Factors affecting the seasonal movements of Cape mountain zebras in the Mountain Zebra National Park

P.A. Novellie*
Mountain Zebra National Park, P/Bag X66, Cradock, 5880 Republic of South Africa
L.J. Fourie, O.B. Kok and M.C. van der Westhuizen
Department of Zoology, University of the Orange Free State, P.O. Box 339, Bloemfontein, 9300 Republic of South Africa

Received 11 February 1987; accepted 13 July 1987

Factors underlying the movement of mountain zebras from a plateau in the summer to hill slopes and ravines in the winter were investigated. The movement was associated with a relative change in diet quality (as indicated by crude protein contents of preferred food plants and of the faeces) between the summer and winter habitats. In summer faecal and grass protein contents were higher in samples collected on the plateau than in those collected on the hill slopes. In the winter the reverse was the case. On the plateau the cover of grasses in the height range favoured by zebras changed only slightly from summer to winter. It thus seemed unlikely that the movement of zebras was caused by a seasonal change in the height structure of the grass sward. The diet comprised mostly grasses but traces of dicotyledons in the faeces were found more frequently during winter than summer.

Faktore wat die beweging van bergkwaggas vanaf 'n plato gedurende die somer na heuwelhellings en klowe gedurende die winter beïnvloed, is ondersoek. Die bewegingspatroon word geassosieer met 'n relatiewe verandering in voedselkwaliteit (soos aangedui deur die ruproteïen-inhoud van voorkeurvoedselplante en van die mis) tussen die somer- en winterhabitatte. Die ruproteïen-inhoud van grasse en mis wat gedurende die somer op die plato versamel is, was hoër as dié van die heuwelhellings. Gedurende die winter is die omgekeerde egter waar. Die grasbedekking op die plato in die hoogteklas waaraan bergkwaggas voorkeur verleen, het slegs geringe verandering tussen die somer en winter getoon. Dit lyk dus onwaarskynlik dat die beweging van bergkwaggas deur 'n seisoensverandering in die hoogtestruktuur van die grasveld veroorsaak word. Hoewel die dieet hoofsaaklik uit grasse bestaan, het spore van dikotiele meer dikwels gedurende die winter as gedurende die somer in die mis voorgekom.

*To whom correspondence should be addressed

Seasonal migrations are characteristic of many populations of the indigenous grass-eating ungulates of Africa (Smuts 1972; Sinclair 1977; McNaughton 1979; Sinclair & Fryxell 1985). It has been suggested that the seasonal rotation of grazing pressure resulting from these migrations allows the system to support a higher density of grazers than would be the case if the animals were confined to only a part of their annual range (Sinclair & Fryxell 1985). This has serious implications for conservation areas that are too small to allow seasonal movements of ungulates, and lack of space for such movements is often regarded as one of the main justifications for culling. An understanding of the principles underlying seasonal changes in habitat use is of value for the successful management of wild ungulates in small reserves.

The Mountain Zebra National Park (eastern Cape Province, Republic of South Africa) is the main stronghold of the rare Cape mountain zebra (*Equus zebra zebra*). This Park covers an area of only 6536 ha, but despite its small size the mountain zebra population does show a regular seasonal movement, from an open grassy plateau in the summer to more wooded hill slopes and ravines in the winter (Penzhorn 1982; Grobler 1983).

This study investigated two factors that might govern this seasonal movement: (i) a change in the nutrient content of the diet of zebras in the summer and winter habitats and (ii) a change in the cover and height distribution of the grass sward in the two habitats.

The cover and height distribution of the sward were measured because these factors influence the rate of nutrient intake in grazing ungulates (Chacon & Stobbs 1976, 1977; Owen-Smith 1985), and they have been shown to be of potential importance in determining seasonal changes in habitat use (Bell 1970). Grobler (1983) showed that grass height has an important influence on food selection in Cape mountain zebras. In common with plains zebras (Bell 1970), they favour taller grass than most antelope species, harvesting most of their food between 50 mm and 150 mm from the ground (Grobler 1983).

Crude protein content was chosen as a measure of food value because it provides a rough indication of the concentration of available nutrients in plant material (Owen-Smith & Novellie 1982). Several studies have shown that for large herbivores that feed mainly on grasses it is possible to use the protein content of the faeces as an index of dietary protein content (Arman, Hopcraft & McDonald 1975; Erasmus, Penzhorn & Fairall 1978; Zimmerman 1980). But if browse (leaves and shoots of woody plants or forbs) comprises a major proportion of the diet then the relationship between dietary and faecal protein contents is much less close (Mould & Robbins 1981). Grobler's (1983) finding that mountain zebras feed largely on grasses implies that faecal protein contents would provide a satisfactory indication of diet quality. It was nevertheless necessary to check on the proportion of browse in the zebra's diet during the study period. This was done by identification of plant fragments in the faeces.

Thus the winter and summer habitats were compared with respect to (i) the crude protein content of important food plants, (ii) the protein content of the diet of the zebras as indicated by faecal protein content, (iii) grass height and cover, and (iv) the proportion of browse in the diet.

Study area

The Mountain Zebra National Park, situated 24 km south-west of the town of Cradock, lies in the transitional zone between the arid dwarf shrubland of the western and central Karoo and the eastern dry grasslands. The vegetation is typically co-dominated by grasses and dwarf shrubs. Plant communities of the Park are described by Van der Walt (1980).

The mean annual rainfall for the years 1962 to 1986 is 389 mm, of which 70% falls in the summer months October to March. Temperatures can be as high as 42°C in summer and as low as –7°C in winter, with occasional snow on the higher mountains.

A plateau known as Rooiplaat, approximately 1500 ha in area at an elevation of 1300 m to 1400 m above sea level, forms the north-western part of the Park. The terrain in the remainder of the Park is mainly mountainous. Several steep-sided drainage lines or kloofs run from the mountain tops to the Wilgerboom River, which traverses the central valley of the Park. The lowest point, the valley bottom where the Wilgerboom River makes its exit, is 1200 m above sea level and the highest point is 1957 m above sea level.

Precipitation and average monthly temperatures recorded during the study period are shown in Table 1. Precipitation was recorded at one station on the Rooiplaat plateau, the favoured summer grazing area of the zebras, and at two stations in the favoured winter habitat. Temperature was recorded at one station in the winter habitat. June and July were the coldest months and January the hottest. The seasonal distribution of rainfall was similar at all three stations.

During the study period (January 1985 to August 1986) the mountain zebra population fluctuated between 130 and 160 individuals. Other ungulates present in the Park were black wildebeest (*Connochaetes gnou),* blesbok (*Damaliscus dorcas phillipsi),* eland *(Taurotragus oryx),* grey duiker (*Svlvicapra grimmia),* klipspringer *(Oreotragus oreotragus),* kudu *(Tragelaphus strepsiceros),* mountain reedbuck *(Redunca fulvorufula),* red hartebeest (*Alcelaphus buselaphus),* springbok *(Antidorcas marsupialis)* and steenbok (*Raphicerus campestris).*

Methods

Counts of mountain zebras

The numbers of zebras on the Rooiplaat plateau were counted once or twice per month from January 1985 to August 1986 (with the exception of April 1985) by an observer in a vehicle. Most parts of the plateau are visible from a circuit road, and the open nature of the terrain allowed a reasonably accurate count. Because of the broken terrain and the higher density of woody cover, regular counts of zebra numbers were not made on the hill slopes that provide the favoured winter habitat.

Table 1 Monthly precipitation (in mm) and average temperatures (°C) recorded in the Mountain Zebra National Park between January 1985 and August 1986. The stations Babylonstoren and Grootkloof are in the winter habitat of the zebras, Rooiplaat is in summer habitat

	Station			
Month	Babylonstoren Temperature	Babylonstoren Rain	Grootkloof Rain	Rooiplaat Rain
Jan.	22,3	90,6	129,5	148,4
Feb.	20,1	125,5	76,8	92,7
Mar.	18,0	21,3	22,9	27,4
Apr.	15,9	18,0	21,2	20,6
May	11,3	3,6	0	0
Jun.	9,9	12,7	22,0	43,6
Jul.	8,9	0,8	1,6	0
Aug.	12,3	0	0	0
Sep.	14,0	14,8	14,5	14,2
Oct.	17,6	64,1	50,5	51,0
Nov.	19,4	76,5	82,3	88,2
Dec.	18,2	149,4	118,1	150,5
Jan.	20,6	102,6	102,3	63,3
Feb.	19,5	39,0	57,8	47,2
Mar.	18,3	49,9	60,5	61,0
Apr.	16,1	4,3	3,0	34,3
May	13,2	0	0	0
Jun.	9,0	6,3	8,0	3,0
Jul.	8,5	0	0	0
Aug.	10,7	17,1	25,5	17,3

Collection and crude protein analysis of food plants

The following grass species were chosen for analyses of crude protein content:

(i) *Themeda triandra,* a species which occurs in both the summer and winter habitats, and which was found by Grobler (1983) to be the grass most favoured by the zebras.

(ii) *Setaria sphacelata,* which occurs on the hill slopes and valleys of the northeastern part of the Park (winter habitat). It is also favoured by mountain zebras (Grobler 1983).

(iii) *Eragrostis curvula,* common on the Rooiplaat plateau but rare elsewhere. It is only moderately favoured by the zebras (Grobler 1983) but by virtue of its dominance on the plateau it probably contributes significantly to their diet.

Samples of *Eragrostis curvula, Setaria sphacelata* and

Themeda triandra were collected at four- to five-week intervals between January and December 1985. On the plateau the samples were collected during the last weeks of January, February and March, and during the first weeks of each of the months May to December. On the hill slopes collection times were as above except that no samples were collected during January.

In each sampling period the following numbers of samples of each grass species were clipped:

Themeda triandra (i) plateau: 10–12 samples
(ii) hill slopes: 4–7 samples
Setaria sphacelata (hill slopes only): 5–7 samples
Eragrostis curvula (plateau only): 10–12 samples.

The dry weight of each sample was 5–15 g. The grass tufts were clipped off at heights of 30–50 mm from ground level. Culms were removed from the samples, which therefore included mostly leaves with some sheaths. Each sample was collected from a different locality, chosen in areas frequented by mountain zebras. Care was taken not to resample grass tufts that had been clipped in previous sampling periods.

The samples were dried in a forced-draught oven, milled and analysed for crude protein content using the standard Kjeldahl nitrogen determination.

Collection and analysis of faeces for crude protein content and plant fragments

Fresh mountain zebra faeces were collected during the same periods as the grass samples. In each sampling period 7–12 samples from the hill slopes, and 8–12 samples from the plateau, were collected. Each sample of faeces was divided into two subsamples. One of these was oven-dried and analysed for crude protein using the Kjeldahl procedure. The other was kept for microscopic examination of plant fragments. The fragments were separated and classified as either grass, woody stems, or other parts of dicotyledons. After drying and weighing the percentage contribution of each of these groups to the total weight of identified fragments was calculated.

Changes in grass cover and height

The magnitude of seasonal variation in grass cover and height were assessed by means of point surveys conducted at permanently marked sites, using the method of Roux (1963) and Vorster (1982). The survey sites were chosen in areas known to be utilized by mountain zebras. Distribution maps (Grobler unpublished) of sightings of zebra groups were used as a guide to choosing the sites. Thirteen sites were located on the plateau and six on the hill slopes.

The points surveyed at each site were arranged in rows of 25, with 1-m spacing between points. The rows were spaced 3 m apart. From 6 to 10 rows were sampled at each site giving 150 to 250 points. Each point was recorded as either a 'miss' if it contacted bare earth or rock or a 'strike' if it fell within the perimeter of the canopy of a plant (see Roux 1963). For each strike the plant species and the height from ground level to the tallest leaf (measured for grasses only) were recorded.

The sites were surveyed in March–April 1986, when large numbers of zebras were on the plateau, and again in August–September 1986, when most of the zebras had moved away from the plateau to the hill slopes. The sites were marked with stakes so that the repeat surveys were conducted at the same locations as the initial ones. The numbers of sites surveyed were not sufficient to be representative of conditions prevailing over the whole of the summer and winter ranges of the zebras. The intention was to examine the magnitude of seasonal variation in grass height and cover in selected examples of favoured summer and winter habitat.

Statistical analysis

To test whether the seasonal movement of the zebras could be related to a change in diet quality the grass and faeces samples were grouped into two periods:

Period I. February to May, and December, i.e. those months when more than 40 zebras were counted on the plateau (Figure 4).
Period II. June to November, those months when less than 40 zebras were counted on the plateau (Figure 4).

The protein content of food plants and faeces were compared between (i) the hill slopes and the plateau and (ii) Period I and Period II by means of two-factor analysis of variance. The grass and faecal protein contents did not meet the requirements for analysis of variance in that variances were heterogeneous (variances were higher during the wet season than during the dry season). The analysis was therefore performed on log transformed data (Snedecor & Cochran 1967).

Results

In general the pattern of seasonal variation in the crude protein content of the faeces was similar to that of the grasses, i.e. high during the summer months (January to March and November–December) and low during the winter (June to August) (Figures 1, 2 and 3). This supports the conclusion that the faecal protein content

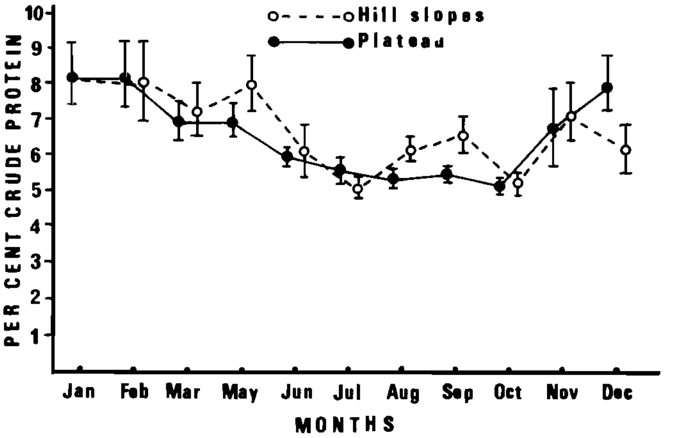

Figure 1 Changes in the crude protein contents of mountain zebra faeces collected on the plateau and on the hill slopes, January to December 1985. Means are shown with 95% confidence limits.

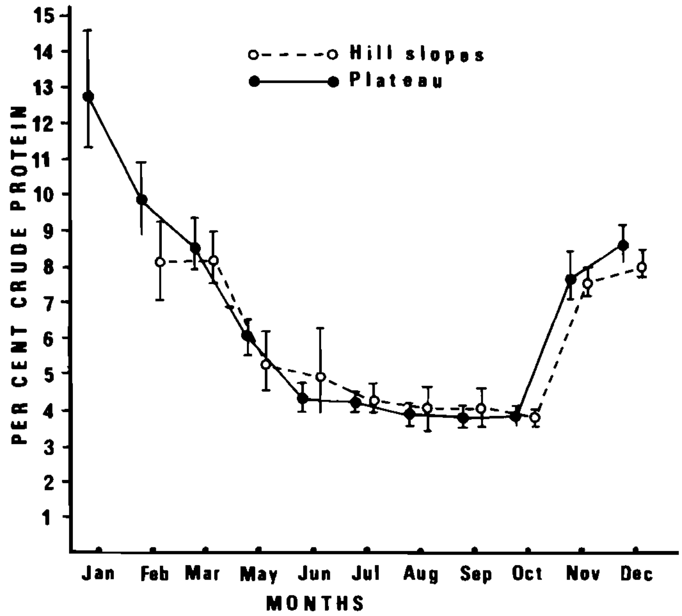

Figure 2 Changes in the crude protein contents of the grass *Themeda triandra* collected on the plateau and on the hill slopes, January to December 1985. Means are shown with 95% confidence limits.

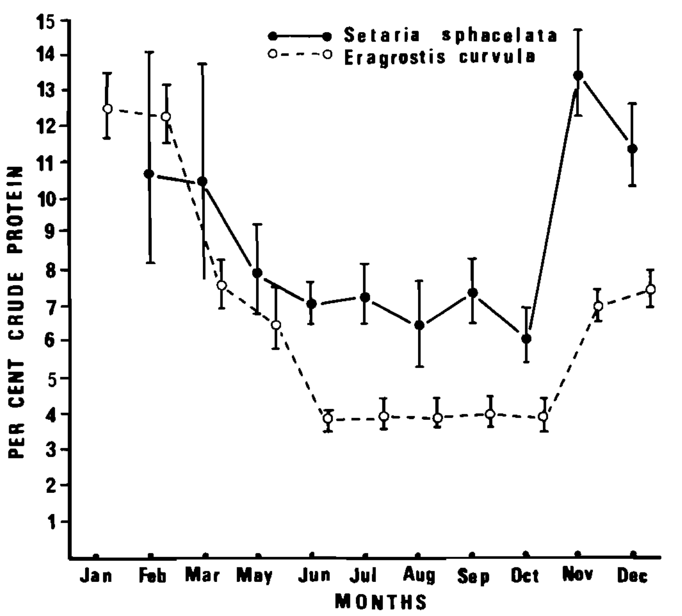

Figure 3 Changes in the crude protein contents of the grasses *Setaria sphacelata* (collected on the hill slopes), and *Eragrostis curvula* (collected on the plateau), January to December 1985. Means are shown with 95% confidence limits.

provided a reasonable index of diet quality.

The protein contents of *Setaria sphacelata* and *Eragrostis curvula* showed essentially the same pattern of seasonal variation as that of *Themeda triandra* (Figures 2 and 3). The results confirm the conclusion of Grobler (1983) that there is little difference in protein content between *Themeda triandra* and *Eragrostis curvula* but that the protein content of *S. sphacelata* is considerably higher than the other two species. Values

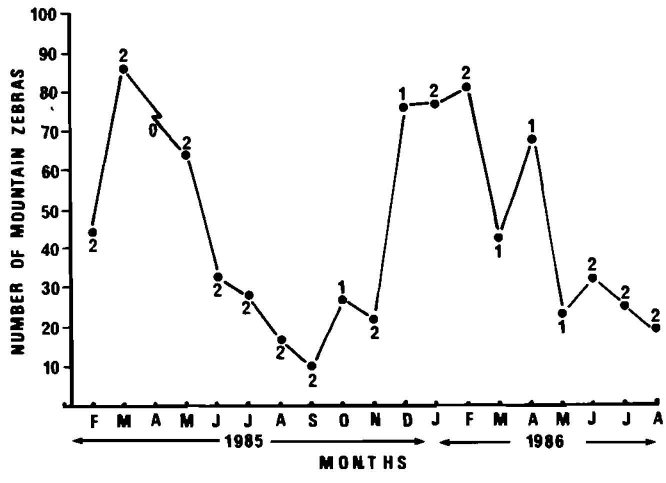

Figure 4 Changes in the numbers of mountain zebras counted on the Rooiplaat plateau, February 1985 to August 1986. The numbers of counts in each month are shown on the graph. For those months in which two counts were made the value presented is the mean of the two.

Table 2 Crude protein (CP) content (% dry mass) of mountain zebra faeces compared between the plateau and the hill slopes during summer–autumn (Period I) and winter–spring (Period II)

		Plateau	Hill slopes
Period I	Mean CP content	7,36	7,25
	N (sample size)	42	41
Period II	Mean CP content	5,47	5,92
	N (sample size)	60	58

for the latter species never declined below 5% at any time of the year (Figure 3).

The number of zebras on the Rooiplaat plateau during the study period is shown in Figure 4. The seasonal trends were similar to those described by Penzhorn (1982) and Grobler (1983), with highest values in summer (December to March) and lowest numbers in late winter (August and September).

The faecal protein contents are compared between habitats and seasons in Table 2. During Period I (summer and autumn) the mean protein content for the plateau was slightly higher than that for the hill slopes. In Period II (winter and spring) the value for the hill slopes was higher than that for the plateau. The analysis of variance yielded a significant *F* value for interaction ($F = 5{,}23$; *df* 1 & 197; $P < 0{,}05$), which shows that the relative difference between the hill slopes and the plateau varied depending on the season. Comparisons between means showed no significant difference between the plateau and the hill slopes in Period I ($F = 0{,}2$; *df* 1 & 197). But in Period II the mean for the hill slopes is significantly higher than that for the plateau ($F = 8{,}7$; *df* 1 & 197; $P < 0{,}01$).

The differences between the habitats and seasons in the protein content of *Themeda triandra* followed a similar pattern (Table 3), i.e. during Period I the mean for the plateau was higher than that for the hill slopes, whereas in Period II the reverse was the case. The *F* value for interaction is almost significant at the 5% level ($F = 3{,}71$; *df* 1 & 153; whereas an *F* value of 3,9 is required for significance at $P < 0{,}05$). Comparison of means showed the difference between the plateau and the hill slopes in Period I to be significant at $P < 0{,}10$ but not at $P < 0{,}05$ ($F = 3{,}7$; *df* 1 & 153). In Period II the difference between the plateau and the hill slopes is not significant ($F = 0{,}5$; *df* 1 & 153).

The plant parts identified in the faeces were predominantly grasses. Dicotyledon fragments never made up more than 1% of the weight of identified fragments in any month of the study period, either on the plateau or the hill slopes. Seasonal changes in the proportion of faeces samples that contained traces of dicotyledons are shown in Figure 5. On both the plateau and the hill slopes these values show a pronounced seasonal trend, with peak values during the dry season.

Table 3 Crude protein (CP) content (% dry mass) of *Themeda triandra* compared between the plateau and the hill slopes during summer–autumn (Period I) and winter–spring (Period II)

		Plateau	Hill slopes
Period I	Mean CP content	8,07	7,17
	N (sample size)	42	24
Period II	Mean CP content	4,39	4,56
	N (sample size)	61	30

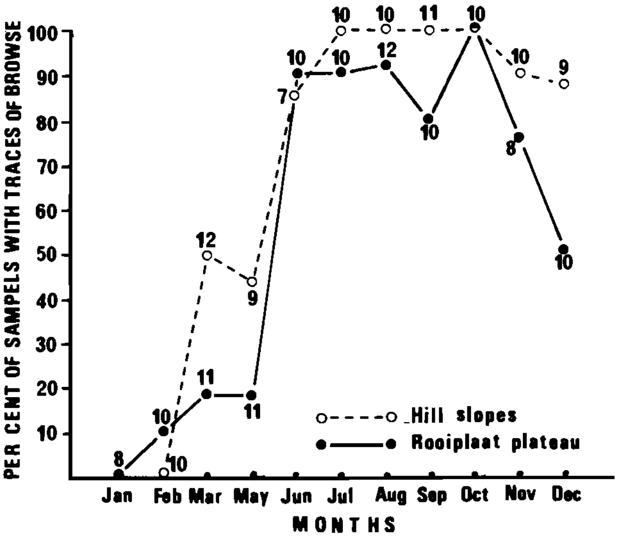

Figure 5 Changes in the percentage of faeces samples which contained traces of browse, compared between the hill slopes and the plateau, January to December 1985. The number of faeces samples examined in each month is shown on the graphs.

Table 4 The canopy spread cover of grass (all species) in three height classes in 13 plots on the Rooiplaat plateau, compared between two seasons

			Canopy spread cover	
Height class	Number of tufts measured	Per cent of tufts	Mean	Standard error
Late summer March – April 1986				
< 50 mm	321	20,8	14,5	2,8
50–150 mm	597	38,8	25,1	3,4
> 150 mm	622	40,4	27,4	5,3
Total	1540	100,0		
Late winter August – September 1986				
< 50 mm	388	24,2	17,1	4,5
50–150 mm	720	44,9	29,5	2,9
> 150 mm	496	30,9	21,4	4,9
Total	1604	100,0		

Table 5 The canopy spread cover of grass (all species) in three height classes in six plots on the hill slopes, compared between two seasons

			Canopy spread cover	
Height class	Number of tufts measured	Per cent of tufts	Mean	Standard error
Late summer March – April 1986				
< 50 mm	60	14,8	5,8	2,5
50–150 mm	184	45,3	18,8	8,2
> 150 mm	162	39,9	17,5	5,6
Total	406	100,0		
Late winter August – September 1986				
< 50 mm	65	17,0	5,8	2,8
50–150 mm	185	48,3	17,0	6,2
> 150 mm	133	34,7	13,2	4,1
Total	383	100,0		

It appears that when grass becomes scarce the zebras tend to accept more browse.

The canopy cover of grass and percentage of grass tufts in three different height classes are compared between seasons and habitats in Tables 4 and 5. On both the plateau and the hill slopes the height distribution of grass tufts changed from the summer to the winter, the proportion in the taller class (> 150 mm) declined relative to the shorter classes. However the change was relatively slight. On the plateau the cover of grass within the height range normally grazed by zebras (taller than 50 mm, Grobler 1983) did not decline significantly from the summer to the winter (analysis of variance, $F = 0{,}4$; *df* 1 & 12, see Table 4).

Discussion

If the seasonal movement of zebras was due to a change in the nutritional value of the available forage, one would expect that faecal and grass protein contents would have been higher on the plateau than the hill slopes in the summer and autumn, but in winter and spring the reverse should have been true. The protein contents of both the faeces and *Themeda triandra* (Tables 2 and 3) are in accord with this prediction. The results therefore support the hypothesis that the movement of zebras was associated with a change in the nutrient content of the diet obtainable from the two habitat types. In terms of dietary protein content the plateau appeared to be the more profitable of the two habitats in summer, whereas the hill slopes were evidently the more profitable in winter.

The magnitude of the difference in grass and faecal protein content between the plateau and the hill slopes might appear small (see Tables 2 and 3). However, a small difference in food nutrient content is likely to have a significant effect on accumulated nutrient gain over a long period.

The reason for the difference between the two habitats in the crude protein contents of grass and faeces is not clear. The distribution of rainfall over the seasons was similar on both the plateau and the hill slopes (Table 1). It therefore seems unlikely that the difference was due to a patchy distribution of rainfall over the summer and winter habitats. It is possible, however, that the effective availability of moisture for plants differed between the two habitats because of differences in soil, microclimate or topography. Penzhorn (1982) suggested that the more sheltered hill slopes provided less arid conditions in the dry season than those prevailing on the more exposed plateau.

Setaria sphacelata maintained a higher dry season protein content than the other grasses. Thus an increased intake of this species may have (at least partly) accounted for the relatively high protein content of faeces collected on the hill slopes in the dry season. The presence of *S. sphacelata* in part of the winter habitat may therefore be an attraction for the zebras. However the availability of this grass cannot be the sole reason for the seasonal movement, because it is confined to the northern and eastern part of the Park. Some of the zebra groups that occupy the plateau in the summer move to the southern and central parts of the Park in winter, where no *Setaria sphacelata* occurs (Grobler unpubl., pers. obs.).

Browse fragments made up only a very small proportion of the mass of the faeces in both habitats. It therefore seems unlikely that the presence of browse in the diet could have seriously distorted results. However, the zebras increased their intake of browse when the quantity and quality of available grass declined. Thus under very dry conditions the amount of browse in the diet may be higher than it was during this study. During a very dry spell in 1984, when grass abundance was low, zebras were observed feeding extensively on karoo bushes (P.N. pers. obs.). Therefore if faecal protein content is to be used to monitor long-term changes in diet quality it would be advisable to also monitor the proportion of browse in the diet.

The antelope species that favour short grass, black wildebeest, blesbok and springbok, are common on the plateau but relatively rare on the hill slopes, and they do not show the same pattern of seasonal movement as the zebras. The plateau therefore carries a higher biomass of herbivores than the hill slopes and experiences a heavier grazing pressure throughout the year (Van der Walt 1980). Because of the high density of short grass grazers on the plateau there is a danger that the grass may be grazed down to below the height required by zebras (Grobler 1983). This is most likely to occur in the winter when grass production is low. Thus another explanation for the seasonal movement is that a shortage of grass in the optimum height range forces the zebra off the plateau in the winter. However the very slight seasonal change in the cover of grass in the height range favoured by zebras does not support this explanation (Table 4).

Migrations of grazers are often influenced by the presence of surface water (Smuts 1972; Sinclair & Fryxell 1985). This is not a factor in the Mountain Zebra Park as water is available in both summer and winter habitats throughout the year.

Thermoregulatory behaviour may also exert an influence on the seasonal movements of the zebras. Since the plateau has less shelter than the hill slopes it is possible that low temperatures and exposure to wind in winter cause the animals to leave the plateau. However Penzhorn (1982) pointed out that seasonal variations in zebra numbers on the plateau tended to be more closely associated with variations in rainfall than with temperature. During Penzhorn's study period the numbers of zebras on the plateau were lowest during the driest time of the year (August and September), rather than the coldest (June and July). The same phenomenon was observed during the present study, zebra numbers on the plateau being lowest during August and September (Figure 4), which were on average warmer than June and July (Table 1).

This suggests that temperature does not play a primary role in determining the seasonal movement. It is possible that wind together with temperature plays a more important role than temperature alone, but further work on relationships between zebra movements and climatic conditions would be required to confirm this.

Rotational grazing is widely practised in the management of domestic livestock, and evidence suggests that it is less likely to lead to range deterioration than continuous grazing (Sinclair & Fryxell 1985). It would therefore be advantageous if conservation areas could be planned so as to encourage the type of voluntary rotational grazing evident in the mountain zebras. This study suggests that a diversity of habitats, such as that present in the Mountain Zebra National Park (Van der Walt 1980), is particularly desirable. Seasonal shifts in grazing pressure are more likely to develop in reserves offering a variety of grassland types, differing in sward structure, height distribution and phenology.

Acknowledgements

We are grateful to C. Pieterse for the rainfall and temperature records, and to K. Mazwai for assistance in the field.

References

ARMAN, PAMELA, HOPCRAFT, D. & MACDONALD, I. 1975. Nutritional studies on East African herbivores. 2. Losses of nitrogen in the faeces. *Br. J. Nutr.* 33: 265–276.

BELL, R.H.V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. In: Animal populations in relation to their food resources. pp. 111–124. *Symp. Brit. Ecol. Soc.* Ed. A. Watson. Blackwell, Oxford.

CHACON, E. & STOBBS, T.H. 1976. Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Aust. J. agric. Res.* 27: 709–727.

CHACON, E. & STOBBS, T.H. 1977. The effects of fasting prior to sampling and diurnal variation on certain aspects of grazing behaviour in cattle. *Appl. Anim. Ethol.* 3: 163–171.

ERASMUS, T., PENZHORN, B.L. & FAIRALL, N. 1978. Chemical composition of faeces as an index of veld quality. *S. Afr. J. Wildl. Res.* 8: 19–24.

GROBLER, J.H. 1983. Feeding habits of the Cape mountain zebra *Equus zebra zebra* Linn. 1758. *Koedoe* 26: 159–168.

McNAUGHTON, S.J. 1979. Grassland–herbivore dynamics. In: Serengeti: dynamics of an ecosystem. pp. 46–81. Eds. A.R.E. Sinclair and M. Norton-Griffiths. Chicago University Press, Chicago.

MOULD, E.D. & ROBBINS, C.T. 1981. Nitrogen metabolism in elk. *J. Wild. Manage.* 45: 323–334.

OWEN-SMITH, N. 1985. Niche separation among African ungulates. In: Species and speciation. pp. 167–171. Ed. E. Vrba. Transvaal Museum Monographs No. 4., Transvaal Museum, Pretoria.

OWEN-SMITH, N. & NOVELLIE, P. 1982. What should a clever ungulate eat? *Amer. Nat.* 119: 151–178.

PENZHORN, B.L. 1982. Habitat selection by Cape mountain zebras in the Mountain Zebra National Park. *S. Afr. J. Wildl. Res.* 12: 48–54.

ROUX, P.W. 1963. The descending-point method of vegetation survey. A point-sampling method for the measurement of semi-open grasslands and Karoo vegetation in South Africa. *S. Afr. J. agric. Sci.* 6: 273–288.

SINCLAIR, A.R.E. 1977. The African buffalo. University of Chicago Press, Chicago.

SINCLAIR, A.R.E. & FRYXELL, J.M. 1985. The Sahel of Africa: ecology of a disaster. *Can. J. Zool.* 63: 987–994.

SMUTS, G.L. 1972. Seasonal movements, migration and age determination of Burchell's zebra *(Equus burchelli antiquorum* H. Smith, 1841) in the Kruger National Park. M.Sc. thesis, University of Pretoria.

SNEDECOR, G.W. & COCHRAN, W.G. 1967. Statistical Methods. Iowa State University Press, Iowa.

VAN DER WALT, P.T. 1980. A phytosociological reconnaissance of the Mountain Zebra National Park. *Koedoe* 23: 1–32.

VORSTER, M. 1982. The development of the ecological index method for assessing veld condition in the Karoo. *Proc. Grassld. Soc. sth. Afr.* 17: 84–89.

ZIMMERMAN, I. 1980. Predicting diet quality from measurement of nitrogen and moisture in cattle dung. *S. Afr. J. Wildl. Res.* 10: 56–60.