Habitat utilisation by Cape mountain zebras in the Mountain Zebra National Park, South Africa

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This study investigated the seasonal patterns of vegetation community use by the Cape mountain zebra within the Mountain Zebra National Park over one seasonal cycle. Day-time censuses revealed that the zebras utilised all the different vegetation communities that were defined in the park, with the exception of the riparian bush community. Year-round the zebras made greatest use of the grassland vegetation communities, together with those shrubland and dwarf shrubland communities that offered high grass biomasses. Selectivity for vegetation communities was greatest during the wet season, when the zebras favoured those grassland communities on the plateaus over other vegetation communities on the mountain slopes and in the ravines. During the dry season the zebras showed a greater diversity in their use of vegetation communities, and made greater use of those vegetation communities on the mountain slopes and in the ravines. The results suggest that the seasonal variations in vegetation community use by the zebras were in response to changes in the annual rainfall pattern.

Key words: Cape mountain zebra, vegetation community use, selectivity, diversity, nonruminant grazers, nutritional value, grass biomass

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Introduction

Large herbivores are not evenly distributed across a region while foraging, but rather favour certain habitat types over others (McNaughton & Georgiadis 1986). Preference for a given habitat type is largely determined by the available vegetation within the area, which provides the herbivore with food, water, minerals, shelter from climatic extremes and cover from predators (Jarman & Sinclair 1979). Of these vegetation features, food is considered to be the most important factor influencing habitat use among large herbivores (McNaughton 1987). Hence, herbivores favour those habitat types or vegetation communities in which they can maximise their nutrient intake at any time of the year (Westoby 1974; Owen-Smith & Novellie 1982; Owen-Smith 1985).

Food resources, however, not only vary between different habitat types, but also show marked seasonal variations within a given habitat, in response to changes in rainfall patterns (Phillipson 1975; Sinclair 1975). As a result, large herbivores move seasonally between the different habitat types to feed in those vegetation communities offering the highest forage quality and abundance at any given time (Bell 1971; McNaughton 1987). These movements occur either in the form of long-distance migrations, as can be seen among blue wildebeest (*Connochaetes*

taurinus) and plains zebras (*Equus burchellii*) in the vast ecosytems of the East African plains (Pennycuick 1975), or in the form of more irregular nomadic movements, characteristic for many large herbivores in smaller conservation areas (Hirst 1975; Melton 1987).

The Mountain Zebra National Park is a small conservation area, which was established to safeguard the endangered Cape mountain zebra (*Equus zebra zebra*) from extinction (Grobler & Hall-Martin 1982). When considering management objectives for the conservation of the zebras, it is important to know how these animals utilise the different vegetation communities available to them. Hence, the objective of this paper was to assess the seasonal changes in vegetation community use by the Cape mountain zebra in the Mountain Zebra National Park, and to determine which vegetation communities were favoured for feeding.

Study area

The Mountain Zebra National Park (MZNP), covering an area of 6 536 ha, is situated on the north-facing slopes of the Bankberg mountain range near the town of Cradock in the eastern Cape Province. Eight steep-sided ravines run from the Bankberg range to the Wilgerboom River, which traverses the central valley of the MZNP in a north-easterly direction at 1 200 m above sea level. Along the western boundary of the MZNP the Kranskop mountain ridge runs parallel to the river at an altitude of 1 800 m above sea level. Northward this ridge opens into the extensive low-lying Rooiplaat plateau. The highest point of the MZNP, Bakenkop, extends from the Bankberg range, reaching a height of 1957 m above sea level. The mean annual rainfall in the MZNP over the period 1962-1989 was 392 mm (range 351-651 mm). Daily temperatures can exceed 40 °C in the hottest month, while winter temperatures regularly drop below 0 °C. The vegetation in the MZNP is dominated by an abundance of grasses and dwarf shrubs, classified as Eastern Mixed Karoo (Van der Walt 1980). In addition to Cape mountain zebras, other large herbivores present in the MZNP included mountain reedbuck (*Redunca fulvorufula*), springbok (*Antidorcas marsupialis*), black wildebeest (*Connochaetes gnou*), blesbok (*Antidorcas marsupialis*), red hartebeest (*Alcelaphus buselaphus*), eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), klipspringer (*Oreotragus oreotragus*), steenbok (*Raphicerus campestris*), and grey duiker (*Sylvicapra grimmia*).

Methods

Habitat classification for the analyses in this paper was based on the vegetation communities in the MZNP that were described in detail by Van der Walt (1980). Thirteen habitat types (vegetation communities) were identified, on the basis of their floristic and physiognomic characteristics (see Van der Walt 1980) (Table 1). The extent of some of these vegetation communities has changed in recent years under the influence of rainfall (see Novellie & Strydom 1987).

Seasonal changes in the use of the vegetation communities by the zebras in the MZNP were determined during day-time censuses by locating the zebras from the circuit road that runs through the park. Most parts of the MZNP are visible from vantage points along the roads which allowed for accurate locations of the zebras in the field. Night censuses were not feasible during this study because of the nature of the terrain and the relative nervousness of the animals at night.

The data on vegetation community use was collected at the group level rather than at the individual level for two practical reasons. Firstly, the social structure of mountain zebras takes the form of small groups in the forms of breeding herds and bachelor

groups, rather than of lone individuals (Penzhorn 1979). Secondly, individual animals are easily overlooked during censuses when hidden behind trees or rocky outcrops, thus presenting room for bias in the data analysis.

Emphasis in this study was placed on breeding herds only. Breeding herds occur in stable social units which remain together at most times (Penzhorn 1979). Each breeding herd was individually known to the observer since each individual zebra could be identified on the basis of its distinct striping pattern. A total of 21 breeding herds occupied the MZNP during the course of the study period, varying in group size from three to nine animals. Contrary to the breeding herds, bachelor groups commonly change in composition, with group sizes varying from two to over 10 animals, while sightings of individual males are not uncommon (Penzhorn 1979). Hence bachelor groups were excluded from the analyses, since each census rarely represented a total count of the entire zebra population. Breeding herd sightings, however, were complete during each census.

At each sighting of a breeding herd, the vegetation community in which the group was located was recorded. A minimum of three censuses was carried out each month, with a total of 43 censuses for the entire year. Independence between individual observation periods was ensured since successive censuses were carried out during different weeks in each month.

The censuses collected over the study period were grouped into four seasons which were identified on the basis of changing grass sward characteristics as a result of the annual rainfall pattern. These were: (i) late growing season (December-February) when the sward was tall with an abundant supply of green material; (ii) early dormant season (March-May) when the grasses were mature and green but plant growth had ceased; (iii) late dormant season (June-August) when the grasses were dry and senescent; and (iv) early growing season (September-November) when the grasses were mainly dry but some new growth had emerged.

Seasonal habitat use by the zebras was calculated for each month of the study period as the proportional number of breeding herds that were sighted within each vegetation community. A Chi-square test of homogeneity (Zar 1984) was used to test for seasonal variations in vegetation community use.

To test whether observations of habitat use followed the expected patterns of occurrence based upon proportional habitat availability, a Chi-square goodness-of-fit analysis (Zar 1984) was applied. When the Chi-square test detected a significant difference in habitat use versus habitat availability, the Bonferroni z-statistic (Neu, Byers & Peek 1974) was employed to determine which habitat types were used more or less frequently than expected.

The use of the above methods for determining habitat preferences was based on several assumptions. For the Chi-square goodness-of-fit analyses, independence between successive observations was required, which was ensured since successive observations were carried out during different weeks in each month. A further assumption was that a large sample size was used for a normal distribution approximation to the binomial distribution to be valid. In this study the Chi-square test was applied under the condition that ± 20% of all habitat types contained <5 expected observations.

Overall selectivity for habitat types was quantified using the selectivity index S of McNaughton (1978), where

$$S = \Sigma\ |P_{io} - P_i|/2,$$

and where P_{io} was defined as the observed proportion of zebra breeding herds occurring in habitat i. P_i expressed the expected proportion of zebra breeding herds in habitat i. This index could vary from 0 to 1, where higher values denoted increasing selectivity.

The Shannon-Wiener diversity index H' (Zar 1984) was used to indicate seasonal changes in diversity of habitat use, where

$$H' = -\Sigma\ P_{io} \log P_{io}.$$

Table 1.

The vegetation communities in the Mountain Zebra National Park, with descriptions, areas and the percentage of the total study area covered by each community (modified from Van der Walt, 1980)

Vegetation community (Abbreviation)	Description	Area (ha)	%
Riparian bush (RB)	Tall, woody riverine vegetation, dominated by tall *Acacia* and *Diospyros* shrubs.	153	2.3
Peak afromontane grassland (PGL)	Mesic grass- and shrubland community on summits and higher slopes, dominated by the grass species *Merxmuellera disticha*.	548	8.4
Slope afromontane grassland (SGL)	Mesic grass- and shrubland community on steep slopes, dominated by *Euryops* and *Elytropappus* dwarf shrubs, and by the grass species *Merxmuellera disticha*.	1081	16.5
Rocky plateau grassland (RGL)	Grass- and shrubland community on plateaus on hot shaly slopes, dominated by the grass species *Themeda triandra* and by *Filicia* dwarf shrubs.	669	10.2
Degraded plateau grassland (DGL)	Plateau grass- and shrubland community on sandstone, dominated by *Eragrostis* grass species and by *Pentzia* dwarf shrubs.	856	13.1
Trampled plateau grassland (TGL)	Degraded grassland on plateaus, dominated by the low-growing grass species *Cynodon incompletus*.	162	2.5
Higher dolerite shrubland (HSL)	Xeric shrubland on higher doleritic pediment, dominated by the tall shrub *Rhus erosa* and by *Aristida*, *Eragrostis*, and *Heteropogon* grass species.	331	5.1
Lower doleritic shrubland (LSL)	Xeric shrubland on lower doleritic pediment, dominated by tall *Diospyros*, *Grewia*, and *Rhus* shrubs, and by *Aristida*, *Eragrostis* and *Themeda* grass species.	1275	19.5
Shaly slope shrubland (SSL)	Shrubland on hot shaly slopes, dominated by tall *Acacia* and *Diospyros* shrubs, and by *Cymbopogon*, *Digitaria*, *Heteropogon*, and *Setaria* grasses.	387	5.9
Lower slope dwarf shrubland (SDSL)	Xeric dwarf shrubland community on lower slopes, dominated by *Filicia* and *Walafrida* dwarf shrubs, and by *Aristida*, *Digitaria*, and *Heteropogon* grasses.	481	7.4
Dwarf shrubland on exposed soil (EDSL)	Degraded dwarf shrubland community on exposed subsoil, dominated by *Pentzia* dwarf shrubs and by *Eragrostis* grass species.	212	3.2
Overgrazed dwarf shrubland (ODSL)	Overgrazed dwarf shrubland community, dominated by *Becium* and *Eriocephalus* dwarf shrubs, and by *Eragrostis* and *Tragus* grass species.	37	0.6
Valley bottom dwarf shrubland (VDSL)	Dwarf shrubland community in the alluvium region of the Wilgerboom river, dominated by the dwarf shrub *Pentzia sphaerocephala* and by *Eragrostis* grasses.	344	5.3

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Table 2

Simultaneous confidence intervals using the Bonferroni z-statistic to determine utilization and preference of the different vegetation communities by Cape mountain zebras in the Mountain Zebra National Park. See text for definition of Bonferroni z-statistic. Abbreviations for vegetation communities are given in Table 1

		Late growing (N=252)		Early dormant (N=294)		Late dormant (N=168)		Early growing (N=189)	
Vegetation community	Expected proportion of usage (P_i)	Observed proportion of usage (P_{io})	Bonferroni intervals for (P_{io})	Observed proportion of usage (P_{io})	Bonferroni intervals for (P_{io})	Observed proportion of usage (P_{io})	Bonferroni intervals for (P_{io})	Observed proportion of usage (P_{io})	Bonferroni intervals for (P_{io})
RB	0.023	0	-	0	-	0	-	0	-
PGL	0.084	0.032	0.000-0.064*	0.027	0.000-0.055	0.047	0.000-0.094	0.020	0.000-0.050*
SGL	0.165	0.090	0.038-0.142*	0.133	0.075-0.190	0.171	0.087-0.255	0.189	0.107-0.271
RGL	0.102	0.339	0.253-0.425*	0.320	0.241-0.399*	0.224	0.131-0.317*	0.306	0.209-0.403*
DGL	0.131	0.146	0.082-0.210	0.109	0.056-0.162	0.124	0.050-0.198	0.076	0.020-0.132
TGL	0.025	0.012	0.000-0.032	0.014	0.000-0.033	0.006	-	0.015	-
HSL	0.051	0.047	0.008-0.086	0.044	0.009-0.079	0.041	0.000-0.085	0.046	0.002-0.090
LSL	0.195	0.154	0.088-0.220	0.194	0.127-0.261	0.218	0.126-0.310	0.168	0.089-0.246
SSL	0.059	0.055	0.013-0.097	0.051	0.014-0.088	0.082	0.021-0.143	0.051	0.005-0.097
SDSL	0.074	0.098	0.044-0.152	0.095	0.046-0.145	0.047	0.000-0.094	0.107	0.042-0.172
EDSL	0.032	0.004	0.000-0.016*	0.003	0.000-0.013*	0.012	0.000-0.036	0.005	0.000-0.020*
ODSL	0.006	0.004	-	0.003	-	0.012	-	0.005	-
VDSL	0.053	0.020	0.000-0.046*	0.007	0.000-0.021*	0.018	0.000-0.048*	0.012	0.000-0.035*

P_i defined as the expected proportion of the total number of zebra breeding herds occurring in habitat i.

P_{io} defined as the observed proportion of the total number of zebra breeding herds occurring in habitat i.

Bonferroni intervals calculated only for P_i when $NP_i \geq 5$

* indicates statistical significance at $P < 0.05$

Late growing (December-February)

Early dormant (March-May)

Late dormant (June-August)

Early growing (September-November)

N = number of observations.

P_{io} was defined as above. A zero value denoted no diversity, while higher values represented increasing diversity.

Both the selectivity index S and the diversity index H' did not represent absolute values, but rather relative indices which allowed for comparisons of the results between seasons.

Results

The zebras were found to utilise all the different vegetation communities that were identified in the MZNP, except in the case of the riparian bush community (RB) along the Wilgerboom River in the central valley of the park (Fig. 1). The zebras made greater use of the grassland communities, most notably those grasslands on the Rooiplaat plateau, than of the available shrubland and dwarf shrubland communities. Year-round, the rocky plateau grassland (RGL) community was used most frequently by the zebra breeding herds.

The Chi-square test of homogeneity revealed that habitat use by the zebras varied significantly between seasons ($\chi^2 = 36.5$, $\chi^2_{0.05,12} = 21.0$, $P < 0.001$). During the wet season period the zebras largely utilised the rocky plateau grassland community (RGL), with almost 40% of all breeding herds recorded in this community. However, use of this plateau community decreased during the dry season period, when the zebras made greater use of certain montane vegetation communities, in particular the lower doleritic shrubland (LSL) and the slope afromontane grassland community (SGL).

In all seasons, zebra breeding herds were selective in their choice of vegetation communities in which to feed (Table 2). The rocky plateau grassland (RGL) was the only vegetation community that was strongly selected for in each season, while other plateau grassland communities, including degraded plateau grassland (DGL) and trampled plateau grassland (TGL), were utilised as expected from availability. The peak afromontane grassland (PGL) was consistently selected against, except during the late dormant season when it was used as expected from availability, while the slope afromontane grassland (SGL) was avoided only during the late growing season. All shrubland communities were used as expected from availability, while certain dwarf shrubland communities, notably dwarf shrubland on exposed soil (EDSL) and valley bottom dwarf shrubland (VDSL), were avoided at all times.

Selectivity for habitat types by the zebras was greatest during the late growing season, but markedly decreased during the dry season periods, with the lowest selectivity during the late dormant season (Table 3). Conversely, diversity of habitats used by the zebras increased during the dry season periods, with the highest diversity recorded during the late dormant season.

Table 3
Seasonal variations in habitat selectivity (S) and habitat diversity (H'). See text for definitions of S and H'.

Season		S	H'
Late growing	(Dec-Feb)	0.276	0.842
Early dormant	(Mar-May)	0.220	0.864
Late dormant	(Jun-Aug)	0.178	0.894
Early growing	(Sep-Nov)	0.212	0.840

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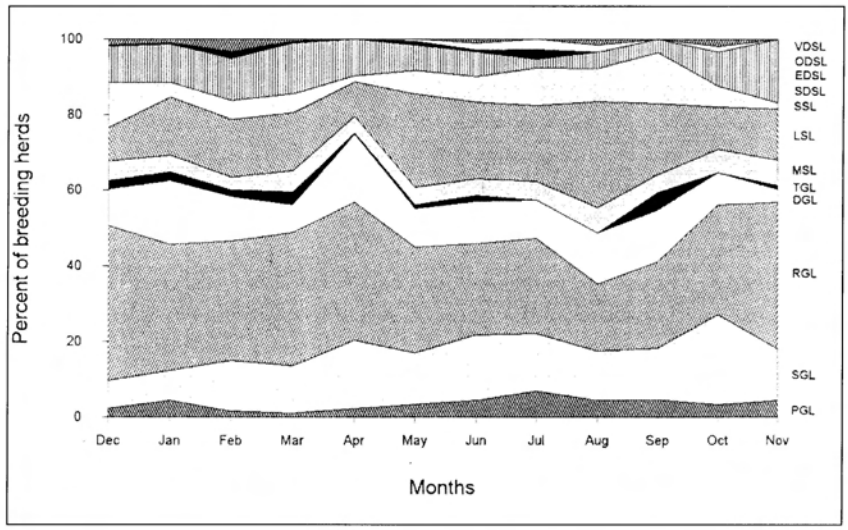

Fig. 1. Seasonal variations in vegetation community use by Cape mountain zebras in the Mountain Zebra National Park (as a percentage of the total sightings of all breeding herds in each vegetation community for each month of the study period). Abbreviations for vegetation communities are given in Table 1.

Discussion

The wide dispersion of the zebras across the different vegetation communities that were defined in the MZNP was in accord with theoretical predictions concerning habitat use among wild equids (Janis 1976; Owen-Smith 1982, 1985). Zebras, like other equids, are nonruminant, hindgut fermenters that do not achieve as high a digestive coefficient for a given forage as do ruminant or foregut fermenters of comparable body size (Janis 1976; Owen-Smith 1982). As a result, intake requirements per unit body weight are higher among nonruminants than among comparable herbivores with a foregut digestive system. In order to meet these high intake demands, theory suggests that nonruminants achieve their optimal foraging performance feeding on a diversity of available food plants in vegetation communities with high plant biomasses (Bell 1971; Janis 1976; Jarman & Sinclair 1979; Owen-Smith 1982). Winkler (1993) demonstrated that Cape mountain zebras feed on a diversity of available grass species, while the present study revealed a preference for vegetation communities with high grass abundance. The results from these studies, together with those from earlier research on Cape mountain zebras (Penzhorn 1982), thus lend support to the above theory. Similar observations were noted during studies on other nonruminant grazers, including Hartmann mountain zebras (*Equus zebra hartmannae*) (Joubert 1973), plains zebras (*Equus burchellii*) (Hirst 1975; Melton 1987) and feral horses (*Equus caballus*) (Duncan 1983; Pratt *et al.* 1986).

In spite of the above theoretical implications on nonruminant habitat use, the day-time censuses revealed that the zebras consistently avoided the riparian bush community along the Wilgerboom River

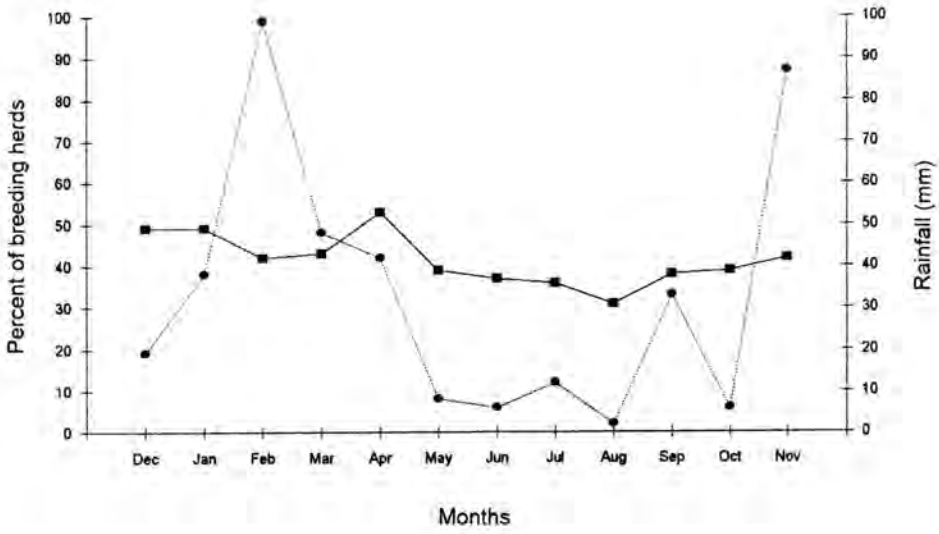

Fig. 2. Monthly sightings of Cape mountain zebra breeding herds on the Rooiplaat plateau (expressed as the percentage of the total sightings of all breeding herds over the entire park for each month of the study period) (solid line), plotted with the monthly rainfall totals in the Mountain Zebra National Park (dashed line).

valley, although grass availability within this community was high year-round. The zebras possibly avoided this community during day-time hours, because of the presence and activities of humans in the staff and visitor facilities, which were situated along the river valley.

The zebras rarely utilised the dwarf shrubland communities for feeding. Van der Walt (1980) noted that grasses were rare in these vegetation communities, while the most abundant grass species were of relatively low nutritional value, including *Aristida*, *Eragrostis* and *Tragus* species. It thus appears most likely that the zebras avoided these communities because the available grass biomass and the nutritional quality of the available grass plants were too low throughout the year for the zebras to meet their high intake and nutrient demands. Notably, the lower dwarf shrubland community, which was regularly utilised by the zebras year-round, was characterised by a high grass diversity and grass availability (Van der Walt 1980). Similarly, the zebras favoured those tall shrubland communities with high grass biomasses, while largely avoiding those shrubland communities where grass availabilities were low.

The study demonstrated that, on a year-round basis, the zebras tended to favour certain grassland vegetation communities for feeding. This was to be expected from a grazing herbivore (Owen-Smith 1982;

McNaughton & Georgiadis 1986), since grass biomass was naturally high in each season within these communities (Van der Walt 1980). The trampled plateau grassland was the only grassland community that was rarely utilised by the zebras for feeding, presumably because the most abundant grass plants in these areas were below the feeding height required by the zebras (Grobler 1983). The rocky plateau grassland community, in contrast, was strongly selected for by the zebras throughout the year. This community carries the highest biomass of grazing herbivores in the MZNP, including not only the mountain zebras, but also other large herbivores, such as springbok, blesbok, red hartebeest, and black wildebeest (Novellie *et al.* 1988). Preference for this community was probably related to the dominant grass species in this community, *Themeda triandra* (Van der Walt 1980), which is known to be the favoured food plant of Cape mountain zebras (Grobler 1983; Winkler 1993; Novellie & Winkler 1993), and of most of the other grazing herbivores that are common on the plateau (Grobler 1983).

Marked seasonal variations in vegetation community use by the zebras were previously recorded by Penzhorn (1982), who noted seasonal movements of the zebras from the Rooiplaat plateau to the mountain slopes. The results from the present study showed that the zebras were most selective in their choice of vegetation communities during growing seasons, when largely feeding in the rocky plateau grassland on Rooiplaat. Vegetation community use became more diverse during the dry season periods when the zebras made greater use of those communities on the mountain slopes and in the ravines. Similar patterns in seasonal vegetation community use have been noted for other zebras, including Hartmann mountain zebras (Joubert 1973) and plains zebras (Melton 1987).

Novellie *et al.*(1988) noted that the seasonal movements of the zebras in the MZNP were associated with a change in diet quality, as indicated by the crude protein contents of the preferred food plants and in the faeces of the zebras. However, if the nutritional content of the available forage was to be considered the overriding factor influencing the seasonal variations in vegetation community use by the zebras, one would expect all zebras to move into those areas offering the highest available nutrients at a given time. Yet, the results from the present study showed that the zebras were widely dispersed across all vegetation communities at any time of the year, rather than concentrated within those areas offering the highest available nutrients.

Thus, during the growing season several breeding herds remained in the mountain vegetation communities, although Novellie *et al.* (1988) found that the nutrient contents were highest among the grasses on the Rooiplaat plateau.

Conversely, during the dry season periods, when the nutrient contents of the available forage were highest in the vegetation communities on the mountain slopes (Novellie *et al.* 1988), certain breeding herds did not leave the plateau grasslands. Furthermore, although zebra numbers on the plateau fluctuated during the course of the year, the rocky plateau grassland community on Rooiplaat remained favoured by the zebras throughout the year, in spite of the relatively low nutrient contents of grasses in this community during the dry periods. These observations indicate that, in addition to nutrient availability, other factors were of importance in influencing the seasonal movements of the zebras between the different vegetation communities.

Optimal foraging theory suggests that a herbivore's choice of a vegetation community

for feeding is aimed at maximising the net rate of nutrient intake (Westoby 1974; Owen-Smith & Novellie 1982). Hence, habitat use is not only influenced by the nutritional contents of the available food plants, but also by the overall food availability in terms of grass biomass (Senft *et al.* 1987). This is particularly important for nonruminant grazers, in view of their high intake requirements, as discussed above.

The grass biomass available within a given vegetation community is influenced primarily by variations in the annual rainfall pattern (Phillipson 1975; Sinclair 1975). Hence, several studies investigating the seasonal variations in vegetation community use among large herbivores in African grasslands have related these movements to periodic changes in rainfall (Bell 1971; Hirst 1975; Pennycuick 1975).

The same phenomenon was noted during the present study, where zebra numbers on the plateau grasslands were closely associated with variations in rainfall (Fig. 2). Similar observations were made by Penzhorn (1982) and Novellie *et al.* (1988). The observations suggest that the seasonal fluctuations of zebra numbers on the Rooiplaat plateau were related to changes in grass biomass, as a result of the annual rainfall pattern. Thus, zebra numbers on the plateau grasslands were lowest during the dry season period, when the available grass biomass within these communities was low. The reverse was the case during the growing season.

The observations thus suggest that the seasonal variations in vegetation community use by the zebras were not only influenced by changes in grass quality (in terms of the nutritional value of the available forage), but also by variations in grass quantity (in terms of the available grass biomass). However, it is important not to view these factors in isolation, since aspects other than food availability, including water, mineral licks, shelter, as well as social factors, are also known to influence habitat use among other large herbivores (Jarman & Sinclair 1979; McNaughton 1987).

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