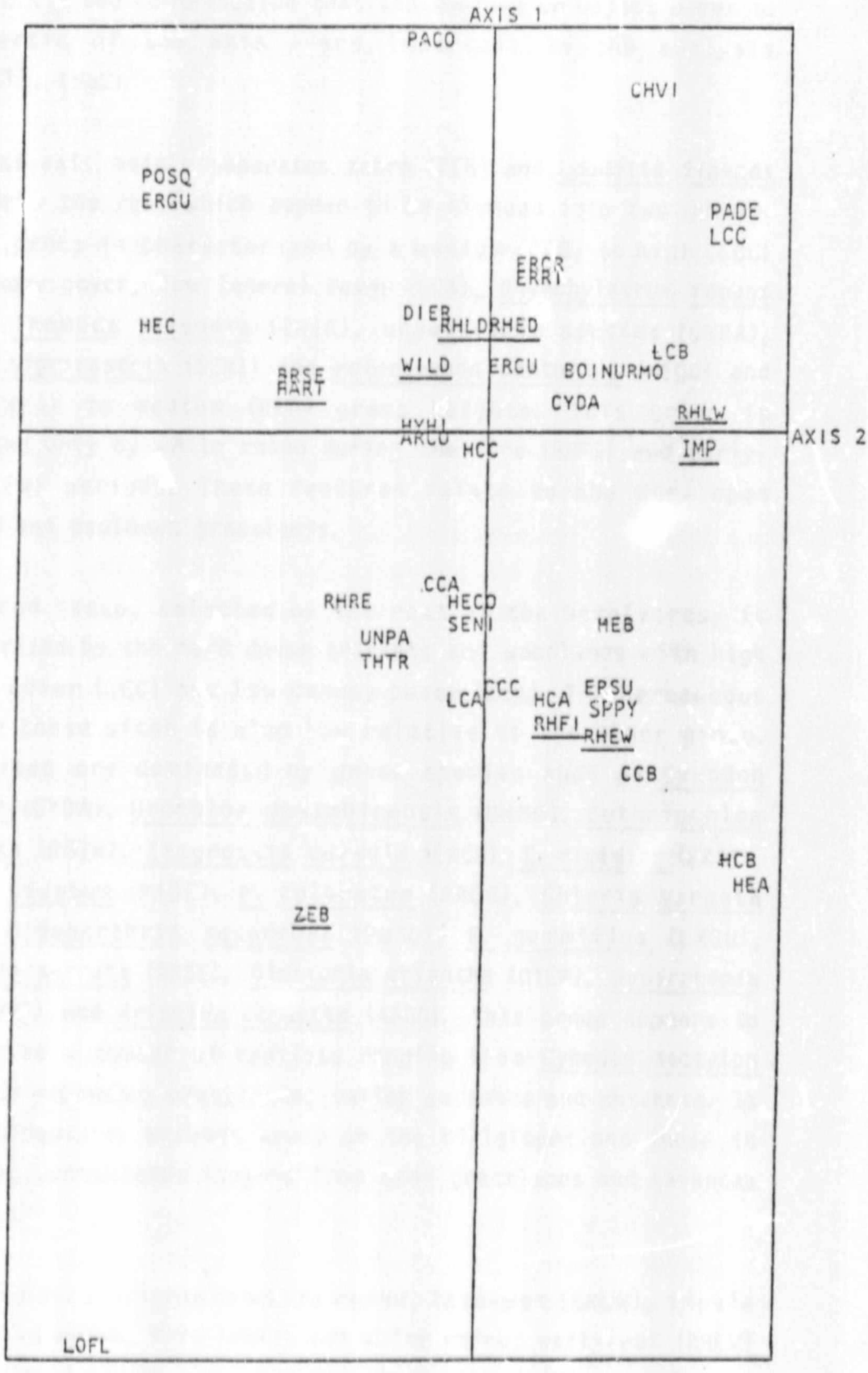

Figure 4.6 : Projections of herbivore species and habitat factors onto a plane of principal axes 1 and 2. A key to the species names and habitat factors is given in Appendix F.

column CTR - the contribution that the subject or object makes to the inertia of the axis - are important in the analysis (Beardall, 1982).

The first axis mainly separates zebra (ZEB) and Loudetia flavada (LOFL) from the rest which appear to be clumped into two groups. The one group is characterized by a medium (CCB) to high (CCC) tree canopy cover, low lateral cover (LCA), Rhynchyletrum repens (RHRE), Themeda triandra (THTR), unpalatable species (UNPA), Setaria nigrirostris (SENI) and Heteropogon contortus (HECO) and short (HEA) to medium (HEB) grass heights. This group is frequented only by white rhino during the fire (RHFI) and early-wet (RHEW) periods. These features relate to the more open savannas and pediment grasslands.

The second group, selected by the rest of the herbivores, is characterized by the more dense thickets and woodlands with high lateral cover (LCC) and low canopy cover (CCA). The herbaceous cover in these sites is also low relative to the other group. These sites are dominated by grass species such as Cynodon dactylon (CYDA), Urochloa mosambicensis (URMO), Bothriochloa insculpta (BOIN), Eragrostis curvula (ERCU), E. rigidior (ERRI), Panicum deustum (PADE), P. coloratum (PACO), Chloris virgata (CHVI), Pogonarthria squarrosa (POSQ), E. gummiflua (ERGU), Brachyaria serrata (BRSE), Digitaria eriantha (DIER), Hyparrhenia hirta (HYHI) and Aristida congesta (ARCO). This group appears to characterize a number of habitats ranging from Cynodon dactylon "lawns" to secondary grasslands, valley savannas and thickets. It also distinguishes between areas on the hillslopes and those in the valley bottomlands ranging from open grasslands and savannas to thickets.

The second axis contrasts white rhino, late-wet (RHLW), impala (IMP), white rhino, fire (RHFI) and white rhino, early-wet (RHEW) and habitat factors, short (HEA) to medium (HEB) grasslands, medium (LCB) to high (LCC) lateral cover, Panicum deustum (PADE) and Urochloa mosambicensis (URMO), with hartebeest (HART) and zebra (ZEB), and tall grasslands (HEC), Eragrostis gummiflua

(ERGU), Brachyaria serrata (BRSE) and Loudetia flavada (LOFL). This axis describes a gradient based on grass height, and lateral canopy cover.

Axis three (not displayed) contrasts white rhino, early-wet (RHEW) and white rhino, fire (RHFI) with zebra (ZEB) and white rhino, late-wet (RHLW). The habitat factors depict a gradient of short grasslands (HEA) with low (HCA) to medium (HCB) herbaceous cover, low canopy cover (CCA) and Setaria nigrirostris (SENI) to high canopy cover (CCC), Loudetia flavada (LOFL), Sporobous pyrimedalis (SPPY), Bothriochloa insculpta (BOIN) and Chloris virgata (CHVI).

Table 4.6 summarizes the output from this analysis by giving the "Importance Indices" of each habitat factor to the herbivore species. The index ranges from 0 (no preference or avoidance) to 1 (high preference). Thus the importance of each habitat factor to herbivore habitat selection can be analyzed.

Similar preferences were shown by the white rhino both after a burn, and during the early wet season. There is a high selection for short grasslands dominated by Rhynchyletrum repens (RHRE), Heteropogon contortus (HECO), Themeda triandra (THTR), Eragrostis superba (ERSU), unpalatable species (UNPA) and Setaria nigrirostris (SENI). These grasslands are typical of both the secondary grasslands and valley savannas classified in section 3.3.1. There is also a high preference for areas both of low (CCA) and high (CCC) canopy cover, suggesting that canopy cover probably plays a minor role during this period. There is however, a selection for habitats consisting of a low lateral cover index (LCA) and grass heights ranging from 0 to 10 cm (HEA). The structural feature, grass height therefore appears to play a major role in influencing white rhino habitat selection during the fire period.

During the late-wet season a greater selection is shown for the sites supporting the more palatable grass species, such as, Cynodon dactylon, Eragrostis curvula (ERCU), E. superba (ERSU),

Table 4.6 : Importance indices for each habitat factor by the herbivore species. A key to the habitat factors is given in Table 4.1

SPECIES . SEASON	Cover									Grass Height			Grass Species							
	Canopy			Lateral			Herbaceous													
	CCA	CCB	CCC	LCA	LCB	LCC	HCA	HCB	HCC	HEA	HEB	HEC	CYDA	ARCO	RHRE	HECO	THTR	ERCU	ERSU	ERRI
White rhino: Fire	0.8	0.9	0.9	0.9	0.5	0.4	1.0	0.9	0.8	0.9	0.9	0.3	0.5	0.4	0.7	0.9	0.8	0.2	0.9	0.2
Early wet	0.8	1.0	0.9	0.8	0.5	0.4	0.9	0.9	0.9	0.9	0.9	0.3	0.5	0.4	0.7	0.8	0.8	0.3	1.0	0.9
Late wet	0.4	0.5	0.5	0.5	0.9	0.8	0.5	0.6	0.3	0.6	0.6	0.1	0.9	0.0	0.2	0.4	0.3	0.6	0.6	0.7
Early dry	0.1	0.2	0.1	0.1	0.7	0.8	0.1	0.3	0.2	0.3	0.3	0.5	0.7	0.4	0.1	0.1	0.1	0.9	0.2	1.0
Late dry	0.2	0.1	0.1	0.1	0.6	0.6	0.0	0.1	0.2	0.1	0.1	0.7	0.5	0.6	0.3	0.1	0.2	0.8	0.8	0.1
Wildebeest: Dry	0.3	0.1	0.2	0.3	0.6	0.5	0.2	0.1	0.8	0.1	0.6	0.8	0.6	0.7	0.5	0.3	0.4	0.6	0.1	0.7
Hartebeest: Dry	0.5	0.3	0.4	0.4	0.3	0.3	0.5	0.3	0.6	0.3	0.2	0.9	0.2	0.9	0.6	0.5	0.6	0.5	0.3	0.5
Zebra . Dry	1.0	0.8	0.9	0.9	0.3	0.2	0.8	0.7	1.0	0.7	0.7	0.5	0.3	0.6	0.9	0.9	0.9	0.0	0.7	0.0
Impala : Dry	0.4	0.6	0.5	0.5	0.8	0.8	0.6	0.7	0.3	0.6	0.7	0.1	0.5	0.0	0.3	0.5	0.4	0.6	0.6	0.7

Table 4.4 : Decomposition of the first 3 Moments of Inertia in terms of the Herbivore Species and Seasons (subjects).

NAME		QLT	MASS	INR	1 F	COR	CTR	2 F	COR	CTR	3 F	COR	CTR
White rhino:	Fire	997	45	78	119	31	8	-248	138	52	-164	60	23
	Early wet	998	170	154	160	107	52	-283	336	252	-347	507	391
	Late wet	996	127	152	464	684	324	53	8	7	213	144	111
	Early dry	996	208	66	57	39	8	200	475	154	80	77	26
	Late dry	996	81	51	-27	4	1	175	184	46	1	0	0
Wildebeest:	Dry	995	148	70	-231	336	80	138	152	53	-37	11	4
Hartebeest:	Dry	997	123	137	-481	790	338	107	39	27	-111	42	29
Zebra:	Dry	997	62	199	-392	183	113	-595	420	408	575	390	391
Impala:	Dry	995	31	90	455	272	77	11	0	0	207	56	26

E. rigidior (ERRI), Urochloa mosambicensis (URMO) and Panicum deustum (PADE). Selection also occurs for sites of high lateral cover (LCC), eg. thickets with relatively short to medium grass heights. This period, relative to the first two depicts a greater preference for areas comprising of both greater lateral cover and high ratios of palatable to intermediate grass species. Hence, in comparison to the previous two periods, the structural components play only a minor role in the white rhinos' habitat selection with grass species composition being important.

Although still selecting for sites of high lateral cover, the white rhinos during the late-dry season show a high preference for the taller grasslands again with high palatable to intermediate ratios. The unpalatable grass species such as Elyonuris argenteus (ELAR), Cymbopogon species and Bothriochloa insculpta (BOIN) were either avoided or at least played no major role in habitat selection during this period.

To conclude, the factors important in white rhino habitat selection differ seasonally, thus suggesting that habitat diversity is neccessary for the survival of these animals in the reserve. In addition, the herbivores are still at reasonably low densities and yet there are still marked seasonal differences in their habitat selection. This again indicates the dependence on habitat diversity or heterogeneity for survival.

The wildebeest during the dry-season selected for similar habitat factors as the white rhinoceros. However, a greater preference was shown for areas of higher lateral cover, higher herbaceous cover and taller grasslands. Differences occurred in their selection for the dominant grass species in that higher selection indices were shown for areas dominated by Cynodon dactylon (CYDA), Aristida congesta (ARCO), Eragrostis rigidior (ERRI), Hyparrhenia hirta (HYHI), Brachyaria serrata (BRSE) and Pogonarthria squarrosa (POSQ). Thus, wildebeest tend to select for the taller grasslands with a high herbaceous cover.

The hartebeest selected for tall grasslands of relatively low

canopy and low lateral cover but with high herbaceous covers. Grass species characteristic of the relatively lower successional stages were preferred, eg. Aristida congesta (ARCO), Rhynchyletrum repens (RHRE), Themeda triandra (THTR), E. gummiflua (ERGU), Hyparrhenia hirta (HYHI), Brachyaria serrata (BRSE), Digitaria eriantha (DIER) and Pogonarthria squarrosa (POSQ). Thus the only important structural feature in determining the hartebeests' habitat selection was grass height.

The zebra depict interesting results in that either a high selection or complete avoidance for certain habitat factors occurred. They were highly selective for the open woodlands with grasses ranging from 10 to 15 cm in height. Sites of low canopy cover (CCA), low lateral cover (LCA) and low (HEA) to medium (HCB) herbaceous cover were also preferred. Sites dominated by grass species such as Rhynchyletrum repens (RHRE), Heteropogon contortus (HECO), Themeda triandra (THTR), unpalatable species (UNPA), Loudetia flavada (LOFL), Sporobolus pyrimedalis (SPPY) and Setaria nigrirostris (SENI) were highly preferred whereas, sites dominated by Cynodon dactylon (CYDA), E. curvula (ERCU), E. rigidior (ERRI), E. gummiflua (ERGU), Bothriochloa insculpta (BOIN), Urochloa mosambicensis (URMO), Digitaria eriantha (DIER), Panicum deustum (PADE), P. coloratum (PACO), Chloris virgata (CHVI) and Eragrostis. species (ERCR) were generally avoided. The areas selected by the zebra were characteristic of the hillside savannas which supported a relatively higher density of zebra during the dry season. Hence in this species habitat selection was based to a large extent on the structural components.

Impala selected for areas of relatively high canopy and lateral cover with short to medium grass heights typical of Acacia and riverine thickets. Grass species such as Bothriochloa insculpta (BOIN), Urochloa mosambicensis (URMO), Sporobolus pyramidalis (SPPY), Chloris virgata (CHVI) and Eragrostis species (ERCR) were highly selected with relatively complete avoidance for site factors typical of the more open habitats. Hence both the structural components and the grass species composition play an important role in the impalas' habitat selection

To conclude, Correspondence Analysis was able to extract and identify those habitat factors to which the herbivores either selected or avoided. However, this study was only able to analyze habitat selection based on the general habitat factors. The more subtle features, such as the effects of different nutritional values of the plant species, would have to be analyzed using experimental studies where comparisons can be made on both the feeding and non-feeding sites.

It is suggested from this analysis that certain physical characteristics of the habitat influences the habitat selection by the herbivores. The next section deals with dietary selection and its relationship to certain habitat factors.

4.4.3 Dietary Selection of the Five Main Grazers

4.4.3.1 Seasonality in the White Rhinos Diet

4.4.3.1.1 Overall Diet

The seasonal variation in the diet of the white rhinoceros is first considered and then related to the dietary selection of the other four grazers during the dry season.

Table 4.7 and Appendix F gives the results of the seasonal changes in the dietary preferences of the white rhinos, averaged for all habitat types. Only the grasses comprising over five percent of the diet or over five percent availability for at least one of the grazers are considered in the analyses. The seasons cover the months discussed in section 3.3.3.

Eighteen different grass species were recorded in the diet of the white rhinoceros population at Pilanesberg. However, only 6 of the species comprised about 70% of their diet with Eragrostis superba (average 10.3%), Heteropogon contortus (average 19.2%), Hyparrhenia hirta (average 12.5%), Panicum deustum (average 11.6%) and Urochloa mosambicensis (average 9.4%) being the most

Table 4.7.

Seasonal changes in the Percentage Contribution in the diet, of the grass species, for the white rhino at Pilanesberg. Standard errors are given in parentheses. A key to the grass species is given in Appendix F.

Species	Fire	Early wet	Late wet	Early dry	Late dry
CYDA	20.9(8.0)	0.8(1.5)	5.8(3.3)	2.3(1.8)	4.3(3.7)
RHRE	1.9(1.1)	4.4(1.4)	0.2(0.6)	4.5(2.5)	4.9(4.0)
HECO	21.2(5.1)	13.0(6.1)	11.3(4.9)	26.5(6.5)	24.1(9.3)
THTR	4.1(0.7)	0.7(1.3)	1.4(1.7)	6.6(3.1)	4.4(3.8)
ERCU	5.0(3.5)	4.2(3.4)	10.1(4.6)	4.3(2.5)	3.4(3.3)
ERSU	12.9(3.9)	23.8(8.4)	4.3(2.9)	2.3(1.8)	8.2(5.2)
ERRI	2.9(1.6)	1.6(2.1)	6.6(3.7)	4.1(2.4)	3.1(3.1)
ERGU	3.8(3.3)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.6(1.3)
HYHI	23.2(5.5)	19.0(7.4)	1.5(1.7)	3.7(2.3)	15.0(7.2)
BOIN	0.0(0.0)	0.0(0.0)	2.5(2.2)	0.7(1.0)	0.0(0.0)
BRSE	0.3(0.3)	6.2(4.1)	0.1(0.4)	6.8(3.1)	2.1(2.6)
URMO	1.7(1.4)	9.4(5.1)	27.4(7.8)	5.3(2.8)	3.1(3.1)
LOFL	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)
DIER	2.2(1.2)	3.4(3.0)	5.2(3.3)	5.4(2.8)	5.0(4.0)
PADE	0.0(0.0)	6.3(4.1)	18.8(6.4)	20.6(5.7)	12.5(6.5)
PACO	0.0(0.0)	0.0(0.0)	3.5(2.7)	5.6(2.8)	9.3(5.6)
SPPY	0.0(0.0)	7.3(4.5)	1.5(1.7)	1.2(1.2)	0.0(0.0)
UNPA	8.0(2.3)	15.0(6.5)	2.0(2.0)	1.0(1.2)	0.0(0.0)

important throughout the year. Similar results were found by Owen-Smith (1973) in the Umfolozi population with Themeda triandra (35.5%) being the most important grass species.

The main seasonal differences in the white rhinos diet concerns the significant increas or decrease in one or more of the following species (refer to Appendix); Digitaria eriantha (DE), Cynodon dactylon (CD), E. superba (ES), E. rigidior (ER), Heteropogon contortus (HC), Hyparrhenia hirta (HH), E. curvula (EC), Brachyaria serrata (BS), Themeda triandra (TT), Panicum deustum (PD), P. coloratum (PC), Urochloa mosambicensis (UM), Sporobolus pyramidalis (SP) and unpalatable species (UP).

Dietary selection during the fire and early-wet seasons both appear to be similar in terms of grass species selection, except for a significant decrease in the use of Cynodon dactylon ($t=7.77$, $p<0.001$) and increase in Heteropogon contortus ($t=3.24$, $p<0.001$). Thus the bulk of the white rhino's diet during these periods consisted of Eragrostis superba (ES), Heteropogon contortus (HC), Hyparrhenia hirta (HH) and to a lesser extent, Cynodon dactylon (CD) and unpalatable species (UP).

It is interesting to note that during the flush after a burn, and during the early-wet season, unpalatable grass species (UP) such as Cymbopogon excavatus and Elyonurus argenteus were present in their diet.

During the latter part of the wet season, the white rhinos showed an increase in selection for Panicum deustum (PD) and Urochloa mosambicensis (UM) and, to a lesser extent Digitaria eriantha (DE), Cynodon dactylon (CD), E. rigidior (ER), Panicum coloratum (PC) and Bothriochloa insculpta (BI). In contrast, the selection for E. superba ($t=7.40$, $p<0.001$), Hyparrhenia hirta ($t=7.38$, $p<0.001$), Brachyaria serrata ($t=4.64$, $p<0.001$), Sporobolus pyrimedalis ($t=3.23$, $p<0.01$) and unpalatable species ($t=5.65$, $p<0.001$) declined during the late wet season.

The early-dry season showed a similar dietary selection as the

previous season with only significant differences in Rhynchyletrum repens ($t=-4.96$, $p<0.001$), Heteropogon contortus ($t=-5.88$, $p<0.001$), Brachyaria serrata ($t=-7.21$, $p<0.001$), Themeda triandra ($t=-4.91$, $p<0.001$) and which increase, and Cynodon dactylon ($t=3.51$, $p<0.01$), Eragrostis curvula ($t=3.25$, $p<0.01$) and Urochloa mosambicensis ($t=8.14$, $p<0.001$) which decrease. Both Heteropogon contortus (HC) and Panicum deustum (PD) account for just under 50% of their diet during this period.

Significant dietary changes occurred during the late-dry season in selection for Eragrostis superba ($t=-3.52$, $p<0.01$) and Hyparrhenia hirta ($t=-4.78$, $p<0.001$) which increase, and Brachyaria serrata ($t=3.73$, $p<0.01$) and Panicum deustum ($t=2.74$, $p<0.01$) which decrease. The white rhinos' diet during this period consists mainly of Heteropogon contortus (HC), Hyparrhenia hirta (HH), Panicum deustum (PD) and P. coloratum (PC) totalling to approximately 51%.

To summarize, high selection for palatable species such as Eragrostis superba (ES), Heteropogon contortus (HC), Hyparrhenia hirta (HH), Panicum deustum (PD), P. coloratum and Urochloa mosambicensis (UM) was evident and together accounted for over 60% of their annual diet. Significant changes occur between one or more of the above grass species depending on the season and the habitat (see below). Minor changes occurred between the less dominant species such as Cynodon dactylon (CD), Rhynchyletrum repens (RR), Eragrostis rigidior (ER), E. curvula (EC), Brachyaria serrata (BS), Themeda triandra (TT) and Panicum coloratum (PC).

4.4.3.1.2 **Relationship between Diet and Habitat Choice**

Appendix G shows the seasonal differences in the percentage contribution to the diet (PC), and the preference indices (PI) for the grasses eaten by the white rhinos within each habitat type. It is evident that diet changes not only seasonally but also within each habitat type. However because of the small sample size per habitat, the grass species were categorized as

either palatable-tall, palatable-creeper, intermediate or unpalatable (see Table 3.). The percentage contribution of each dietary type is given in Table 4.8

During the fire period, valley savannas and secondary grasslands were mainly selected (see Figure 4.1), hence dietary differences only within these two habitats were considered. In both habitats the palatable species such as E. superba (ES) and Heteropogon contortus (HC), the intermediate species such as Themeda triandra (TT), Eragrostis curvula (EC), E. rigidior (ER), Hyparrhenia hirta (HH) and Digitaria eriantha (DE), and unpalatable species (UP) were preferred.

Similarities in the overall feeding patterns in both habitat types is confirmed by the Chi-square test results. However there was a slight preference for the two palatable feeding categories in the secondary grasslands. There was no significant difference in the selection for the various dietary types in the valley savannas, thus indicating that no preference for the particular grass species occurred during this period. A similar phenomenon of no preference for dietary types also occured during the early-wet season, and may be attributed to the fact that most grass species tend to be highly nutritious during the rainy season.

The late-wet season showed a tendency for the white rhinos to select Acacia and riverine thickets, valley savannas and termitaria to a greater extent than during the previous two seasons. There was no significant difference in the white rhinos' feeding pattern between the valley savannas and termitaria, except avoidance for the unpalatable species was apparent in the valley savannas. However, significant differences did result between the intermediate and the two palatable feeding types in the termitaria. Despite this, significant differences were shown in their diets between the habitats, with a high preference for Heteropogon contortus ($t=6.20$, $p<0.001$), E. superba ($t=3.51$, $p<0.001$), and Sporobolus pyrimedalis ($t=4.03$, $p<0.001$) in the valley savannas, and Urochloa mosambicensis ($t=3.11$, $p<0.001$), Digitaria eriantha ($t=4.09$, $p<0.001$) P. deustum ($t=7.79$, $p<0.001$)