Estimating seasonal diet selectivity and quality of four ungulates species using stable isotopes in Hluhluwe-Umfolozi Game Reserve, Natal, South Africa

Susan Botha
Botany honours
University of Cape Town
2001

Botany Honours Project 2001
Supervisor: W.D. Stock

Abstract

Faecal samples collected over a year period from Hluhluwe-Umfolozi National Park were analyzed using stable carbon and nitrogen isotopes to determine seasonal diet selectivity and forage quality of four ungulate species, impala, nyala, warthog and wildebeest. The results showed that wildebeest and warthog remained grazers throughout the year. Nyala and impala were able to sustain more nutritious diets than wildebeest and warthog by selecting more C_3 material when grass quality declined during the winter months. Faecal N content was significantly higher in spring (2%) compared to all other seasons for impala ($p < 0.001$, $n = 107$) and significantly lower in winter (1.1%) compared to summer for wildebeest ($P < 0.05$; $n = 56$). Faecal nitrogen content was higher for the mix-feeders, nyala and impapa (1.8%) throughout the year compared to the pure grazers (1.4%). It is suggested that warthog can tolerate a decline in grass quality during the winter months by digging up the root systems of grasses. Faecal isotope analysis provides a useful tool for monitoring the quality of the veld and animal species.

Introduction

Methods for analyzing mammalian diet include analysis of mouth and stomach content of recently shot animals (van Rooyen, 1992; van Hoven and Boomker, 1980), oesophagel sampling and observing animals whilst feeding. These methods hold several disadvantages: rumen samples of shot animals represent only the last meal of one individual whilst the sampling method is both impractical and socially objectionable. On the other hand it is difficult to get close to shy, wild animals to obtain an accurate assessment of quantities eaten or to correctly identify what they are eating. Oesophageal sampling may interfere with the normal grazing habits of animals and is often impossible to use on free-ranging animals (McAllister and Bornman, 1972). Microhistological analysis of faeces makes it easier to obtain quantitative and qualitative samples representative of the whole population over longer time periods but the identification of plant species from minute fragments is difficult or impossible and time-consuming (McAllister and Bornman, 1972).

Using stable isotopes to analyze animal tissue, gut content and faeces is an alternative method to reconstruct prehistoric and modern diets of both animals and humans (Vogel 1978; Tieszen *et al.*, 1979; van der Merwe; Jones *et al.*, 1981; Schoeninger, M.J., 1983; Witt *et al.*, 1998). This method is based on the differential fractionation of the stable carbon isotope ratio ($^{13}C/^{12}C$) by plants, depending on which photosynthetic pathway they utilize. C_3 plants (Calvin photosynthetic cycle) discriminate more against the heavy isotope (^{13}C) with foliage averaging –26.5‰ (relative to the Pee Dee Belemnite (PDB) standard) and C_4 plants (Hatch-Slack cycle) foliage averaging –12.5‰. Plants with a crassulacean acid metabolism (CAM) photosynthetic system, common to succulents and E*uphorbia* spp., are capable of both C_3 and C_4

photosynthesis depending on environmental conditions. In areas where CAM plants are abundant (for example Addo Elephant National park in the Eastern Cape) it becomes difficult to establish the carbon derived from grass (C_4) and that derived from other C_3 sources (trees, shrubs and dicotyledonous forbs) (van der Merwe *et al.*, 1988).

In South Africa, 90% of the grass-cover along the eastern coast and interior is C_4 whilst C_3 grasses are dominant in the winter rainfall area of the Western Cape. C_4 trees and shrubs are rare, and savannas thus provide a unique isotopic signature difference between C_3 trees, shrubs and some dicotyledonous forbs and C_4 grasses. Vogel (1978) used this distinction to show that the ^{13}C content of animal tissue reflect the amount of browse and graze ingested by animals. van der Merwe *et al.* (1988) used bone collagen carbon isotopic ($\delta^{13}C$) values to distinguish between the proportion of C_3 to C_4 consumed by elephants in areas with different mixtures of C_3 trees and C_4 grasses.

However, since carbon turnover in bone collagen is slow, $\delta^{13}C$ values represent dietary averages over a long time span. This makes it difficult to infer whether species exhibit short-term selectivity. Isotopic analyses of faeces present a way to test for short-term selectivity of large herbivores (van der Merwe, 1988). Faecal isotopic $\delta^{13}C$ values are similar to the feed ingested (Jones *et al.*, 1979) and the method has been utilized to indicate diet preference in some east African mammalian herbivores (Tieszen and Imbamba, 1988).

A long-term project studying the effects of herbivores on grassland dynamics in Hluhluwe-Umfolozi National park, allowed the opportunity to collect dung samples in experimental plots over a year period. The park has a unique climate and high rainfall (especially the northern areas of the park in Hluhluwe) and hence has a high availability of palatable grasses at different heights. However, during the drier months, grass quality declines, particularly in terms of crude protein and the cellulose: protein ratio of grasses increases (Bell, 1971). Animals are thus forced to move to areas with more palatable grasses or change to less favored plant species. Analysis of faeces allows a way to identify, monitor and compare the response of different animal species to seasonal declines in food quantity and quality.

The chemical composition of the fodder ingested by animals is related to the chemical composition of their faeces (Erasmus *et al.*, 1978; Putman, R.J., 1984). Faecal nitrogen and phosphorus have been used to assess nutritional value of the veld as well as indicating nutritional intake differences between grazers, browsers and herbivore species that feed on both trees and grasses (mix-feeders) (Grant *et al.*, 1995; Erasmus *et al.*, 1978).

Although dietary N concentration can be predicted from faecal nitrogen, this relationship is influenced by tannin content and low digestibility (Wrench *et al.*, 1997; Wehausen J.D., 1995; Zimmerman, 1979). Soluble phenolics that are more common in browse inhibit protein digestion, which can cause excess protein to reach the faeces (Robbins *et al.*, 1987).

Similarly low digestibility of forage influences the accuracy of predicting dietary N concentrations from faeces (Holochek *et al.*, 1982; Wrench *et al.*, 1997). C_4 grasses might be less digestible than C_3 shrub-leaves and forbs and will thus be over-represented in the faeces. This will cause an underestimation of foliage protein content where C_3 plants have higher nitrogen than C_4 plants. On the other hand, contamination of faeces by the excretion of gut microbes, might overestimate foliage protein content. However, faecal nitrogen analysis should reflect trends in feed composition and quality and regular monitoring of faecal composition of a species should give an indication of a decline in forage quality during critical times such as drought or winter (Grant *et al.*, 1995).

This paper examine the diet selectivity of four ruminants, wildebeest (*Connochaetes taurinus*), warthog (*Phacochoerus aethiopicus*), nyala (*Tragelaphus angasii*) and impala (*Aepyceros melampus*) by isotopic analysis of nitrogen and carbon of their faeces over the period of a year. Nitrogen content (%) and C: N ratios were used as indicators of forage quality.

Study area

The Hluhluwe-Umfolozi Game Reserve (225km^2) is situated in central Zululand, South Africa. Hot, wet summers and cold dry winters characterize the reserve. Mean annual rainfall is between 800 mm and a 1000 mm that peaks between October and March. The majority of the reserve area is covered by woodland, savanna and thicket communities that are dominated by various *Acacia* species (van Wilgen and Wills, 1988). Two overlapping grassland types co-occur in the reserve: tall, fire-prone bunch grasslands dominated by andropogonoid grasses such as *Themeda triandra* and short grasslands or "grazing lawns" dominated by sod-forming stoloniferous cloridoids species such as *Digitara longiflora*, *Dactyloctenium australe* and *Urochloa mossambicensis*.

Tall bunch grasslands dominate higher rainfall and altitudinal ranges and carry fire if sufficient fuel is left in the dry season. Grazing lawns occur over a wide altitudinal range, are excluded from high rainfall areas and do not burn or only carry low intensity fires. The grassland types support different suite of animals and tree species. Nearly all the grasses are C_4 (Vogel 1978) and the shrubs and trees are C_3.

Methods

The experiment is part of a long-term study on the effects of herbivory and fire on grassland dynamics. The ten experimental sites already established, cover a wide rainfall gradient from pure bunch grasslands (high rainfall) through mixed grasslands (a mosaic of lawn and bunch grasses) to extensive grazing lawns (Table 1). At each site, half of the exclosure (25 X 25 m) is fenced to exclude all mammals larger than a hare. The other half is strung with cable wire to exclude rhinos and elephants but not other herbivores.

Dung samples were collected and identified from the rhino-excluded treatments on a monthly basis since March 2000. Faeces were grounded, homogenized, weighed to approximately 2.25mg and analyzed for stable carbon and nitrogen isotope ratios by comparing the sample to a reference gas and calibrating it against 3 standards, using a Carloerba mass spectrometer Finnigan MAT, 252, Germany). Rainfall data was obtained from permanently mounted gauges at each site.

The ratio of C_3 to C_4 vegetation in the faeces can be expressed as a percentage with a $\delta^{13}C$ value of –12.5 ‰ representing a 100% C_4 diet and -26.5 ‰ a 100% C_3 diet. Intermediate values would thus represent a percentage mixture of C_3 and C_4. The raw data is attached as appendix A.

Table 1: Vegetation type, position and names of experimental sites.

Vegetation type	Hluhluwe	Umfolozi
Mixed grass, lawn/tuft	Nombali	Gqoyeni
Mixed grass, lawn/tuft	Maquanda	Mbuzane
Tall grass	Le Dube	Sokwazela
Lawn	Seme	Thobothi
Herb	Klazana	Mona

Statistical analysis

The number of dung samples per species varied widely between months. To increase the power of a one-way ANOVA, monthly samples were pooled into four seasons, logged and analyzed for statistical differences. Significant seasons were identified using the Tukey honest significant difference (HSD) for unequal n test. The months were divided into four seasons: Summer (December, January and February), autumn (March, April and May), winter (June, July and August) and spring (September, October and November).

Results

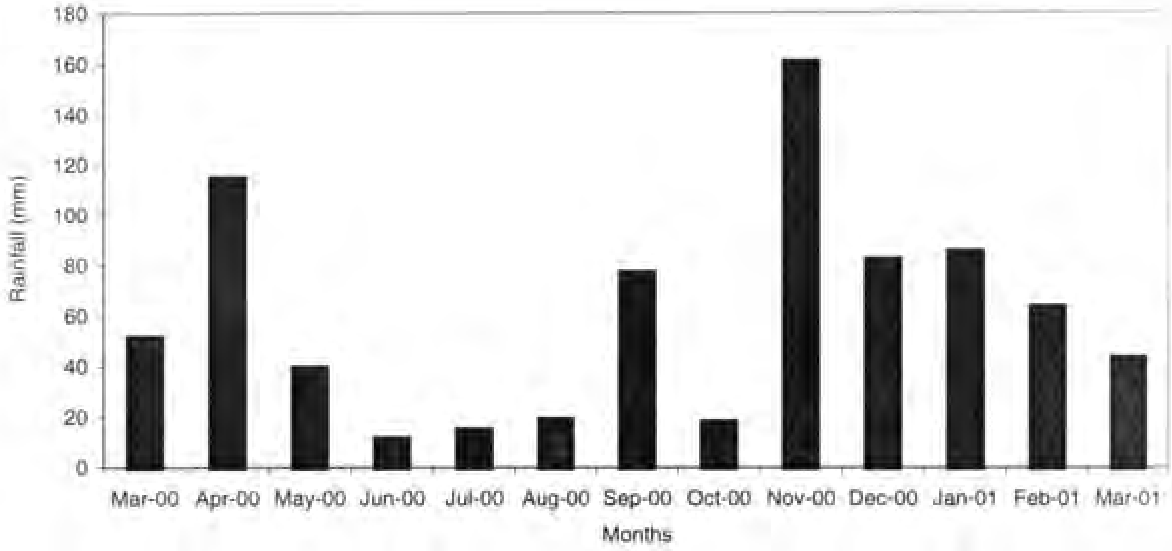

Figure 1 The monthly rainfall (averaged across all ten sites) for Hluhluwe-Umfolozi National Park from March 2000 to March 2001. Rainfall was collected on a regular basis from mounted gauges at ten permanent sites within the reserve.

The average monthly rainfall reaches a low in the winter months of June, July and August. Rainfall is higher during the summer, from November to January and then drops off again. The average rainfall recorded from the rain gauges is lower than the average rainfall recorded for the park, which falls between 800 and 1000 mm per year. This might be due to the size of the gauges, that easily fill up and then overflow, and some sites are not easily accessible to check the gauges on a daily basis. The general seasonal trend in rainfall is however apparent.

% **Graze: C3 ratio**

Figure 2

Warthog's diet remained largely C_4 throughout the year, selecting 10% C_3 during the drier months of June, July and August (fig.2). Similarly, Wildebeest had a predominant grazer diet throughout the year, selecting 10 to 20% C_3 during some of the drier months (fig.2). Impala ate significantly more C_3 during the winter months ($p < 0.01$, $n = 107$). Nyala ($p < 0.51$; $n= 44$) also tended to be a mix-feeder, selecting a large percentage of C_3 during the winter months.

Large coefficients of variation around mean C_4 values of the average %C_4 values for impala could be indicative that individuals show a high degree of variation in vegetation selection. Large coefficients of variation were especially evident for nyala, especially during the winter months. Similarly, wildebeest showed larger coefficients of variance around the drier months, suggesting that individuals will include a larger percentage of C_3 when optimal food sources become limited. The small coefficients of variation for $\delta^{13}C$ values of warthog throughout the year indicate a high degree of uniformity in the vegetation selected.

%Nitrogen

Figure 3

The nitrogen content in impala dung was significantly higher in spring ($p < 0.01$; $n = 107$) when compared to all other seasons. Wildebeest dung had significantly higher nitrogen values in summer than in winter ($p < 0.01$; $n = 56$). No significant seasonal variation in nitrogen content was found for warthog ($p < 0.191$; $n = 15$) or nyala ($p < 0.93$; $n = 44$). Impala and nyala had slightly higher nitrogen values, fluctuating around 1.8% throughout the year, whereas yearly fluctuations in nitrogen values for wildebeest and warthog were slightly lower (around 1.4 %).

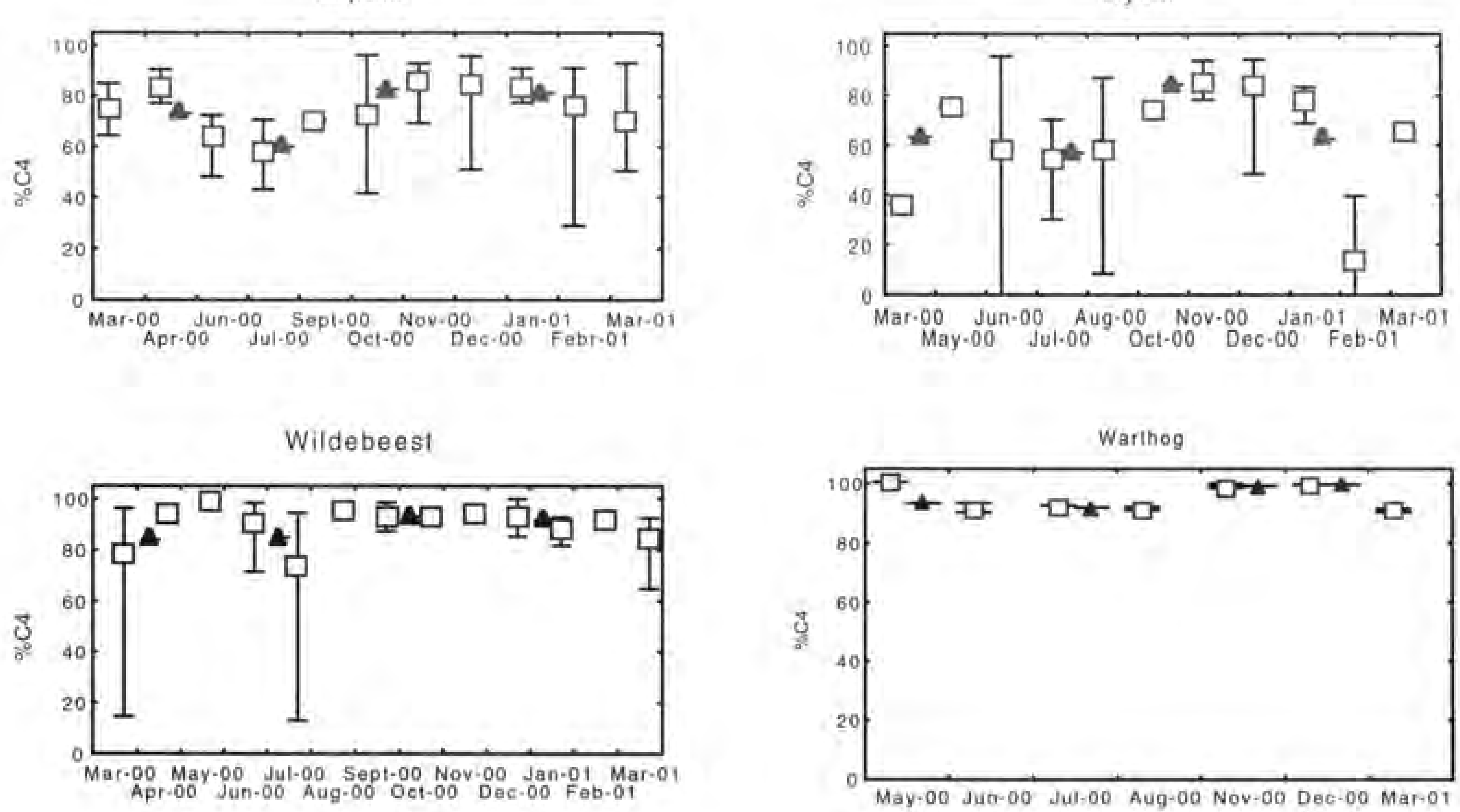

Figure 2. Average monthly and seasonal %C_4 as calculated from isotopic analysis of the faeces of four ruminant species: impala, nyala, wildebeest and warthog, from March 2000 to March 2001. The ratio of C_3 to C_4 vegetation in the faeces is expressed as a percentage with a $\delta^{13}C$ value of –12.5 ‰ representing a 100% C_4 diet and –26.5 ‰ a 100% C_3 diet (or 0% C_4). The months were divided into four seasons: summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). Lines indicate min, max values. (□-mean, monthly %C_4 values; ▲-mean, seasonal %C_4 values)

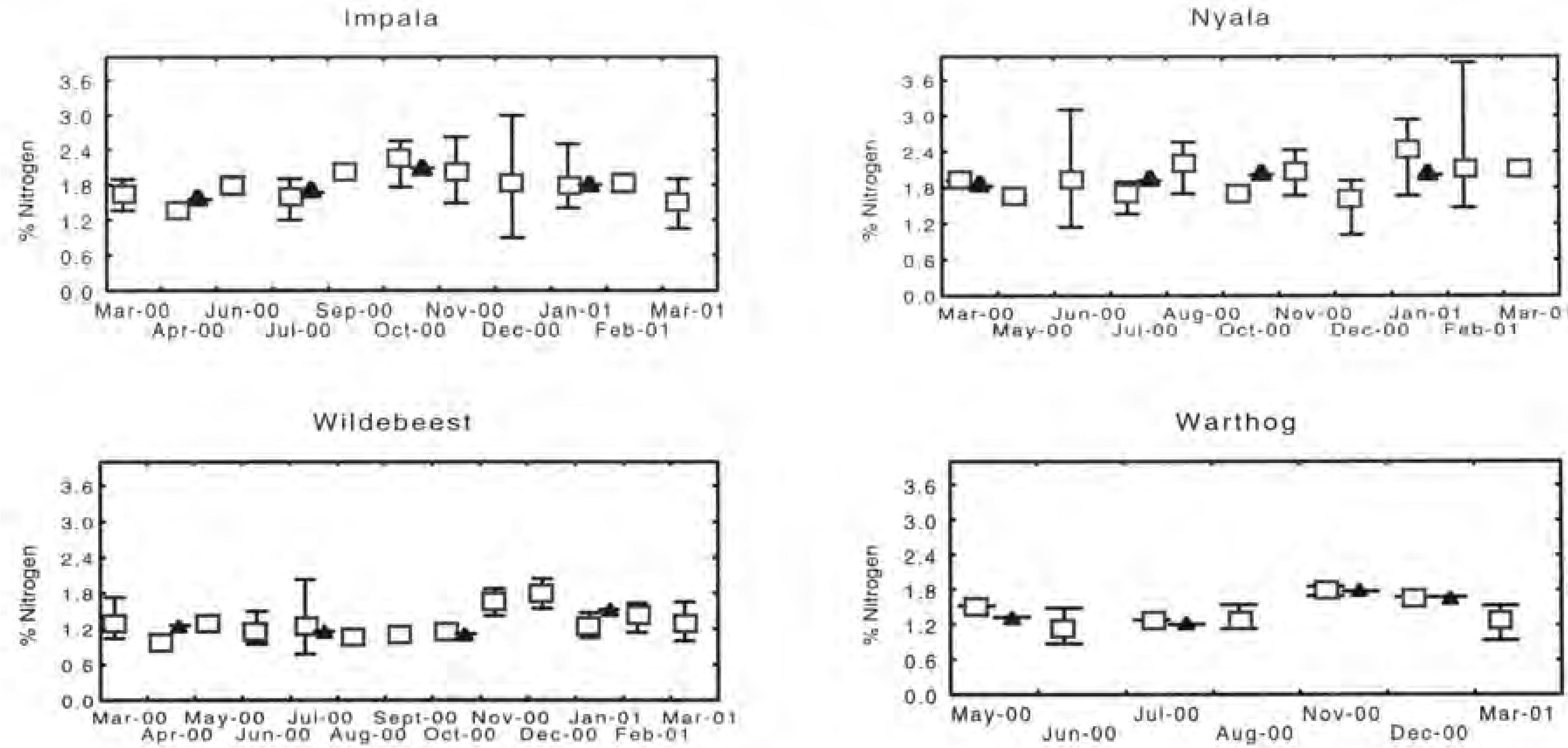

Figure 3: Average monthly and seasonal % nitrogen content in the faeces of four ruminant species: impala, nyala, wildebeest and warthog from March 2000 to March 2001. The months were divided into four seasons: summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). Lines indicate min, max values. (□-mean monthly % nitrogen; ▲-mean seasonal % nitrogen).

C: N ratios

Figure 4

The C: N faecal values give an indication of cellulose: protein ratios of the food ingested. Wildebeest had significantly higher C: N values in winter than summer ($p < 0.01$; $n = 56$) (fig. 4) whereas impala ingested significantly better food quality in spring than all the other seasons ($p < 0.01$, $n = 107$). This suggests that impala and wildebeest consume nutritious grasses during spring and summer respectively. No significant differences in C: N ratios between seasons were noted for nyala ($p < 0.19$; $n = 44$) or warthog ($p < 0.14$; $n = 15$). Average C: N ratios were slightly higher for wildebeest and warthog (generally higher than 25) than for impala and nyala (between 20 and 25).

Large coefficient of variations around monthly C: N means for warthog (where $n > 1$), suggests that food ingested vary considerably in digestibility throughout the year. Wildebeest showed large coefficient of variation around the C: N means of June, July and March. This suggests that individuals eat a range of foods that vary in digestibility during the drier months when food quality is low.

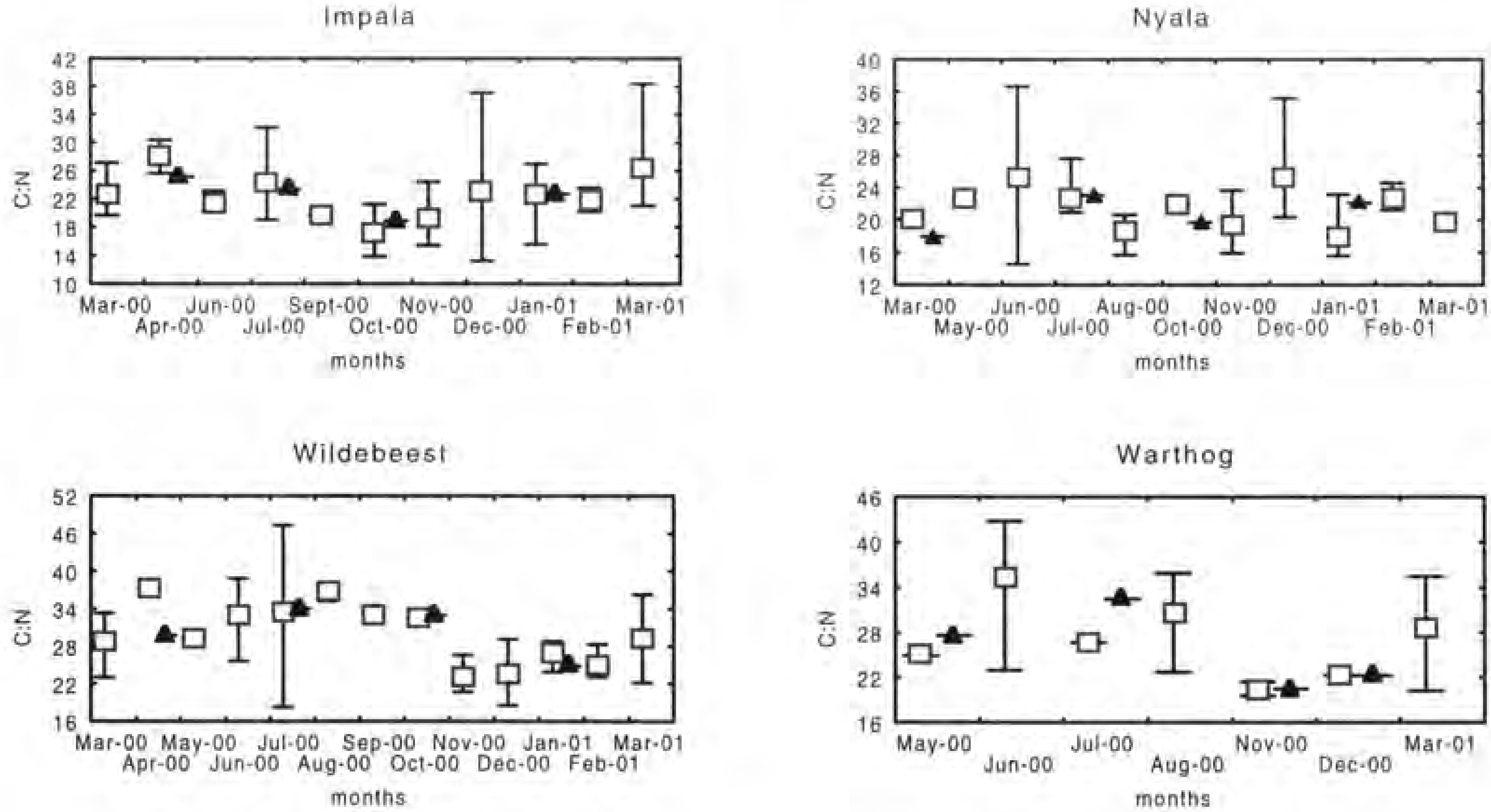

Figure 4. Average monthly and seasonal C: N content in the faeces of four ruminant species: impala, nyala, wildebeest and warthog from March 2000 to March 2001. C: N values were calculated from isotopic analysis of the faeces. The months were divided into four seasons: summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). Lines indicate min, max values. (□-mean monthly C: N; ▲-mean seasonal C: N)

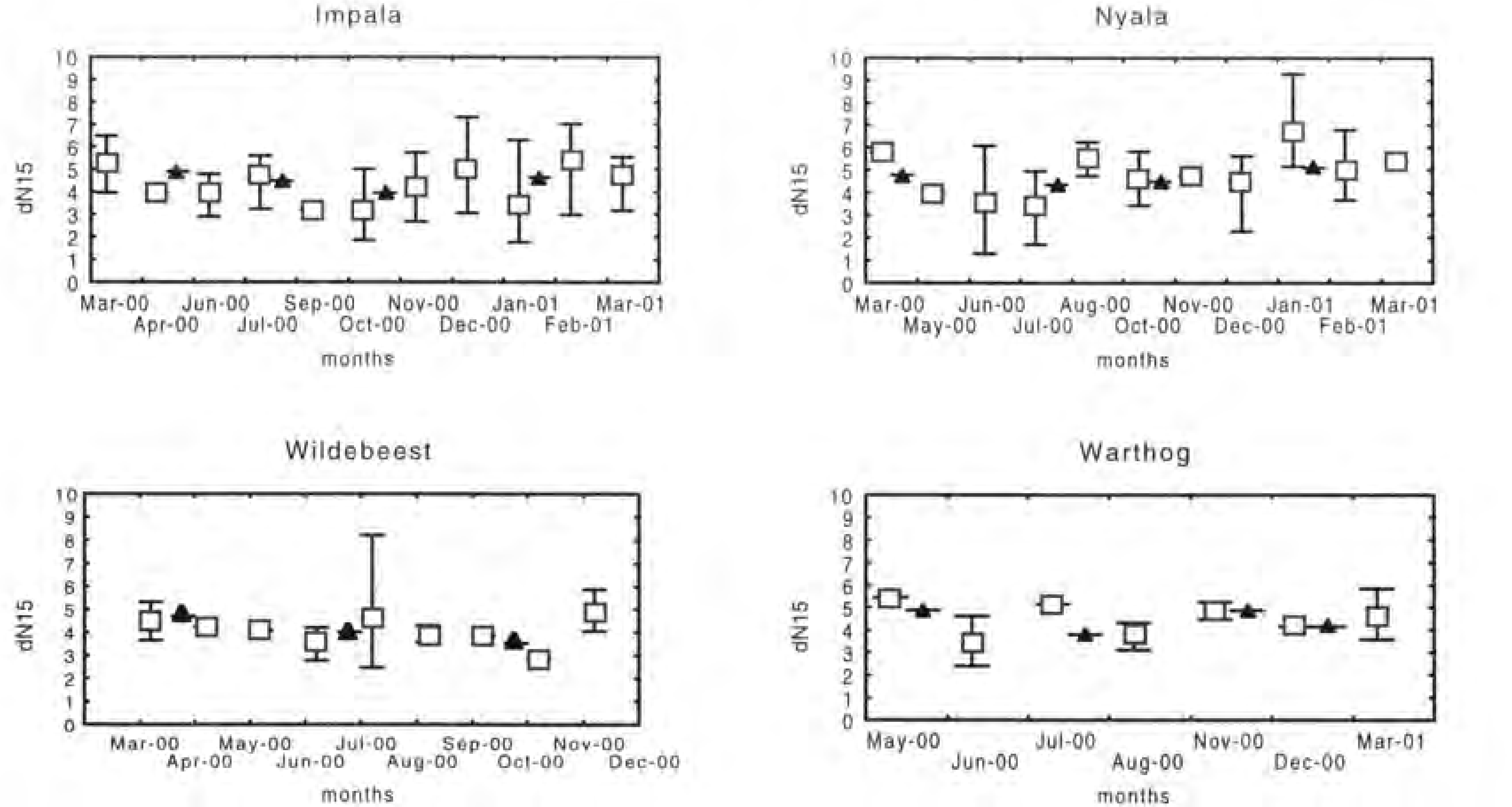

Figure 5. Monthly and average seasonal $\delta^{15}N$ content in the faeces of four ruminant species: impala, nyala, wildebeest and warthog from March 2000 to March 2001. The months were divided into four seasons: summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). Lines indicate min, max values. (□-mean monthly $\delta^{15}N$; ▲-mean seasonal $\delta^{15}N$).

$\delta^{15}N$ values

An increase in $\delta^{15}N$ values in the summer months was particularly evident for wildebeest and nyala and to a lesser degree, impala. The $\delta^{15}N$ values were significantly higher in spring compared to autumn for impala ($p < 0.028$; $n = 107$), whilst $\delta^{15}N$ values were significantly higher in summer than in winter for wildebeest ($p < 0.003$; $n = 56$). No seasonal differences in $\delta^{15}N$ values were evident for nyala ($p < 0.83$; $n = 44$) or warthog ($p < 0.27$; $n = 15$).

Discussion

Carbon isotope analysis of animal tissue is useful for the reconstruction of prehistoric diets, or the average long-term diet, but is less useful for the assessment of intermediate dietary changes. Isoptopic faecal analysis provides a useful tool to determine short-term shifts in diet. Tieszen et al. (1979) used isotopic analysis of faeces to show that some herbivore species with flexible feeding habits, such as impala (*Aepyceros melampus*), Grant's (*Gazelle granti*) and Thomson's (*Gazelle thomsoni*) gazelle, can rapidly change their diet from browse to grass within a few days following rain. Similarly, van der Merwe (1988) showed that $\delta^{13}C$ values of elephant dung changed seasonally to show higher values (incorporation of browse) during the months with low rainfall.

This study showed a similar pattern for impala and nyala to incorporate more C_4 material with the onset of the rainy season. Carbon isotopic analysis of faeces indicates that impala and nyala tended to be mix-feeders, selecting more C_3 plant material during the winter months. The proportion of dietary monocotyledonous material declined from approximately 80% in the wet season to near equal proportions of graminoids: dicotyledons towards July, the middle of the dry season. Impala, especially, ingested significantly more C_3 vegetation during June, July and September, when rainfall was low, compared to all other seasons.

Both species shifted back towards grass with the onset of the rainy season, starting in October through to January. This is similar to van Rooyen's (1992) findings that showed that dicot content of rumen samples of nyala and impala varies seasonally, with C_4 uptake increasing at the start of the rainy season.

The change in nutrient quality of C_4 and C_3 plant material is probably the reason for dietary shifts in these two ungulate species. Where the quality of grass in terms of protein, mineral and fibre content decrease with time from the rainy season (Bell 1971), crude protein content of woody species often increases before the onset of the rainy season. It is thus likely that a selection of browse is not simply because it is more available in the dry winter season, but woody dicotyledons have higher crude protein levels compared to that of grasses. This was found for the greater kudu, *Tragelaphus strepsiceros*, whose nutritional status was influenced more by diet quality than food abundance (Owen-Smith, 1990).

Contrary to impala and nyala, wildebeest and warthog remained pure grazers throughout the year. Thus even during the dry season these species were totally dependent on grass material. Wildebeest is known to be a pure grazer (Vogel 1978; Tieszen *et al.*, 1978) but work from East Africa (Tieszen *et al.* 1978) identified warthog as a mix-feeder that selected grasses but also incorporated significant quantities of C_3 material.

The overwhelming dependence of wildebeest and warthog on grasses for food throughout the year suggests that these species will be more vulnerable to weight loss during winter or times of drought, when crude protein levels of grass is low (Wrench *et al.*, 1995).The results showed that nitrogen content for the two pure grazers (wildebeest and warthog) was lower during the dry season compared to that of the mix-feeders (impala and nyala). This suggests that the nutritional status of grazers may be more vulnerable in the dry season than that of mix-feeders.

Several studies have reported critical faecal nitrogen levels necessary for grazers not to lose weight (Gates and Hudson, 1981; Wofford 1985; Wrench *et al.*, 1997). Gates and Hudson (1981) reported a weight loss in elk where faecal N levels dropped below 1.6 %. Wofford (1985) reported that deficiencies in the diets of steers should be suspected where faecal N fell below 1.7 %. Wrench *et al.* (1997) calculated that a faecal N concentration of less than 14 g N/ kg (2.24%) would indicate a nitrogen shortage in grazers, like wildebeest. The annual faecal nitrogen values of wildebeest and warthog in this study fluctuated around 1.4 %. During the drier months, faecal nitrogen values dropped to around 1.2 %.

Therefore faecal nitrogen levels below 1.2 % for wildebeest and warthog could indicate a nitrogen deficit in their diets. However, the small incorporation of browse during the dry months (where faecal nitrogen levels were around 1.2 %) may indicate that these species already become nutritionally strained at faecal nitrogen levels below 1.4 %.

Large coefficients of variance around the months of June and July of C_4 values for wildebeest suggest that individuals will eat a larger variety of food sources in times when their favored C_4 food sources have low nutritional value. It is unclear why these two grazer species should have critical faecal nitrogen concentration lower to that found for other species (elk and steers) (Gates and Hudson 1981; Wofford 1985) or even the same species (wildebeest) (Wrench *et al.*, 1997).

For that matter, how can wildebeest and warthog survive on a pure C_4 diet, whereas impala and nyala tend to incorporate more nutritious C_3 when grass quality declines? Larger bodied animals have to eat more per day than smaller animals, but as larger animals have lower metabolic rates, they require less energy and thus less nutritious food per day than smaller bodied animals. Thus where warthog are able to tolerate diets that depart from optimum in quantity rather than quality, the opposite holds for wildebeest (Bell 1971). Thus, due to the smaller absolute daily requirements of warthog, they have more time available to select nutritious items.

It has been found that dietary nitrogen to carbon (C: N) or digestible production nutrient concentration is associated with the metabolic rate of the animal (Seydack *et al.*, 2000). This could also suggest that within species, smaller females may be more selective than bigger males.

It is known that warthog dig up roots of grasses, which is a more nutritious part of the plant than the shoots, especially during winter. Although, wildebeest have also been shown to be selective, choosing more grass-leaf as oppose to grass-stem (Mentis and Duke, 1976), their larger size alone means that they are less selective for nutritional food than say warthog.

Impala and nyala also tend to be more selective, choosing the nutritious parts of C_3 plants during winter and the new C_4 grass growth during summer (van Rooyen 1992). It has also been shown that some herbivore species (like impala) tend not to select food that has high tannin levels. Cooper and Owen-Smith (1985) showed that palatability of 14 species of woody plant for three browsing ruminant species, impala, kudu and goats was related to leaf contents of condensed tannins. Furthermore plant species that contained leaf concentrations of condensed tannins in excess of 5% were rejected as food during the wet season (Cooper and Owen-Smith, 1985).

This is in support of other studies that showed reduced intake of foliage with high tannin-levels (Robbins *et al.*, 1987; Owen-Smith and Cooper, 1987). Owen-Smith and Cooper (1987) further showed that unpalatable plant species become temporarily more acceptable when new leaves emerge and during the dry season. These studies indicate that herbivores generally do not ingest C_3 with high tannin levels and that such plant species only become acceptable during critical times when food is scarce.

Whether or not impala and nyala eat large amounts of tannins becomes important when protein content of faecal samples is examined. Deterrent compounds such as condensed or hydrolysable tannins that are common in C_3 decrease protein digestibility (Holocheck *et al.*, 1982; Wehausen 1995). This results in too much N being represented in faecal samples and therefore an overestimation of fodder digestibility and available nitrogen (Grant *et al.*, 1995). On the other hand, faecal nitrogen concentrations are lower in grass than in C_3, because C_3 maintains its nutritive quality in winter, whereas grass loses its nutritive quality when maturing or becoming dormant (Grant *et al.*, 1995). If herbivores select against eating C_3 plants with high tannin contents, differences in faecal nitrogen can be described to differences in food quality between C_3 and C_4 material.

Nitrogen content of the faeces was not significantly higher in the months when impala (June and July) and nyala (June, July and August) ingested C_3. Similarly C: N ratios were not lower during these months. This would have been expected if C_3 contained significantly more nitrogen than grass eaten at other times of the year, or if high tannin-levels resulted in more nitrogen reaching the faeces. Impala, especially ate significantly more C_3 during the winter months, yet nitrogen content of faeces was significantly higher in spring compared to all other seasons. The increase in food quality ingested by impala during spring was also reflected in the C: N ratios that were significantly lower in spring to all other seasons. This suggests that mix-feeders did not ingest C_3 that contained high tannin-levels during the winter months, or that C_3 was more nutritious than the grass fed on outside the winter months.

Wildebeest and warthog remained grazers throughout the year and showed a decrease in protein content of grass during the winter months. Similarly C_4 material eaten became less digestible during winter, as illustrated by the high C: N values.

$\delta^{15}N$ values of faeces tended to increase towards the summer months for nyala, impala and wildebeest. This is not related to grass quality. Heaton *et al.* (1986) showed that although senescent, brown and actively-growing green leaves have significantly different N contents, there is no difference in their $\delta^{15}N$ values. Furthermore, photosynthetic pathway appears to have no influence on the $^{15}N/^{14}N$ ratio of plants. Higher $\delta^{15}N$ values have also been noted in areas with more intense grazing. However, these patterns are still unclear (Frank and Evans, 1997).

Higher $\delta^{15}N$ values are commonly related to increased aridity (Handley *et al.*, 1999). However the opposite trend is apparent in this study, with faecal $\delta^{15}N$ increasing towards the wet season. Higher $\delta^{15}N$ values might be evidence of herbivores foraging on grass regrowing after fire (Kathawaroo 2000). Burnt areas have higher $\delta^{15}N$ values, as ^{14}N is volatilized in the fire. Thus, in summer, many of the herbivores would take advantage of the new grass growth in these burned areas, and this might be reflected in their diet.

To conclude, impala and nyala are able to maintain nutritious diets throughout the year by selecting more browse during the drier months when grass quality declines. Warthog probably survive on a pure graze diet by feeding on the root system of grasses, which is more nutritious compared to grass-shoots during winter. Their minimum absolute daily energy requirements allow them more time to search for more nutritious items. Wildebeest might be vulnerable in times of drought when there is a shortage of food, but is less affected by declines in food quality.

Some of the disadvantages of using stable isotopes to determine selectivity and forage quality are that it is impossible to distinguish between different C_3 or between different C_4 plant species eaten. It is also uncertain how much of the faeces have been contaminated by endogenous or other materials. High tannin levels and digestibility might further influence the precision of predicting the quality of forage ingested.

To my knowledge, this is one of the first studies to use isotope composition of faeces collected over a one-year period, to determine seasonal ungulate diet selectivity and quality (see van der Merwe *et al.*, 1988 for elephants). Others have used once-off isotopic analysis of rumen and animal tissue to differentiate between grazers and browsers and (Vogel 1978) the immediate dependence of some East African herbivores on plant growth forms from the isotopic composition of faecal samples (Tieszen and Imbamba, 1988).

This study shows that faecal isotope analysis can presents a quick and effective way to determine immediate and seasonal diet selectivity of free-ranging animals.

Acknowledgements

I would like to thank my supervisor, W. D. Stock for his guidance and useful suggestions on an earlier draft. To everyone who helped to collect, identify, and ground dung. To my family, for supporting me throughout my studies.

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Appendix A The $\delta^{13}C$ and $\delta^{15}N$ values, %C and %N and C: N values of faeces of different herbivore species, collected at ten different sites, in Hluhluwe- Umfolozi National Park, Natal, South Africa from March 2000 to March 2001.

Site name	Species	Month	$\delta^{13}C$	$\delta^{15}N$	C%	N%	C/N
Thobothi	Impala	Mar-00	-16.9331	5.3	38.27251	1.64916	23.20728
Thobothi	Impala	Mar-00	-14.6089	3.95	36.69427	1.36412	26.89959
Gqoyeni	Impala	Mar-00	-15.4181	4.07	36.94791	1.36412	27.08553
Gqoyeni	Impala	Mar-00	-15.9263	4.57	37.17273	1.525532	24.36705
Mona	Impala	Mar-00	-17.4883	6.485	37.27578	1.896826	19.65166
Mona	Impala	Mar-00	-15.9921	6.371	35.00871	1.717233	20.3867
Mona	Impala	Mar-00	-15.9921	5.936	38.12802	1.862522	20.47118
Mona	Impala	Mar-00	-16.3685	5.795	36.60735	1.779788	20.56838
Thobothi	Impala	Apr-00	-13.8561	4.01	40.34447	1.328756	30.36258
Thobothi	Impala	Apr-00	-15.7193	3.97	35.23869	1.374714	25.63347
Klazana	black rhino	Jun-00	-26.2114	3.03	45.16093	1.102365	40.96731
Nombali	Impala	Jun-00	-17.2813	3.758	38.25207	1.756238	21.78068
Nombali	Impala	Jun-00	-17.7424	3.78	37.52358	1.833304	20.46773
Nombali	Impala	Jun-00	-17.2437	4.51	35.15796	1.729139	20.33264
Nombali	Impala	Jun-00	-19.7656	2.91	39.83482	1.895803	21.01211
Gqoyeni	Impala	Jun-00	-16.792	3.9	38.08154	1.64384	23.16621
Mona	Impala	Jun-00	-17.2719	4.79	41.752	1.94535	21.46246
Seme	Impala	Jun-00	-16.378	3.69	38.93978	1.74432	22.32376
Thobothi	Impala	Jul-00	-17.4319	3.6	38.59334	1.202472	32.095
Thobothi	Impala	Jul-00	-18.2882	3.78	39.68778	1.234116	32.15887
Mona	Impala	Jul-00	-19.822	5.38	40.98382	1.518912	26.98236
Mona	Impala	Jul-00	-19.775	5.41	39.48438	1.81204	21.79002
Mona	Impala	Jul-00	-17.7236	4.98	36.6379	1.85276	19.77477
Mona	Impala	Jul-00	-19.3797	5.31	39.96349	1.85276	21.56971
Mbuzane	Impala	Jul-00	-19.1821	5.52	39.37165	1.7306	22.75029
Thobothi	Impala	Jul-00	-20.4619	4.67	39.4562	1.71024	23.07056
Gqoyeni	Impala	Jul-00	-18.7493	3.23	38.27856	1.458908	26.23782
Thobothi	Impala	Jul-00	-16.9614	3.9	36.15695	1.345792	26.86667
Thobothi	Impala	Jul-00	-16.952	5.6	33.69805	1.535044	21.9525
Mbuzane	Impala	Jul-00	-17.3378	5.13	40.44656	1.6813	24.05672
Mbuzane	Impala	Jul-00	-19.7656	5.34	35.29773	1.854375	19.03484
Mbuzane	Impala	Jul-00	-16.632	4.66	36.87512	1.53295	24.055
Mona	Impala	Jul-00	-16.8202	4.91	39.24688	1.906443	20.58644
Maquanda	Nyala	Aug-00	-14.2983	5.82	40.12237	2.559946	15.67313
Ledube	Nyala	Aug-00	-25.2986	3.43	46.27454	2.429858	19.04413
Seme	Nyala	Aug-00	-15.7381	4.44	35.0931	1.698816	20.65739
Gqoyeni	Impala	Sep-00	-16.6508	3.21	39.56291	2.020801	19.57783
Sokhwezela	Impala	Oct-00	-17.2625	1.85	37.49816	1.766352	21.22916
Sokhwezela	Impala	Oct-00	-20.6689	2.77	40.32031	2.018688	19.97352
Sokhwezela	Impala	Oct-00	-13.809	2.26	36.79961	2.481304	14.83076
Sokhwezela	Impala	Oct-00	-17.0084	5	40.92275	2.4725	16.55116
Sokhwezela	Impala	Oct-00	-13.0374	3.65	35.43552	2.554986	13.86916
Mona	Impala	Nov-00	-15.3052	5.4	42.08939	1.988426	21.16719
Mona	Impala	Nov-00	-14.4489	5.33	37.27759	1.71252	21.76768
Mona	Impala	Nov-00	-14.2231	5.02	34.73342	1.769604	19.62779

Mona	Impala	Nov-00	-13.8278	4.63	40.04299	1.826688	21.92109
Mona	Impala	Nov-00	-14.8065	5.73	38.43906	2.055024	18.70492
Mona	Impala	Nov-00	-14.9194	5.58	38.54968	2.169192	17.77144
Mona	Impala	Nov-00	-15.7381	4.95	40.95557	1.9028	21.52385
Thobothi	Impala	Nov-00	-13.5832	4.32	39.0828	1.602744	24.38493
Mbuzane	Impala	Nov-00	-15.7663	5.74	41.0856	1.812471	22.66828
Seme	Impala	Nov-00	-14.3642	3.75	39.99796	2.312463	17.29669
Seme	Impala	Nov-00	-14.1478	3.93	40.43302	2.624958	15.4033
Nombali	Impala	Nov-00	-14.176	3.32	38.61122	2.104133	18.35018
Nombali	Impala	Nov-00	-13.4985	2.67	35.70178	1.87497	19.04126
Seme	Impala	Nov-00	-13.9031	3.88	39.76502	2.302843	17.2678
Seme	Impala	Nov-00	-14.2983	4.32	37.20618	2.345097	15.86552
Seme	Impala	Nov-00	-13.8467	3.62	38.26501	2.1127	18.1119
Ledube	Impala	Nov-00	-14.6653	3.74	40.57178	2.271024	17.86497
Ledube	Impala	Nov-00	-14.2042	3.57	37.47022	2.20794	16.97067
Ledube	Impala	Nov-00	-14.8629	2.87	41.07474	2.081772	19.73066
Ledube	Impala	Nov-00	-14.5524	3.38	39.14674	2.20794	17.72998
Ledube	Impala	Nov-00	-14.3548	3.41	42.19242	2.165884	19.48046
Thobothi	Impala	Nov-00	-16.8108	4.29	35.40251	1.492988	23.71252
Seme	Impala	Dec-00	-13.1127	4.026	39.82408	1.553136	25.64107
Seme	Impala	Dec-00	-13.5832	3.72	41.03755	1.9912	20.60946
Seme	Impala	Dec-00	-14.4583	4.21	41.42366	1.967306	21.05604
Mona	Impala	Dec-00	-15.0888	5.4	52.02693	2.5553	20.3604
Mona	Impala	Dec-00	-14.91	3.06	43.76481	1.593578	27.46323
Mona	Impala	Dec-00	-19.3515	4.11	38.00131	1.658622	22.91137
Mona	Impala	Dec-00	-15.0041	5.63	33.28617	0.914928	36.38119
Mona	Impala	Dec-00	-16.3027	7.32	33.90612	1.012956	33.47245
Sokhwezela	Impala	Dec-00	-14.5712	4.91	33.29528	0.89859	37.05281
Mona	Impala	Dec-00	-14.5712	5.87	42.90678	2.342405	18.3174
Mona	Impala	Dec-00	-15.3899	6.26	38.01123	1.945998	19.53302
Mbuzane	Impala	Dec-00	-15.9921	6.18	31.51646	1.621665	19.43463
Gqoyeni	Impala	Dec-00	-15.5687	5.54	39.55604	2.991071	13.22471
Gqoyeni	Impala	Dec-00	-13.6208	4.88	38.74619	1.914192	20.24154
Gqoyeni	Impala	Dec-00	-13.602	4.2	38.45182	2.004912	19.17881
Gqoyeni	Impala	Dec-00	-13.9972	5.28	39.01296	2.186352	17.84386
Thobothi	Impala	Dec-00	-14.3454	5.53	38.26784	1.914192	19.99164
Thobothi	Impala	Dec-00	-13.555	5.09	38.88417	1.900584	20.45907
Thobothi	Impala	Dec-00	-13.2727	5.03	39.16014	1.646568	23.78289
Mona	Impala	Jan-01	-22.438	6.3	43.91768	2.101428	20.89897
Nombali	Impala	Jan-01	-13.9502	4.07	37.04626	2.026377	18.28202
Nombali	Impala	Jan-01	-15.5687	3.66	38.44034	2.00136	19.20711
Nombali	Impala	Jan-01	-15.9357	3.58	38.92703	2.5017	15.56023
Nombali	Impala	Jan-01	-15.0794	1.84	38.65481	1.724688	22.41264
Nombali	Impala	Jan-01	-14.1854	1.76	37.9454	1.407504	26.95936
Sokhwezela	Impala	Jan-01	-13.9031	2.73	37.9289	1.526448	24.84782
Sokhwezela	Impala	Jan-01	-13.762	3.63	36.44408	1.526448	23.87509
Ledube	Impala	Jan-01	-17.2907	3.14	40.1436	1.710336	23.47118
Ledube	Impala	Jan-01	-15.1452	3.83	39.9087	1.50144	26.58028
Ledube	Impala	Jan-01	-16.1051	3.17	40.4352	1.540608	26.24626
Ledube	Impala	Jan-01	-17.3472	3.06	42.5574	1.66464	25.56553
Sokhwezela	Impala	Feb-01	-14.1196	2.98	40.2003	1.804992	22.27173

Mona	Impala	Feb-01	-15.0135	7.03	40.3137	1.90944	21.11284
Mona	Impala	Feb-01	-15.6816	6.71	40.0464	1.981248	20.21271
Mona	Impala	Feb-01	-15.0982	6.32	39.4146	1.824576	21.60206
Thobothi	Impala	Feb-01	-15.1923	4.15	39.76728	1.759488	22.60162
Thobothi	Impala	Feb-01	-14.9382	6.03	38.51621	1.887784	20.40287
Thobothi	Impala	Feb-01	-13.7902	4.71	39.5557	1.677012	23.58701
Mbuzane	Impala	Mar-01	-14.1101	3.17	40.69521	1.059548	38.40809
Thobothi	Impala	Mar-01	-13.4797	4.72	37.37419	1.270787	29.41027
Thobothi	Impala	Mar-01	-17.7048	5.55	35.82325	1.50885	23.74209
Thobothi	Impala	Mar-01	-13.9972	5.51	34.27231	1.109843	30.88033
Thobothi	Impala	Mar-01	-19.4362	4.96	37.27304	1.505497	24.75796
Maquanda	Impala	Mar-01	-16.999	5.51	39.33756	1.727176	22.77565
Mona	Impala	Mar-01	-18.1282	4.25	41.53265	1.739572	23.87521
Mona	Impala	Mar-01	-18.8151	4.74	40.14017	1.908984	21.02698
Mona	Impala	Mar-01	-18.147	4.24	43.62137	1.813948	24.04775
Thobothi	Wildebeest Apr		-13.2727	4.25	36.15232	0.968352	37.33386
Klazana	Warthog	Aug-00	-13.5926	3.91	34.96763	1.541642	22.68207
Klazana	Warthog	Aug-00	-13.7243	4.33	40.55839	1.13014	35.88793
Seme	warthog	Aug-00	-13.6114	3.11	38.05818	1.154241	32.97247
Nombali	white rhino	Aug-00	-14.3454	3.11	32.81208	0.473802	69.25273
Klazana	Wildebeest	Aug-00	-12.9715	3.71	39.291	1.062483	36.98035
Klazana	Wildebeest	Aug-00	-13.075	3.85	38.77437	1.062483	36.4941
Klazana	Wildebeest	Aug-00	-13.0939	4.3	38.44744	1.089044	35.30384
Seme	Wildebeest	Aug-00	-13.3103	3.81	38.91208	1.035223	37.58811
Seme	Wildebeest	Aug-00	-13.4514	3.57	37.38265	0.992969	37.64735
Nombali	Wildebeest	Aug-00	-26.6537	3.11	40.9171	1.486758	27.52102
Seme	Nyala	Dec-00	-13.4044	4.283	38.84502	1.837878	21.1358
Seme	Nyala	Dec-00	-13.2538	4.057	40.87208	1.879693	21.74402
Seme	Nyala	Dec-00	-13.5964	3.678	40.23776	1.867746	21.54349
Mona	Nyala	Dec-00	-19.7373	3.74	44.46442	1.807294	24.60276
Mona	Nyala	Dec-00	-13.9125	6.72	33.93347	1.029294	32.96772
Mona	Nyala	Dec-00	-14.543	6.14	35.59277	1.012956	35.13753
Mona	Nyala	Dec-00	-15.1923	6.78	39.03385	1.91862	20.34475
Gqoyeni	warthog	Dec-00	-12.5481	4.15	37.11797	1.669248	22.23634
Gqoyeni	Wildebeest	Dec-00	-14.5618	5.07	46.23575	2.0412	22.65126
Gqoyeni	Wildebeest	Dec-00	-12.5199	4.43	45.16961	1.551312	29.11704
Gqoyeni	Wildebeest	Dec-00	-13.5455	5.4	36.97998	1.99584	18.52853
Thobothi	Wildebeest	Dec-00	-13.1786	5.04	38.24024	1.54224	24.79526
Mona	Nyala	Feb-01	-14.7877	6.63	34.425	1.4688	23.4375
Mona	Nyala	Feb-01	-15.0888	9.28	37.098	1.687488	21.98416
Mona	Nyala	Feb-01	-15.484	6.74	37.3734	1.521024	24.57121
Thobothi	Nyala	Feb-01	-16.8485	5.44	42.25101	1.988588	21.24674
Thobothi	Nyala	Feb-01	-15.9639	5.15	84.30884	3.903864	21.59625
Thobothi	Wildebeest	Feb-01	-15.0511	6.14	34.8948	1.439424	24.2422
Thobothi	Wildebeest	Feb-01	-15.0606	5.59	34.4655	1.40352	24.55647
Mbuzane	Wildebeest	Feb-01	-13.8373	6.18	32.0841	1.135872	28.24623
Mbuzane	Wildebeest	Feb-01	-13.5644	6.81	37.7251	1.631192	23.12732
Thobothi	Wildebeest	Feb-01	-13.6302	5.34	38.07466	1.567044	24.29712
Thobothi	Wildebeest	Feb-01	-13.5173	5.51	39.05895	1.498314	26.0686
Mona	Nyala	Jan-01	-20.97	6.08	36.13062	1.976343	18.28155
Ledube	Nyala	Jan-01	-28.2251	1.3	45.69946	2.940864	15.53947

Ledube	Nyala	Jan-01	-27.9899	1.93	45.7893	2.931072	15.62203
Mona	Nyala	Jan-01	-24.367	3.53	44.84946	2.76844	16.20026
Klazana	Nyala	Jan-01	-21.1865	5.23	38.57363	1.665196	23.16462
Thobothi	Wildebeest	Jan-01	-13.5738	4.14	33.25172	1.18944	27.95578
Thobothi	Wildebeest	Jan-01	-13.7432	4.19	35.05825	1.4688	23.86863
Thobothi	Wildebeest	Jan-01	-13.4891	3.84	30.40581	1.054272	28.84058
Thobothi	Wildebeest	Jan-01	-13.6302	4.58	34.3764	1.246848	27.57064
Thobothi	Nyala	Jul-00	-19.1539	4.74	37.61411	1.360692	27.64337
Thobothi	Nyala	Jul-00	-19.1821	5.37	39.4562	1.79168	22.0219
Thobothi	Nyala	Jul-00	-22.2686	6.24	39.68166	1.89348	20.957
Thobothi	Nyala	Jul-00	-16.952	5.6	36.74373	1.745324	21.05267
Mbuzane	Nyala	Jul-00	-16.6508	5.45	37.76798	1.755475	21.51439
Mona	Warthog	Jul-00	-13.5267	5.16	34.1578	1.28268	26.63002
Thobothi	Wildebeest	Jul-00	-13.762	2.475	35.94365	0.806922	44.54414
Thobothi	Wildebeest	Jul-00	-13.5267	3.24	36.69247	0.775278	47.32815
Thobothi	Wildebeest	Jul-00	-13.2538	3.81	37.12449	0.886032	41.89972
Mona	Wildebeest	Jul-00	-13.2538	4.53	35.02202	0.806922	43.40198
Mona	Wildebeest	Jul-00	-13.5644	5.19	34.80601	1.1198	31.08234
Thobothi	Wildebeest	Jul-00	-13.3197	4.53	35.53876	1.16052	30.62314
Mbuzane	Wildebeest	Jul-00	-24.687	5.89	39.79179	2.002725	19.86883
Mbuzane	Wildebeest	Jul-00	-23.9248	8.21	37.05369	2.02745	18.27601
Seme	Wildebeest	Jul-00	-15.9263	3.31	37.17263	1.476352	25.1787
Mqanda	Nyala	Jun-00	-18.5554	3.639	38.65197	1.961332	19.707
Klazana	Nyala	Jun-00	-18.514	4.945	45.04283	2.6537	16.97359
Seme	Nyala	Jun-00	-13.8937	3.055	41.76285	1.2488	33.44238
Seme	Nyala	Jun-00	-13.0845	3.415	41.63295	1.1373	36.60683
Seme	Nyala	Jun-00	-24.3294	3.575	45.52995	2.2077	20.62325
Seme	Nyala	Jun-00	-13.1221	3.765	44.23095	1.2488	35.41876
Seme	Nyala	Jun-00	-26.9077	1.7	45.18221	3.112144	14.51803
Mqanda	Warthog	Jun-00	-13.4173	3.447	34.03249	1.483444	22.94154
Nombali	Warthog	Jun-00	-13.7714	3.38	37.41482	0.874986	42.76047
Gqoyeni	Warthog	Jun-00	-13.4609	4.61	36.81497	1.068496	34.45494
Klazana	Warthog	Jun-00	-13.8467	2.385	44.5557	1.0704	41.62528
Gqoyeni	Wildebeest	Jun-00	-13.9219	3.32	36.73053	1.109592	33.10274
Gqoyeni	Wildebeest	Jun-00	-12.8304	3.82	37.54676	0.965756	38.87811
Gqoyeni	Wildebeest	Jun-00	-13.1691	3.2	35.66098	0.945208	37.72818
Klazana	Wildebeest	Jun-00	-12.7175	3.245	40.59375	1.1373	35.69309
Klazana	Wildebeest	Jun-00	-27.6229	2.355	0	0	
Seme	Wildebeest	Jun-00	-13.4232	4.21	37.58854	1.204239	31.21352
Thobothi	Wildebeest	Jun-00	-16.4909	4.16	38.28054	1.492988	25.64022
Thobothi	Wildebeest	Jun-00	-15.7004	3.51	35.01133	1.303736	26.85461
Seme	Wildebeest	Jun-00	-13.2162	2.78	37.81258	1.059135	35.70138
Thobothi	Wildebeest	Jun-00	-13.4609	3.59	36.12285	1.08075	33.42387
Mona	Nyala	Mar-00	-21.3991	5.774	38.72682	1.919023	20.18049
Thobothi	Wildebeest	Mar-00	-13.0092	3.99	35.98969	1.07908	33.3522
Thobothi	Wildebeest	Mar-00	-13.4514	4.87	35.25693	1.16052	30.38029
Gqoyeni	Wildebeest	Mar-00	-24.4423	5.33	39.76621	1.7306	22.97828
Gqoyeni	Wildebeest	Mar-00	-13.028	3.65	36.1506	1.432709	25.23234
Mona	Wildebeest	Mar-00	-13.5023	4.54	34.22888	1.041236	32.8733
Mona	Nyala	Mar-01	-17.366	5.45	41.05882	2.094924	19.59919
Sokhwezela	warthog	Mar-01	-13.6773	5.85	30.81642	1.525615	20.19935

Thobothi	warthog	Mar-01	-13.7526	4.56	39.42243	1.321082	29.84102
Thobothi	warthog	Mar-01	-13.8373	3.58	32.95739	0.928781	35.48457
Klazana	white rhino	Mar-01	-13.4797	3.39	29.59422	1.280846	23.10521
Mbuzane	Wildebeest	Mar-01	-17.4413	5.42	36.59029	1.649676	22.18029
Mbuzane	Wildebeest	Mar-01	-13.9878	4.74	36.22784	1.099784	32.94087
Mbuzane	Wildebeest	Mar-01	-14.5995	5.75	35.6041	1.498791	23.75521
Mbuzane	Wildebeest	Mar-01	-13.7902	5.05	35.29222	1.136667	31.04887
Maquanda	Wildebeest	Mar-01	-13.555	4.7	36.11827	0.995841	36.26911
Seme	Nyala	May-00	-15.8228	4.05	37.35113	1.683648	22.18464
Seme	Nyala	May-00	-15.9451	3.83	37.38683	1.59264	23.47475
Seme	warthog	May-00	-12.4352	5.46	37.94588	1.524096	24.8973
Seme	Wildebeest	May-00	-12.6986	4.07	38.22578	1.299392	29.4182
Mona	Nyala	Nov-00	-15.5216	5.62	37.85833	2.055024	18.42233
Mona	Nyala	Nov-00	-15.1923	5.59	41.1712	2.198636	18.72579
Thobothi	Nyala	Nov-00	-15.0135	5.06	39.3269	2.013704	19.52963
Mbuzane	Nyala	Nov-00	-15.1547	4.34	39.35402	1.664388	23.64474
Nombali	Nyala	Nov-00	-13.3197	2.28	37.38763	1.66664	22.43293
Seme	Nyala	Nov-00	-13.9219	4.29	37.58854	2.366224	15.88545
Seme	Nyala	Nov-00	-13.5267	4.61	40.79444	2.429605	16.79057
Sokhwezela	Warthog	Nov-00	-12.6892	4.48	36.10965	1.687473	21.39865
Klazana	Warthog	Nov-00	-12.5199	5.26	36.21841	1.854137	19.53384
Mbuzane	Wildebeest	Nov-00	-13.5267	4.97	37.69958	1.417812	26.58997
Mbuzane	Wildebeest	Nov-00	-13.3009	5.87	38.32339	1.828772	20.9558
Thobothi	Wildebeest	Nov-00	-13.0656	4.05	38.56748	1.5411	25.02595
Thobothi	Wildebeest	Nov-00	-13.3573	4.47	38.78446	1.869868	20.74182
Maquanda	Wildebeest	Nov-00	-22.6262	3.56	33.83319	1.22535	27.61104
Seme	Nyala	Oct-00	-16.0674	4.75	37.8063	1.708928	22.12282
Sokhwezela	Wildebeest	Oct-00	-13.442	2.87	36.93932	1.135512	32.53099
Mbuzane	Wildebeest	Sep-00	-14.2795	3.87	34.31559	1.03845	33.04501
Seme	Wildebeest	Sep-00	-12.6986	3.85	39.14505	1.172992	33.37197