Dietary Ecology of Chacma Baboons (*Papio Ursinus* (Kerr, 1792)) and Pleistocene Cercopithecoidea in Savanna Environments of South Africa

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DECLARATION

I declare that this work is my own, and has not been submitted before for any other degree at any other university.

Signed by candidate

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ABSTRACT

This dissertation deals with the dietary ecology of savanna-dwelling chacma baboons (*Papio ursinus*), and a number of fossil cercopithecoids, from modern and Pleistocene environments of South Africa, respectively, using principles of stable light isotope ecology. Previous studies of baboon ecology, based largely on direct observations, have not quantified spatial and temporal dietary variability. The dietary ecology of fossil cercopithecoids is even less clear.

The primary focus of this study was to document inter-habitat, intra-habitat, and intra-individual variability in dietary ecology of South African savanna baboons within the context of sympatric mammal communities. Results of isotopic analysis of plants, faeces, hair, and skeletal material show that modern baboons exhibit considerable variability in the type of diet they consume, in response to fluctuations in habitat conditions. Succulents were an important component of baboon diets, in at least one savanna habitat type. Grasses were utilized very little, even in areas where this resource was available in abundance. Most importantly, baboons appear to consistently select for forage of high nutritive value.

Carbon and oxygen isotope data from tooth enamel carbonate of Pleistocene cercopithecoids show that these primates utilized savanna resources to a greater extent than do modern South African chacma baboons. Most specimens of *Papio robinsoni* and members of the genus *Parapapio* nevertheless had diets dominated by C_3-based foods, while the extinct *Theropithecus oswaldi* was largely graminivorous. The diet of the large-bodied *Papio (Dinopithecus) ingens* was more variable than previously proposed. One dietary group of *Cercopithecoides williamsi* specimens (assumed to be a colobine monkey) relied on grasses and other savanna-based resources. At least two groups of both *Parapapio* and *C. williamsi* can be identified based on differences in dietary behaviour, and these do not correspond well with taxonomic assignments.

As savanna-dwelling primates, baboons are an appropriate model on which to base interpretations of early hominid behavioural ecology. The findings of this study support previously suggested ecological similarities between baboons and hominids, providing evidence for the requirement of highly nutritious foods by large-bodied, terrestrial, savanna primates.

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CHAPTER 1

INTRODUCTION

Baboons are among the most versatile and successful of all living nonhuman primates. However, because of the extent of baboon ecological variability, we have a poor understanding of their dietary adaptations. This problem is even more acute amongst the fossil cercopithecoids found in South African Pleistocene deposits, despite the diversity of taxa that are represented here. As savanna-dwelling primates, baboons are a more appropriate primate than extant hominoids, such as chimpanzees, on which to base models of early hominid ecology (Jolly, 2001; Lee-Thorp *et al.*, 2003). Similarly, contemporary cercopithecoids of the African Pleistocene can be deemed ecological analogues for early hominid differentiation, but ecological patterns in both modern and fossil baboons are not as well understood as they should be for effective palaeoecological modelling.

Baboon behavioural ecology is influenced by factors such as social transmission of habits, trade-offs between predation risk and resources gained, availability of water, availability of secure sleeping sites, and troop size (e.g. Cambefort, 1981; Anderson, 1982; Hamilton III, 1986; Cowlishaw, 1997; Henzi *et al.*, 1997). However, dietary selection is probably the most fundamental mechanism structuring any primate's ranging pattern and social relationships, since an animal's diet is largely dependant upon the consumable items available (Rodman, 1999). Rodman (1999) further states that animal diets define the parameters of their respective microhabitats. Behavioural adaptations of modern and fossil baboons are therefore probably best explained through dietary studies.

The diet of baboons represents one of the most extreme examples of primate ecological complexity and adaptability (e.g. DeVore & Hall, 1965; Whiten *et al.*, 1991). Baboons incorporate a wide range of items into their diets, including leaves, fruits, underground storage organs, herbs and forbs, grasses, and animal matter, in extremely variable proportions (e.g. DeVore & Hall, 1965; Dunbar & Dunbar, 1974; Strum, 1975; Moolman & Breytenbach, 1976; Hamilton III & Busse, 1982; Whiten *et al.*, 1991; Byrne *et al.*, 1993).

Although it has been suggested that baboons display some dietary selectivity, responding to certain biochemical nutrients in plant foods (e.g. Whiten *et al.*, 1991; Barton *et al.*, 1993), resource availability is believed to be the most important factor influencing their diets (DeVore & Hall, 1965; Barton *et al.* 1993). Dietary ecology in baboons should therefore be studied in terms of a broader community ecology framework, but no existing studies have attempted to compare baboon diets with sympatric mammal species.

Baboon feeding ecology has been extensively studied in East African environments (e.g. Dunbar, 1976 & 1983; Norton *et al.*, 1987), and in the desert environments of Namibia (e.g. Hamilton III, 1986; Brain, 1988). In South Africa, chacma baboons are abundant throughout, but studies have been restricted mostly to the Western Cape (DeVore & Hall, 1965; Davidge, 1978) and the Drakensberg mountains of Kwazulu-Natal (e.g. Byrne *et al.*, 1993). Baboons are commonly considered to be "problem animals" in both agricultural and wildlife management circles, further contributing to them being poorly studied.

Cercopithecoids in South African Pleistocene deposits are represented by a diversity of taxa (Freedman, 1976; Brain, 1981; Delson, 1992). Apart from insights gained from limited isotopic data (Lee-Thorp *et al.*, 1989a; Lee-Thorp & van der Merwe, 1993; Lee-Thorp *et al.*, 1994; Luyt, 2001; Lee-Thorp, 2002), almost nothing is known of the dietary habits of these taxa. Some dental microwear evidence of dietary habits has been presented for *Theropithecus brumpti* and *T. oswaldi* from the Omo Sequence of East Africa (Teaford, 1993).

The sympatric existence of several species observed in Pleistocene primates, is absent amongst modern savanna primates, although species do appear to co-exist through feeding niche separation. For example, in southern African savannas, baboons are the most terrestrial primate species, while monkeys are somewhat more arboreal, and the ranges of *Cercopithecus aethiops* and *C. mitis* seldom overlap (Skinner & Smithers, 1990). These primates are also not in competition with the nocturnal prosimian species that occupy the subcontinent. A similar situation is present in East Africa, where *Theropithecus gelada*, *Cercopithecus aethiops*, and *Papio anubis* achieve differential habitat utilization through terrestrial, arboreal, and intermediate generalist lifestyles, respectively (Dunbar & Dunbar, 1974).

Similar niche separation may have occurred in cercopithecoids of the South African Pleistocene, but because so little is known of the dietary ecology of South African fossil baboons, it remains to be tested whether differential resource utilization enabled co-existence. Lee-Thorp *et al.* (1989a) reported some evidence for this, demonstrating that sympatric *Theropithecus darti (oswaldi)* and *Papio robinsoni* exploited different resources in the Pleistocene environments around Swartkrans.

Models of early hominid behavioural ecology have relied heavily on analogies with chimpanzees, and other extant hominoids. However, chimpanzees, along with most other primate species, are forest-dwellers, and therefore have different ecological requirements to early hominids that, even if they themselves resided in forests, utilized savanna resources (e.g. Lee-Thorp *et al.*, 2003; Sponheimer & Lee-Thorp, 2003; van der Merwe *et al.*, 2003). Following earlier suggestions (Jolly, 1970; Dunbar, 1976 & 1983), primatologists and anthropologists are turning their attentions to baboons, particularly the genus *Papio*, considering them suitable models for several aspects of early hominid differentiation (e.g. Jolly, 2001; Lee-Thorp, *et al.*, 2003). This is supported by stable carbon isotopic evidence, in that early hominids and extant great apes utilized resources differently, even in similar environments, with only australopithecine diets having a significant savanna component (see Schoeninger *et al.*, 1999; Carter, 2001; Lee-Thorp *et al.*, 2003; Sponheimer & Lee-Thorp, 2003).

Such modelling can be extended to baboon species that lived contemporaneously with early hominids. Current knowledge of early hominid behavioural adaptation is based partly on assessments of the resources that were available to them (e.g. Vrba, 1974, 1975; Spencer, 1997). It can therefore be argued that insight into resource utilization by contemporary primate taxa would cast light onto the resources available to hominids foraging in the same environments. The co-existence of a diversity of savanna primates can probably reflect patterns of sympatric habitat utilization by several hominid species in the African Pleistocene.

Baboon and hominid evolutionary radiation patterns are believed to have been somewhat similar. Today this is portrayed by the savanna lifestyle of both groups. It appears that cercopithecines and colobines diverged around the same time as did Asian and African hominoids, possibly resulting in similar levels of biodiversity within these respective clades (Delson, 1992). Jolly (2001) exploited this and proposed a comparable level of genetic diversity across the genus *Papio* as would have been found in Pleistocene hominids.

Patterns of variability resulting from comparable evolutionary radiation in hominoids and papionins would lead to repetitive trends in exploitation of available niches. In Africa, hominoids are represented by gorillas, chimpanzees, and modern humans. These taxa represent specialist folivores, adaptive frugivores, and ecological generalists, respectively. The cercopithecoids can be divided into the same ecological sub-groupings. In this respect, colobine monkeys would be the counterparts of gorillas, *Cercopithecus* spp. (being generalist feeders, but limited to riparian and forest habitats) are comparable with chimpanzees, and baboons of the genus *Papio* might reflect the ecological responses of humans (and therefore early hominids) to changes in the environment. Such patterns of biodiversity and niche exploitation suggest that, amongst extant primates, *Papio* baboons offer the most suitable analogue on which to base interpretations of early hominid ecology (Jolly, 2001).

Jolly (1970) first suggested that papionin ecology might provide valuable insight into early hominid differentiation. Drawing from similarities in dental and hand morphology in australopithecines and *Theropithecus gelada*, Jolly (1970) proposed that early hominids relied heavily on a graminoid diet in the grassland habitats of the African Pleistocene. Stable light isotopes and dental microwear show that this was not the case (e.g. Lee-Thorp *et al*., 1994). In any event, gelada baboons are highly specialized feeders, while hominids appear to have been generalists (Dunbar, 1983).

Papio baboons exhibit a more marked generalist behaviour than most other extant primates, and thus Dunbar (1976, 1983) and Jolly (2001) conclude that early hominid ecology was probably more similar to that of modern *Papio* spp.

Jolly (1970, 2001) and Dunbar (1976, 1983) point out that when using taxa as models for fossil fauna, it is not a direct comparison that is being made, but an expression of the variability that may have existed. Therefore, it is important that a suitable model be used, and that one does *not expect a direct comparison* to be plausible. For example, Rose (1976) makes use of bipedal behaviour in baboons in order to hypothesize mechanisms underlying the evolution of this behaviour in humans. As Jolly (2001) points out, such comparison could be made with gerenuks, kangaroos, and a variety of other species. This could be further extended to megaherbivores such as African elephants, which often stand on their hind legs in order to reach the young leaves at the tops of trees (personal observation).

The baboon/hominid ecological model suggested here is made on the premise that modern and fossil baboons may provide clues as to how early hominids would have responded to a changing savanna habitat in the Pleistocene. Such a model is merely an expression of the ecological variability that might have been displayed by these hominids.

Stable light isotope ecology offers an empirical technique for quantifying such fundamental ecological principles as diet and habitat selection, in the absence of time-consuming and subjective field observations (e.g. DeNiro & Epstein, 1978; Vogel, 1978; Ambrose, 1986). In contrast to other methods of dietary analysis, such as gut morphology, dental morphology, and dental microwear (e.g. Hylander, 1975; Walker, 1976; Milton, 1993; Strait, 1993; Lambert, 1998; Ungar, 1998), it is possible to make use of materials such as faeces and hair, and thus in modern situations, animals need not be killed. It is difficult to distinguish differences in dietary habits such as frugivory and folivory using stable light isotopes, but the method offers insights into an alternative range of ecological variables.

The method is based on measurements of the ratios of stable isotopes of various elements in biological tissues. In this study, $^{13}C/^{12}C$, $^{15}N/^{14}N$, and $^{18}O/^{16}O$ ratios are employed for assessing environmental variables.

Natural abundances of these isotopes (for example $^{13}C/^{12}C$) are measured against international standards, and converted to standard delta (δ) notation using the equation:

$$\delta^{13}C = (R_{sample} / R_{standard} - 1) * 1000,$$

where R = $^{13}C/^{12}C$. Values are expressed here in terms of the heavier isotope of each element ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$) in parts per thousand, or per mil (‰).

Stable carbon isotope ratios in African savanna mammals are dependent on the ratio of C_3 to C_4 photosynthetic plants at the base of the foodweb (Vogel, 1978). This is founded in that the trees and shrubs of these environments use the C_3 photosynthetic pathway, and are isotopically distinct from grasses that mostly follow the C_4 pathway (Vogel *et al.*, 1978). Therefore $\delta^{13}C$ values in herbivore tissues are used to quantify the ratio of grass to browse consumed, and in carnivores to identify the feeding habits of their prey. Animal $\delta^{13}C$ values are also informative about habitat utilization, reflecting environmental factors that affect plant $\delta^{13}C$ values, such as foliage density and water availability (e.g. Tieszen, 1991; van der Merwe & Medina, 1991).

Nitrogen isotope ratios are influenced by a number of variables, indicative of the physiological responses of an animal to the conditions and fluctuations of its immediate environment (Ambrose, 1991). Authors have suggested that $\delta^{15}N$ values of animal tissues vary with digestive anatomy (Sponheimer *et al.*, 2003a), dietary quality (Schoeninger *et al.*, 1997; Sponheimer *et al.*, 2003a), trophic level (Sealy *et al.*, 1987), aridity (Ambrose, 1991), and age (Ambrose, 2000).

A useful adjunct to measurements of $\delta^{15}N$ is the concurrent measurement of percentage nitrogen, which in plants and faeces is a measure of crude protein content, and a rough indicator of dietary quality (e.g. Leslie & Starkey, 1985).

Stable oxygen isotope ratios have been shown to vary with local precipitation (Dansgaard, 1964), and thus $\delta^{18}O$ values in animals from different habitats, or during different time periods, reflect climatic conditions and seasonality (Koch *et al.*, 1989). More importantly, however, is that between individuals and species from the same habitat, $\delta^{18}O$ values are related to differences in water sources. $\delta^{18}O$ values in animal tissues are expected to reflect differences in water acquisition (whether by drinking or from water bound in food), should differ between faunivores and herbivores, and between animals that lose water predominantly via panting and those that sweat (Kohn *et al.*, 1996; Sponheimer & Lee-Thorp, 1999a, 2001; Smith *et al.*, 2002).

Stable isotope ecology has been used for interpretations of early hominid (Lee-Thorp *et al.*, 1994; Sponheimer & Lee-Thorp, 1999b; Lee-Thorp *et al.*, 2000; Lee-Thorp *et al.*, 2003; Sponheimer & Lee-Thorp, 2003; van der Merwe *et al.*, 2003) and nonhuman primate palaeoecology (Lee-Thorp *et al.*, 1989a; Lee-Thorp, 2002). Palaeodietary studies, however, utilize extinct and extant ungulate and other mammal species of known diets as controls, and yet the behaviour of stable isotopes in living nonhuman primates has seldom been researched.

Some studies have approached modern primate feeding ecology using stable isotopes, but have dealt mainly with forest-dwelling species, such as prosimians, platyrrhine monkeys, colobines, and chimpanzees (e.g. Schoeninger *et al.*, 1997; Schoeninger *et al.*, 1998; Schoeninger *et al.*, 1999; Carter, 2001; McGee & Wright, 2001). Thackeray *et al.* (1996) analysed stable carbon and nitrogen isotope ratios from a small number of bone collagen samples in an attempt to document ecological variability of southern African chacma baboons.

This project forms the first extensive investigation into the behaviour of stable light isotopes in South African chacma baboons and thus contributes to a more rigorous understanding of baboon dietary ecology, and of isotopic measurements taken from South African fossil primate taxa.

Different biological tissues provide insights into environmental variables at slightly different time scales, based on growth and turnover rates of each material (see Jones *et al.*, 1981; Tieszen *et al.*, 1983; Ambrose & Norr, 1993; Tieszen & Fagre, 1993; Sponheimer *et al.*, 2003b). In this study, faeces have been analysed to access dietary information for the few days prior to deposition. A large number of plant samples have been used, as well as faeces from a variety of mammal species, providing an appropriate ecological context. Hairs and tooth dentine were sampled in serial increments so as to obtain temporal variability within an individual. Tooth enamel carbonate of fossil primates from Swartkrans Members 1 and 2 were analysed, and compared with data from previously published work, and with the information obtained from modern baboon enamel. It must be noted that teeth form early on during an individual's life, and thus analysis of this tissue only provides ecological information for the first few years of life. In sum, the work comprises data from a vast number and diversity of materials, providing an ideal backdrop for reaching the objectives of the project.

In the following chapter, available literature relevant to the ecology of modern and fossil baboons is reviewed. Chapter 2 also contains a review of previous studies of modern and fossil primate ecology based on stable light isotopes. Chapter 3 elaborates on the principles of stable light isotope ecology, outlines the use of percentage nitrogen as an indicator of dietary quality, and presents a model of the different scales of ecological information archived in different biological materials. In chapter 4, the study areas for this project, and the techniques employed for field collection, sample preparation, and laboratory analysis are described. The results of all analyses are presented in chapter 5, although raw data are given in Appendices I through V. These results are discussed in chapter 6, in terms of baboon dietary variability within savanna communities, Pleistocene cercopithecoid dietary adaptations, and the implications of these results for the baboon/hominid model.

CHAPTER 2

CHACMA BABOONS AND SOUTH AFRICAN PLEISTOCENE CERCOPITHECOIDEA

This chapter reviews the current geographical distribution of baboons, and literature pertaining to the ecology of the genus *Papio*. The content essentially describes baboons as the extreme dietary generalists of the modern primate world. Previous work involving stable light isotope ecology in modern primates and in South African Pleistocene cercopithecoids, and the insights that have thereby been gained into the feeding ecology of these fauna, is reviewed. The last section also includes an introduction to members of the South African Pleistocene Cercopithecoidea analysed in this study.

2.1. Taxonomy of African Papionins, and the Genus *Papio*

The cercopithecine tribe Papionini is comprised of six genera, including macaques, mandrills, mangabeys, and baboons. All but one of these genera (*Macaca*) are indigenous to sub-Saharan Africa. Recently, molecular phylogenetic studies have resulted in a revision of the clades occurring within the tribe. Singleton (2001) showed that the two mangabey genera, *Cercocebus* and *Lophocebus*, are not sister groups, as morphological data had previously suggested, and similarly, *Mandrillus* is not a sister group of the baboons *Papio* and *Theropithecus*. Singleton (2001) points out that *Cercocebus* and *Mandrillus* form a single clade within the papionins, and that *Lophocebus* shares its Most Recent Common Ancestor (MRCA) with the baboon clade. This taxonomy has been supported by phylogenetic reconstructions based on postcranial morphological character traits (Collard & Elton, 2001; Fleagle & McGraw, 2002).

Subgeneric taxonomy of the genus *Papio* is unclear; confusion surrounds the distinction of species, subspecies, and varieties. There are five generally recognized forms, namely chacma, yellow, olive, hamadryas, and guinea baboons. If each form is recognized as a species, these are ascribed the epithets *P. ursinus* (chacma baboons), *P. cynocephalus* (yellow baboons), *P. anubis* (olive baboons), *P. hamadryas* (hamadryas baboons), and *P. papio* (guinea baboons). Guinea baboons, which occur only in a small part of West Africa, are probably the least well-known members of the genus. The distribution range of olive baboons includes parts of West Africa, the southeastern Congo Basin, and East Africa. Hamadryas baboons occur in montane areas of Eritrea, and a population also exists in southeastern parts of the Arabian Peninsula. Yellow baboons are common in Malawi, Tanzania, northern Mozambique, and in Ethiopia. A second type of yellow baboon, sometimes referred to as *P. c. kindae*, occurs in south-central Africa, in parts of Zambia and Angola. In southern Africa, that is the area south of the Zambezi River, only chacma baboons occur.

Interpretations vary as to how many of these forms should be considered distinct species, and how many should be included as subspecies of another form. Part of this problem can be ascribed to the overlap in geographical ranges, leading to hybrids and hybrid zones (reviewed in Jolly, 2001).

There are three common usages of baboon nomenclature (Jolly, 1997). Some authors have divided the five forms into *P. hamadryas* and *P. cynocephalus* (with four subspecies). However, as Jolly (1997) points out, this nomenclature presents a paraphyly, since hamadryas and olive baboons are more closely related to each other than either is to chacma baboons. According to Jolly (1997), placement of all five forms within a single *Papio* species, *P. hamadryas*, best fits the Linnaean species concept, but he suggests that considering all five forms as distinct species is also acceptable.

Hayes *et al.* (1989) support the separation of *P. anubis*, *P. cynocephalus*, and *P. ursinus* into three species, based on morphological variations and the apparent distinctness of hybrid forms. Aldridge & Richtsmeier (1999) found that craniofacial character traits displayed significant localized differences between the olive, yellow, and chacma baboon morphotypes. However, mtDNA sequences of baboons suggest that yellow and olive baboons share a MRCA, and form a larger clade with the hamadryas baboons (Newman *et al.*, 2000). The results indicate that guinea baboons are basal to the yellow-olive-hamadryas baboon clade, and that chacma baboons are basal to all four morphotypes. Interestingly, the hamadryas baboons exhibit two paraphyletic lineages that Newman *et al.* (2000) ascribe only partially to hybridization with yellow baboons.

There is also variability within the chacma baboons, leading to further taxonomic confusion. Generally, *Papio ursinus* are considered as a sister species to other *Papio* baboons, or as a subspecies within the single *P. hamadryas* species. Meester *et al.* (1986)

(in Skinner & Smithers, 1990) recognized six subspecies of *Papio ursinus*, while Jolly (2001) displays only three allopatric taxa within the chacma group (Jolly, 2001, Fig. 1, p.95).

In this dissertation, the "five-species" nomenclature is used, as further subdivision of the baboon morphotypes has hitherto been largely unsuccessful. Wherever possible, different baboon morphotypes are referred to by their common names, which seems reasonable until a more definitive nomenclature has been established. In this chapter, the term "baboons" will be applied to all members of the genus *Papio*, unless specifically indicated. However, for comparisons between other mammal species, and for discussions of the results, the term "baboons" refers to chacma baboons (unless otherwise indicated), as this is the only of the baboon morphotypes included in this study.

2.2. Ecology of Modern Baboons

Jolly (2001) argues that all *Papio* baboons are ecological generalists, and that each baboon morphotype's particular habitat-specific modifications are not extreme enough to exclude them from thriving in environments other than those in which they occur. In East Africa, Dunbar & Dunbar (1974) concluded that baboons displayed a more generalized behaviour, in terms of habitat utilization and dietary selectivity, than other primate species (including *Theropithecus gelada* and the generalist *Cercopithecus aethiops*). The adaptability of baboons is noted by Aldridge & Richtsmeier (1999), who found that ecological boundaries between baboon groups defined their craniofacial character traits more consistently than did taxonomic groupings. The observation of Phillips-Conroy & Jolly (1988), showing that baboon tooth eruption varied significantly between wild and captive situations, indicates that the adaptive plasticity of baboons to their environment extends even to the dental development of these primates.

In ecological terms, baboons exhibit a high degree of flexibility and adaptability. These primates flourish in African savanna ecosystems, but also occur in desert, swamp, forest, and montane habitats (e.g. Whiten *et al.*, 1991). Dietary flexibility in baboons was noted by DeVore & Hall (1965), stating that it is easier to list the non-dietary items than the items utilized by baboons in a given area.

Whiten *et al.* (1991) reported that, throughout Africa, baboons incorporate between 3 and 74% fruits, 8 and 53% leaves, and 1 and 53% subterranean items. Dunbar & Dunbar

(1974) found that the diet of *Papio anubis* living in the Bole Valley in Ethiopia was comprised of about 40% grasses and herbs, 20% shrubs and 35% trees. Fruits comprised about 55% of the diet of these baboons, while leaves accounted for almost 33%. In Laikipia, Kenya, baboons reportedly incorporate as much foliage into their diets as do the folivorous colobine monkeys (Barton *et al.*, 1993). In other cases, baboons rely heavily on grasses, such as those observed in Kenya by DeVore & Hall (1965). Moolman & Breytenbach (1976) analyzed stomach contents from chacma baboons near the Loskop Dam in the Gauteng Province, South Africa, and reported that annual intake of dicotyledonous plants was 80.5%, while 11,1% of the diet consisted of monocotyledonous plant species.

Underground storage organs (such as roots and rhizomes) are often heavily utilized by baboons, especially in arid conditions, as these plant organs have a high water content and nutritive value (DeVore & Hall, 1965). Chacma baboons in the Western Cape were observed to dig up subterranean plant parts from as deep as 18 inches below the ground (Hall, 1961). Baboons also include varying amounts of animal matter into their diets (e.g. DeVore & Hall, 1965).

Patterns of dietary selectivity are often consistent in primates, especially in species with specialized ecological adaptations. For example, Ganzhorn (1992) reported that the distribution of folivorous primates in forests closely follows the distribution of high quality (protein/fibre ratio) leaves. While nutrients are the most important factor dictating primate food choice, plant secondary compounds also influence their diets (Glander, 1982).

Several long-term studies have been carried out on baboons in an attempt to explain dietary selectivity in these primates. Whiten *et al.* (1991) argued for the selection of high quality diets (high protein/fibre ratios) and lipid-rich food items, and added that digestion inhibitors such as plant secondary compounds are generally selected against. Baboons in Laikipia in Kenya have diets with a higher protein content than do gorillas, and lower fibre than colobines (Barton *et al.*, 1993). Barton *et al.* (1993) suggested that because baboons lack the specialized foregut of folivorous colobines, and do not rely on body size to compensate for low dietary quality as gorillas do, they are forced into selecting diets of high quality and low digestion-inhibiting secondary compounds. Barton & Whiten (1994) provide data for olive baboons that supports these general rules of baboon dietary selectivity.

A study spanning five years in duration on yellow baboons in Mikumi in Tanzania revealed that in this area, yellow baboons utilized less than 25% of the available plant species (Norton *et al.*, 1987). The variability of these yellow baboon diets was also restricted in that there appeared to be a set of dietary staple plant parts that were utilized every month throughout the study period, and only perimeter items varied (Norton *et al.*, 1987), indicating a high degree of selectivity.

Glander (1982) predicted that generalist primate taxa should be less adapted to feeding on plants that produce high quantities of secondary compounds, compared to species with more specialized diets. Furthermore, non-folivorous primates are not distributed in correlation with foliage quality in the same way as folivorous species are (Ganzhorn, 1992). Thus, baboon diets should be delimited by plant secondary compounds, and to a lesser extent, plant nutrient content. In some generalist species, plant secondary compounds are important dietary deterrents, such as in *Cercopithecus aethiops* (Wrangham & Waterman, 1981). It has been suggested that this is also the case for baboons (e.g. Norton *et al.*, 1987; Whiten *et al.*, 1991; Barton *et al.*, 1993), but food availability (and plant biomass) is considered a more important determinant of dietary composition than is selectivity (Barton & Whiten, 1994). This implies that dietary selectivity observed in some studies does not place major constraints on baboon feeding.

The highly selective feeding behaviour of baboons in the study by Norton *et al.* (1987) could be considered a result of the lack of extreme seasonality in the tropical environment of this population. The authors themselves suggest that generalist, adaptive feeding behaviour may have been more apparent if conditions had changed and resulted in an absence or a decrease in the availability of baboon staple foods. Baboons in subtropical regions experience a higher degree of seasonality than those living closer to the tropics, which should result in seasonal fluctuations in available foods and thus resources utilized (Anderson, 1982). Byrne *et al.* (1993) found a strong seasonality in the plants eaten by chacma baboons in the Kwazulu-Natal Drakensberg, with the widest range of plants and plant parts being incorporated during the spring months. The same study also showed that two baboon troops, separated by an altitudinal cline of only 400m, had completely different diets, so much so that even the staple food items differed. Moolman & Breytenbach (1976) found that while monocotyledonous plant species accounted for only 11.1% of the baboon diet, as much as 56.3% of the baboon diet was comprised of this resource in June.

Moolman & Breytenbach (1976) further showed that tree bark was utilized by baboons more often during winter months than in summer months. In Byrne *et al*. (1993) and Moolman & Breytenbach (1976), the pattern holds that baboon diets are dictated by the availability of resources, and fluctuate seasonally in the subtropical environments of South Africa.

Contrasting with prediction of Glander (1982), as discussed above, baboons have been reported to feed on plants known to be toxic to other mammal species (Hamilton III *et al*., 1978). Baboons in Queen Elizabeth National Park in Uganda reportedly feed so heavily on *Euphorbia ingens* (= *candelabrum*) trees growing there that they affected the plant's appearance, and it was at one stage believed that two separate species of the tree occurred there (Lock, 1972). It was later shown that the spatial separation of the two morphologically different forms of this tree was correlated with the reserve's baboon population, and that baboon utilization of the plant in some areas and not in others was responsible for the emergence of the "two forms" (Lock, 1972).

Another example of the generalist behaviour of baboons is their ability to survive, and thrive, in the harsh environmental conditions of the Namib Desert in Namibia. The Namib baboons have developed many foraging and other survival strategies that enable them to live there. Hamilton III (1985) found that the Namib baboons often turned to toxic plants, such as *Datura* and *Euphorbia* spp., as a source of nutrition in times of staple food shortages. Apart from obtaining water by digging in holes created by other mammals such as *Oryx* (Hamilton III, 1985), the Namib baboons are able to conserve water by decreasing their activity levels, and as such have sometimes survived for up to 11 consecutive days without drinking water (Brain, 1988). These baboons obtain most of their water from within dietary items, especially fruits, but in times of food abundance, even this dietary selectivity becomes less apparent (Brain, 1988).

Faunivory in baboons is well documented, and further reflects their generalist and opportunistic behaviour. Omnivory merely allows baboons to adapt their diets when other food items become depleted (Hamilton III *et al*.; 1978). Insects often form a major component of baboon diets, though only when available (DeVore & Hall, 1965; Hamilton III *et al*. 1978). In the Namib Desert, Brain (1990) observed baboons feeding almost exclusively on butterflies when these insects arrived at the waterholes in the area. Previously, Hamilton III (1986) observed a similar dietary response by the Namib baboons to the appearance of grasshoppers. In the Okavango of Botswana, mopane scale insects (when these appeared) dominated the diet of one baboon troop, but were almost excluded from feeding by a troop only a few kilometers away (Hamilton III *et al.*, 1978). The vegetarian troop almost never came into contact with these insects, and the resultant dietary difference between the two troops is a phenomenon that almost entirely excludes the concept of dietary selectivity from baboon ecology.

Vertebrates are sometimes incorporated into baboon diets, including reptiles, birds (and their eggs), and mammals (DeVore & Hall, 1965). This behaviour is extremely opportunistic, however, and is most common in areas where baboons are in close contact with domestic livestock (e.g. Jackson, 1978; McKee, 1992; Butler, 2000). Strum (1975) observed an East African baboon troop that developed a social tradition of systematic predation, including co-operative hunting, but this remains an isolated case. All in all, vertebrate predation by baboons is rare, and hunts are very often unsuccessful (e.g. Moolman & Breytenbach, 1976; Hamilton III & Busse, 1982; Irby, 1984; Hill, 1999).

The ranging patterns of baboons are also correlated with resource availability. Stoltz & Keith (1973) reported that baboons in the Limpopo Province (formerly the Northern Transvaal) were distributed according to the availability of water. In the Namib Desert, baboon home ranges cover relatively large areas, in comparison with environments having a richer supply of food and water, such as the Okavango (Hamilton III *et al.*, 1976). A slightly different hypothesis of baboon ranging patterns is presented by Cowlishaw (1997), suggesting that it is not dietary quality, but risk of predation that places constraints on baboon habitat choice.

The only consistent pattern in baboon behavioural ecology that emerges from the studies discussed above is that baboons exhibit adaptations that enable them to utilize whichever resources are available in a given area in order to optimize nutritional uptake, as predicted by DeVore & Hall in 1965, almost four decades ago.

2.3. Stable Light Isotope Ecology of Modern and Fossil Primates

Although for more than two decades stable isotope ecology has been used to assist in archaeological and palaeo-anthropological ecological studies, relatively little is known about the stable light isotope ratios of modern primate taxa, and how these are related to environmental parameters defining primate behavioural ecology. However, several researchers have approached modern primate isotope ecology, and valuable information has been gained from extinct primate taxa, both human and nonhuman alike.

2.3.1. Modern Primates

Existing studies using stable light isotope ratios to interpret extant primate ecology have generally aimed to document feeding habits and niche separation amongst sympatric forest species. These studies have, for the most part, been limited in scope, sample sizes have been small, and primates have not been well placed in the context of mammal communities occupying the same habitats.

Schoeninger *et al.* (1998) used stable carbon and nitrogen isotopes from the hair of two species of *Galago* from Kenya, and *Lepilemur leucopus* from Madagascar, to elucidate aspects of these species' ecologies. Their study showed that $\delta^{13}C$ values correlated with foraging at different levels of the canopy, and that $\delta^{15}N$ values indicated trophic levels, with the more insectivorous species being more ^{15}N-enriched. *Propithecus diadema edwardsi* from Madagascar showed $\delta^{13}C$ values higher than that expected for a closed canopy species (McGee & Wright, 2001). They suggest that stable light isotopes may be useful in primate conservation, through identifying and qualifying habitat disturbances due to human activity.

Schoeninger *et al.* (1997) found that, among four species of platyrrhine monkeys, carbon isotope ratios from hair distinguished ^{13}C-depleted closed canopy feeders (*Cebus* and *Ateles*) from more ^{13}C-enriched species that feed mainly in open canopy, deciduous forests (*Alouatta* and *Brachyteles*). In their study, nitrogen isotope ratios were significantly different between species having slightly different diets. *Cebus*, an omnivorous genus, had the highest $\delta^{15}N$ values, while the frugivorous and folivorous genera (*Alouatta*, *Brachyteles*, and *Ateles*) had hair that was lower in ^{15}N.

Chimpanzees (*Pan troglodytes*) from Ugalla in Tanzania and Ishasha in the Democratic Republic of Congo were shown to feed primarily on forest plants (Schoeninger *et al.*, 1999), implying very little utilization of savanna-based resources. Schoeninger *et al.* (1999) also suggested that termites and other animal matter were relatively scarce in the chimpanzee diet (Schoeninger *et al.*, 1999).

Carter (2001) found similar results for chimpanzees living in the Kibale Forest in Uganda. She concluded that chimpanzees did not consume sufficient animal matter to affect $\delta^{15}N$ values of their body tissues, and that $\delta^{13}C$ values in chimpanzee tissues only indicate utilization of savanna-type resources when agricultural plants make significant inputs into their diets. In her study of five primate species in Kibale Forest, Carter (2001) also showed that differential foraging by these species is indicated by stable light isotope ratios. She suggested that oxygen isotopes in bone and enamel apatite carbonate were the most consistent indicator of niche separation in forest primates, with the more folivorous species having the highest carbonate $\delta^{18}O$ values.

Limited data are available for modern *Papio* spp. Ambrose (1986) reported that baboons from East Africa had diets dominated by C_3-based foods, and that baboon collagen was more depleted in ^{15}N than any other herbivore. Because baboons are omnivorous, at least to some extent, Ambrose (1986) ascribed their low collagen $\delta^{15}N$ to high utilization of nitrogen fixing plants, such as *Acacia* spp., although it has since been shown that nitrogen fixing plants are not necessarily depleted in ^{15}N compared to other plant species (e.g. Muzuka, 1999).

Papio anubis from Kibale Forest also had tissue $\delta^{13}C$ values indicating C_3-based diets, although the highest values amongst five primate species from that area were observed in baboon tissues (Carter, 2001). This is in keeping with the idea that baboons have a more varied diet than other primate groups, and also that utilization of open area, savanna resources does occur more regularly than is the case with other primates, including chimpanzees. Carter (2001) also found that baboons (*Papio anubis*) had lower $\delta^{18}O$ values than other primate species, and suggested that this was due to baboons drinking more regularly than the other primates studied.

There has hitherto been only one study aimed at documenting baboon diets using stable light isotopes. Using new and previously published data on chacma baboon bone collagen from several areas in southern Africa (Lee-Thorp *et al.*, 1989a, 1989b), Thackeray *et al.* (1996) examined intra- and inter-habitat dietary variability in baboons. This study noted that baboon collagen $\delta^{13}C$ values are highest in areas where grasses are more commonly available (Drakensberg and Messina). Thackeray *et al.* (1996) also found considerable variability in baboon collagen carbon isotope ratios when comparing animals from a variety of different environments, but within any one environment, dietary variability was more limited.

Thackeray *et al.* (1996) observed the highest $\delta^{15}N$ values in specimens from the extremely dry Namib Desert, and from Mkuze in Kwazulu-Natal, where mean annual rainfall exceeds 1 000mm. Since $\delta^{15}N$ is often believed to be higher in arid areas, they ascribed the ^{15}N-enrichment of Mkuze baboons to higher rates of evaporation that decreased the amount of water actually available to baboons. This interpretation is not supported by current understandings of nitrogen isotope fractionation in mammals (see Chapter 3).

2.3.2. South African Pleistocene Cercopithecoidea

The fossil cercopithecoids found in South African Pleistocene deposits comprise a wider diversity of genera and species than is encountered in the savanna environments of today. However, confusion still surrounds the taxonomy of these primates. Moreover, almost nothing is known about their dietary and behavioural adaptations. I will provide a brief account of some of the previously described taxa that pertain to this study. Notably, no specimens of *Gorgopithecus* were obtained for analysis, and this taxon is therefore omitted from this description.

Theropithecus

These were relatively large baboons with high, flat faces. They are closely related to the modern *Theropithecus gelada* (Brain, 1981). Specimens of this genus were previously regarded as *Simopithecus* sp., but Freedman (1976) suggested that *Simopithecus* be included as a subgenus of *Theropithecus*. In a review of African and Indian *Theropithecus* fossils, Delson (1993) proposed that the name *Simopithecus* be altogether deleted from the taxonomy. Currently, two species are recognized in South African deposits, *T. darti*, which appears slightly earlier in the fossil record, and *T. oswaldi* (Delson, 1983). At Swartkrans in particular, Delson *et al.* (1993) recognize the presence of only *T. oswaldi*, but Delson (1992) points out that the distinction between these two species is in any case arbitrarily based on differences in incisal tooth size. From an adaptive behavioural perspective, these primates had high-cusped cheek teeth and reduced incisors, similar to that of modern gelada baboons, which have a grass-based diet (Jolly, 1970). Stable carbon isotopic data indicates that extinct members of the *Theropithecus* genus were also primarily graminivores (Lee-Thorp *et al.*, 1989a), furthering the phylogenetic and ecological connection between them and modern geladas. Dental microwear evidence also suggests that *T. oswaldi* from the Omo Sequence in East Africa had a diet very similar to that of modern geladas, although *T. oswaldi* appears to have consumed a slightly higher proportion of leaves (Teaford, 1993).

Parapapio

These baboons differed from the genus *Papio* in having shorter, less concave, frontals and nasals (Brain, 1981). However, Brain (1981) noted that this character trait exists in modern *Papio ursinus* populations as well, confusing the issue of separating these two genera. Furthermore, several species of *Parapapio* have been described from South African Pleistocene deposits, and thus the subgeneric taxonomy of the genus also remains a matter of much debate. Freedman (1976) supports the distinction of *P. jonesi*, *P. whitei*, and *P. broomi* based on taxonomic sub-grouping according to body size, with *P. whitei* being the largest and *P. jonesi* being the smallest of the three species. According to Brain (1981), there is very little evidence that the three species even form a chronocline, and he states that the presence of three *Parapapio* species co-existing in the same place and at the same time is remarkable. However, as Freedman (1976) pointed out, subgeneric classification of *Parapapio* specimens is based on teeth, as very little cranial material has been recovered. Nevertheless, these three species are currently accepted as biologically accurate, and it can only be supposed that differential resource utilization and/or temporal separation favoured this sympatry in the South African Pleistocene. Luyt (2001) provides some evidence for dietary separation of *P. jonesi* and *P. broomi*, but she cautions that the difference in their $\delta^{13}C$ values could also possibly be a sex or age related phenomenon occurring within a single species.

Papio (Dinopithecus) ingens

Dinopithecus was previously considered as its own genus, but is currently recognized as a subspecies of the genus *Papio* (Brain, 1981). These were very large cercopithecoids with long muzzles and robust skulls (e.g. Freedman, 1976). Morphologically, they appear to have been large-bodied folivorous primates (as are modern gorillas), and this is supported by limited ($n = 3$) stable carbon and oxygen isotopic evidence (Lee-Thorp & van der Merwe, 1993).

Papio robinsoni

Along with *Theropithecus*, *Papio robinsoni* is the most common cercopithecoid in South African Pleistocene deposits (Delson, 1992). Morphologically, this baboon is very similar to the modern *P. ursinus*, and "almost certainly ancestral to it" (Brain, 1981, p.153). Stable carbon isotope ratios of *P. robinsoni* indicate that it had a diet very similar to that of modern *P. ursinus*, being primarily C_3-based, probably consisting of a blend of leaves, fruits, and other plant material present in the diets of chacma baboons (Lee-Thorp *et al.*, 1989a).

Cercopithecoides

Cercopithecoides are members of the Colobinae, the cercopithecoid subfamily that is totally absent from modern savanna ecosystems. Freedman (1976) recognizes only a single species, *C. williamsi*, from South African deposits. Colobines are generally exclusive folivores living high in the canopy of equatorial rain forests, and thus their presence in the South African, as well as East African, Plio- and Pleistocene savanna is surprising. *Cercopithecoides* has been considered an important indicator of past habitat conditions, most notably in deposits in which they occur contemporaneously with early hominids. In Aramis, Ethiopia, their presence and abundance was suggested to reflect closed, woodland palaeo-environments (WoldeGabriel *et al.*, 1994; Leakey *et al.*, 1995). Delson (1992), however, suggested that these monkeys were adapted to a terrestrial lifestyle, which is in complete contrast with that of modern colobines. Delson's prediction is in agreement with existing carbon isotope data, which suggests that these animals consumed higher amounts of C_4-based foods than all contemporary primates, barring *Theropithecus* (Luyt, 2001).

From the above, it is clear that the dietary adaptations of these primates are poorly known, although several attempts have been made to resolve this issue using stable light isotope ratios from apatite carbonate. Lee-Thorp et al. (1989a) showed that two sympatric primate species from the Pleistocene deposits of Swartkrans Members 1 and 2 were able to co-exist through competition avoidance due to isotopically different feeding habits. *Papio robinsoni* had a diet similar to modern baboons, being C_3-based, while *Theropithecus darti* had a C_4-based diet comparable with the modern graminivorous diets of *Theropithecus gelada* living in the Ethiopian Highlands. Amongst other Swartkrans baboons, *Papio*

(*Dinopithecus*) *ingens* also showed $\delta^{13}C$ values indicating reliance on C_3-based foods (Lee-Thorp & van der Merwe, 1993). *Parapapio jonesi* exhibited greater variability (>3°/₀₀) in $\delta^{13}C$ values between specimens, which was ascribed to be indicative of different feeding strategies at different sites, or due to taxonomic confusion of one or both of the specimens analysed (Lee-Thorp & van der Merwe, 1993). Luyt (2001) analysed carbon and oxygen isotope ratios from a variety of primate taxa from Sterkfontein, and these are considered alongside the fossil cercopithecoids included in this dissertation.

SUMMARY

Disparity between morphological and molecular phylogenies, complications arising from hybridization, and discrepancies in understandings of the species concept, has resulted in there being an as yet unresolved nomenclature for the *Papio* baboons. For the remainder of this manuscript, chacma baboons will be referred to as either *P. ursinus*, or simply baboons.

In general, leaves and fruits are the most important dietary item consumed by baboons, although subterranean items may be a more important resource in arid conditions. Grasses and grass parts are utilized, but are not relied on as a food source in most environments. Dietary selectivity for high quality foods, and selection against secondary compounds does occur, although this appears to be limited for baboons. Instead, baboons are extreme generalist and opportunist feeders, readily adapting to environmental conditions to exploit available resources in order to meet their nutritional needs.

The South African Pleistocene Cercopithecoidea are represented by a variety of sympatric taxa. Stable light isotope studies have provided some important insights into the diets of these fauna, but the behavioural adaptations of each species, and differential resource utilization in relation to their co-existence, remains poorly documented.

CHAPTER 3

STABLE ISOTOPE ECOLOGY

Stable isotope ecology has proven to be a powerful tool in ecological and palaeoecological research. This chapter presents background information on the major processes responsible for the abundances of stable carbon, nitrogen, and oxygen isotopes in biological tissues found in terrestrial ecosystems. The types of ecological information that can be obtained from stable light isotope analysis of a variety of animal tissues, including the possibility of establishing temporal ecological records from serial analysis of hair and teeth, is discussed. Faecal nitrogen content is widely accepted to reflect dietary quality, i.e. the crude protein content of a mammal's diet, and a brief account of the benefits and problems associated with analysis of faecal nitrogen is provided.

3.1. Stable Carbon Isotope Ratios: Photosynthesis, Diet Selectivity and Habitat Utilization

The fractionation and abundance of stable carbon isotopes in biological tissues is by now relatively well understood, and has been used to qualify and quantify the diets of a range of modern and fossil fauna. The major fractionation of the stable isotopes of carbon in terrestrial ecosystems occurs in plants during photosynthesis, and mammal tissues faithfully record this fractionation in the carbon of their tissues, which is obtained from ingestion of carbon-containing foods.

3.1.1. Photosynthesis and the Carbon Isotope Ratios of Terrestrial Plants

Smith & Epstein (1971) described a bimodal distribution of $^{13}C/^{12}C$ ratios in plants associated with two different photosynthetic pathways: plants following the Calvin Benson cycle (C_3 photosynthetic plants) are consistently depleted in ^{13}C compared to plants that follow the Hatch-Slack method of photosynthesis (C_4 photosynthetic plants). C_4 photosynthesis occurs in plants where the photosynthetic structures (usually leaves) have a particular design known as Kranz anatomy, with a prominent, radially aligned bundle sheath. Smith & Epstein (1971) concluded that Kranz anatomy, and therefore C_4 photosynthesis, can be consistently predicted from a plant's $\delta^{13}C$ value.

Smith & Epstein (1971) observed that Kranz anatomy was not necessarily correlated with taxonomic groupings, although it proved to be more common in monocotyledonous species. C_4 photosynthesis seems to be an evolutionary adaptation of plants (mostly grasses) for survival in tropical and subtropical environments where the growth season is characterized by high temperatures. In other words, C_4 grasses dominate in low-altitude, summer rainfall, tropical or subtropical environments (Vogel *et al.*, 1978). This evolutionary step has occurred at least 31 times among 18 families of angiosperms and is attributed to the vascular leaf anatomy and gene code of C_3 plants being readily susceptible for conversion to Kranz anatomy (Hibberd & Quick, 2002). Because C_4 photosynthesis is most common in the Poaceae (=Gramineae), Vogel *et al.* (1978) examined the distribution of C_3 versus C_4 grasses in South Africa. The results of the survey showed that in the warm, summer rainfall, savanna environments of South Africa, grasses are predominantly C_4, while C_3 grasses dominate in high altitude areas, such as the Lesotho Drakensberg, and in the winter rainfall environment of the Western Cape. In most areas of South Africa, the trees and shrubs are almost exclusively C_3 (Vogel *et al.*, 1978).

Although $\delta^{13}C$ values may vary in plants growing in different environmental conditions, particularly in C_3 plants, the ranges of $\delta^{13}C$ values found in C_3 and C_4 plants respectively, do not overlap (Vogel, 1980). The basis for this difference is that during photosynthesis, C_3 and C_4 plants discriminate against ^{13}C in different amounts.

The greatest fractionation occurs during carboxylation (CO_2-fixation) (Vogel, 1980; O'Leary, 1988). In C_3 plants, the enzyme responsible for the carboxylation of CO_2 is *ribulose bisphosphate carboxylase* (Rubisco) that converts absorbed CO_2 into phosphoglyceric acid (PGA) consisting of three carbon atoms. During C_4 photosynthesis, CO_2 is converted into oxaloacetic acid (OAA), a four-carbon compound, by the action of the enzyme *phosphoenolpyruvate carboxylase* (PEP). Rubisco discriminates against ^{13}C more heavily than does PEP (Farquhar *et al.*, 1982; O'Leary, 1988). The isotopic fractionation that occurs during carboxylation by PEP or Rubisco is irreversible, and it follows that although Rubisco is involved in C_4 photosynthesis later on, further fractionation is limited (Vogel, 1980). The nett result is that C_3 plants are more depleted in ^{13}C than C_4 plants (Vogel, 1980; Farquhar *et al.*, 1982; O'Leary, 1988). $\delta^{13}C$ values of C_3 plants generally range from -24 to $-27^{o}/_{oo}$, while $\delta^{13}C$ in C_4 plants ranges from about -12 to $-14^{o}/_{oo}$ (Vogel *et al.*, 1978; Vogel, 1980; O'Leary, 1988).

The $\delta^{13}C$ values of plants exhibit some degree of variation depending on the circumstances in which these plants are growing. Because C_4 plants irreversibly fix CO_2 (and thus ^{13}C) early on during photosynthesis, they show less within-group $\delta^{13}C$ variation than do C_3 plants (O'Leary, 1988; Tieszen, 1991).

Fractionation of stable carbon isotopes in C_3 plants is understood from the expression:

$$F = [a + (b - a)C_i/C_a - d] \ldots\ldots\ldots\ldots\ldots\ldots(1)$$

In equation 1, F is the magnitude of isotopic fractionation that occurs in C_3 plants. The co-efficient *a* is the discrimination against ^{13}C due to diffusion (4.4‰), *b* is the discrimination due to carboxylation (~30‰), and *d* represents the minimal effect that respiration, liquid-phase diffusion, carbon export and other factors have on isotopic exchange during photosynthesis (after O'Leary, 1993). C_i is the concentration of CO_2 in the interstitial spaces of a photosynthesising leaf, and C_a is the ambient atmospheric CO_2 concentration. Variations in C_3 plant $\delta^{13}C$ values stem largely from variations in C_i/C_a ratios. During photosynthesis, the higher the C_i/C_a ratio, the lower the discrimination against ^{13}C in absorbed CO_2, thus effecting an overall enrichment in plant ^{13}C (Farquhar *et al.*, 1982).

There is a consistent depletion of ^{13}C in dense forests as compared to more open habitats, with intensive recycling of atmospheric CO_2 progressively increasing C_a, resulting in $\delta^{13}C$ values as low as -37‰ in some Amazonian rain forest plants (Farquhar *et al.*, 1982; van der Merwe & Medina, 1989). Thus, the $\delta^{13}C$ of forest C_3 plants is more depleted than that of woodland or savannah C_3 plants (van der Merwe & Medina, 1991). Van der Merwe & Medina (1989) also showed a $\delta^{13}C$ cline within forest plants, lower level foliage being the most depleted in ^{13}C, with leaf $\delta^{13}C$ gradually increasing further up the canopy. Concomitantly, the $\delta^{13}C$ values of plants growing in more open habitats increases with a decrease in foliage density, owing to the effects of radiation on discrimination against ^{13}C (e.g. Tieszen, 1991). Together with this, $\delta^{13}C$ in woodland and savanna plants may increase with height above the ground, even within different parts of a single plant.

Other environmental factors affect $\delta^{13}C$ values of C_3 plants, albeit that these effects are small, in the order of less than 2‰ (but sometimes as much as 5‰). Firstly, C_3 plants growing in wetter habitats are slightly more depleted in ^{13}C than plants from drier areas because water stress causes stomatal closures that in turn cause a reduced C_i/C_a. In effect, ^{13}C is not as heavily discriminated against during photosynthesis in plants growing in dry areas as it is in plants from wetter areas (Tieszen, 1991). Thus, $\delta^{13}C$

values of C_3 plant leaves are inversely related to the amount of water available to these plants (Stewart *et al.*, 1995). The study of Stewart *et al.* (1995) showed that this correlation is consistent for plants from different areas with mean annual rainfall ranging between 350mm and 1700mm. Secondly, $\delta^{13}C$ values of C_3 plants decreases if ambient temperatures deviate from the optimum for any plant species, due to reduced enzyme activity resulting in decreased C_i/C_a (Tieszen, 1991). Thirdly, there is a relationship between the $\delta^{13}C$ values of C_3 plants and altitude, due to air pressure affects on C_i/C_a ratios, with plants growing at the highest altitudes exhibiting the lowest $\delta^{13}C$ values (Tieszen, 1991).

Variation in $\delta^{13}C$ also exists within C_4 plants, although not as pronounced as that observed in C_3 plants. Three sub-pathways of C_4 photosynthesis are known to occur, based on different enzymes involved in the process. Variation in $\delta^{13}C$ between these C_4 subtypes is small, and there is overlap between the ranges of $\delta^{13}C$ values exhibited by each type, but the means reportedly differ significantly (Hattersley, 1982). Hattersley (1982) presented means and standard deviations for NADP-ME, PCK, and NAD-ME grasses of $-11.35 \pm 0.13‰$, $-11.95 \pm 0.19‰$, and $-12.7 \pm 0.21‰$, respectively. In the Turkana Basin, Kenya, Cerling & Harris (1999) found that the mean $\delta^{13}C$ values of NADP-ME grasses, adapted to mesic environments, was $-11.8 \pm 0.7‰$, while that for xeric adapted NAD-ME and PCK grasses combined was $-12.8 \pm 0.8‰$.

A third photosynthetic pathway, Crassulacean Acid Metabolism (CAM), has a different effect on carbon isotope fractionation. Plants with CAM photosynthesis may engage in slight modifications of both C_3 photosynthesis (if the stomata are opened and CO_2 is absorbed during the day) and C_4 photosynthesis (if the stomata are opened at night) (O'Leary, 1988). In fact, C_3-like and C_4-like photosynthesis in CAM plants often occur simultaneously in proportions dependant on the plant's metabolism and on certain environmental conditions, such as temperature, so that the $\delta^{13}C$ of CAM plants varies with climatic and other fluctuations (Vogel, 1980). In arid conditions, CAM plants can close their stomata during the day, and open them at night to reduce water loss via evapotranspiration, thereby fixing CO_2 at night. This fixated CO_2 is stored in leaf vacuoles until daylight, when the C_3 photosynthetic cycle takes over (Vogel, 1980; O'Leary, 1988). The overall result is that the $\delta^{13}C$ of these plants is very similar to that of C_4 plants, but in wetter conditions, the plant may fixate CO_2 during the day, and thus their $\delta^{13}C$ values would then be more similar to those of C_3 plants. However, not all

CAM plants are able to switch to C_3 photosynthesis in more favourable conditions, but retain CAM photosynthesis (with C_4-like $\delta^{13}C$ values) in any environment (Stock, 2003, pers. comm.). CAM photosynthesis is most common amongst succulents and other plants adapted to the xeric conditions of desert and semi-desert regions, and apart from a few exceptions, is seldom observed in the woody plants of tropical and subtropical savannas.

3.1.2. Fractionation of Stable Carbon Isotopes between Diet and Terrestrial Mammal Tissues

Plant $\delta^{13}C$ values are reflected in the carbon of tissues of animals feeding on those plants, either directly in herbivores, or indirectly in animals feeding at higher trophic levels (e.g. Minson *et al.*, 1975; Vogel, 1978; DeNiro & Epstein, 1978). Therefore, in environments where C_4 grasses predominate, the ratio of graze to browse incorporated into the diet of an animal, either directly by herbivores, or indirectly by carnivores, are qualitatively reflected by tissue $\delta^{13}C$ values (Vogel, 1978). In areas where CAM plants make significant contributions to animal diets, animal tissue ^{13}C-content is intermediate between the depleted C_3 browsing and enriched C_4 grazing signals, creating an overlap of ranges that may complicate interpretations of diet. One such area is the Addo Elephant National Park in the Eastern Cape of South Africa, where the succulent *Portulacaria afra* is an abundant food source for the African elephants (*Loxodonta africana*) that live there (van der Merwe *et al.*, 1988).

Animal $\delta^{13}C$, being dependant on the $\delta^{13}C$ of the basic plant diet, also varies with variations in the $\delta^{13}C$ of plants growing in different environmental conditions. Therefore, taking into account the canopy effect (van der Merwe & Medina, 1989, 1991), and the observations of Tieszen (1991), animal $\delta^{13}C$ values are expected to be most depleted if they habitually feed on C_3 plants growing in: dense stands of vegetation; lower levels of the canopy (or at least on shorter plants or plant parts found closest to the ground); shaded areas; well-watered areas; and higher altitudes.

It is thus possible to use the carbon isotope ratios of animals to extract information regarding the habitats utilized by those animals, provided that this is interpreted within a particular dietary regime. For example, Ambrose (1986) found that within C_3 browsing species, forest herbivores were depleted in ^{13}C compared to savanna species, and also that forest floor feeders were ^{13}C-depleted when compared to higher canopy level feeders.

It has also been claimed that enamel carbonate $\delta^{13}C$ values of grazers reflected differential feeding on either NADP-ME or NAD-ME and PCK C_4 grasses, even though mean $\delta^{13}C$ values of these plants differ by very small amounts (Cerling & Harris, 1999).

Different animal tissues show different degrees of fractionation of stable carbon isotopes, which should also be taken into account for stable carbon isotope analysis of diet. Lipids from fatty tissue are depleted in ^{13}C by $3^o/_{oo}$ compared to the dietary $\delta^{13}C$ value, while muscle and other visceral tissues are slightly more enriched (Tieszen *et al.*, 1983). Faeces usually exhibit $\delta^{13}C$ values that are $0.9^o/_{oo}$ less than the dietary value (Sponheimer *et al.* 2003b & 2003c). Mammalian hair, comprised predominantly of a protein called keratin, was initially reported as being $1.8^o/_{oo}$ more enriched in ^{13}C than the animal's diet (Jones *et al.*, 1981), but this value is probably closer to $3^o/_{oo}$ (e.g. Nakamura *et al.*, 1982; Sponheimer *et al.*, 2003b). Bone is traditionally the most commonly used tissue for isotopic dietary studies. Collagen, the protein component of bone, has a $\delta^{13}C$ value that is between 4.5 and $6^o/_{oo}$ higher than that of the diet (Ambrose & Norr, 1993).

The mineral, inorganic phase of bone (apatite) can also be isolated and used for isotopic dietary investigations, based on $\delta^{13}C$ of apatite carbonate (Lee-Thorp & van der Merwe, 1987; Lee-Thorp, 1989b). The fractionation of dietary carbon isotope ratios in biological apatite is, however, more intricate than is the case with organic tissues. Apatite carbonate in herbivores is enriched in ^{13}C by between 12 and $14^o/_{oo}$ relative to the diet, while in carnivores, the difference is only 8 or $9^o/_{oo}$, and omnivores exhibit intermediate diet-apatite $\delta^{13}C$ differences (Lee-Thorp *et al.*, 1989b; Ambrose & Norr, 1993; Cerling & Harris, 1993).

Despite early controversy (Sullivan & Krueger, 1981, 1983; Schoeninger & DeNiro, 1982, 1983; reviewed in Lee-Thorp, 1989), bioapatite $\delta^{13}C$ signals are reliable dietary indicators (Lee-Thorp *et al.*, 1989b; Lee-Thorp & van der Merwe, 1991). The persistence of bone mineral in fossil samples allows for the use of stable isotopic analysis of this material for ecological studies (e.g. Lee-Thorp & van de Merwe, 1987; Wang & Cerling, 1994).

Bone apatite in fossil material does, however, undergo post-mortem diagenesis, due to recrystallization of the carbonate molecules. Lee-Thorp & van der Merwe (1987) showed that the effects of this diagenesis on the isotopic integrity of biogenic carbonates over time is limited and therefore $\delta^{13}C$ values of carbonate from fossil bone apatite as old as three million years still accurately reflect the $\delta^{13}C$ of the animal's lifetime diet. Lee-Thorp & van der Merwe (1991) identified tooth enamel as the most reliable source of $\delta^{13}C$ in fossil samples. It was further noted that the proportion of carbonate ions in fossil enamel crystalline structures undergoes a small amount of change early on during the fossilization process, after which no noticeable change occurs (Sponheimer & Lee-Thorp, 1999c). Using fossil tooth enamel carbonate, reliable $\delta^{13}C$ values have been obtained from samples dating back to the Miocene, ca. fourteen million years old (e.g. Quade *et al.*, 1995; Cerling *et al.*, 1997).

3.1.3. Changes in $\delta^{13}C$ of Atmospheric Carbon Dioxide and Implications for Dietary Analysis

Twentieth century industrialization and the burning of fossil fuels have resulted in a global decrease in $\delta^{13}C$ of atmospheric carbon dioxide of about 1.5‰ since the early 1900's (Friedli *et al.*, 1986; and see Arens *et al.*, 2000). Marino & McElroy (1991) showed that this change is reflected in the $\delta^{13}C$ values of C_4 plants, the most significant shift in $\delta^{13}C$ values occurring during the 1950's. C_3 plant $\delta^{13}C$ values also record changes in the $\delta^{13}C$ of atmospheric CO_2 (Arens *et al.*, 2000). Because animal tissues faithfully reflect the carbon isotopic composition of the basic plant diet, it is necessary to consider this atmospheric change, especially for dietary interpretations of $\delta^{13}C$ in animal tissues from before 1950. Thus, when comparing older material (pre-1950, including prehistoric and palaeontological material) with modern samples, ~1.5‰ should be subtracted from the $\delta^{13}C$ value obtained from the older specimens to more accurately understand diet.

3.2. Stable Nitrogen Isotopes in Terrestrial Ecosystems

Fractionation of the stable isotopes of nitrogen is more complex, and a poorly understood combination of factors is responsible for the abundance of ^{15}N in biological materials. It has been suggested that, due to the large number of variables influencing biological fractionation of stable nitrogen isotopes, $\delta^{15}N$ values cannot be used as dietary or environmental tracers (Handley & Raven, 1992). $\delta^{15}N$ analysis does, however, seem to bear useful ecological information, provided that all factors that contribute to natural ^{15}N abundances, and other lines of evidence such as $\delta^{13}C$ values, are considered. Used in combination with $\delta^{13}C$, $\delta^{15}N$ in animal tissues can, for example, provide insights into niche differentiation between species (Schoeninger *et al.*, 1997).

There is a close relationship between soils, plants, and the nitrogen cycle, with plant $\delta^{15}N$ values being influenced by nitrification and denitrification rates, soil pH and salinity, soil clay content, and aridity (Heaton, 1987; Handley & Raven, 1992; Robinson, 2001; Muzuka, 1999; Schmidt & Stewart, 2003).

Nitrogen fixation tends to add ^{15}N-depleted nitrogen to the soil, and thus nitrogen-fixing plants (such as legumes) often have lower $\delta^{15}N$ values than non-fixing plants (Delwiche & Steyn, 1970; Virginia & Delwiche, 1982). However, this is not always the case (e.g. Handley *et al.*, 1994; Muzuka, 1999; Schmidt & Stewart, 2003), and it appears that only those nitrogen-fixing plants that have mycorrhizal associations fractionate nitrogen isotopes differently to other plants (Robinson, 2001; Schmidt & Stewart, 2003). In contrast to nitrogen fixation, denitrification processes result in overall enrichment of soil ^{15}N content, due to the loss of ^{15}N-depleted mineral compounds (Handley & Raven, 1992). Thus plants growing in swampy areas or on lake margins should also be ^{15}N-enriched, as denitrification in these areas is often slower than the rate of decomposition (Muzuka, 1999). Plant $\delta^{15}N$ values should also be higher in environments with clay-rich soils, and in dry, overgrazed areas (Muzuka, 1999). Heaton (1987) found that plant $\delta^{15}N$ values are higher in arid environments than in areas receiving more annual rainfall, but this effect is small, in the order of 1 to 2‰.

Variations in plant $\delta^{15}N$ values are not clearly reflected in animal tissues, as a great deal of further isotopic fractionation occurs in animals during metabolic processes.

In animal tissues, it is widely accepted that fractionation exists between terrestrial herbivores and carnivores within a particular ecosystem, with animals feeding at higher trophic levels having $\delta^{15}N$ values 3 to 4‰ greater than primary consumers (Schoeninger & De Niro, 1984; Sealy *et al.*, 1987). However, Sponheimer *et al.* (2003a) observed that within a trophic level, the amount of protein in the diet of an herbivorous animal is positively correlated with $\delta^{15}N$. In their experiments, dietary protein levels influenced $\delta^{15}N$ by up to 3.6‰, suggesting that differences in nitrogen isotope ratios of species at different trophic levels is a function of protein intake, and not merely a fractionation effect that takes place between trophic levels (Sponheimer *et al.*, 2003a).

There is evidence that in arid conditions, especially in areas receiving less than 400mm of rain per year, animal tissues become more enriched in ^{15}N (Heaton *et al.*, 1986; Sealy *et al.*, 1987; Ambrose, 1991).

Taking into account observations of Steele & Daniel (1978), who showed that urine is depleted in ^{15}N relative to an animal's diet, Ambrose & DeNiro (1986) proposed a mass balance model between urea excretion and nitrogen isotope ratios to explain the apparent ^{15}N-enrichment of stressed animals living in arid environments (reviewed and summarized in Ambrose, 1991). Ambrose (1991) argued that an increase in excretion of ^{15}N-depleted urea would result in more ^{15}N remaining in the body's nitrogen pool, and thus lead to higher tissue δ^{15}N values. Animals that experience water stress or heat stress tend to show an increase in urea excretion, thereby increasing tissue δ^{15}N values. Total protein intake also affects an animal's urea excretion, as there is a positive trend between available protein and osmolality in the kidneys, and thus animals on high protein diets excrete more concentrated urine (higher levels of urea) and show higher tissue δ^{15}N. Thus, in drought-tolerant herbivores that perhaps excrete more urea than obligate drinkers to increase water retention, δ^{15}N values should be higher than in obligate drinkers.

Ambrose (1991) points out that browsing herbivores tend to be drought tolerant, and that their diets are higher in nitrogen than that of grazing herbivores, which are also generally forced to drink to obtain body water, and thus browsers should be more ^{15}N-enriched than grazing species.

Sealy *et al.* (1987) found that the patterns predicted by the Ambrose & DeNiro (1986) model were true for most environments, but not in Addo Elephant National Park. Grazers, as well as obligate drinkers, in Addo were enriched in ^{15}N compared to browsers and drought-tolerant herbivores. Sealy *et al.* (1987) proposed that available forage in Addo is low in protein, and thus the herbivores there retain protein (and thus urea) in order to sustain their microbial gut flora. In ruminants at least, this might cause a progressive recycling of urea within the animal, progressively increasing δ^{15}N as the gut flora are more enriched in ^{15}N than the recycled substrate. However, as Ambrose (1991) points out, the flora of Addo is comprised of 50% CAM photosynthesising succulent plant species. These plants would provide water to animals that fed on these plants, and it is likely that in Addo, which receives less than 400mm of rain annually, browsing and grazing species do utilize these plants, creating dietary overlap that might be responsible for the disparity in δ^{15}N signals in mammals from this area. In addition, Muzuka (1999) showed that succulents are ^{15}N-enriched compared to other plants, and perhaps grazers in Addo (obligate drinkers) supplemented their diets with water-rich CAM plants more readily than did drought tolerant browsing species, thereby increasing tissue δ^{15}N.

The model presented by Ambrose (1991) could be considered to account for the stepwise enrichment of ^{15}N between trophic levels, as well as for the observed pattern of ^{15}N-enrichment observed in water stressed animals. However, this mass-balance model does not consider that significant amounts of nitrogen are excreted in the form of faeces. Mammalian faeces are enriched in ^{15}N relative to their diet, as opposed to urea which is ^{15}N-depleted (Steele & Daniel, 1978). Mammals on high protein diets tend to excrete a higher proportion of protein in the form of ^{15}N-depleted urea, thereby increasing the overall amount of ^{15}N available for tissue synthesis. In contrast, mammals on low protein diets lose more protein in the form of ^{15}N-enriched faeces, and thus tissue $\delta^{15}N$ decreases (Sponheimer *et al.*, 2003a).

It seems that dietary protein and the nitrogen metabolism associated with different digestive anatomies may influence nitrogen isotope fractionation in animals more directly than other environmental variables (Sponheimer *et al.*, 2003a). The effect of protein intake on animal $\delta^{15}N$ values (Schoeninger *et al.*, 1997; Sponheimer *et al.*, 2003a) suggests that this isotope might simply be a function of the relative quality of an animal's diet, which in turn is influenced by factors such as climate, aridity, and ecological stress.

Another poorly understood variable that may influence stable nitrogen isotope trends is the cumulative effect of ^{15}N retention and excretion associated with aging. In controlled climate and feeding experiments with rats, Ambrose (2000) found no relationship between $\delta^{15}N$ and dietary protein, water stress, or heat stress, but noted that $\delta^{15}N$ showed a slight increase with age. The premise for this may be that during an animal's lifetime, selective retention and/or discrimination against ^{15}N may result in a shift in that animal's long-term nitrogen balance, thereby causing a temporal trend in observed $\delta^{15}N$ values. Ambrose (2000) does express caution here, however, noting that rats are not necessarily an appropriate model for predicting stable nitrogen isotope fractionation in larger mammals.

3.3. Stable Oxygen Isotope Abundances

Animal tissue $\delta^{18}O$ values are influenced by their water sources (e.g. Longinelli, 1984; Luz & Kolodny, 1985). $\delta^{18}O$ values of meteoric water vary with latitude, altitude, temperature, and precipitation (Dansgaard, 1964). Accordingly, across different habitats, mammalian carbonate $\delta^{18}O$ values reflect local climatic conditions (e.g. Koch *et al.*, 1989).

Within similar habitats, mammalian $\delta^{18}O$ values vary across different taxa having different ecological adaptations (Kohn, 1996). Variation in mammalian $\delta^{18}O$ values is a function of differences in drinking water, and $\delta^{18}O$ values of the water bound within their food sources.

The leaves of terrestrial plants are ^{18}O-enriched relative to local meteoric water, as water evaporation from leaf surfaces involves a discrimination against the lighter isotope (^{16}O) resulting in an overall increase in leaf $\delta^{18}O$ (Epstein *et al.*, 1977). As such, animals that obtain water mostly from within their food (usually browsing species) appear to be more enriched in ^{18}O relative to taxa that obtain water by drinking (usually grazers) (e.g. Kohn *et al.*, 1996; Sponheimer & Lee-Thorp, 1999a, 2001; Carter, 2001; Smith *et al.*, 2002). Plant roots, however, are less ^{18}O-enriched than are leaves (Epstein *et al.*, 1977; Yakir, 1992), and this may further complicate dietary interpretations.

Well irradiated plants, such as C_4 grasses and the uppermost leaves of C_3 plants, have higher rates of evapotranspiration than shaded plants, and thus appear to be enriched in ^{18}O (Yakir, 1992). This potentially provides for differentiation of mammal feeding habits into open versus dense habitats, and differential canopy level feeding (e.g. Quade *et al.*, 1995).

Kohn (1996) showed that animal foods are more ^{18}O-depleted than are plants, and it has been found that carnivorous fauna from the Pleistocene deposits of Swartkrans had lower $\delta^{18}O$ values than herbivorous taxa (Sponheimer & Lee-Thorp, 1999a). This pattern was also evident among modern fauna from Morea Estate (Sponheimer & Lee-Thorp, 2001), and amongst desert-dwelling omnivorous mammals compared to herbivores from the same region (Smith *et al.*, 2002). However, the lower $\delta^{18}O$ values of faunivores may reflect reliance on drinking water (Sponheimer & Lee-Thorp, 1999a, 2001).

It has been suggested that differences in physiologies between taxa affect mammal $\delta^{18}O$ values. Luz *et al.* (1984) proposed that, amongst small mammal species, smaller species with higher metabolic rates had different $\delta^{18}O$ values to slightly larger species. Bryant & Froelich (1995) attempted to extend this observation to larger mammals, and suggested that mammalian $\delta^{18}O$ is negatively correlated with body size. However, Bryant & Froelich (1995) noted that, at least for species examined in their study, dependence on the water bound in food decreases with increasing body size. Given the observation that drinking mammals display higher $\delta^{18}O$ values than taxa that obtain water from their food (Kohn *et al.*, 1996; Sponheimer & Lee-Thorp, 1999a, 2001; Smith *et al.*, 2002), the results obtained by Bryant & Froelich (1995) probably represent differential reliance on drinking water as opposed to water bound in food.

Sponheimer & Lee-Thorp (2001) suggest that the mode of water loss by mammals may also be reflected in their $\delta^{18}O$ values. Respiratory carbon dioxide, urine, faeces, and sweat all consist of water with a similar oxygen isotopic composition to that of an animal's body water, but water vapour that an animal excretes is relatively depleted in ^{18}O (Wong *et al.*, 1988). Therefore, Sponheimer & Lee-Thorp (1999a, 2001) have suggested that animals that lose water through panting should have $\delta^{18}O$ values that are higher than values observed in animals that sweat, but empirical data for testing this hypothesis is lacking.

Early studies of mammalian stable oxygen isotope ratios showed that the $\delta^{18}O$ of local meteoric water is directly related to $\delta^{18}O$ values in body water and bone phosphate (Longinelli, 1984; Luz *et al.*, 1984). Oxygen isotope ratios from apatite carbonate are measured routinely along with carbon isotope ratios, and tooth and bone apatite carbonate $\delta^{18}O$ values reflect water sources in the same way as do body water and bone phosphate values (Bryant *et al.*, 1996; Iacumin *et al.*, 1996). Stable oxygen isotope ratios in apatite carbonate of a fossil animal are also consistent with the $\delta^{18}O$ values that were present in its tissues while it was still alive, as is the case with stable carbon isotopes (Wang & Cerling, 1994; Sponheimer & Lee-Thorp, 1999c).

3.4. Isotopic Information Archived in Different Tissues

Depending on the rate of growth and turnover of a particular tissue, stable light isotope ratios measured in different tissues offer insights into animal diets at different time scales. Faeces, hair, bone collagen, dentine collagen, and enamel apatite carbonate differ in the type of ecological information that each tissue can provide. The following is a description of these variations, and a discussion of the implications for interpreting ecological variability in baboons from these tissues.

3.4.1. Faeces

Carbon and nitrogen isotope ratios in faeces have previously been used to document savanna mammal diets, providing short-term ecological information (e.g. Tieszen *et al.*, 1989; Sponheimer *et al.*, 2003c). For steers fed a sequence of C_4-, C_3-, and C_4-based diets, only seven days were required before the isotopic composition of faeces reached equilibrium with the dietary isotopic composition (Jones *et al.*, 1981). Clemens &

Phillips (1980) reported that the baboon caecum and colon retains fluid and particulate matter for three to five days before total evacuation of a meal. Lambert (1998) pointed out that this retention time may vary according to the nutritive composition of the diet. Nevertheless, it remains that faecal matter contains information about the past few days of a baboon's (and other mammal species') ecological activity. It is therefore expected that seasonal fluctuations in diet should be fully represented in faeces, and by isotopic analysis of faeces, should seasonally different diets comprise different isotopic signatures.

Faeces are informative regarding mainly the portion of the diet that is not digested and so isotopic analysis of diet may be biased towards less digestible food items. For example, baboons are unable to masticate leaves well, and do not have the specialized digestive tract of the folivorous colobine monkeys. Undigested food remains (commonly grass blades) are often observed in baboon faeces (e.g. Dunbar, 1976 & 1983). This may play a critical role when comparing information obtained from different tissues, but between species, and more so between different individuals of the same species, undigested foods in faeces should consistently indicate variations in dietary habits.

A further factor complicating faecal analysis is that the majority of nitrogen in herbivore faces is not of dietary origin. Most of the nitrogen in faeces is actually comprised of sloughed endogenous gut tissues and microbial cell walls (van Soest, 1994, in Sponheimer *et al.*, 2003d). This factor may complicate interpretations of faecal $\delta^{15}N$ values (and %N) as an ecological indicator.

3.4.2. Hair

Hair has often been used for stable light isotope ecological studies (e.g. Nakamura *et al.*, 1982; Schoeninger *et al.*, 1997 & 1999). Carbon and nitrogen isotope ratios in hair provide a longer-term insight into mammal feeding ecology than faeces, as a result of the tissue's longer formation time.

To examine a species' ecological variability from stable isotope ratios in hair, hairs can be removed from different animals at different time intervals. Hair follicles would be the best material for this purpose, as this is the part of the hair that is still growing, and thus the period in which this portion of the hair grew would be known (Zlotkin, 1985).

Temporal ecological variability of an animal can also be obtained through an analysis of several segments along the shaft of a single hair strand. Carbon isotope analysis of hair from equids fed controlled diets reflected changes in the isotopic composition of the diet within a few days (Sponheimer *et al.* 2003b). Due to a longer attenuation time, however, these changes do not reflect the full extent of dietary shifts, thus quantifying dietary fluctuations through serial analysis of mammal hair is difficult, even though qualitative shifts should be evident. Two to two-and-a-half months worth of growth are required before a mammal's hair reaches isotopic equilibrium with its diet (Jones *et al.*, 1981). In other words, a complete dietary shift (with a different isotopic composition) will only be fully expressed in hair after two or three months of consistent feeding on the new diet, as this is the time required for total replacement of the body's carbon and nitrogen pool.

Another factor complicating serial analysis, especially of wild animals, is the variability that exists in the rate at which hair grows. Human scalp hair grows at a rate of 0.3mm per day, or 10mm per month, on average (Zlotkin, 1985). Inagaki & Nigi (1988) showed that the growth rate of the hair of the Japanese monkey (*Macaca fuscata fuscata*) varies between 4.2 and 26.2mm per month, according to season, an individual's nutritional state, and that pregnant females exhibit a different rate of hair growth to males and non-pregnant females. Their data indicate that hair of these monkeys (and perhaps all cercopithecoids) grows an average 12.4mm per month (extrapolated from Inagaki & Nigi, 1988, Table 5, P. 85). Cercopithecoids, specifically *Macaca fuscata fuscata* and *Cercopithecus* spp. undergo seasonal moulting, with hair being wholly replaced once a year (Inagaki & Nigi, 1988; Isbell, 1995). If chacma baboons were to experience similar seasonal hair length changes, fallen hair strands should reflect a growth span of about one year. It seems reasonable to accept that baboon hair length increases by 10 to 12mm a month *on average*. Due to the variation in mammalian hair growth rates however, it is unlikely that a precise time frame can be posited on a serially sectioned mammalian (and baboon) hair collected from a wild animal. In short, factors affecting hair growth rates, and the moulting patterns of species, should be considered for this purpose, even though information on this topic is limited.

3.4.3. Bone Collagen

Bone collagen has traditionally been the most commonly used tissue for isotopic analysis of animal diets, in both modern and prehistoric contexts (e.g. van der Merwe, 1982; Ambrose, 1986; Cormie & Schwarcz, 1996). Bone undergoes turnover throughout an animal's life, and thus isotopic data obtained from this tissue provides an integrated lifetime average of ecological variables.

About 65% of bone is comprised of inorganic material (apatite), while 25 to 35% is comprised of a fibrous protein called collagen (LeGeros, 1991). The mineral phase of bone does not form part of this study. Ambrose & Norr (1993) showed that bone collagen, a protein, is derived from the protein component of an animal's diet, and thus stable carbon and nitrogen isotope ratios of bone collagen reflect an animal's protein food source.

3.4.4. Dentine Collagen

About 20% of tooth dentine is collagen (LeGeros, 1991), from where carbon and nitrogen isotopes can, and have previously been measured (e.g. Bocherens *et al.*, 1994; Sealy *et al.*, 1995; Balasse *et al.*, 2001). As is the case with hair and bone collagen, dentine collagen is formed from a nutrient pool derived from the protein component of an animal's diet (Ambrose & Norr, 1993).

Unlike bones, teeth do not turnover, as no calcium withdrawals occur once the dentine has been deposited, and thus the growth records are permanent (Schour & Hoffman, 1939a). During calcification, dentine is deposited in daily increments (microscopically visible as alternating light and dark bands), known as Lines of von Ebner, which form in concentric patterns starting at the dentino-enamel junction and progressing towards the root.

The rate of dentine apposition averages 4μm per day in humans and rhesus macaques (e.g. Molnar *et al.*, 1981), but calcification rates vary between species, and between individuals. Molnar *et al.* (1981) found that heat stress decreased the rate of dentine apposition in rhesus macaques, and that the daily increase in dentine in these animals is related to age. Schour & Hoffman (1939b) reported that the daily increments in rhesus macaque dentine vary between 2.4 and 12.2μm. In baboons from the Awash National Park in Ethiopia, Dirks *et al.* (2002) found that nutritional and other types of stress caused accentuated growth increments in the dentine. Therefore, the case for serial analysis of dentine is similar to that for hair, in that the variability in the growth rate makes it difficult to place a series of samples within a well-defined time frame.

The nutrient pool from which dentine collagen is derived also undergoes a relatively long turnover time in the event of a dietary shift. Balasse *et al.* (2001) performed serial analysis on cattle dentine collagen, reporting that an abrupt change in the diet of the study animals (from C_3-based to a mixture of C_3- and C_4-based foods) was reflected by a gradual change in the isotopic composition of the dentine collagen. The diet-tissue equilibration time for dentine collagen in cattle is at least two months (Balasse *et al.*, 2001), not dissimilar to the equilibration time for hair.

In primates, and other mammals that do not have continuously growing teeth, isotopic analysis of dentine (and enamel) provides information about the first few years of the animal's life. The temporal perspective gained through serial analysis of dentine requires consideration of the animal's age at which a particular tooth is formed. The average age of baboons at eruption of each tooth is given by Phillips-Conroy & Jolly (1988) for *Papio cynocephalus*, and by Kahumbu & Eley (1991) for *Papio anubis.* However, an animal's age at eruption of a particular tooth also shows variability, based on sex and ecological condition. For example, Phillips-Conroy & Jolly (1988) showed that the mean age of eruption of baboon teeth was accelerated in captive compared to wild individuals. The age at which calcification begins also varies considerably between individuals, as this may be pre- or post-natal. Thus, the ages of baboons at tooth eruption are used here only as a broad guideline for inferring the range of possible ages of an individual when a particular tooth, and particular increment from within that tooth, was formed.

3.4.5. Tooth Enamel Carbonate

Carbon and oxygen isotope ratios measured from tooth enamel carbonate have been useful in assessing the diets and ecology of a number of modern and fossil fauna (e.g. Lee-Thorp *et al.*, 1989b; Cerling *et al.*, 1997; Cerling & Harris, 1999; Smith *et al.*, 2002; Sponheimer *et al.*, 2003e).

More than 95% of the composition of mammalian tooth enamel is inorganic apatite (LeGeros, 1991). As suggested by Krueger & Sullivan (1984) and later by Lee-Thorp *et al.* (1989b), apatite carbonate is derived from a combination of all of the constituents of an animal's diet. In essence, isotopic analysis of enamel carbonate reflects the isotopic composition of the whole diet, as opposed to proteinaceous tissues that reflect only the protein component of the diet (Ambrose & Norr, 1983; Tieszen & Fagre, 1993). For fossilized fauna, where organic tissues are absent, tooth enamel is usually more well preserved and subject to less isotopic diagenesis than bone apatite (Lee-Thorp & van der Merwe, 1991; Wang & Cerling, 1994).

3.5. Faecal Nitrogen as an Indicator of Dietary Quality

Faecal nitrogen (percentage nitrogen) is a representation of the crude protein content of the faeces. Protein levels in mammalian faeces are widely accepted to reflect the crude protein content of the diet, and have been used to monitor the spatial and seasonal quality of domestic and wild animal diets (e.g. Erasmus *et al.*, 1978; Leslie & Starkey, 1985). However, faecal nitrogen is not necessarily correlated with dietary crude protein, as pointed out by Hobbs (1987). The protein-precipitating effects of plant secondary compounds, such as condensed tannins, often alter the levels of nitrogen in the faeces of herbivores (Robbins *et al.*, 1987). Additionally, much of the nitrogen in plants occurs in the form of insoluble proteins and is unavailable to herbivores for effective digestion. Grant *et al*. (2000) showed that, amongst large-bodied herbivorous mammals in the Kruger National Park, faecal nitrogen predicted about 70% of the protein content of the diet. Thus, faecal nitrogen levels are a reasonable indicator of dietary quality, although results should be treated as a crude, not absolute, measure of protein intake.

SUMMARY

Stable light isotopes in terrestrial ecosystems provide an empirical method for qualifying and quantifying a range of ecological variables displayed by the flora and fauna inhabiting these environments, as well as the amount of variability across different spatial and temporal scales. Stable carbon isotopes are informative about habitats, photosynthesis in plants, and animal diet selectivity and habitat utilization, while nitrogen isotopes can provide insight into a combination of dietary, climatic, and physiological factors. Stable oxygen isotopes in apatite carbonate of modern and fossil fauna reflect differences in water sources. Considered in combination, and measured from a variety of tissues providing slightly different types of information, carbon, nitrogen, and oxygen isotopes provide valuable insight into the ecology and palaeoecology of mammalian fauna. Percentage nitrogen is measured routinely during mass spectrometry, and in plants and faeces this information is useful for predicting variations in mammalian dietary quality.

CHAPTER 4

RESEARCH METHODOLOGY

This chapter describes the climate, geology, and flora and fauna of the study areas that were selected to investigate variability of modern baboon diets, and provides information about the Pleistocene deposits of Swartkrans, from where fossil material was obtained. The second section deals with the techniques followed for selecting and collecting plant, faecal, hair, bone, and tooth samples for laboratory analysis. Finally, the chapter includes a discussion of methods used for laboratory treatment of samples, and measurements of stable light isotope ratios using previously established methods for stable light isotope ratio mass spectrometry.

4.1. Study Areas

For collection of modern material, fieldwork for this project was carried out in the Waterberg and in the southern parts of the Kruger National Park (Fig. 4.1). Both areas represent South African savanna ecosystems. As this was a comparative study, these areas were selected on the basis of differences in resources available to chacma baboons inhabiting slightly different savanna environments. The Waterberg is a high altitude, mountainous region, and differs somewhat in climate and vegetational composition to the lower altitude Kruger Park. Both of these study areas support a rich diversity of mammal species, and thus provided the opportunity to compare the variability in resources utilized by baboons living in different circumstances with other species in a similar ecological context.

Fossil material was obtained from the Pleistocene deposits of Swartkrans Members 1 and 2, South Africa. A number of primate taxa are available from this site, providing the opportunity for ecological comparisons of modern baboons with a variety of extinct savanna-dwelling primate taxa.

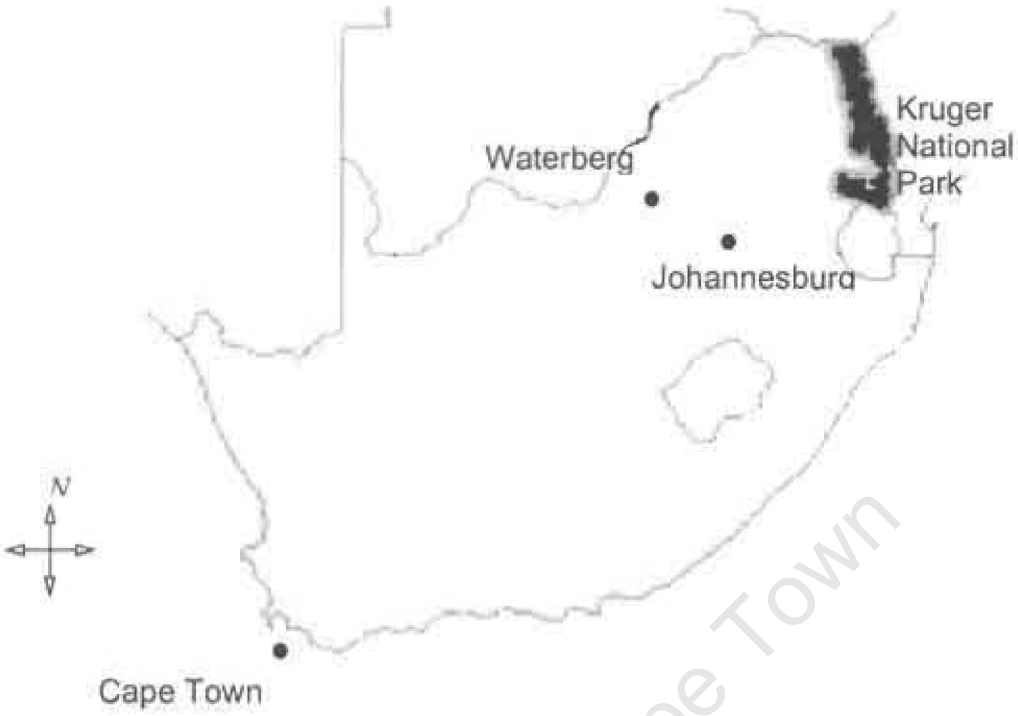


Figure 4.1 – Map of South Africa showing approximate location of the Waterberg and the Kruger National Park in relation to the major cities Cape Town and Johannesburg (map not to scale).

4.1.1. The Waterberg

The Waterberg is an area of mountainous bushveld situated in the southwestern parts of South Africa's Limpopo Province. Fieldwork was carried out in two reserves in the Waterberg. Zoetfontein Private Game Farm is a small (ca. 7km^2), privately owned plot of land, located about 40km south of the town Ellisras. The Welgevonden Private Game Reserve, about 60km to the south of Zoetfontein and 10km west of Vaalwater, is a larger reserve of roughly 330km^2.

Climate

The Waterberg falls within the warm, temperate, summer rainfall area of South Africa. The wet season occurs between October and March, while April to September are characteristically dry months (Fig 4.2.). Annual rainfall often exceeds 600mm, although the Vaalwater Weather Station, about 25km east of Welgevonden, recorded a higher mean annual rainfall than the Ellisras Station, nearer to Zoetfontein, between 1968 and 2002 (Fig 4.3.). The Welgevonden Office recorded an average of 634mm of rain per annum between 1993 and 2002, although annual rainfall during this period is 562mm if the floods of 2000 are excluded. Average daily maximum temperature recorded at the Vaalwater Weather Station is 26.5°C, but during the summer months temperatures often rise above 35°C. The Waterberg usually experiences moderate frost during the winter months.

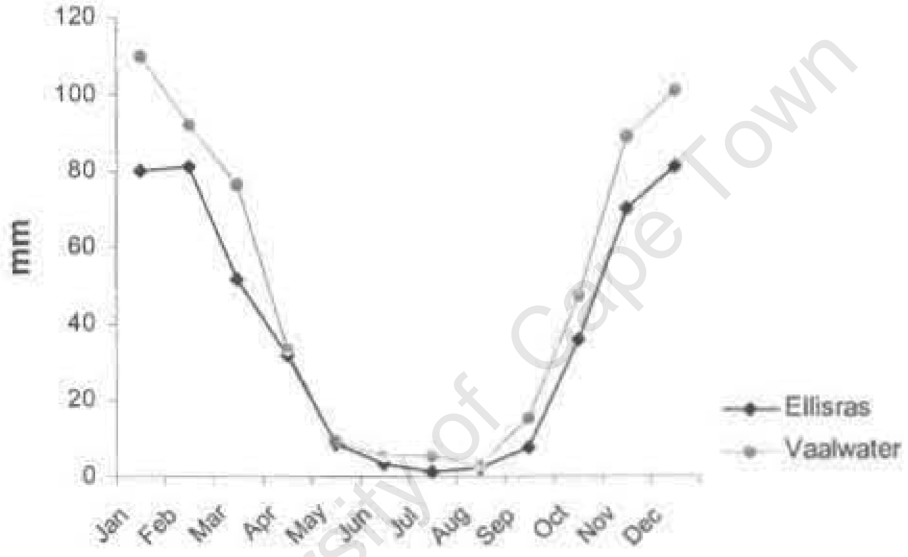


Figure 4.2 – Mean monthly rainfall recorded at the Ellisras and Vaalwater Weather Stations between 1968 and 2002, indicating seasonal rainfall patterns in the Waterberg (Data supplied by the South African Weather Bureau).

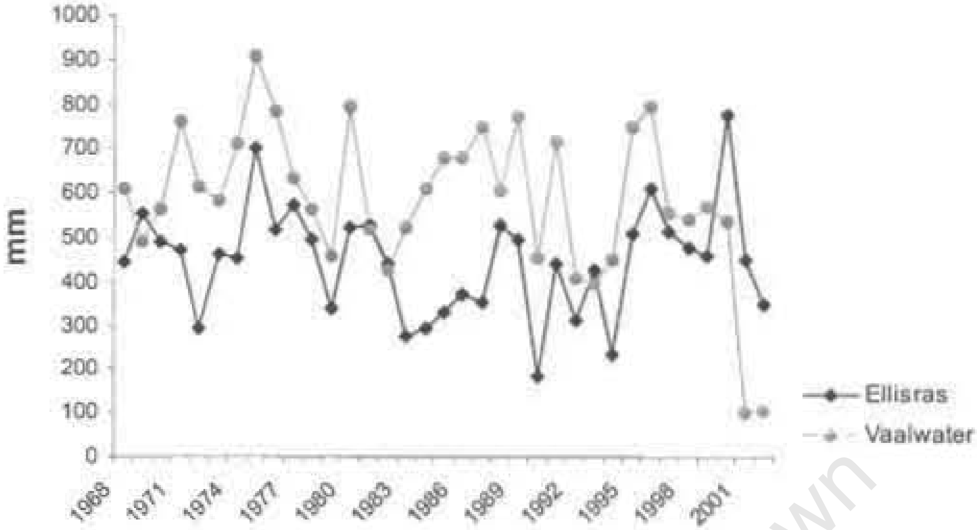


Figure 4.3 – Annual rainfall recorded at the Vaalwater and Ellisras Weather Stations between 1968 and 2002. The former station is nearest to the Welgevonden Private Game Reserve, while the latter is closest to Zoetfontein Game Farm (Data supplied by the South African Weather Bureau).

Vegetation

Acocks (1988) classifies the Waterberg as "sour bushveld", comprised of tall straight trees (predominantly *Faurea saligna*, the Transvaal Beech) with tufted sour grassveld in the less rocky areas. The area displays a characteristically high herbaceous productivity. For ecological purposes, the vegetation of the Waterberg is divided into three vegetational landscapes, namely plateaus, hillsides, and valley bottoms (Fig. 4.4). The plateaus are characteristically woodland savanna, while open grassland is common on the valley bottoms. Hillsides are heavily wooded, especially at the footslopes where dense riparian vegetation dominates the fringes of rivers and streams that flow between the mountains.

Faunal Composition

Because much of the Waterberg's conservation land has been reclaimed from earlier agricultural lands, many species of African mammals have been re-introduced to the area, particularly on Welgevonden. Only a few large mammal species occur on Zoetfontein (although browsing, grazing, and mixed feeding ungulates are present on the farm). A wider range of species is found in Welgevonden, including African elephant (*Loxodonta africana*), lion (*Panthera leo*), square-lipped rhinoceros (*Ceratotherium simum*), giraffe (*Giraffa camelopardalis*), and a diversity of other ungulate species not found in Zoetfontein. Thus the mammalian-plant ecosystem of Welgevonden is somewhat more complete than Zoetfontein, which lacks several megaherbivore species usually associated with southern African savannas.

Baboons occur in high numbers on both reserves. In Zoetfontein these animals are often seen throughout the farm, some individuals and troops residing permanently within its boundaries, while others periodically traverse the farm. In Welgevonden, as many as 25 baboon troops have been counted during annual game counts. This figure may be an overestimate, however, since solitary individuals are, on occasion, counted as one troop (Burger 2002, pers. comm.).

Conspicuously, the Waterberg baboons are extremely wary of people. On Welgevonden, this can be ascribed to the fact that tourist densities are relatively low, thus baboons here are not as habituated to humans as they are in some other parts of southern Africa. On Zoetfontein, baboons display a fear for humans, probably because they are often shot as pests on surrounding agricultural farms.

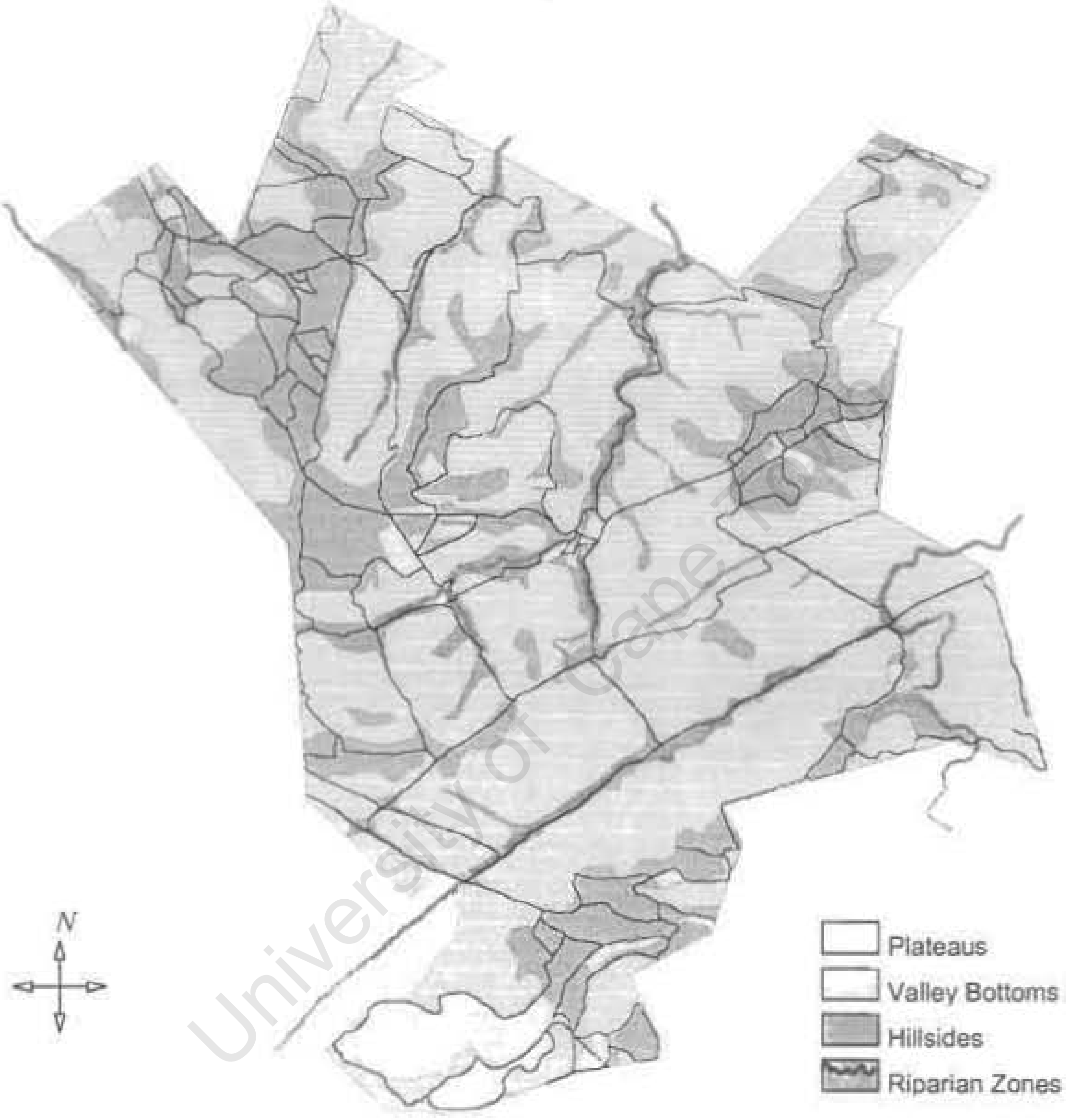


Figure 4.4 – Map of Welgevonden Private Game Reserve showing distribution of landscapes, based on topography and vegetation (Map provided by Welgevonden Private Game Reserve).

4.1.2. The Kruger National Park

Kruger National Park is situated in the northeast of South Africa, between 22° 20' and 25° 32' S and 30° 32' and 32° 02' E, stretching more than 400km from north to south along the border between South Africa and Mozambique, and 60km from west to east at its widest point. The entire area covers almost 20 000km^2 of deciduous lowveld savanna between the Drakensberg mountains to the west and the Lebombo mountain range on the eastern boundary. The Crocodile River forms the southern boundary, and the Limpopo River runs along the northern border.

Climate

Average annual rainfall for Kruger Park is about 500mm, but this varies throughout the reserve, generally decreasing from south to north, and to a lesser extent from west to east (Fig. 4.5). Thus, mean annual rainfall varies from ca. 740mm in the southwest to ca. 440mm in the northeast (Venter & Gertenbach, 1986). The minor decrease in rainfall from west to east corresponds to an altitudinal cline, from about 900m at Pretoriuskop in the southwest to about 200m in the east. Rainfall is highly seasonal, with December, January, and February being the wettest months, while July and August are the driest (Fig. 4.6.). There appears to be an eighteen- to twenty-year cyclical rainfall pattern, drier and wetter periods each lasting nine or ten years (Gertenbach, 1980). During the summer months, daily temperatures often exceed 40°C, with more moderate temperatures characterizing the winter months.

Geology and Vegetation

Venter (1986) described seven soil classes, based on the underlying parent rock, which are more or less longitudinally differentiated throughout the Park. The current study was carried out only in the southern parts of Kruger Park, i.e. south of the Sabie River, or within a few kilometers to the north of it. For the purposes of this study, the geology can be crudely divided into two major groupings: the western granites associated with sandy soils, and the basaltic, clay-rich soils of the eastern regions. These geological units are closely associated with the distribution of vegetational landscapes within the Park. Crests and midslopes on the sandy, granitic soils are characterized by *Combretum* spp. and *Terminalia sericea* woodland savanna, while *Acacia nigrescens*, *Dichrostachys cinerea* and *Euclea* *divinorum* dominate the clayey duplex soils on the footslopes of these areas. Grasses are sparse on the crests, but on the footslopes they occur in denser stands of palatable species (Venter & Gertenbach, 1986). In the east, basaltic soils support a more open grassland savanna, with lush grasses, such as *Themeda triandra*, *Panicum coloratum*, and *Bothriochloa radicans*, interspersed with *Acacia nigrescens* and *Sclerocarya birrea* subsp. *caffra* trees (Venter & Gertenbach, 1986).

The Kruger Park exhibits an extensive habitat and vegetational diversity. Whyte (2001) lists a total of 35 vegetational landscapes previously described for the area. In sum, around 400 species of trees and shrubs, over 200 grass species, more than 1 000 forbs and hydrophytes, 20 aloe species, 17 fern species, and 16 woody lianas occur in the Park (Venter & Gertenbach, 1986).

Faunal Composition

The faunal composition of Kruger Park exhibits a variety that follows that of the vegetation, with species inhabiting and exploiting the rich diversity of available habitat types. Authors have reported totals of 147 mammal species, 505 bird species, 120 reptiles, 35 amphibians, and 53 fish species (see Whyte 2001). Chacma baboons occur throughout Kruger, and are often observed around rest camps and main tourist roads. This has led to these animals being considered as 'problem animals' in the Park, and attempts at keeping them away from tourist vehicles, campsite dustbins, and visitors' cottages have not alleviated the human-baboon interaction. For this reason, Kruger Park may not be the ideal setting for studies of baboon diets, especially when the methods involve chemical analysis of tissues, and not direct observations. Incorporation of human food items may affect the isotopic compositions of these baboons' diets, and must be taken into consideration when interpreting results.

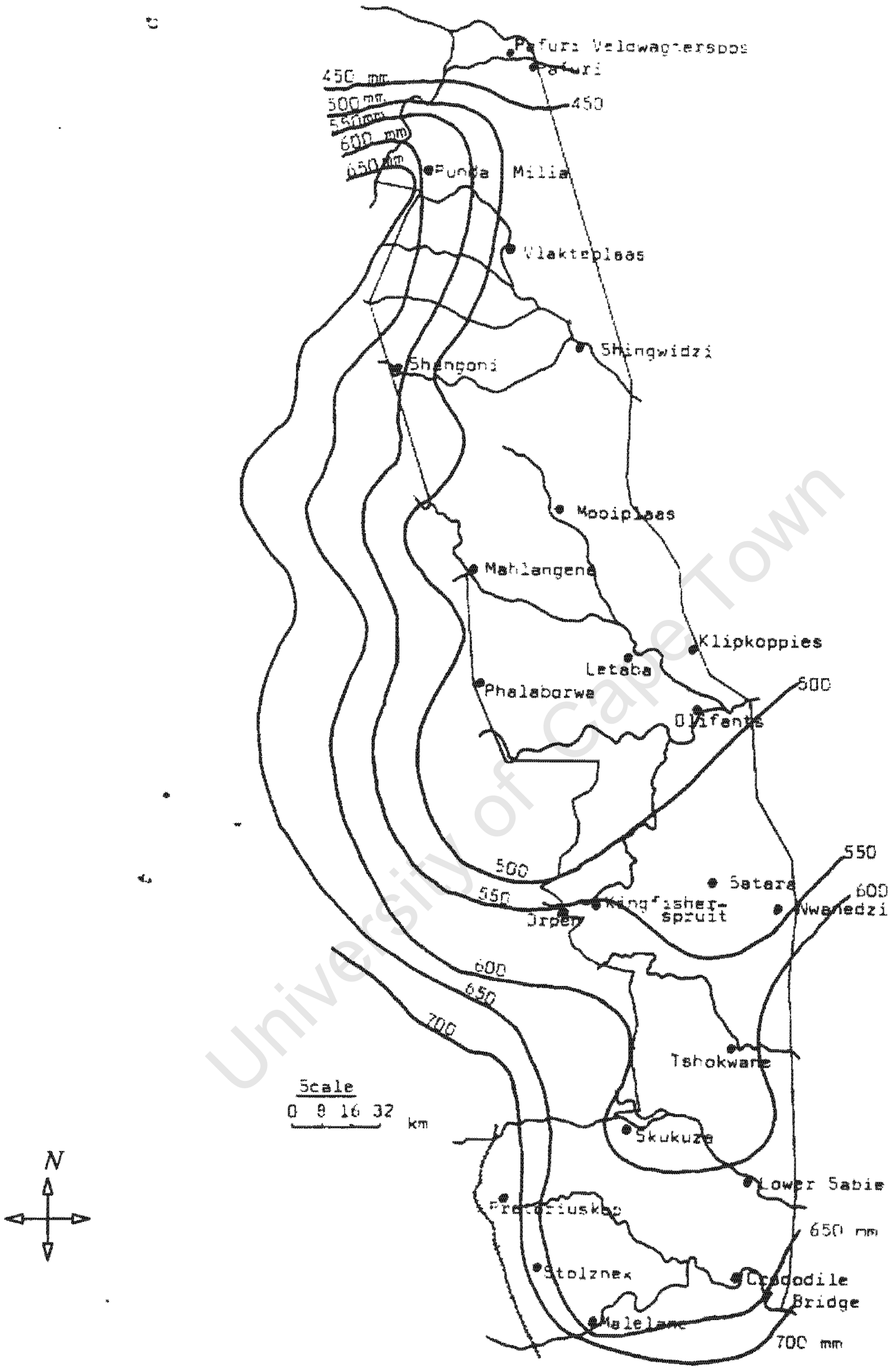


Figure 4.5 – Map of the Kruger National Park with distribution of rainfall patterns (from Gertenbach, 1980).

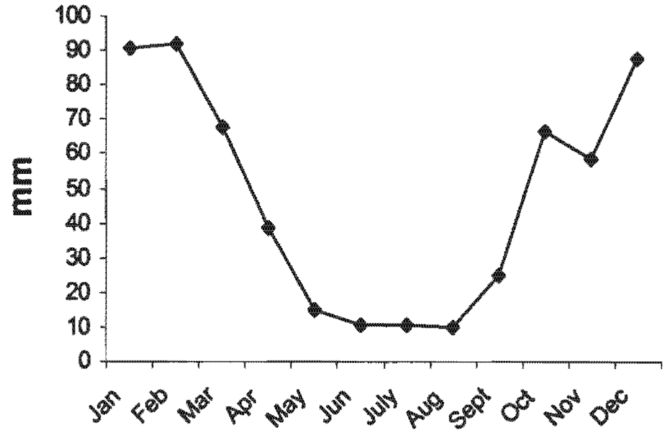


Figure 4.6 – Mean monthly rainfall recorded at the Skukuza Weather Station between 1941 and 2002, indicating seasonal rainfall patterns in the Kruger National Park (Data supplied by the South African Weather Bureau).

4.1.3. Swartkrans

Swartkrans lies in the Sterkfontein Valley in the Gauteng Province, South Africa, now the "Cradle of Humankind World Heritage Site". It is situated about 1km northwest of the Sterkfontein caves, and comprises an abundance of breccia-bound Pleistocene fossil remains, including specimens of *Australopithecus (Paranthropus) robustus* and *Homo erectus* (e.g. Brain, 1981).

Swartkrans is made up of Precambrian dolomitic rocks that form part of the Transvaal Supergroup. The complex stratigraphy of Swartkrans, a result of climatically linked cycles of deposition and erosion, is reviewed in Brain (1994). Sediment layers separate the different Members. Dating of the site is based on biostratigraphy, however, and is thus still insecure. Age estimates for these deposits provided by Brain (1994) are followed here. The age of Member 1, the oldest part of the sequence, is believed to be approximately 1.7 Ma, and consists of deposits of the Lower Bank and includes a Hanging Remnant. Member 3 is estimated at ca. 1 Ma, while Member 2 is intermediate in age between Members 1 and 3. Members 4 and 5 are much more recent, representing the Late Pleistocene. Hominid remains are abundant in Members 1 and 2, especially the robust australopithecines, and some robust hominid specimens have been excavated from Member 3 (Brain, 1994).

A diversity of mammalian fauna has been excavated from the site (Brain, 1981). Mammals are present in high densities; Vrba (1975) for example used the relative abundances of Bovidae in the Swartkrans assemblage to propose a chronological sequence in the site. In addition, nonhuman primates are also well represented in Members 1 and 2. The cercopithecines include members of the genera *Gorgopithecus*, *Theropithecus oswaldi* (after Delson *et al.*, 1993), *Papio (Dinopithecus) ingens*, *Papio robinsoni*, possibly three species of *Parapapio* (*P. jonesi*, *P. broomi*, and *P. whitei*), and *Cercopithecoides* sp., probably a colobine monkey.

4.2. Sampling Protocol

A total of four excursions were made during 2002 and 2003 for the collection of samples for isotopic analysis. Plants and faeces were collected from the Waterberg during September 2002 and January 2003, in order to obtain isotopic and thus dietary information for two seasons. In Kruger Park, plants and faeces were collected during June 2002 and again in January 2003. June and September represent different seasons these respective areas, which would be expected to complicate inter-habitat comparisons, and the effects of this disparity are further noted in the proceeding chapters. Baboon hairs were collected from Welgevonden during September 2002 and from Kruger Park in June 2002. Hairs were only collected from each area on one occasion, since temporal ecological fluctuations can be obtained from this tissue using serial analysis. Baboon crania and teeth were obtained from Zoetfontein in September 2002, and from collections of the Transvaal Museum, Pretoria. Fossil tooth enamel was obtained from fossil primates of the Swartkrans collections at the Transvaal Museum.

4.2.1. Collection of Plants, Faeces, and Hair

A wide variety and number of plants and plant parts were analyzed to provide baseline isotopic and elemental information for qualifying and quantifying isotopic variability in baboon diets, and that of other mammals. Faeces from a wide variety of mammal species were collected in order to provide a comparative data set, including samples from pure browsers, pure grazers, mixed feeding species such as impala, and carnivores (although these were scarce in the field).

Different plant parts (leaves, fruits, bark, stems, roots, inflorescences, and seeds) were obtained from several plant species (including trees, forbs, grasses, sedges, reeds, and a small number of geophytes) collected from a number of transects established in each reserve. Table 4.1 shows details of the sites from where plant samples were collected in the Waterberg and Kruger Park. The January set of Waterberg plants was collected from only three of the five sites listed for Welgevonden (Bushman's Painting, Mziki, and Motswedi) and no collections were made on Zoetfontein during January 2003. This was because isotopic variations beyond the three repeated sites were small, as observed from the September collections, and were considered superfluous for further comparisons.

Table 4.1. List and details of plant collection sites in the Waterberg and in the Kruger National Park (Landscape vegetational data from Venter & Gertenbach (1986)).

Collection Site	Landscape	Vegetation	Elevation	Latitude	Longitude
Waterberg					
Welgevonden					
Bushman's Painting	Hillside	Dense woodland	1115m	24°13'53,3"S	27°50'53,6"E
Mziki	Valley Bottom	Dense / riparian	1159m	24°14'44,8"S	27°50'41,7"E
Motswedi	Plateau	Open woodland	1292m	24°14'47,3"S	27°58'00,1"E
Keg and Fig	Valley Bottom	Open grassland	1268m	24°17'42,8"S	27°49'37,8"E
Acacia Loop	Valley Bottom	Open woodland	1246m	24°13'54,2"S	27°44'02,4"E
Zoetfontein	Plateau	Open woodland	1011m	23°54'08,5"S	27°49'05,5"E
Kruger Park					
Hlanganzwane	Southern basalts	Open grassland	238m	25°14' 12.0"S	31°59' 08.4"E
Crocodile River	Southern basalts	Woodland / riparian	251m	25°20' 30.4"S	31°56' 25.7"E
Renosterkoppies	Southern granites	Open woodland	282m	25°04' 19.1"S	31°36' 37.9"E
N'watimvambu R	Southern granites	Dense / riparian	214m	25°01' 02.3"S	31°46' 55.8"E

All mammal faeces, with the exception of baboon faeces, were collected opportunistically in each reserve, although the majority of faecal collections were made at the same sites from where plant samples were obtained. Baboon faeces were sampled at specific localities in both the Waterberg and Kruger Park (Table 4.2). This was considered necessary due to observed differences in the behaviour of these animals between the two areas.

Collection of plant and faecal samples was made on foot, accompanied by local staff members of the various reserves. Plants and faeces were placed into paper bags, and oven dried at 60°C for 24 hours. This ensured that samples did not become contaminated with fungal growth.

Table 4.2. List and details of baboon faeces collection sites in the Waterberg and in the Kruger National Park (Landscape vegetational data from Burger (2002, pers. comm.).

Collection Site	Landscape	Vegetation	Location of faeces
Waterberg			
Welgevonden			
Bushman's Painting	Hillside	Dense woodland	Baboon sleep site
Mziki	Valley Bottom	Dense / riparian	Baboon sleep site
Tshetshepi	Valley Bottom	Dense / riparian	Baboon sleep site
Nalana	Valley Bottom	*Euphorbia ingens* tree and *Agave* spp. plants	Beneath *Euphorbia*
Motswedi	Plateau	Open woodland	Along road
Zoetfontein	Plateau	Open woodland	Throughout reserve
Kruger Park			
Sabie-Skukuza	Southern Granites	Dense / riparian	Along road
L Sabie Bridge	Southern Basalts	Grassland / riparian	Along road
Salitje River	Southern Basalts	River bed	Dry river bed
Stolsnek	Southern Granites	Open woodland	Rocks and ground
Stevenson Hamilton	Southern Granites	Rocky outcrop	Rocks and ground

Sampling of Baboon Faeces and Hairs in the Waterberg

In the Waterberg, baboons are clearly uncomfortable in the presence of people, usually fleeing at the first sight of human activity. Hence, they seldom utilize the roads in this area, and location of faeces was difficult. These difficulties were, however, beneficial to this study, as this behaviour ensured that human food consumption would not complicate dietary analysis.

In Zoetfontein, several kilometers were traveled each day on foot, in search of baboon faecal samples. In Welgevonden, only a few baboon faecal samples could be obtained by randomly locating the material. During September 2002, five samples were found along the roadsides of the plateau (listed in Table 4.2 as Motswedi), and six samples were collected beneath a solitary *Euphorbia ingens* tree on which baboons had reportedly been feeding (Nalana site). The majority of baboon faecal samples from Welgevonden were obtained from three commonly used sleep sites situated at the lower reaches of cliff faces, surrounded by riparian forest vegetation. At these sleep sites, large "beds" of baboon faeces were present, from where the most recently deposited samples were selected.

Within the sleep site faecal "beds", individual baboon hair strands were located and collected. To be able to ascertain temporal variability within individuals, only the longest hairs (at least 12cm) were retained for serial isotopic analysis. It is not certain that each hair strand came from a different individual, but it seems unlikely that two such randomly selected strands, obtained from dung piles several metres apart, belonged to the same animal. In any case, the objective here was not to document variability between individuals.

Sampling of Baboon Faeces and Hairs in the Kruger Park

Kruger Park has a far higher tourist density than the Waterberg, and interaction between baboons and humans, including raids for food debris on rest camps, are not uncommon. In Kruger, baboon faeces were sampled along the roadsides (Sabie-Skukuza area and the Lower Sabie bridge) and at a tourist lookout point (Stevenson Hamilton).

An attempt was also made to collect faeces from sites where baboons were less likely to come into contact with humans, and where they would be expected to exhibit a more "natural" dietary behaviour (at Stolsnek and the Salitje River). However, time constraints dictated that these "natural" feeding sites could only be sampled during June 2002, and thus faeces from "Stevenson Hamilton" were collected in January 2003 to compensate for this (it was considered likely that baboons utilizing the area around this site, located on one of the Park's secondary gravel roads, also consume less human food items than do those inhabiting areas nearer to the tarred roads and rest camps).

Three strands of hair were obtained from the pelt of a single individual (UCT Lab No. 8639) that had been culled and was in the keeping of Kruger Park staff.

4.2.2. Bones and Teeth

In order to document intra-individual variability from dental material, teeth were analyzed sequentially. Teeth of just a few individuals were available for this purpose. A description of each specimen sampled is presented in Table 4.3.

Crania and teeth of two adult males that died in November 2001 were obtained from local ground staff in Zoetfontein, who had previous knowledge of these dead animals' whereabouts. Due to weathering processes, and the activity of hyaenas, further location of baboon skeletal material in the field was impossible. To compensate, specimens from the collections of the Transvaal Museum were obtained. These were selected so as to obtain data from baboons that had lived in the vicinity of the Waterberg and Kruger Park. Crania and teeth of museum specimens from the D'Nyala Reserve in Ellisras, and from Blydepoort in the Mpumalanga lowveld were selected, as these were baboons from areas in the closest available proximity to the current study areas. Museum specimens all pre-dated the current study, as most had died in 1986, and one specimen (TM 911) died in 1926, providing the opportunity to make some historical comparisons.

Table 4.3. List of baboon specimens from where bone and tooth samples were obtained.

Specimen ID	Region	Reserve	Death	Sex	Age Group	Jaw	Side	Teeth Sampled
UCT 9786	Waterberg	Zoetfontein	Nov-01	M	Adult	Maxilla	Right	M1, M2, M3
UCT 9787	Waterberg	Zoetfontein	Nov-01	M	Adult	Maxilla	Right	M1, M2, M3
AZ 769	Waterberg	D'Nyala	Jul-86	M	Adult	Mandible	Left	M1, M2, M3
AZ 770	Waterberg	D'Nyala	Jul-86	F	Adult	Mandible	Left	M1, M2, M3
AZ 790	Waterberg	D'Nyala	Jul-86	M	Juvenile	Mandible	Left	M1, M2, M3
AZ 792	Waterberg	D'Nyala	Jul-86	F	Sub-adult	Mandible	Left	M1, M2
TM 911	Lowveld	Blydepoort	1926	M	Adult	Mandible	Left	M3
AZ 798	Lowveld	Blydepoort	1984	?	Adult	Mandible	Left	M2, M3
AZ 797	Lowveld	Blydepoort	1984	F	Sub-adult	Mandible	Left	M1, M2, M3
AZ 806	Lowveld	Blydepoort	1984	?	Infant	Mandible	Left	dM1, dM2

4.2.3. Sampling of Fossil Material

Several South African Plio-Pleistocene cercopithecoids from Swartkrans and Sterkfontein have already been analyzed for stable light isotope ratios (Lee-Thorp *et al.*, 1989a; Lee-Thorp & van der Merwe, 1993; Lee-Thorp *et al.*, 1994; Luyt, 2001; Lee-Thorp, 2002). Attention was paid to previously unsampled specimens, so as to increase the number of specimens of each species for which data would become available, thereby obtaining a more robust data set for interpreting fossil cercopithecoid ecology. Samples were taken from *Theropithecus oswaldi*, *Papio (Dinopithecus) ingens*, *Papio robinsoni*, *Parapapio* cf. *jonesi*, and *Cercopithecoides williamsi*. This provided a reasonable representation of the Swartkrans baboons, and *C. williamsi* was sampled as it can be considered an unusual cercopithecoid in the savanna biome (see Chapter 2). Where possible, samples were selected so that the same taxon could be analyzed from both Members 1 and 2, in order to obtain a temporal trend in dietary ecology.

Enamel powder was removed from selected specimens of the Transvaal Museum collections with the use of a diamond-tipped microdrill. Tooth enamel is the most suitable tissue for analyzing stable light isotope ratios in fossil material (Lee-Thorp & van der Merwe, 1987 & 1991; Wang & Cerling, 1994).

4.3. Laboratory Techniques

4.3.1. Preparation of Plants and Faeces

Once in the laboratory, each plant and faecal sample was assigned a UCT Laboratory Reference Number. Different parts of the same plant were given the same UCT number so that future studies of intra-individual variation in plants would be possible. However, in order to facilitate analysis of the large number of samples collected, a field number was ascribed to each plant and faecal sample. Samples were thus labeled as ZP, ZF, WP, WF, KP, and KF, for plants and faeces from Zoetfontein, Welgevonden, and Kruger Park, respectively. This field numbering system allowed for assignation of a unique number to different parts of the same plant.

Previously dried plant and faecal samples were ground in order to homogenize each sample prior to isotopic analysis. 2mg of each plant and faecal sample was weighed into a tin capsule in preparation for isotopic measurements.

A total of 70 plant samples from Zoetfontein were analyzed, 131 from Welgevonden, and 289 from Kruger Park, representing a range of plant species, growth forms, and plant parts. For some plants, if a sample was considered too small for isotopic analysis, different parts of the same species from the same collection site were combined. In addition, not all plants were separated into the various parts available, especially in the case of grasses. Therefore, some plant parts were labeled as 'Whole' (when all available parts of a plant specimen were homogenized), or 'No Roots' (if the whole plant was sampled, but the roots were analyzed separately).

A large number of mammal faeces, from a variety of species, were analyzed, further providing an appropriate ecological context. Including baboon faeces, 106 samples representing 12 mammal species from Zoetfontein, 206 (16 species) from Welgevonden, and 225 (10 species) from Kruger Park were analyzed. Thus, a baseline for comparing the responses of baboons to environmental fluctuations with patterns observed in other mammal species was established. Sample size for baboon faeces totaled 50 from Zoetfontein, 135 from Welgevonden, and 86 from Kruger Park. The portion of this project that was carried out in Kruger Park formed part of a larger, team-based research project, and of all the plant and faecal samples analyzed, only those relevant to this study are included here. This explains the lesser diversity of Kruger mammal species compared to the Waterberg reported on in this project.

4.3.2. Preparation of Individual Hair Strands

A total of 12 hair strands (nine from Welgevonden and three from a single Kruger Park individual) were prepared for isotopic analysis. Each strand was wiped clean of all dust. In order to obtain temporal data from hair, every strand was sectioned, starting at the root and working towards the tip. Baboon hair is thin and has low density, and it was determined that each section had to be ~20mm in order to obtain enough material from each section so as to measure both carbon and nitrogen isotope ratios.

Only 0.05mg of hair is required for carbon isotope analysis, while 0.15mg of material is needed for measuring stable nitrogen isotope ratios in hair. However, it was determined that 0.15mg of hair did not yield reliable results for the simultaneous measurement of carbon and nitrogen isotope ratios. This meant that carbon and nitrogen isotopes needed to be analyzed separately, from slightly different portions of each 20mm section.

4.3.3. Preparation of Baboon Bone Collagen and Tooth Dentine

In order to obtain an integrated long-term dietary average from bone collagen, fragments of bone were removed from the crania that were available (for some of the museum specimens, only tooth dentine was sampled).

For temporal data, tooth dentine was sampled sequentially. Molars were the only teeth available in every specimen, thus it was decided that only molars would be analyzed. Entire molar rows were sampled wherever possible, so that intra-tooth and inter-tooth variability could be compared, increasing the time scale that analysis would yield.

Using a diamond-tipped microdrill, with a diameter of 1mm, dentine powder was removed from the available molars. Serial sampling commenced immediately below the dentino-enamel junction and progressed longitudinally towards the root tip. Holes of ~1mm in diameter were drilled, each being 0.5mm apart. In cases where insufficient powder was obtained for isotopic analysis, the holes were extended transversely, avoiding overlap with the transverse growth plane of the previous sample. In this way, at least four or five samples were obtained for almost all molars used.

Bone collagen was isolated from bone fragments and dentine powder according to current methods used by the Archaeometry Laboratory at the University of Cape Town (e.g. Sealy, 1997).

Bone fragments were placed in 0.2M HCl (hydrochloric acid) for two to three days, until samples were completely demineralized. Humates were removed by placing these samples in a 0.1M NaOH (sodium hydroxide) solution for 24 hours. Bone fragments were placed in a solution of methanol, chloroform, and water (in the ratio 2:1:0.8) for 24 hours, to remove lipids.

Dentine powder was also demineralized in a 0.2M HCl solution. Sixty minutes of this treatment were required before only collagen remained. Dentine powder was not treated for lipids, as the material did not contain a large enough lipid component to warrant treatment in defatting solution. It was also observed that such treatment caused the samples to separate during centrifugation, and thus the supernatant could not be decanted without losing an unacceptable amount of material.

Bone and dentine collagen samples were freeze-dried at -40°C for 24 hours. Between 0.45 and 0.6mg of clean, dry collagen was weighed into tin capsules for analysis of stable carbon and nitrogen isotope ratios.

4.3.4. Preparation of Baboon Tooth Enamel

Baboon enamel is relatively thin, and thus only one sample of enamel was taken from each molar tooth. Powdered enamel was removed from the teeth using a diamond-tipped microdrill. This enamel powder was treated in a 1.5% sodium hypochlorite (bleach) solution for 30 minutes to remove organic material, and then placed briefly (seven minutes) in a 0.1M acetic acid solution to ensure uniform treatment with fossil material (see section 4.3.4 below). The samples were then freeze-dried at -40°C for 24 hours and weighed for analysis. Although only 1mg of sample is required for isotopic analysis, at least 3mg of enamel was removed from each tooth so that sufficient powder remained after pretreatment, since these procedures usually result in sample loss in the order of 50 percent. One tooth (M1 of specimen AZ 770) lacked sufficient enamel for isotopic analysis.

4.3.5. Preparation of Fossil Tooth Enamel

Fossil tooth enamel powder from the Transvaal Museum was prepared for isotopic analysis using previously published methods (e.g. Koch *et al.*, 1997; Sponheimer, 1999). Bleach was not used in fossil enamel pretreatment, as organic matter does not persist in material of this age, and this also reduced the loss of samples that were already small. A 0,1M acetic acid solution was used, however, as omission of this step may yield unreliable results, due to the presence of more soluble carbonates in hydration layers and amorphous zones. Thus samples were placed in 0.1M acetic acid for five minutes. Prepared fossil enamel was freeze-dried at -40°C for 24 hours and 1mg of each was weighed for analysis.

4.3.6. Mass Spectrometry

Organic tissues (plants, faeces, hair, and collagen) were combusted in an automated Carlo-Erba device and the resultant N_2 and CO_2 gases were measured for $^{13}C/^{12}C$ ratios, $^{15}N/^{14}N$ ratios, percentage carbon, and percentage nitrogen, using a continuous flow-through inlet system attached to a Finnigan MAT 252 Mass Spectrometer. Analytical precision for organic tissues is better than 0.1‰ for $^{13}C/^{12}C$, and 0.3‰ for $^{15}N/^{14}N$, based on replicate measurements of laboratory protein standards (Merck Gel and Valine), plant standards, and a chocolate powder standard.

Modern and fossil enamel carbonate $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios were obtained by reaction in phosphoric acid at 70°C, and cryogenic distillation of the samples, in a Kiel II autocarbonate device from where dry CO_2 was introduced into the Finnigan MAT 252 Mass Spectrometer. For the inorganic material, analytical precision is better than 0.1‰ for $^{13}C/^{12}C$ and 0.2‰ for $^{18}O/^{16}O$, based on replicate measurements of international mineral standards (NBS 18 and NBS 19), and two marble standards (Carrara Z and Cavendish Marble).

Stable light isotope ratios are presented in conventional delta (δ) notation in parts per thousand (‰) relative to the PDB standard ($\delta^{13}C$ and $\delta^{18}O$) and the atmospheric N_2 standard ($\delta^{15}N$). These delta numbers were further corrected for variation using a 3-point regression equation ($y = m.x + c$) obtained from comparison of the known values of laboratory and international standards with observed values for each set of analysis.

4.4. Data Handling and Processing

Results of isotopic analysis and the percentage nitrogen of each plant and faecal sample are given in Appendices I and II. Appendix III provides $\delta^{13}C$, $\delta^{15}N$, and C/N ratio of all hair samples analyzed, and data from dentine and bone collagen, and tooth enamel carbonate from modern specimens, is given in Appendix IV. Data obtained from $\delta^{13}C$ and $\delta^{18}O$ analysis of fossil baboon enamel is provided in Appendix V.

All hair samples analyzed had C/N ratios within the normal range for collagen, a protein similar to keratin (2.9 to 3.6; e.g. DeNiro, 1985). The majority of collagen samples also fell within this range, although samples that showed C/N ratios of 2.8 or 3.7 were not considered as deviating significantly from the normal protein composition. However, most dentine collagen samples obtained from specimen AZ 797 had abnormally high C/N ratios (4.0 to 7.1). It is not known why this was the case, but this specimen may have previously been treated with glue. Museum specimens treated with glue have previously given similar anomalous results (Lee-Thorp, pers. comm.). Dentine and bone collagen data from AZ 797 was excluded from the interpretation of results.

A number of fossil baboon specimens yielded insufficient CO_2 gas during mass spectrometry for reliable results to be obtained (indicated in Appendix V). According to

Luyt (2001), samples yielding gas amplitudes less than 1.5V show unreliable $\delta^{13}C$ values, and those of less than 1.0V give unreliable results for $\delta^{18}O$ analysis. In cases where sufficient sample material remained, such specimens were reanalyzed, but gave similar results. Several fossil primate specimens analyzed by Luyt (2001) displayed a similar problem, especially for $\delta^{18}O$ values. Low CO_2 yields may be the result of the low carbonate content of primate skeletal material (Sponheimer, 2003, pers. comm.). Alternatively, the presence of glue could also play a role here (Luyt, 2001). No glue was visible on these specimens, however, and as such these were not washed in acetone during pretreatment. All fossil samples that offered such results are omitted from the discussion of results in this dissertation.

An estimate of the proportion of C_3-based versus C_4-based foods incorporated into baboon (and other mammal species') diets as reflected by various tissues was calculated. For this purpose, end-member values were obtained by pooling the $\delta^{13}C$ values of all C_3 trees and C_4 grasses (including a combination of different plant parts) for a given area during a given period, and adding previously published diet-tissue carbon isotope fractionation factors to these means. For faeces, seasonally different data for plants from the three reserves were used, while for hair, bone, and tooth material, the seasonal data had to be pooled.

Diet-tissue fractionation factors used were –0.9‰ for faeces (Sponheimer *et al.* 2003b & 2003c), 3.0‰ for hair (Nakamura *et al.* 1982; Cerling & Harris, 1999), 4.5‰ for collagen (e.g. Ambrose & Norr, 1993), and 12.5‰ for enamel carbonate (Lee-Thorp *et al.*, 1989b). Given the atmospheric $\delta^{13}C$-depletion during the twentieth century (e.g. Marino & McElroy, 1991), 1.5‰ was subtracted from $\delta^{13}C$ values of samples of TM 911 (a baboon that died in 1926) in order to compare this individual's diet with that of the modern samples.

The calculation, however, does not account for variations in plant $\delta^{13}C$ values, such as those resulting from the "canopy effect" (van der Merwe & Medina, 1989), variability within different plant parts (as observed in the data), and C_4 photosynthetic subtypes (Hattersley, 1982). Therefore, it must be stressed that the percentage of dietary C_3, as calculated here, is a semi-quantitative estimate of dietary input, and should be treated as a guideline for interpretations (see Chapter 5).

All data were compared for significant differences and variability for inter-specific and intra-specific comparisons. Furthermore, within- and between habitat variations and seasonal fluctuations were tested, as well as differences between plant parts. Significant differences between categories were analysed using one-way Analysis of Variance and Tukey's post-hoc HSD. Differences in individual or mean delta values of less than 1‰ were not considered relevant, as this level of variation is potentially normal within a single sample (e.g. O'Leary, 1993).

The results of all analyses are presented and discussed in the following chapters, in order to divulge information about chacma and fossil baboon dietary ecology within their respective habitats.

CHAPTER 5

RESULTS

This chapter presents the results of all sample analyses, providing an isotopic perspective of the plant and mammal community ecology in the Waterberg and Kruger Park for the study period, and of South African fossil cercopithecoid dietary ecology. The first section reports on results obtained from analysis of plant material. In the second section, intra- and inter-habitat variations in baboon feeding ecology are compared with those of sympatric mammal species. Serial analyses of baboon hair and tooth dentine collagen provide insights into intra-individual dietary flexibility. The chapter includes a discussion of the different types of information obtained from different biological materials, and the benefits and disadvantages associated with analysis of each. Lastly, the dietary habits of South African fossil cercopithecoids from Pleistocene deposits of Swartkrans Members 1 and 2, as observed in isotopic data, are described. These results are compared with previously reported data for specimens from Swartkrans and from the older deposits of Sterkfontein Member 4.

5.1. Plants

A detailed representation of isotopic ($\delta^{13}C$ and $\delta^{15}N$) and crude protein content (expressed by %N) in plants is given in Figs. 5.1 through 5.10. These results are discussed below in terms of the relevance to interpretations of mammalian diets in the study areas. For inter- and intra-habitat comparisons (sections 5.1.1 and 5.1.2), all plant parts (leaves, fruits, bark, roots, and seeds) are pooled. These various organs are considered separately in section 5.1.3.

A summary of the results obtained from trees and grasses is provided in Table 5.1. Table 5.1 serves only to provide mean plant values that were used as isotopic "end-member" values for calculating the percentage dietary C_3 from mammal tissues (see Chapter 4).

Table 5.1. Summary of data from trees and grasses in the Waterberg and the Kruger Park

			$\delta^{13}C$		$\delta^{15}N$		%N	
Plant Form	**Month**	***n***	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Zoetfontein								
Trees	Sept	47	-24.9	1.9	4.4	2.6	1.2	0.5
Grasses		18	-11.4	1.3	2.6	1.9	0.9	0.4
Welgevonden								
Trees	Sept	50	-25.5	1.8	2.7	2.7	1.2	0.6
	Jan	28	-26.4	1.3	4.2	3.6	1.7	1.0
	Average	78	-25.8	1.7	3.2	3.1	1.4	0.8
Grasses	Sept	17	-10.5	1.2	2.7	1.8	0.9	0.2
	Jan	15	-13.3	1.0	4.5	1.4	1.0	0.3
	Average	32	-11.8	1.8	3.5	1.9	0.9	0.3
Waterberg Combined								
Trees		125	-25.5	1.8	3.7	2.9	1.3	0.7
Grasses		50	-11.7	1.6	3.2	1.9	0.9	0.3
Kruger Park								
Trees	June	64	-26.4	1.9	2.5	2.6	1.4	0.6
	January	45	-26.4	1.5	3.8	2.2	2.0	0.6
	Average	109	-26.4	1.7	3.0	2.5	1.6	0.7
Grasses	June	59	-11.7	1.4	2.2	1.7	0.5	0.3
	January	51	-12.6	0.8	3.8	2.0	1.0	0.4
	Average	110	-12.1	1.2	3.0	2.0	0.8	0.4

5.1.1. Comparison Between the Waterberg and Kruger Park

The $\delta^{13}C$ values of plants exhibited the bimodal distribution expected for plants using C_3 and C_4 photosynthetic pathways, respectively. All grasses from the Waterberg and Kruger Park were enriched in ^{13}C, and all trees and forbs were ^{13}C-depleted (Fig. 5.1a). Hence, all grasses analyzed followed the C_4 photosynthetic pathway, while all trees and forbs were uniformly C_3. Succulents all had $\delta^{13}C$ values that were indistinct from those of grasses (Fig. 5.2) and were therefore obligate CAM plants. Many species of *Euphorbia* are in fact C_4 (Sage *et al.*, 1999), and it may be that the *E. ingens* sampled is not CAM, but C_4. In order to maintain a consistent discretion between trees, grasses, forbs, and succulents, *E. ingens* is treated here as a CAM plant.

Inter-habitat differences in plant $\delta^{13}C$ values were observed, but these were generally small. Trees from Zoetfontein were slightly more enriched in ^{13}C ($\delta^{13}C = -24.9 \pm 1.9‰$; $n = 47$) than trees from the other two reserves ($\delta^{13}C = -25.8 \pm 1.7$, $n = 78$, and $\delta^{13}C = -26.4 \pm 1.7‰$, $n = 109$, for trees from the Waterberg and Kruger Park, respectively). This difference is not significant ($p > 0.05$), and the pattern was even less pronounced in forbs and grasses (Fig. 5.1a).

Plant $\delta^{15}N$ values displayed much greater variability than $\delta^{13}C$ values, and it is difficult to discern clear trends. Trees from Zoetfontein were significantly ($p < 0.05$) enriched in ^{15}N compared to trees from both Welgevonden and Kruger Park (Fig. 5.1b). Forbs from Zoetfontein and Kruger Park had slight, but not significantly ($p > 0.05$), higher mean $\delta^{15}N$ values than those from Welgevonden, but the Welgevonden forbs showed greater variability ($\delta^{15}N = 2.7 \pm 2.9‰$, $n = 9$). Conversely, grasses from Welgevonden were ^{15}N-enriched compared to grasses from Zoetfontein and Kruger, and this difference is significant ($p < 0.003$).

Crude protein content of trees and forbs was higher than that of grasses (Fig. 5.1c). Contrary to expectations, plants from Kruger Park did not have a consistently higher crude protein content than plants from the Waterberg. The vegetation of the Waterberg is classified as "sourveld" (Acocks, 1988), and was thus expected to be nutrient-poor compared to the "mixed sourveld" and "sweetveld" of Kruger Park. Additionally, earlier agricultural management practices and overgrazing has created a nutrient deficiency in the soil and vegetation of the Waterberg (Burger, 2003, pers. comm.). While Kruger Park trees had significantly more crude protein than trees from the Waterberg ($p < 0.05$), protein content of forbs and grasses did not differ significantly between these areas.

Seasonal differences in plant isotopic and protein composition are displayed in Figs. 5.2 through 5.4. Waterberg trees showed a slight but not significant ($p > 0.05$) decrease in $\delta^{13}C$ values of about 0.9‰ from September to January. Kruger Park trees showed no differences in mean $\delta^{13}C$ values between June and January (Fig. 5.2). $\delta^{13}C$ values of forbs were lower in January for both areas, but this seasonal difference was only significant in the Waterberg ($p < 0.00001$). In both areas, grasses exhibited a significant ^{13}C-depletion in January ($p < 0.00001$). In Kruger Park, this change was in the order of only 1‰, but grasses from the Waterberg were about 3‰ more depleted in ^{13}C in January compared to September. C_3

plants are reported to display seasonal variation in the order of ±1‰ in their $\delta^{13}C$ values (e.g. Handley *et al.*, 1994; Heaton, 1999), and C_4 plants are expected to be even less variable (e.g. O'Leary, 1988). Thus, the 3‰ difference in $\delta^{13}C$ values of C_4 grasses is unexpected. One possible explanation is that this is due to differences in the species collected during September compared to January (see Appendix I).

Tree, grass, and forb $\delta^{15}N$ values, and crude protein content, displayed an increase from September and June, in the Waterberg and Kruger Park respectively, to January (Figs. 5.3 & 5.4). However, this pattern is only significant for Kruger plants ($p<0.05$). Trees, forbs, and grasses had $\delta^{15}N$ values ranging from about 0 to 5‰, although values as positive as 8‰ were observed in some forbs from Kruger Park. No consistent differences in $\delta^{15}N$ were found between legumes (super-family Fabaceae) and non-leguminous plants. Forbs in Kruger Park contained more crude protein than grasses, during both seasons, but in the Waterberg forbs were surprisingly slightly less proteinaceous than grasses (Fig. 5.4).

Sample sizes of other plant forms, such as sedges, geophytes, and succulents, were too small for seasonal comparison, but values for these plants are included in Figs. 5.2 to 5.4 because of their potential importance to baboon dietary ecology.

The wide range of $\delta^{13}C$ values in sedges (Fig. 5.2) is because some specimens were C_4, while most were C_3. Sedges were not separated into photosynthetic categories due to small sample sizes (n = 6 and n = 12 for the Waterberg and Kruger Park, respectively). Geophytes were all C_3, having $\delta^{13}C$ values slightly lower than the mean values for trees and forbs in both areas. Succulents (*Euphorbia ingens* and *Agave* spp.) from Welgevonden all had $\delta^{13}C$ values indicating obligate CAM photosynthesis, and these were not distinct from the values of C_4 grasses.

In the Waterberg, succulents had the highest $\delta^{15}N$ values, excepting for a single sedge from a mud pool on Welgevonden (Fig. 5.3). This sedge had leaf and root $\delta^{15}N$ values in excess of 20‰. Analysis of this sample was repeated for surety. Such high $\delta^{15}N$ values are probably due to a higher rate of decomposition than soil denitrification in swamp-like microhabitats (Muzuka, 1999; Stock 2003, pers. comm.).

The lowest $\delta^{15}N$ value for any plant was observed in the single geophyte sample from Welgevonden, having a $\delta^{15}N$ value of –3.8‰ (Fig. 5.3). However, because only one sample was obtained, it is unclear whether this result can be considered a general representation of geophytes in the Waterberg.

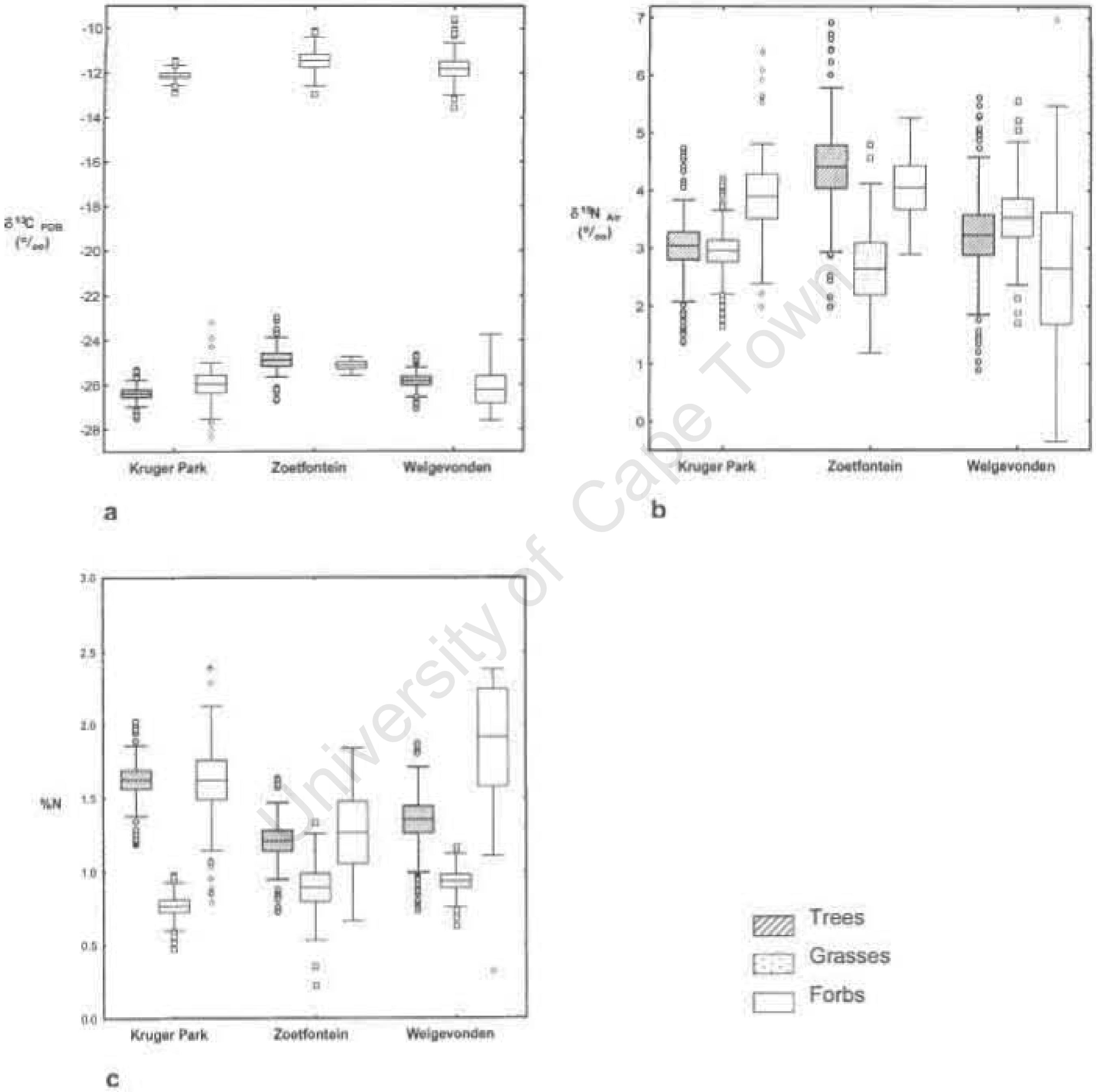
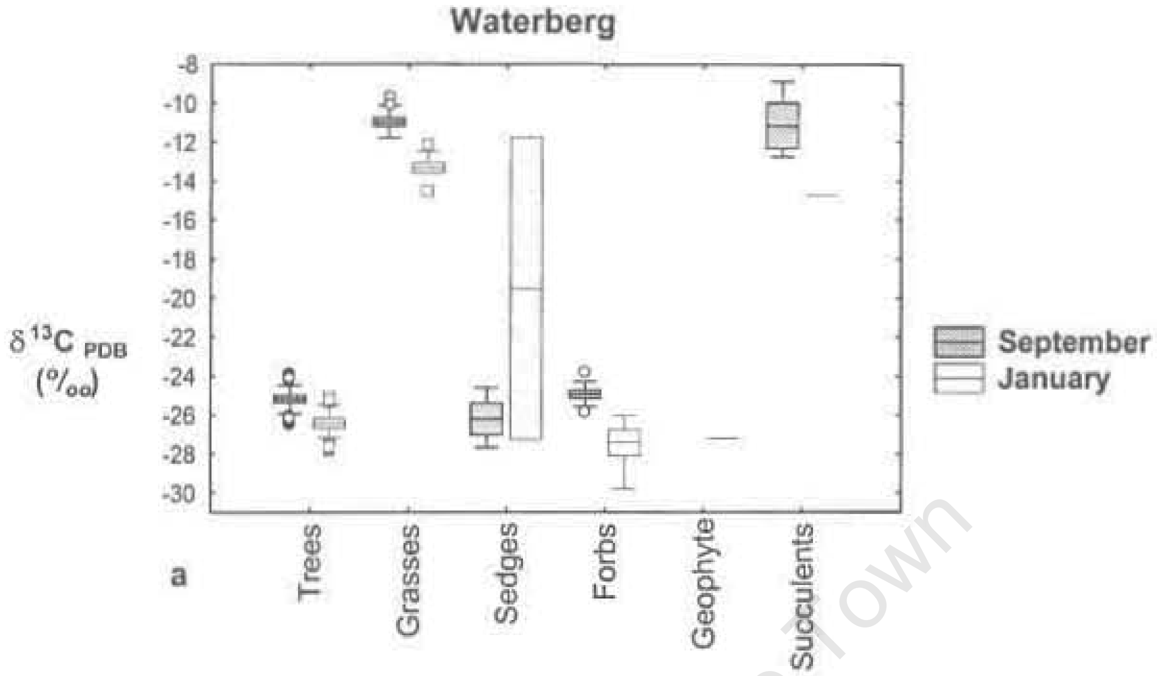


Figure 5.1 a-c – Box plots of means and standard deviations with outliers for $\delta^{13}C$ (a), $\delta^{15}N$ (b), and %N (c) of trees, grasses, and forbs collected in the Kruger Park and the Waterberg.



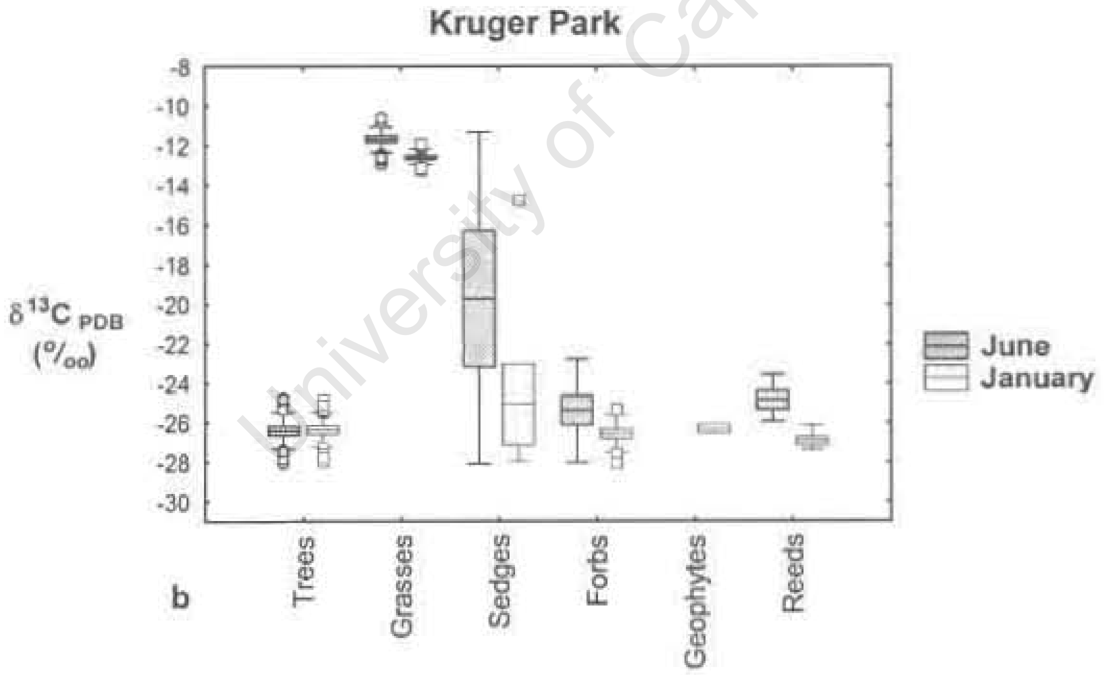
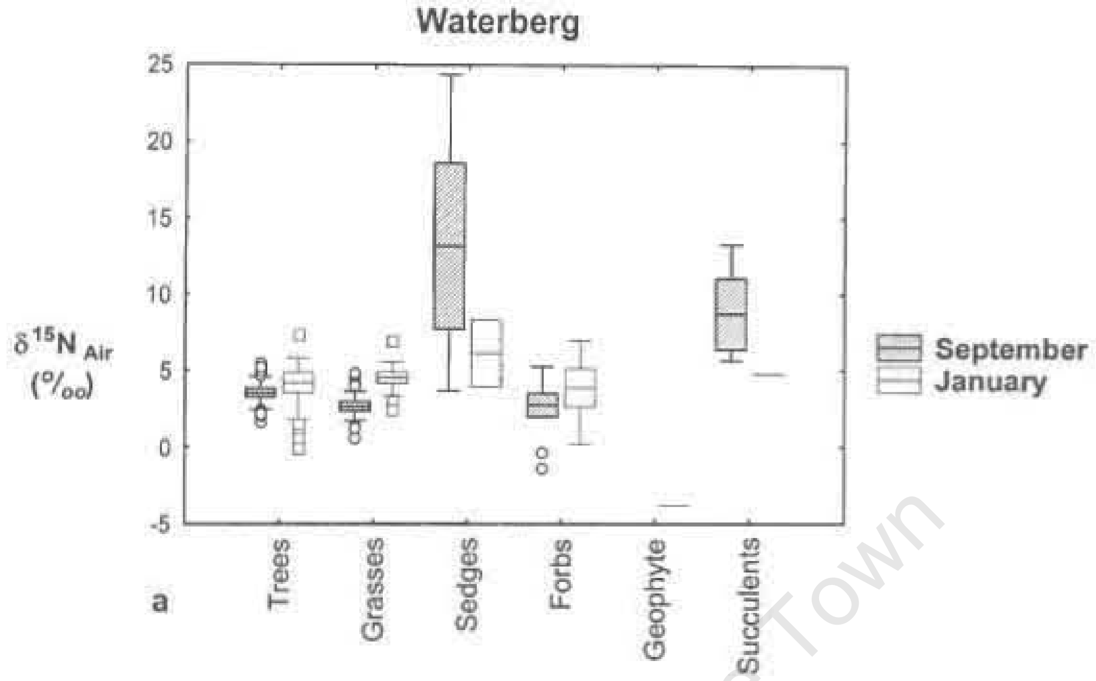


Figure 5.2 a & b – Box plots with means, standard deviations, and outliers, showing seasonal changes in $\delta^{13}C$ of different plant growth forms from the Waterberg (a) and the Kruger Park (b). Each plant grouping consists of pooled data for the different organs analyzed.



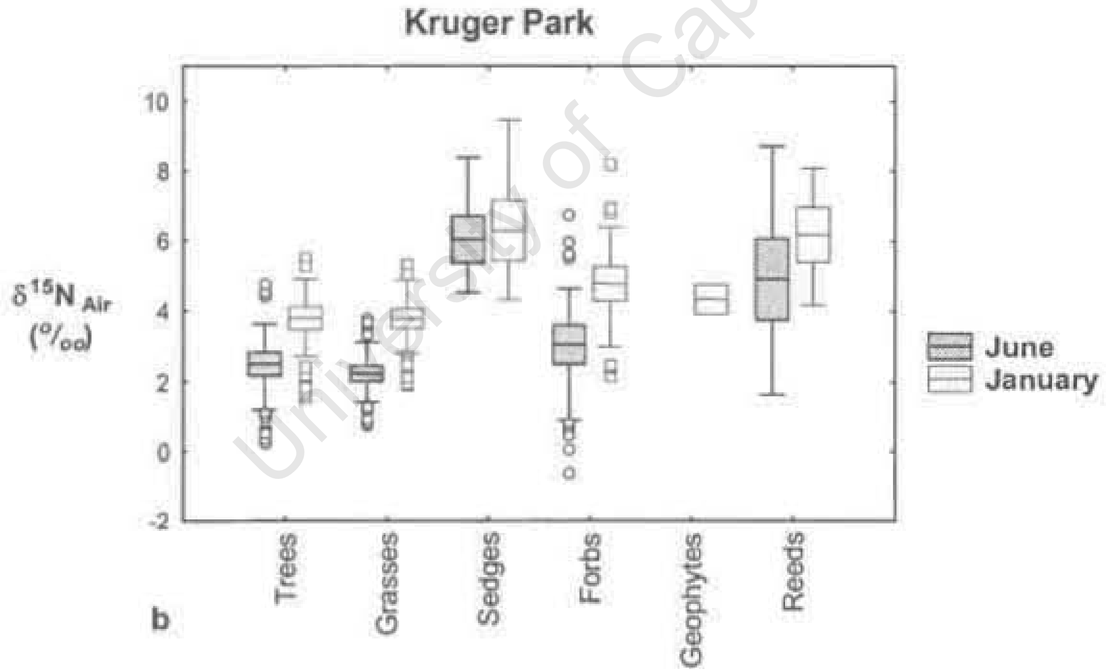


Figure 5.3 a & b – Box plots with means, standard deviations, and outliers, showing seasonal changes in $\delta^{15}N$ of different plant growth forms from the Waterberg (a) and the Kruger Park (b). Each plant grouping consists of pooled data for the different organs analyzed.

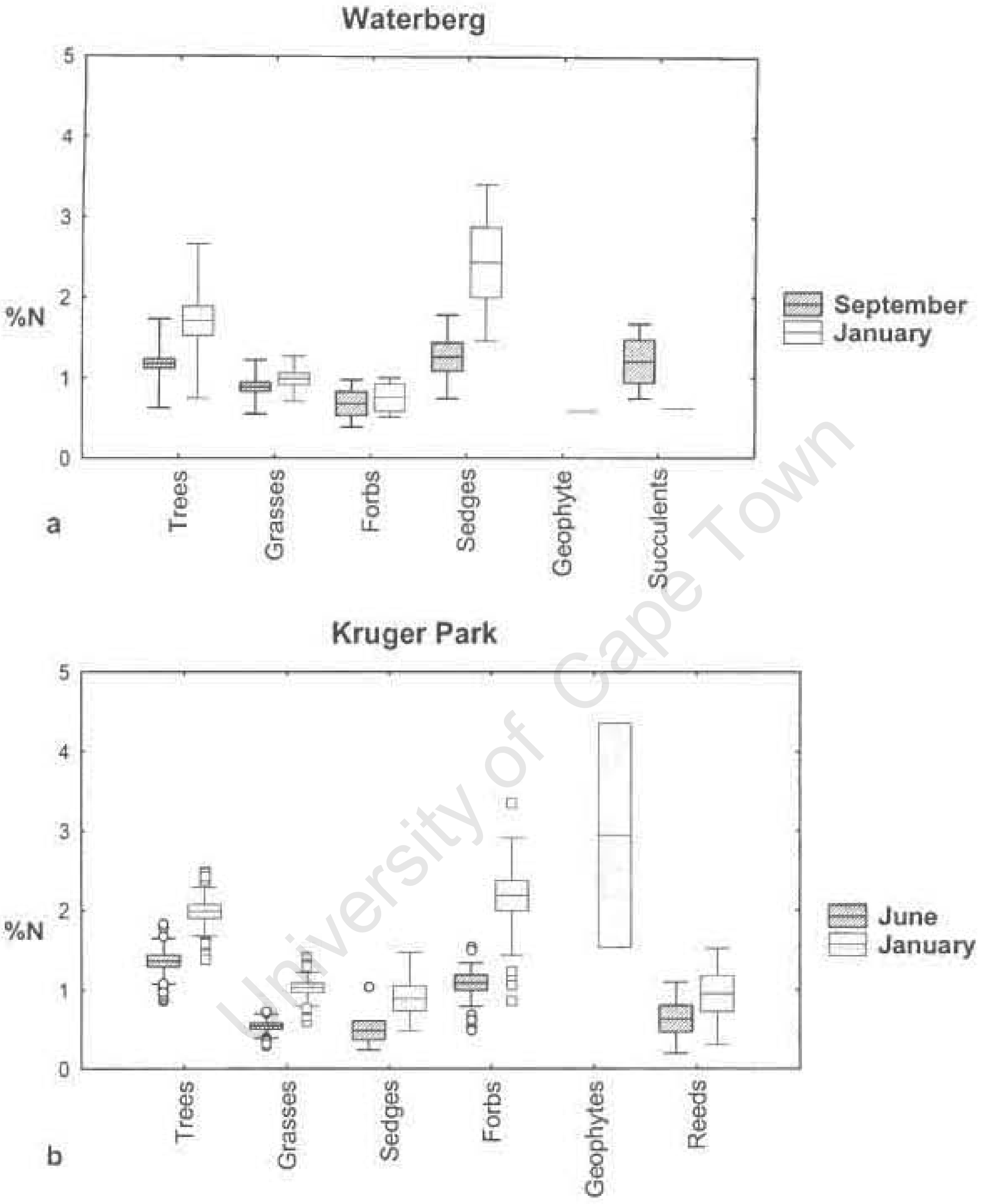


Figure 5.4 a & b – Box plots with means, standard deviations, and outliers, showing seasonal changes in %N of different plant growth forms from the Waterberg (a) and the Kruger Park (b). Each plant grouping consists of pooled data for the different organs analyzed.

5.1.2. Variability Between Microhabitats

Variations in plant isotopic composition between microhabitats of the Waterberg and Kruger Park are presented in Figs. 5.5 to 5.7. Within grasses, no significant differences were observed for species that followed different C_4 sub-pathways (NADP-ME, NAD-ME, PCK). Taxonomic allocation of C_4 subtypes followed Sage *et al.* (1999). This designation of C_4 subtypes is, however, confounded by methodological inconsistencies employed for identifying C_4 sub-pathways. Thus, the lack of differences in mean $\delta^{13}C$ values between NADP-ME, NAD-ME, and PCK grasses in this study may be an artifact of erroneous designation of these sub-pathways to the grass taxa analyzed.

In the Waterberg, grass $\delta^{13}C$ values did not vary significantly between sampling sites, and the ~3‰ decrease in $\delta^{13}C$ values from September to January was evident in all microhabitats (Fig. 5.5a). Waterberg trees had $\delta^{13}C$ values 1 to 2‰ higher in the open woodland site Motswedi compared to the more densely vegetated riparian areas (Bushman's Painting and Mziki) during both September and January (Fig. 5.5a).

Kruger Park plants were no more variable than the Waterberg plants (Fig. 5.5b), even though sampling sites were further apart and there is much more vegetational heterogeneity in this reserve. During each month of sampling, mean $\delta^{13}C$ values of Kruger Park trees and grasses did not differ by more than 1‰ between any of the microhabitats (sites) sampled, with one notable exception. Hlanganzwane, an arid, open grassland site on the basaltic Knobthorn/Marula savanna, had grasses that displayed a mean $\delta^{13}C$ value of -9.8 ± 1.0 ‰ (n = 13) during June. Such a high average for grasses within a single area is largely unknown, and the only reasonable explanation for this seems to be that the soils of this area are highly saline. It is striking, however, that these grasses had amongst the lowest $\delta^{13}C$ values for Kruger Park in January. Analytical error can be ruled out here because sample analysis was not carried out according to collection site, but plants and faeces were in fact analyzed in random order. While this observation remains somewhat unclear, the values noted here do not appear to be reflected in the $\delta^{13}C$ values of mammal faeces from Kruger Park (see section 5.2).

Between-site variations in plant $\delta^{15}N$ values in the Waterberg were small, with all sites having plants exhibiting a similar range of values (Fig. 5.6a). Seasonally, the Waterberg plants showed no significant changes, except for the site Mziki, where trees and grasses increased in δ^{15}N from September to January. In Kruger Park, however, grasses from all four microhabitats shifted to become about $2^{0}/_{00}$ more positive in δ^{15}N in January compared to June (Fig. 5.6b). Trees from Kruger Park sites displayed a similar seasonal trend as observed for grasses, but the Hlanganzwane trees did not differ seasonally.

Trees and grasses displayed an increase in crude protein content from the drier months to January (Fig. 5.7). Apart from the Mziki site, and grasses from Bushman's Painting, the protein content of trees and grasses collected in January is significantly higher ($p<0.02$) than plants collected in September and in June for both the Waterberg and Kruger Park, respectively.

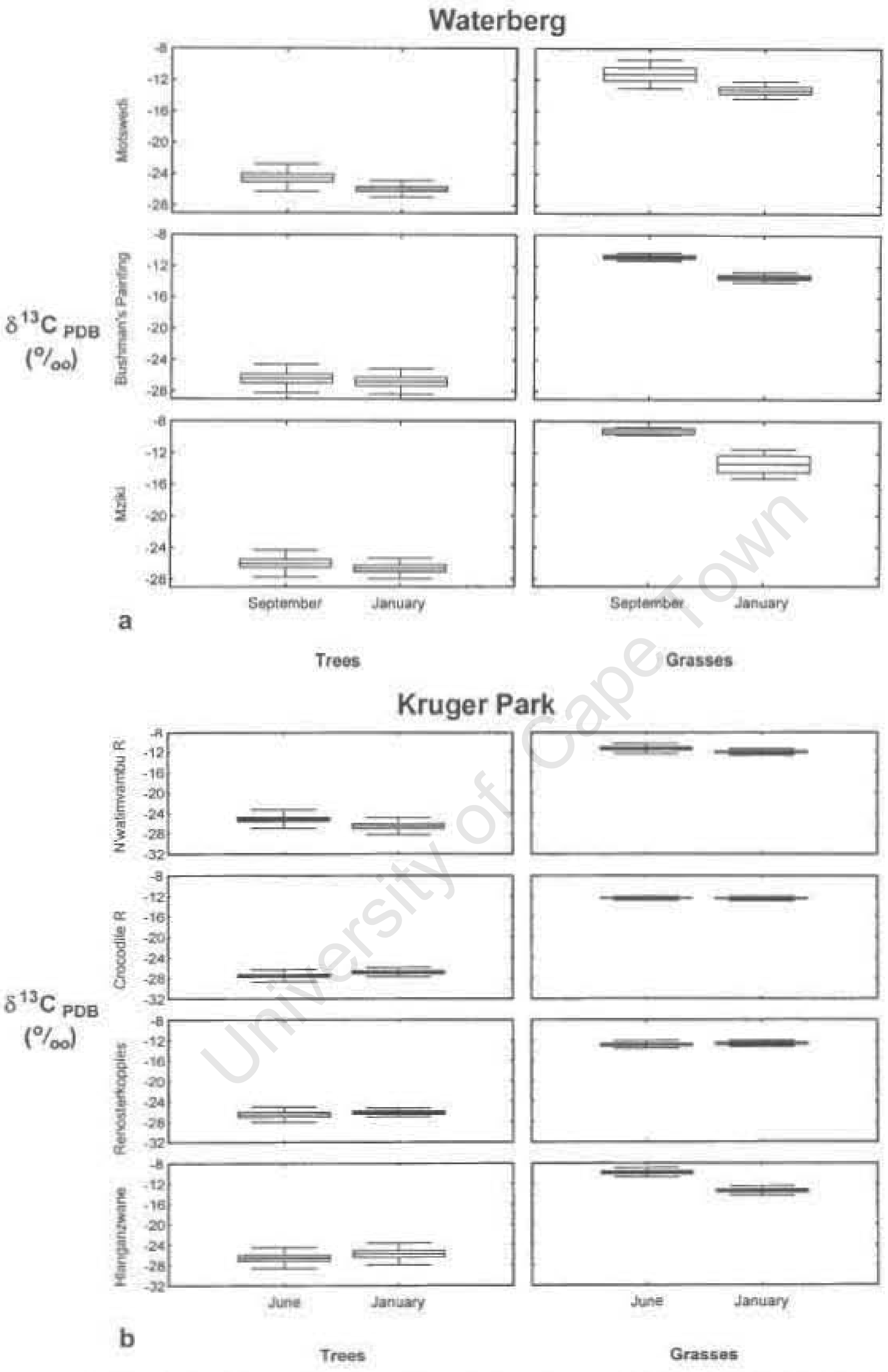


Figure 5.5 – Box plots with means and standard deviations showing seasonal changes in $\delta^{13}C$ of trees and grasses from different collection sites in the Waterberg and the Kruger Park, respectively.

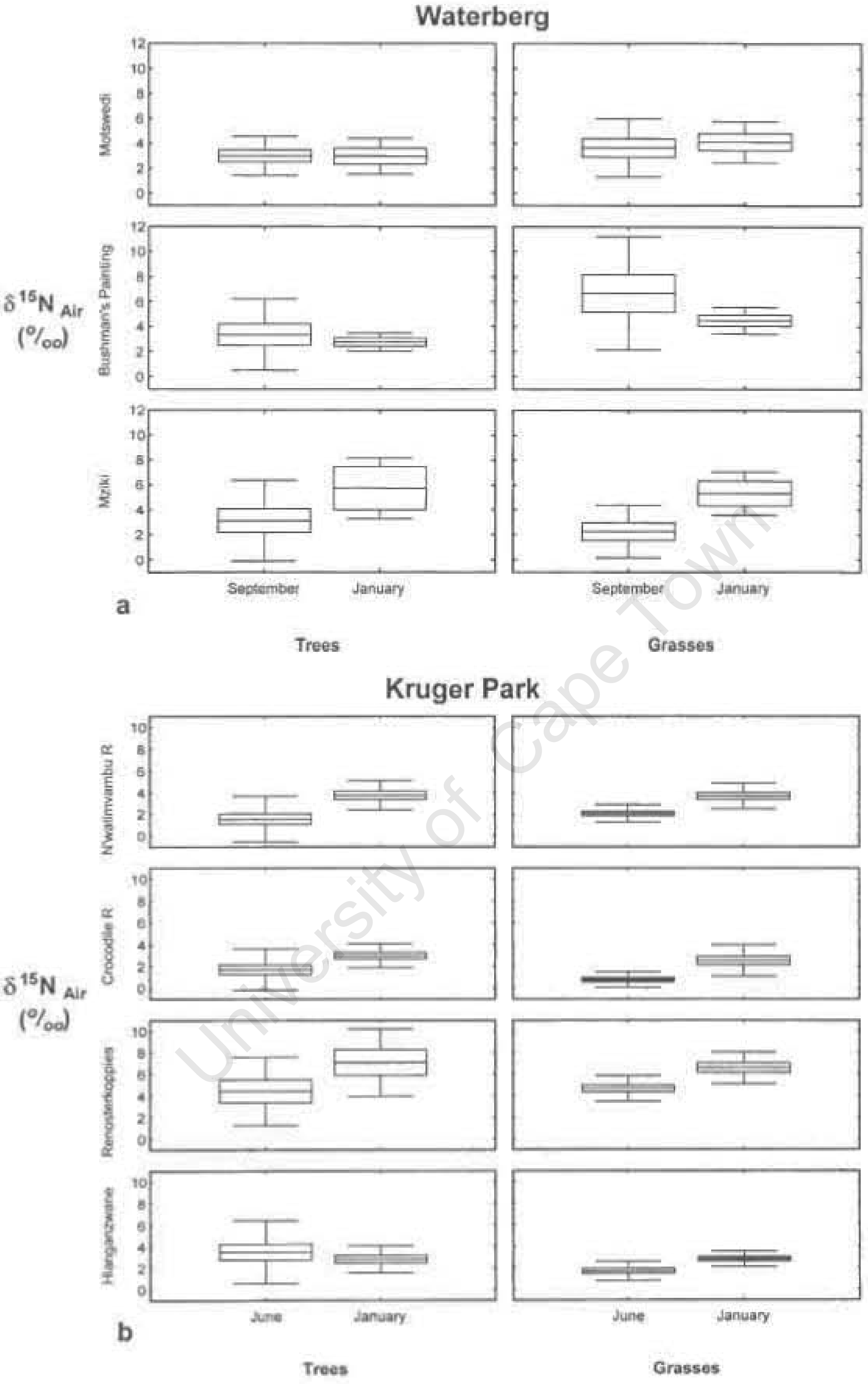


Figure 5.6 – Box plots with means and standard deviations showing seasonal changes in $\delta^{15}N$ of trees and grasses from different collection sites in the Waterberg and the Kruger Park, respectively.

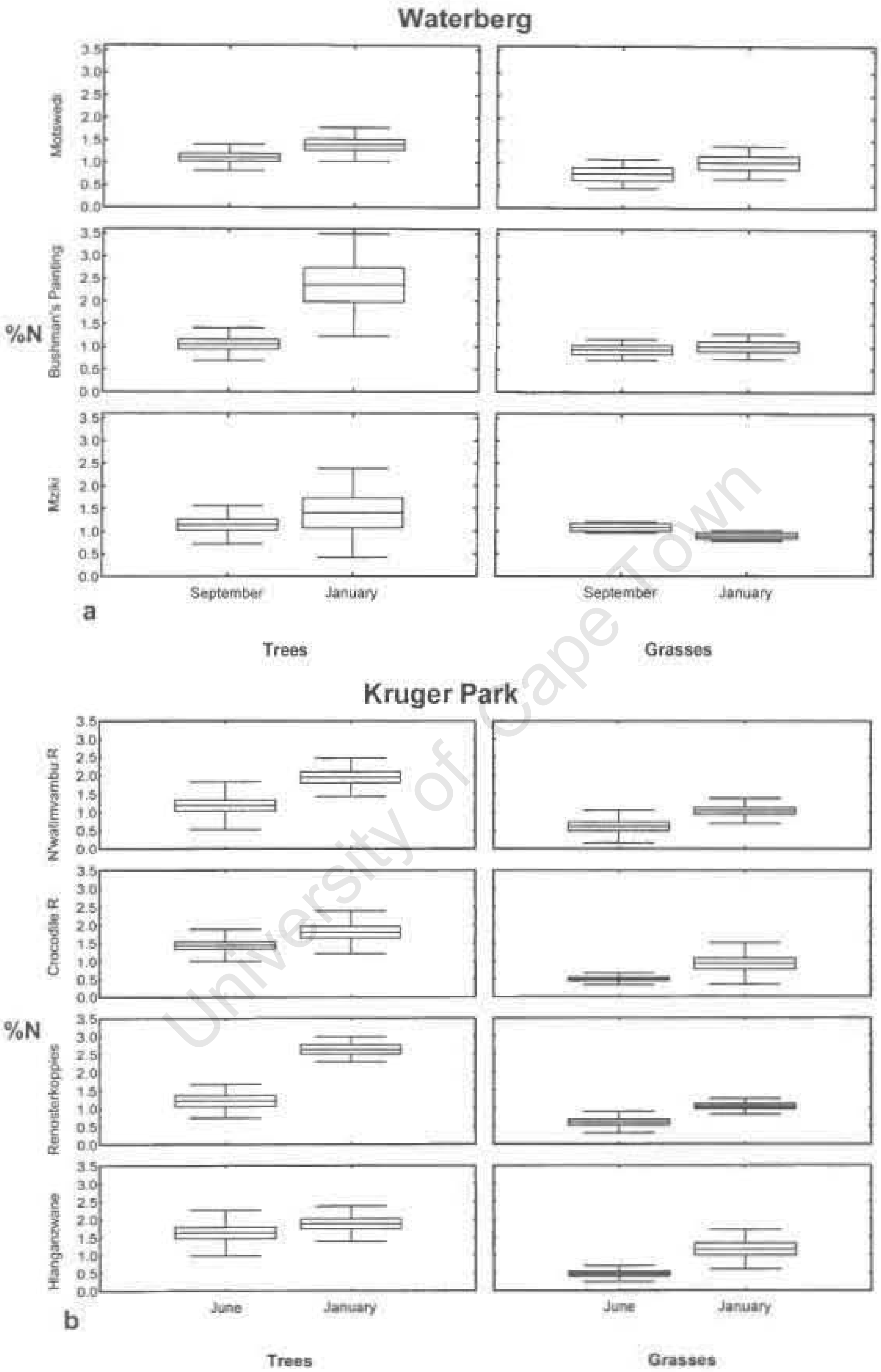


Figure 5.7 – Box plots with means and standard deviations showing seasonal changes in %N of trees and grasses from different collection sites in the Waterberg and the Kruger Park, respectively.

5.1.3. Plant Parts

Different parts of trees, forbs, and grasses from each reserve exhibited some degree of variability in isotopic and protein composition. Notably, δ^{13}C of tree leaves were about 2 to $3^{o}/_{oo}$ lower compared to fruits in both the Waterberg and Kruger Park (Fig. 5.8a). This pattern is consistent for both months of sampling in the respective areas, and the difference is always strongly significant ($p<0.004$). δ^{13}C values of tree bark were intermediate between that of leaves and fruit, but bark was only significantly different ($p<0.01$) from both leaves and fruit in June in Kruger Park. Grass parts did not differ by much in δ^{13}C values, although it appeared that seeds were the most ^{13}C-enriched grass part during January in both areas (Fig. 5.8b).

Tree bark was depleted in ^{15}N by 2 to $4^{o}/_{oo}$, on average, compared to leaves and fruits ($p<0.05$; Fig. 5.9a). The δ^{15}N of different grass parts did not display any consistent patterns (Fig. 5.9b). In June, at least, the roots of forbs had lower δ^{15}N values than leaves, but there were insufficient samples to test whether this held true in the Waterberg (Fig. 5.9c).

The most proteinaceous parts of trees and forbs were the leaves, especially during January (Fig. 5.10a & c). Grass seeds often displayed a higher crude protein content than other parts of grasses from Kruger Park, but in the Waterberg no significant differences between grass seeds and leaves were observed (Fig. 5.10b).

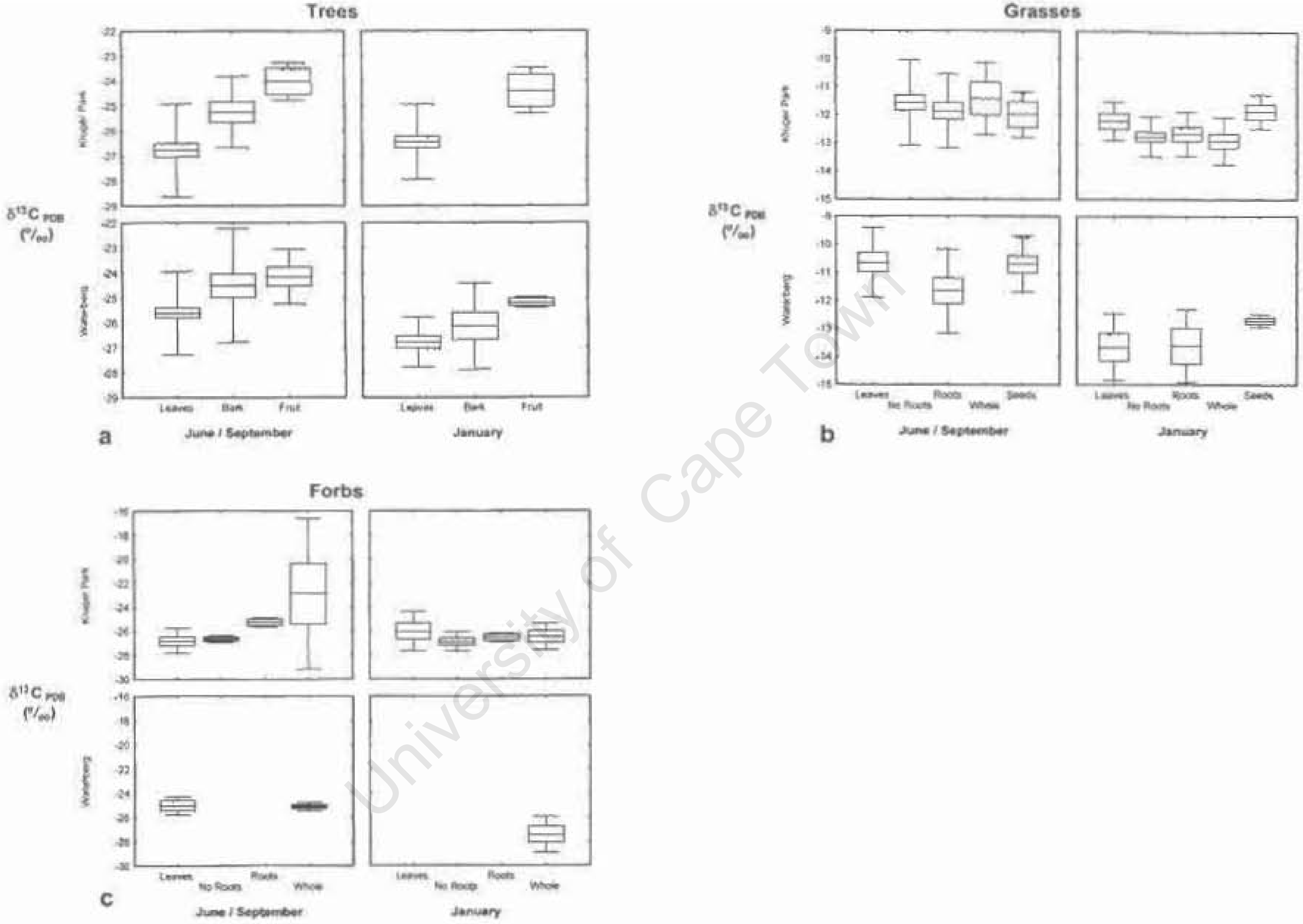


Figure 5.8 – Box plots with means and standard deviations showing seasonal changes in $\delta^{13}C$ of different organs of trees, grasses, and forbs from the Waterberg and the Kruger Park.

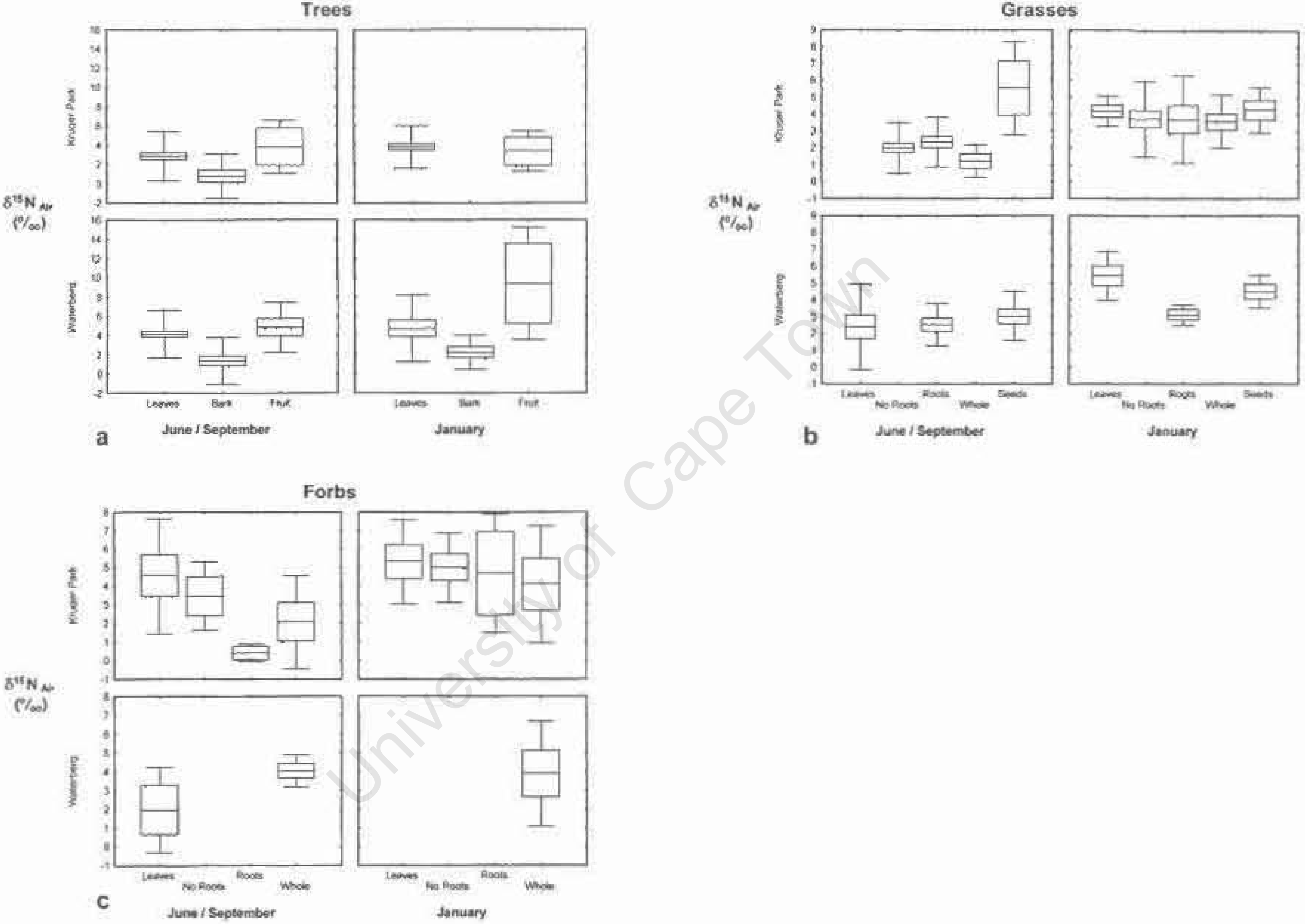


Figure 5.9 – Box plots with means and standard deviations showing seasonal changes in $\delta^{15}N$ of different organs of trees, grasses, and forbs from the Waterberg and the Kruger Park.

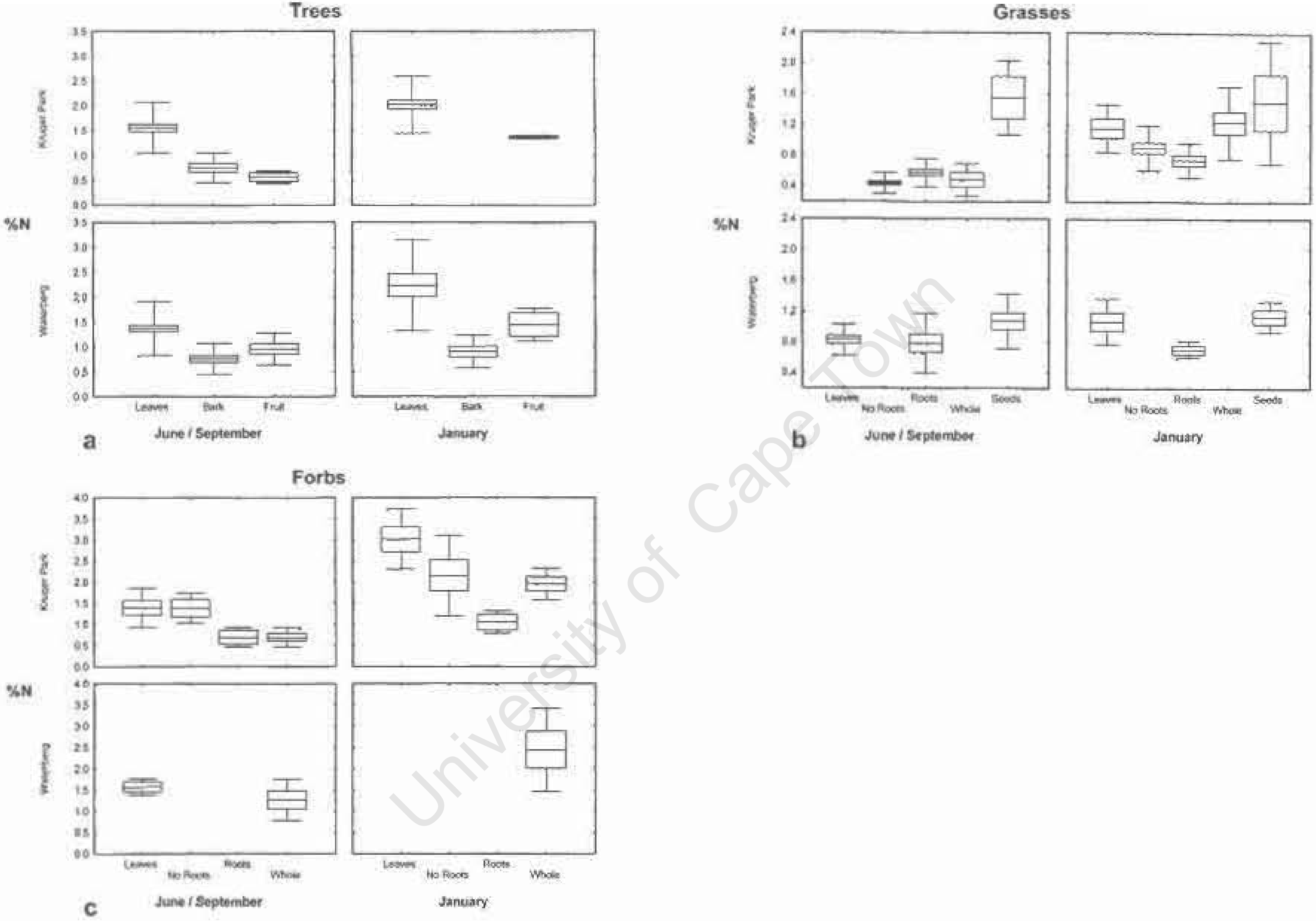


Figure 5.10 – Box plots with means and standard deviations showing seasonal changes in %N of different organs of trees, grasses, and forbs from the Waterberg and the Kruger Park.

5.1.4. Summary of Results from Plants

The results of plant analyses are used here to provide a dietary baseline for interpretation of mammal diets in the Waterberg and Kruger Park. With respect to implications for dietary ecology, several significant points can be made:

- C_4 grass $\delta^{13}C$ values exhibited seasonal variability in both study areas, decreasing from June and September to January.
- Plant $\delta^{15}N$ values and crude protein content were higher during January than during drier months.
- Variations in plant isotopic composition and crude protein content between different microhabitats were small, and thus spatial differences in results observed in animal tissues within each reserve reflect true dietary differences.
- Kruger Park trees contain more crude protein than trees from the Waterberg, and are thus higher quality foods.
- Fruits were enriched in ^{13}C compared to other tree parts, bark was ^{15}N-depleted, and leaves had the highest crude protein composition of all the organs of trees.
- All succulents sampled from the Waterberg had $\delta^{13}C$ values that were indistinguishable from that of C_4 grasses, and were the most ^{15}N-enriched of all plants.
- Data for a single geophyte specimen from the Waterberg hints that these plants may have low $\delta^{15}N$ values in this region.

5.2. Faeces

Faecal samples were grouped by species and results are presented in Tables 5.2 and 5.3. For comparison with baboons, faeces from other mammal species were combined as grazers, browsers, and mixed-feeders, but using only those species for which two months of data were available. Thus, grazers are represented by zebra (*Equus burchellii*); buffalo (*Syncerus caffer*); blue wildebeest (*Connochaetes taurinus*); waterbuck (*Kobus ellipsiprymnus*); and warthog (*Phacochoerus aethiopicus*); in the Waterberg, and by the same species in Kruger Park, barring waterbuck. Browsers are represented by giraffe (*Giraffa camelopardalis*) and kudu (*Tragelaphus strepsiceros*) in both regions. Mixed-feeders are represented only by impala (*Aepyceros melampus*).

These results, indicating dietary variability within and between these groups, and baboons, are presented in Figs. 5.11 to 5.15.

Table 5.2. Data from Waterberg mammal faeces

			$\delta^{13}C$		$\delta^{15}N$		%N	
Species	**Month**	***n***	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Zoetfontein								
Aepyceros melampus	Sept	6	-20.8	3.9	5.3	0.6	1.3	0.2
Connochaetes taurinus		10	-14.5	0.6	5.0	0.6	0.9	0.1
Equus burchellii		11	-14.0	0.4	3.9	0.5	0.8	0.1
Hyaena brunnea		2	-16.9	0.6	8.7	0.0	1.4	0.6
Hystrix africaeaustralis		5	-24.2	1.1	5.4	0.3	1.9	0.1
Mongoose		1	-21.7	-	5.1	-	5.5	-
Oreotragus oreotragus		2	-25.2	0.9	5.7	0.3	1.7	0.1
Oryx gazella		4	-14.4	0.7	4.5	0.8	0.9	0.2
Panthera pardus		1	-17.4	-	8.4	-	6.6	-
Papio ursinus		50	-23.3	1.2	4.4	0.9	2.9	0.7
Phacochoerus aethiopicus		2	-13.0	0.5	4.0	0.4	1.0	0.1
Tragelaphus strepsiceros		12	-25.2	0.9	5.5	0.3	1.8	0.2
Welgevonden								
Aepyceros melampus	Sept	4	-20.6	4.6	5.2	1.3	1.4	0.3
	Jan	4	-16.0	1.5	5.6	0.8	1.6	0.3
Alcelaphus buselaphus	Jan	1	-14.5	-	6.3	-	1.2	-
Ceratotherium simum	Sept	3	-14.5	0.3	4.7	1.2	0.9	0.1
	Jan	1	-14.7	-	4.7	-	0.9	-
Connochaetes taurinus	Sept	5	-13.9	0.3	4.5	0.4	1.1	0.2
	Jan	4	-15.1	1.1	5.4	1.0	1.3	0.3
Equus burchellii	Sept	7	-14.1	0.8	4.3	1.1	0.9	0.2
	Jan	3	-13.0	0.7	4.5	0.2	0.8	0.1
Giraffa camelopardalis	Sept	4	-25.7	0.3	5.2	0.8	1.8	0.1
	Jan	5	-26.2	0.6	4.6	0.8	2.2	0.3
Hyaena brunnea	Sept	5	-15.4	2.6	6.8	0.3	0.8	0.3
Hystrix africaeaustralis	Sept	2	-24.1	0.8	4.2	0.5	1.9	0.2
Kobus ellipsiprymnus	Sept	1	-14.0	-	4.2	-	1.3	-
	Jan	1	-14.4	-	4.6	-	1.0	-
Mongoose	Jan	1	-16.7	-	6.6	-	2.0	-
Papio ursinus	Sept	76	-20.6	1.6	3.6	1.2	2.6	0.8
	Jan	59	-21.2	1.6	3.9	0.7	2.3	0.5
Potamochoerus porcus	Sept	2	-19.7	0.0	3.8	0.2	1.6	0.6
	Jan	1	-24.5	-	3.7	-	2.0	-
Syncerus cafer	Jan	3	-15.2	0.7	5.8	0.7	1.3	0.1
	Sept	3	-14.8	0.5	3.7	0.1	1.1	0.1
Taurotragus oryx	Jan	4	-26.9	0.2	5.7	0.6	2.1	0.1
Tragelaphus scriptus	Sept	1	-26.7	-	4.1	-	2.0	-
Tragelaphus strepsiceros	Sept	3	-26.8	0.2	3.7	0.2	1.9	0.3
	Jan	2	-26.6	0.5	4.9	0.3	2.5	0.0

Table 5.3. Data from Kruger Park mammal faeces

			$\delta^{13}C$		$\delta^{15}N$		%N	
Species	**Month**	*n*	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Aepyceros melampus	June	21	-19.2	2.2	5.3	1.6	2.1	0.4
	Jan	23	-19.8	3.0	6.2	2.5	2.2	0.6
Connochaetes taurinus	June	10	-14.3	0.6	6.7	1.4	1.5	0.2
	Jan	1	-15.0	-	11.3	-	2.6	-
Equus burchellii	June	10	-13.9	0.4	3.4	1.7	1.1	0.3
	Jan	9	-15.2	0.6	5.1	2.4	1.5	1.1
Giraffa camelopardalis	June	8	-27.0	1.0	3.8	1.2	3.1	1.0
	Jan	11	-27.1	0.8	4.6	1.5	2.5	0.6
Kobus ellipsiprymnus	Jan	4	-16.1	0.9	5.7	1.4	1.5	0.8
Panthera leo	June	6	-17.0	1.7	8.9	1.0	6.6	2.8
Papio ursinus	June	50	-25.1	0.8	4.2	1.2	2.6	0.6
	Jan	36	-26.3	1.2	5.4	1.1	3.5	1.4
Phacochoerus aethiopicus	June	7	-14.1	0.4	4.1	0.9	1.5	0.1
	Jan	1	-15.0	-	5.8	-	0.7	-
Syncerus caffer	June	15	-14.7	0.5	3.3	1.2	1.3	0.3
	Jan	5	-16.1	0.8	6.5	2.7	2.0	0.7
Tragelaphus strepsiceros	June	7	-26.6	0.5	6.1	1.0	3.3	0.5
	Jan	1	-28.0	-	3.1	-	3.7	-

5.2.1. Comparison of Mammal Diets Between the Waterberg and Kruger Park

As was the case with plants, $\delta^{13}C$ values from mammal faeces were clearly distinct between grazing (^{13}C-enriched) and browsing (^{13}C-depleted) species (Fig. 5.11a). No significant differences were found in mean grazer or browser $\delta^{13}C$ values between the Waterberg and Kruger Park, although the means for both groups were slightly higher in the Waterberg (Fig. 5.11a). The lack of dietary differences between the two areas is further indicated by the calculated %C_3-intake. Fig. 5.11b shows that the small differences observed in mean $\delta^{13}C$ values of grazers and browsers between the Waterberg and Kruger Park do not reflect differences in the proportions of C_3 to C_4-based foods consumed by these animals. The small inter-habitat differences are attributable to minor differences in plant $\delta^{13}C$ values between these regions. Similarly, no differences were observed in impala diets between the two regions, although they exhibited a wider range dietary flexibility in the Waterberg (~20 to 70% C_3 intake) as compared to Kruger Park (~40 to 55% C_3 intake).

Amongst baboon faeces, a strongly significant difference ($p<0.000001$) was found in mean $\delta^{13}C$ values between the Waterberg and Kruger Park (Fig. 5.11). Baboon faeces from the Waterberg were more enriched in ^{13}C, indicating consumption of between 50 and 70% C_3-based foods, while in Kruger Park baboon faeces had lower δ^{13}C values, indicating utilization of ~80 to 90% C_3-based foods (Fig. 5.11a & b).

It would seem that baboons in the Waterberg commonly utilized grasses during the study period. However, this area comprises a much lower abundance of palatable grass species than Kruger Park (e.g. Acocks, 1988; Burger, 2002, pers. comm.). Furthermore, impala diets were not different between the regions. The possibility that other ^{13}C-enriched dietary items, apart from grasses, form a significant component of the diets of Waterberg baboons must therefore be considered. Given the data obtained from plants, and the observations of baboons feeding on *Euphorbia ingens* in Welgevonden, faecal δ^{13}C trends likely reflect higher utilization of succulents and fruits by baboons living in the Waterberg.

Faecal δ^{15}N values were generally more positive than values from plants, but there was considerable overlap, and thus caution is taken here when interpreting these results as a function of trophic level (Fig. 5.11c). The highest values were observed in mixed-feeding impala from both areas. Browsers were more enriched in ^{15}N than grazers in the Waterberg, but not in Kruger Park. Trees and grasses from these two areas did not differ consistently in mean δ^{15}N values, and thus the difference in faecal δ^{15}N values between browsers and grazers in the Waterberg cannot be ascribed to general trends in local vegetation.

Baboon faecal δ^{15}N values were lower than other mammal species from the Waterberg, and were similar to browser and grazer values from Kruger Park, further extending the argument against using δ^{15}N in faeces as a trophic level indicator (Fig. 5.11c) (but see Kelly, 2000; and Chapter 6). Between the reserves, faecal δ^{15}N values did not differ for any of the dietary sub-groups, but baboons exhibited significantly lower ($p<0.000001$) values in the Waterberg than in Kruger. The low faecal δ^{15}N values in baboon faeces do not necessarily contradict the suggestion that ^{13}C-enriched faeces reflect utilization of ^{13}C- and ^{15}N-enriched succulents, as preferential retention of ^{15}N may occur during digestion (e.g. Ambrose, 1991). It is also possible that the low δ^{15}N values observed in baboon faeces is due to utilization of ^{15}N-depleted geophyte corms and tubers, but insufficient samples of this type of plant material were available to determine whether δ^{15}N values are *consistently* low for geophytes.

Crude protein in faeces was higher in browsers than in grazers, while impala faeces had faecal nitrogen levels intermediate between these groups (Fig. 5.11d). Baboon faeces had a crude protein content similar to that of browsers, although in the Waterberg baboon faeces contained more protein than even the browsing species. In all groups (grazers, browsers, impala, and baboons) faecal protein levels were significantly higher ($p<0.0001$) in Kruger Park than in the Waterberg, even though plants did not differ significantly in %N between these regions.

The higher protein found in Kruger mammal faeces may reflect heterogeneity in Kruger plants, allowing for selection of higher quality foods, whereas the relatively homogenous vegetation of the Waterberg does not provide animals with this option. Alternatively, Kruger plants may be richer in digestion inhibitors such as condensed tannins, and even lignin, which would lead to precipitation of ingested proteins that contribute to raised faecal protein levels.

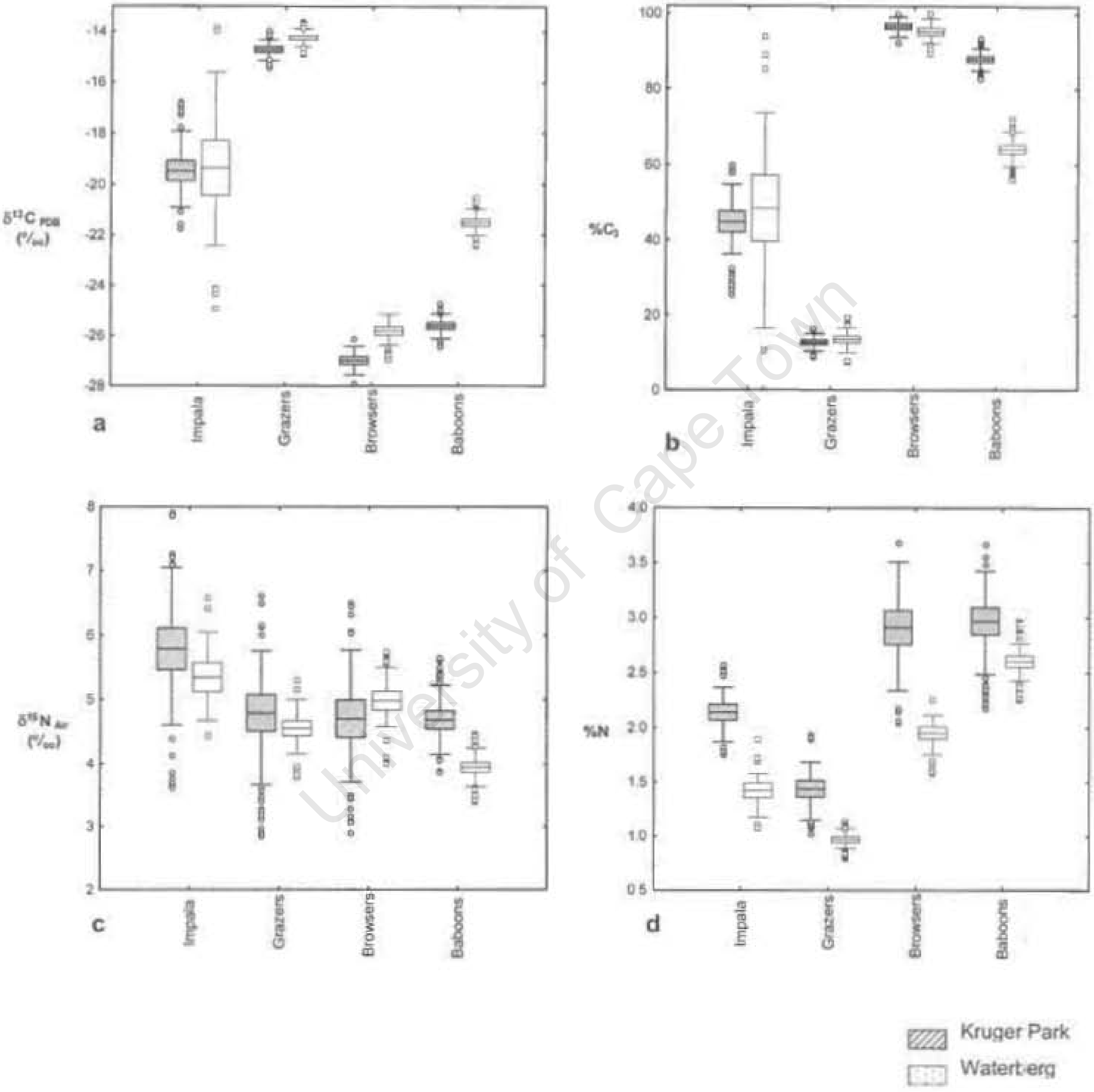


Figure 5.11 – Box plots with means, standard deviations, and outliers, comparing data of mammal faeces from the Waterberg with the Kruger Park.

5.2.2. Seasonality in the Waterberg

The $\delta^{13}C$ values of faeces from grazers and browsers, respectively, indicated no detectable dietary changes between September and January in the Waterberg (Fig. 5.12a & b; Table 5.2). Mixed-feeding impala consumed significantly more grass ($p<0.02$) in January than in September, in some cases faeces having $\delta^{13}C$ values as high as –14‰, reflecting a ~100% grass-based diet (Fig. 5.12a).

Baboon diets did not change significantly, in terms of the ratio of C_3- to C_4-based foods consumed, between these months. At first glance, there appears to be seasonal dietary variation in baboons (Fig. 5.12b). However, the estimated percentage C_3 intake is influenced by the seasonal change of ~3‰ observed in grasses. As discussed above, it appears that grasses do not contribute significantly to the Waterberg baboon diets. Therefore the apparent dietary shift shown in Fig 5.12b is simply a representation of the problem associated with using $\delta^{13}C$ "end-member" values to calculate an absolute percentage dietary C_3 (see Chapter 4).

Faecal $\delta^{15}N$ values exhibited minimal seasonal changes, except for the higher values observed in grazer faeces from January as compared to September (Fig. 5.12c; Table 5.2), which mirrors the seasonal change in grass $\delta^{15}N$ values. The overall lack of seasonal variability in faecal isotopic data can possibly be attributed to the lack of rain in the Waterberg between September 2002 and January 2003, thereby suppressing normal fluctuations in the availability of high quality foods. Nevertheless, grazers, browsers, and mixed feeders all appeared to consume higher quality diets in January than in September, as observed from crude protein content of faeces (Fig. 5.12d; Table 5.2). In contrast, baboon faeces exhibited a small but significant ($p<0.005$) decrease in faecal nitrogen from September to January.

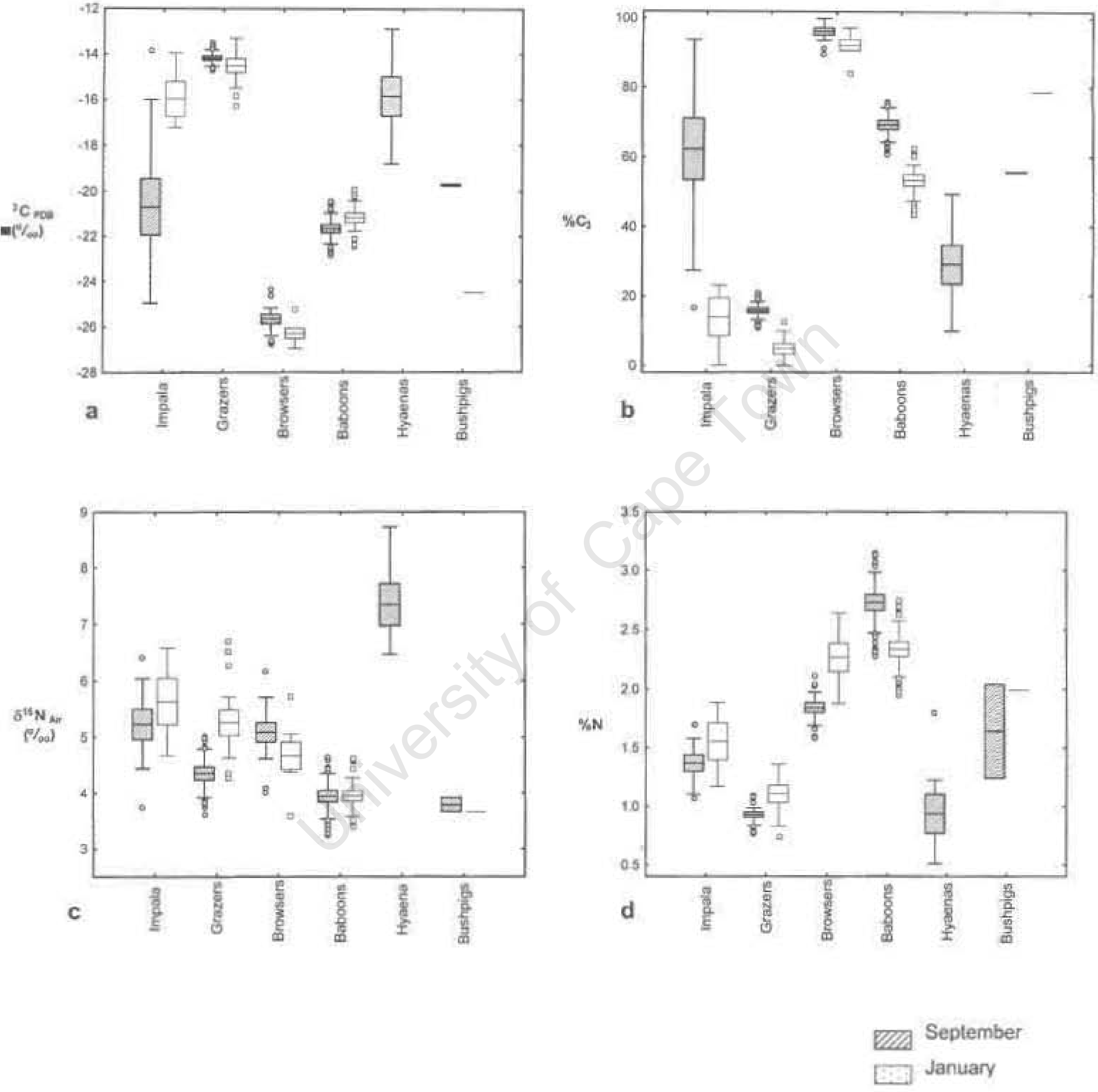


Figure 5.12 – Box plots with means, standard deviations, and outliers, showing interspecific and seasonal ecological variation of mammals in the Waterberg from faecal analysis.

5.2.3. The Waterberg Baboons

The complex combination of dietary items consumed by different baboon groups in the Waterberg is clearly reflected by the results displayed in Fig. 5.13. Faecal $\delta^{13}C$ values averaged around −21 ‰ (Table 5.4). While these values reflect a C_3-dominated diet, these are relatively ^{13}C-enriched given that they were collected primarily from sleep sites enclosed by dense riparian vegetation. Clearly, faecal $\delta^{13}C$ values reflect the utilization of a significant proportion of ^{13}C-enriched items. Such items might include succulents, fruits, and some grasses in and around these habitats. Insects may also form a part of the Waterberg baboon diets, but no analysis were performed on this material to provide support for insectivory. In any event, the Waterberg comprises a relatively low abundance of insects, especially during the drier months (Burger, 2003, pers. comm.).

Although faeces displayed a wide range of $\delta^{13}C$ values, baboon faeces indicated few spatial and seasonal dietary differences throughout the Waterberg, with two notable exceptions: Nalana and Zoetfontein.

The highest faecal $\delta^{13}C$ values for baboons were observed at Nalana (mean = -18.4 ± 2.0 ‰, $n = 6$), where faeces were collected around a CAM photosynthesizing *Euphorbia ingens* tree on which baboons had been observed feeding (Fig. 5.13a & Table 5.4). This observation provides support for the suggestion that succulents, rather than grasses, are an important dietary item in the Waterberg.

The baboons of Zoetfontein had diets significantly more depleted ($p<0.003$) in ^{13}C than the Welgevonden baboons (Fig. 5.13a). This is a further instance for the low importance of grasses for Waterberg baboon diets. It is evident that the Zoetfontein baboons do not supplement their diets with a significant amount of succulent plants, but prefer C_3-based resources. One possibility that must be considered for Zoetfontein is that these baboons commonly utilize agricultural C_3-plants, such as mangos, on farms neighbouring Zoetfontein, a resource that is not available to the Welgevonden population.

$\delta^{15}N$ values of baboon faeces did not display any obviously consistent patterns, and could not be correlated to dietary selectivity ($\delta^{13}C$ values), or dietary quality (%N) (Fig. 5.13c). Some of the highest values were obtained from faeces from Nalana, in keeping with the observation that succulent plants were ^{15}N-enriched, but faeces from the plateau (Motswedi) were as ^{15}N-enriched as Nalana faeces.

It appears that faecal $\delta^{15}N$ values do in some ways reflect feeding at different trophic levels. Brown hyaena (*Hyaena brunnea*) faeces are consistently 2 to 4‰ more enriched in ^{15}N than herbivores (Fig. 5.12c). Bushpigs and baboons both had low faecal $\delta^{15}N$ values. Both of these animals are omnivorous and it is possible that low $\delta^{15}N$ values in their faeces reflect omnivory. Kelly (2000) found that, amongst terrestrial mammals, omnivores had $\delta^{15}N$ values intermediate between those of herbivores and carnivores. Alternatively, bushpigs and baboons commonly utilize underground storage organs, and it is possible that low $\delta^{15}N$ values in their faeces reflect this behaviour, given the extremely low $\delta^{15}N$ value observed in the single geophyte tuber from this area.

The Motswedi faeces exhibited high variability in %N values (mean = 2.8 ± 1.0%; Fig. 5.13d), even though sample size from this locality was small ($n = 5$). Baboons from Zoetfontein appeared to have higher quality diets than those from Welgevonden, but the difference is not significant ($p>0.05$). Notably, faeces from Bushman's Painting had the highest concentration of protein of all sleep sites in Welgevonden, and baboons from this area also had slightly higher faecal $\delta^{13}C$ values in September (Figs. 5.13a & d; Table 5.4). Thus, within Welgevonden, high dietary quality might be correlated with a greater intake of ^{13}C-enriched foods. The opposite pattern is observed for the Waterberg as a whole if Zoetfontein is included in the analysis.

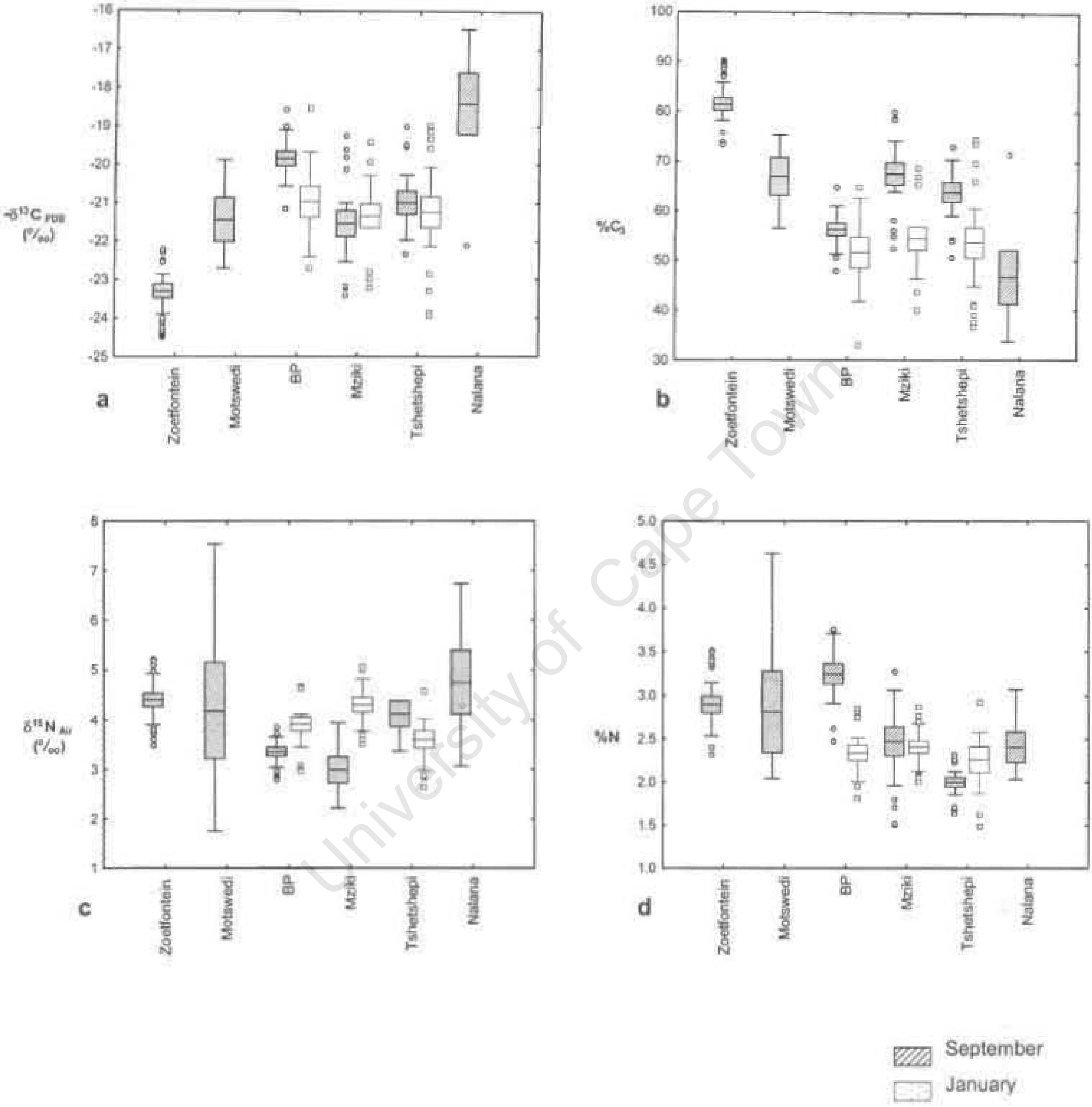


Figure 5.13 – Box plots with means, standard deviations, and outliers, showing seasonal ecological variation in baboons from various microhabitats in the Waterberg from faecal analysis.

Table 5.4. $\delta^{13}C$, $\%C_3$, and %N of baboon faeces showing spatial and temporal differences in dietary habits

				$\delta^{13}C$		$\%C_3$		%N	
Reserve	**Collection Site**	**Month**	***n***	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Kruger Park	L Sabie Bridge	June	5	-24.1	0.7	78.0	4.8	2.8	0.3
		Jan	10	-25.5	0.6	87.0	4.5	3.9	1.3
	Sabie-Skukuza	June	30	-25.4	0.7	87.3	5.0	2.5	0.6
		Jan	12	-26.2	0.5	92.1	3.4	3.3	1.0
	Salitje River	June	6	-25.0	0.7	84.3	4.9	3.0	0.7
	Stolsnek	June	9	-24.6	0.5	81.9	3.7	2.6	0.9
	Steve Hamilton	Jan	14	-27.0	1.6	95.8	10.5	3.3	1.8
Kruger Park Average		**June**	**50**	**-25.1**	**0.8**	**85.0**	**5.6**	**2.6**	**0.6**
		Jan	**36**	**-26.3**	**1.2**	**92.1**	**7.9**	**3.5**	**1.4**
Welgevonden	Bushman's Painting	Sept	25	-19.8	0.9	56.3	6.3	3.2	0.6
		Jan	20	-21.0	1.8	51.7	13.8	2.3	0.4
	Mziki	Sept	20	-21.5	1.5	67.6	10.2	2.5	0.7
		Jan	20	-21.3	1.4	54.5	10.5	2.4	0.3
	Tshetshepi	Sept	20	-21.0	1.4	63.9	9.1	2.0	0.2
		Jan	19	-21.2	1.8	53.7	13.4	2.3	0.7
	Motswedi	Sept	5	-21.4	1.3	67.0	8.6	2.8	1.0
	Nalana	Sept	6	-18.4	2.0	46.7	13.2	2.4	0.4
Zoetfontein	Zoetfontein	Sept	50	-23.3	1.2	81.5	9.2	2.9	0.7
Waterberg Average		**Sept**	**126**	**-21.7**	**2.0**	**69.3**	**14.2**	**2.7**	**0.7**
		Jan	**59**	**-21.2**	**1.6**	**53.3**	**12.5**	**2.3**	**0.5**

5.2.4. Seasonality in the Kruger Park

As was the case in the Waterberg, Kruger Park grazers and browsers exhibited little or no seasonal changes in faecal $\delta^{13}C$ values (Fig. 5.14a & b; Table 5.3). Mixed-feeding impala also displayed no significant seasonal dietary fluctuations. It is surprising that impala diets did not vary seasonally, as these animals have been reported to display radically dietary shifts from season to season (Meissner *et al.*, 1996; Smith, 2003, unpublished data).

Baboon diets shifted from an average calculated 85% utilization of C_3-based foods in June to more than 90% C_3-feeding in January (Fig. 5.14b; Table 5.4). Grass $\delta^{13}C$ values did not change seasonally in Kruger Park by as much as in the Waterberg, and thus monthly differences in faecal $\delta^{13}C$ values are considered to reflect true dietary variations. The significantly lower ($p<0.0003$) utilization of C_4-based resources by baboons in January is not surprising, since the period between June 2002 and January 2003 was particularly dry. It could be expected that after heavy rains there would be an increase in the availability of palatable grasses in Kruger Park. It is possible, but not testable using these data, that baboons may only increase their intake of grasses in this area during higher rainfall periods.

Patterns of variation in $\delta^{15}N$ values of grazer, browser, and impala faeces (Fig. 5.14c; Table 5.3) were similar to those observed in the Waterberg. Trophic level feeding differences were evident in faecal $\delta^{15}N$ values in Kruger Park, in that lions (*Panthera leo*) had faeces roughly 3 to 5‰ more enriched in ^{15}N than herbivores (Fig. 5.14c). Baboons had low faecal $\delta^{15}N$ values, although these were not the most ^{15}N-depleted amongst Kruger Park mammals. This observation again confounds separation of trophic level feeding by $\delta^{15}N$ analysis, at least for omnivores.

In June, browsing species and impala had faeces with higher $\delta^{15}N$ values than did grazers, whereas in January, browser faeces were the most ^{15}N-depleted. Only the change in grazer $\delta^{15}N$ values is significant ($p<0.0002$), which follows the seasonal trend observed in Kruger Park grass $\delta^{15}N$ values. Baboon faeces were as depleted in ^{15}N as were grazer faeces in June, but were significantly more enriched in January ($p<0.0001$). Baboons and grazers in Kruger Park, therefore, exhibited the same seasonal pattern in faecal $\delta^{15}N$ values, even though baboon faecal $\delta^{13}C$ values indicated very little utilization of grass in this area.

Kruger Park mammals had faeces showing similar trends in crude protein content as did Waterberg mammals. Baboons and browsers had the highest faecal protein levels, followed by impala, while grazer faeces had low protein concentrations (Fig. 5.14d; Table 5.3). Except for browsers, in which faecal protein decreased between June and January, Kruger mammal faeces showed a higher crude protein content in January as compared to June. This pattern corresponds to seasonal changes observed in faecal $\delta^{15}N$ values of these animals (Fig. 5.14c).

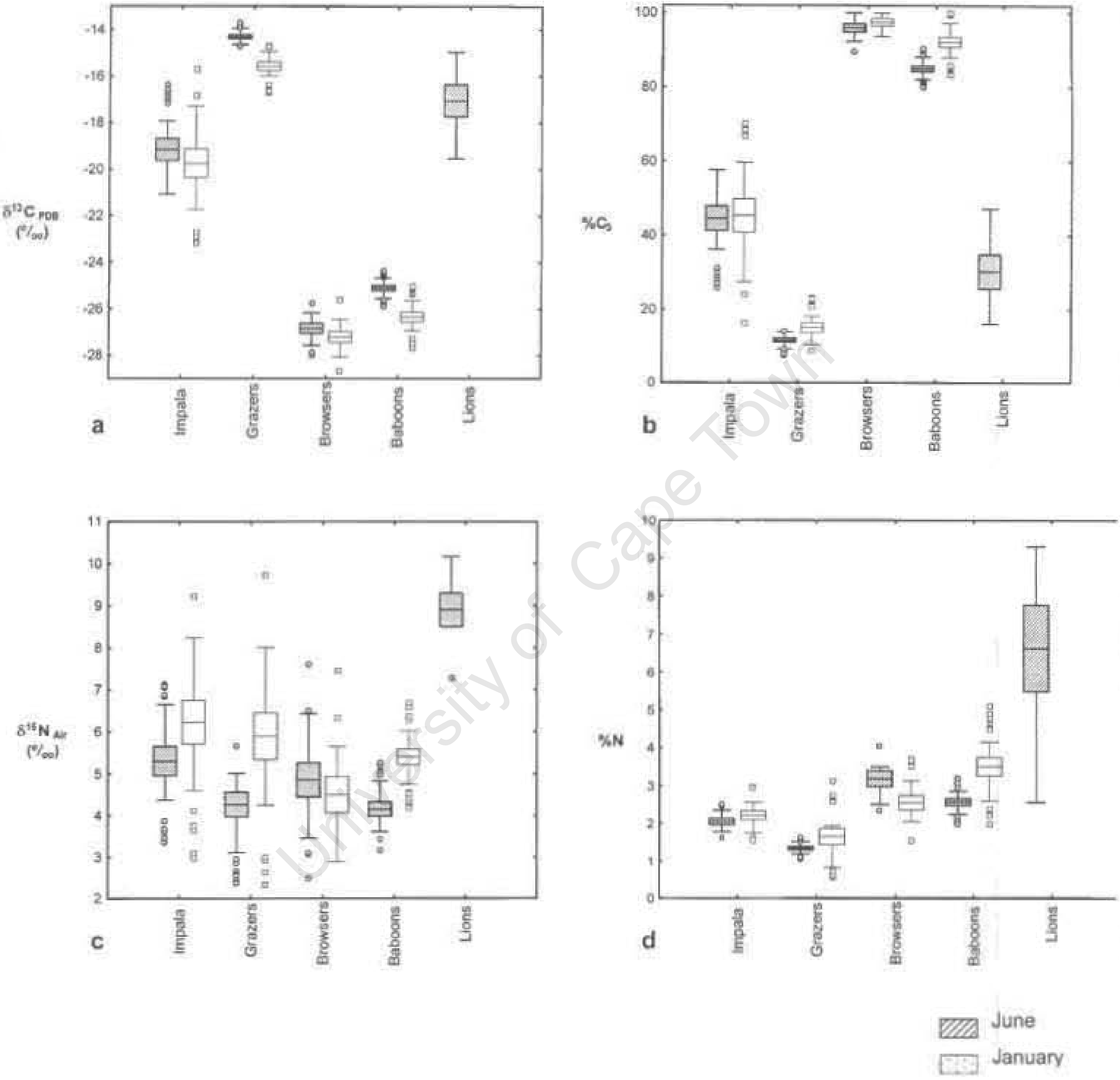


Figure 5.14 – Box plots with means, standard deviations, and outliers, showing interspecific and seasonal ecological variation of mammals in the Kruger Park from faecal analysis.

5.2.5. The Kruger Park Baboons

The Kruger Park baboon faeces displayed a lower range of $\delta^{13}C$ values than those of the Waterberg, which is surprising given the variety of microhabitats that exist in Kruger. Baboons showed a significant seasonal shift to lower $\delta^{13}C$ values in January ($p<0.0003$; see 5.2.4 above). Faeces from Stevenson Hamilton had mean $\delta^{13}C$ values that were significantly lower ($p<0.0001$) from other collection sites, but further significant dietary differences between areas were not observed (Fig. 5.15a & b; Table 5.4). The lack of intra-habitat variability observed in baboon faecal $\delta^{13}C$ values indicates that incorporation of human food items did not significantly alter the carbon isotopic composition of their diets.

Faecal $\delta^{15}N$ values of baboons, on the other hand, may have been affected by feeding on human foods. These values were highest in areas (Sabie-Skukuza; Lower Sabie Bridge) where baboons would commonly consume human food items ($p<0.0003$), as well as at Stevenson Hamilton (Fig. 5.15c). Stevenson Hamilton is not situated on an arterial road, but high faecal $\delta^{15}N$ values in this area could indicate that tourist hand-outs are common here. It is suggested that high faecal $\delta^{15}N$ values might be a response to feeding on human dietary items, as these would be highly digestible, increasing excretion of ^{15}N-enriched protein in faeces (see Steele & Daniel, 1978; Sponheimer *et al.*, 2003a).

Crude protein in baboon faeces did not differ between any of the sites sampled, and was not correlated with the patterns observed in mean $\delta^{15}N$ values (Fig. 5.15d; Table 5.4). This shows that Kruger baboons living in areas with lower tourist densities have diets of as high protein content, and hence nutritional quality, as those that regularly consume human food items.

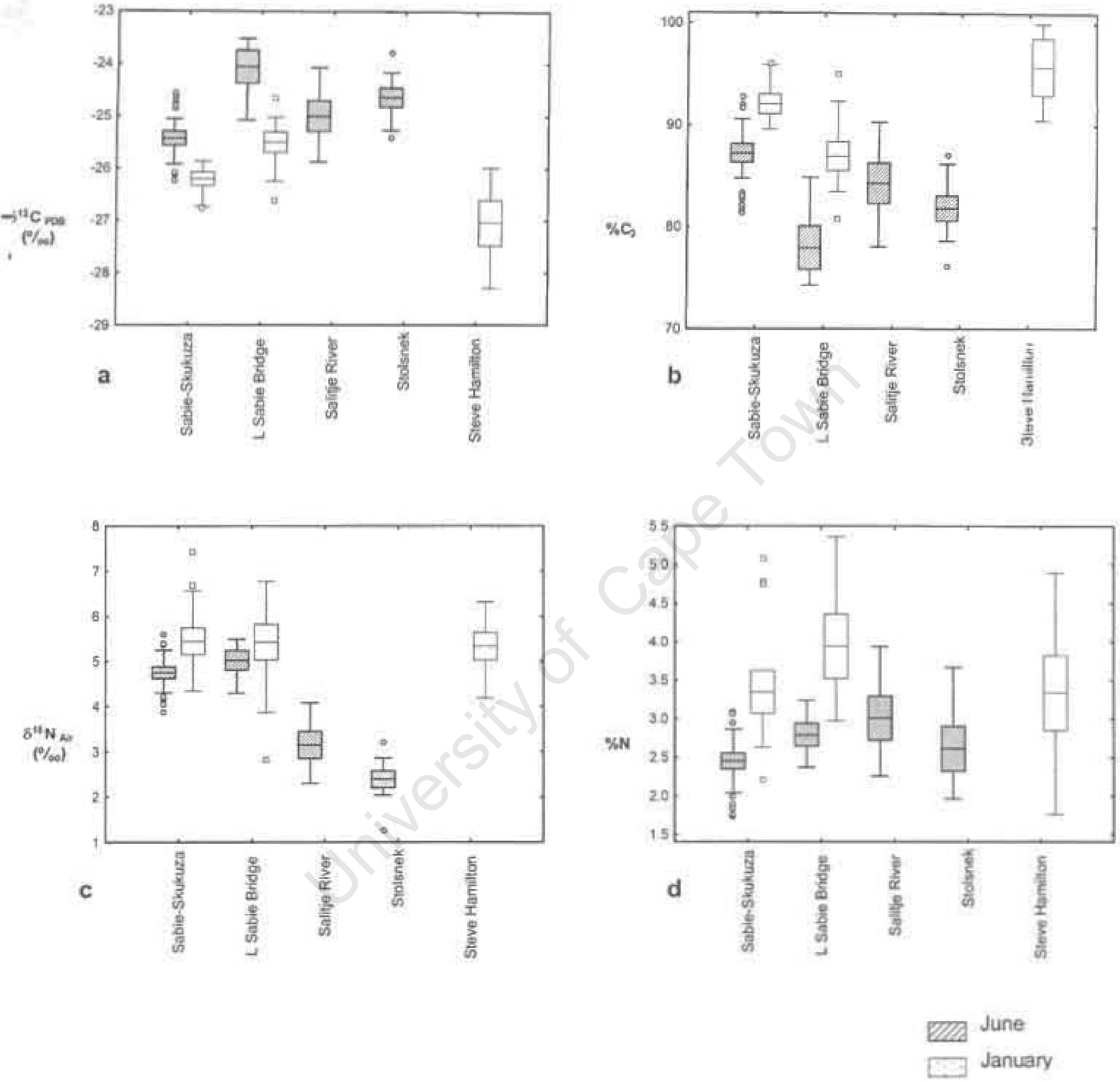


Figure 5.15 – Box plots with means, standard deviations, and outliers, showing seasonal ecological variation in baboons from various microhabitats in the Kruger Park from faecal analysis.

5.2.6. Summary of Results from Faeces

The results obtained from faeces provide the most important insights into baboon feeding ecology for this study, including the following:

- Waterberg baboon faeces were about 4‰ more enriched in ^{13}C, on average, compared to those from Kruger Park
- Baboon faecal $\delta^{13}C$ values exhibited a wide range in the Waterberg, while means did not show any spatial separation in different parts of Kruger Park
- Consumption of *Euphorbia ingens*, and possibly other succulent plants, were reflected by $\delta^{13}C$ values of baboon faeces in the Waterberg
- Percentage nitrogen in baboon faeces was consistently between 2 and 3.5 in all cases
- Seasonal changes in data obtained from baboon faeces were minimal
- Baboon faeces were consistently amongst the lowest in $\delta^{15}N$ for all mammal species

5.3. Serial Analysis of Baboon Hairs

Intra-individual and seasonal dietary variability in baboons was observed in serial isotopic analysis of hair strands (Fig. 5.16 to 5.18). Diet-tissue fractionation of stable carbon isotopes in hair is ~3‰ (e.g. Sponheimer *et al.*, 2003b), thus "end-member" $\delta^{13}C$ values for hair are higher than those for faeces. Variability in $\delta^{13}C$ values, and hence seasonal dietary variability, was greater in the Waterberg than in Kruger Park, but hairs from only one Kruger Park individual were analyzed. Baboon faeces also showed higher $\delta^{13}C$ variability in the Waterberg than in Kruger, thus a similar result obtained from hair analysis is not surprising.

In fig. 5.16 to 5.18, roughly cyclical trends in $\delta^{13}C$ and $\delta^{15}N$ values are evident for most hairs. If baboon hairs grow at a similar rate to macaques, i.e. on average 1cm per month (Inagaki & Nigi, 1988), then every 2cm segment corresponds roughly to two months of growth. Therefore, hairs of 12cm in length represent about one year of growth, and longer hairs reflect dietary shifts over an even longer time period.

$\delta^{13}C$ values tend to show temporal variability in the opposite direction of temporal fluctuations in $\delta^{15}N$ values (especially in UCT# 9789, 9791, 9795, and 9797), but these variables are not consistently correlated ($r^2 = 0.005$ to 0.5353).

Individual Waterberg baboon hair strands showed changes in δ^{13}C values in the order of 3 to 4‰ (Figs. 5.16 & 5.17). From plant δ^{13}C values and the diet-tissue fractionation factor for hair (as discussed in Chapter 4), variability in hair δ^{13}C values correspond to temporal dietary shifts of between 20 and 30% in the amount of C_3-based foods consumed. δ^{13}C values probably underestimate these temporal dietary fluctuations, given the relatively slow attenuation time between the carbon in hair and that of the diet (Jones *et al.*, 1981; Sponheimer *et al.*, 2003b). Hence, individuals in the Waterberg likely had temporal dietary changes greater than 30%. Results from faeces indicate that ^{13}C-enriched items, such as succulent plants, grasses, and fruits, were consumed by baboons in combined amounts fluctuating between ~10 and 50%. Variability in δ^{13}C values of hair indicates greater temporal dietary changes than do faeces, likely due to the fact that only two seasons' worth of faeces were obtained, and because of low rainfall during the study period.

δ^{15}N values in baboon hairs from the Waterberg exhibited fluctuations of between 2 and 3‰ (Fig. 5.16). δ^{15}N patterns along hair strands may reflect climatic changes throughout the seasonal cycle, but the poor correlation between δ^{13}C and δ^{15}N creates uncertainty as to which season is reflected by each segment of hair. It is more likely that the pattern observed in δ^{15}N values reflects temporal changes in the quality of diets consumed, but further information on nitrogen isotope fractionation in mammals, particularly primates, is required to test this.

One hair from the Waterberg (UCT# 9790) displayed an abnormally high deviation in δ^{15}N values of 0.4 to 11.6‰ (Fig. 5.17). The two sections of hair that exhibited this result were adjacent to each other, and both had C/N ratios within the normal range for proteins (see Appendix III). Thus, the results cannot be attributed to analytical error. The sharp increase in δ^{15}N, followed immediately by a radical decline, likely reflects a single event during the individual's life. These extremely variant δ^{15}N values may indicate dietary stress (e.g. Schoeninger *et al.*, 1999). On present evidence, this interpretation is not testable.

Three hairs from a single Kruger Park individual were analyzed (Fig. 5.18). All of these had δ^{13}C values ranging from roughly −19 to -21‰, indicating a similar level of reliance on C_3-based foods as observed in faeces from Kruger Park. δ^{15}N values along these hair strands were relatively static, with only one section from one strand ("Hair A") deviating by more than 1‰ from the average value. It is impossible to make generalizations about

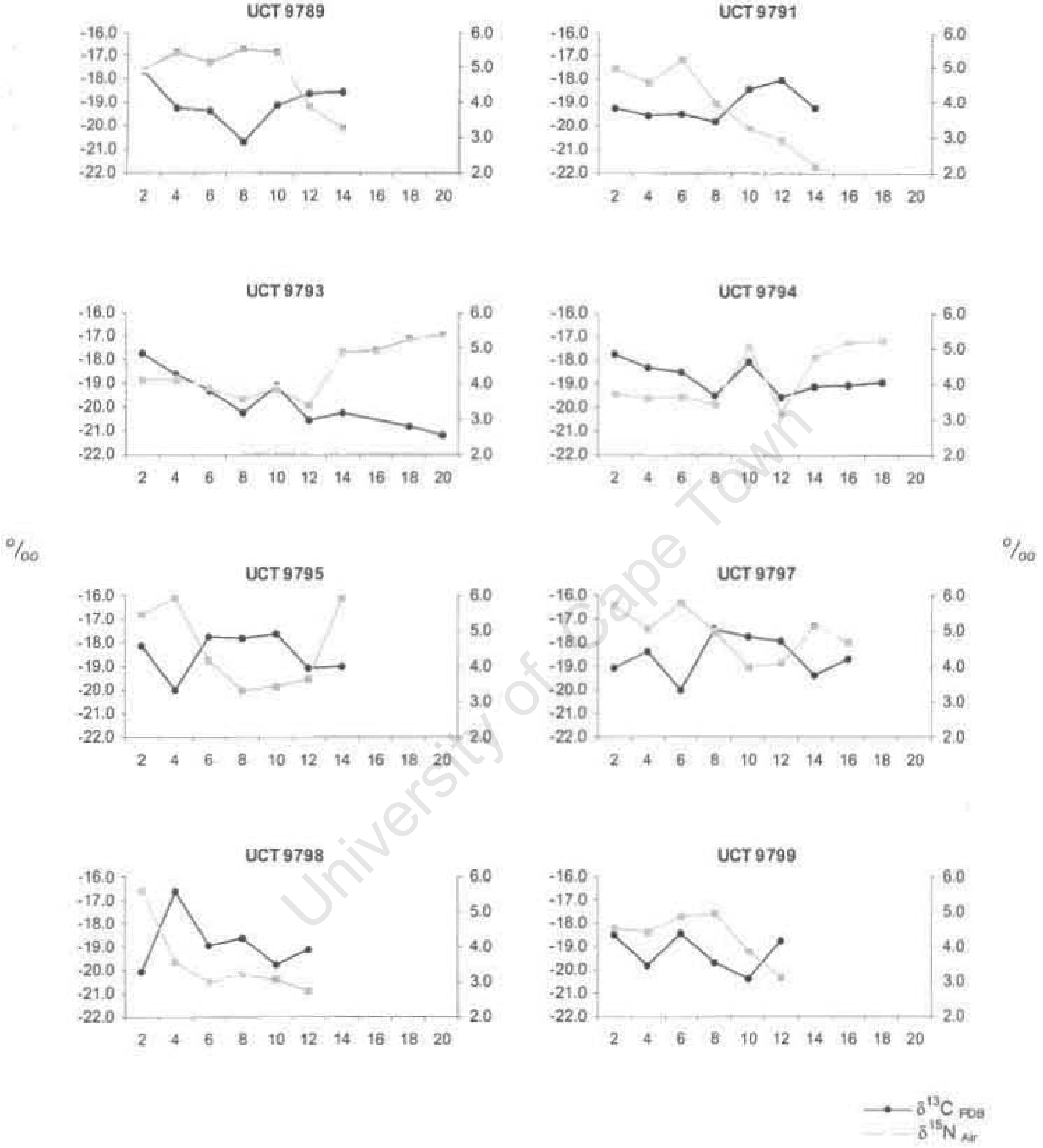


Figure 5.16 – Line graphs of δ^{13}C (left axis) and δ^{15}N (right axis) values obtained from serial analysis of baboon hair strands from the Waterberg, sampled in 2cm increments. The most recent growth is at the hair roots (furthest left on the x-axis of each plot), with the oldest growth at the tip of the hairs (further right along the x-axes).

intra-individual dietary variability for Kruger baboons from such a small sample size. Nevertheless, the results of this analysis indicate that different hairs from the same individual yield compatible results, even though in some cases different life stages may be recorded. This demonstrates the appropriateness of interpreting dietary flexibility from isotopic analysis of baboon hairs from the Waterberg.

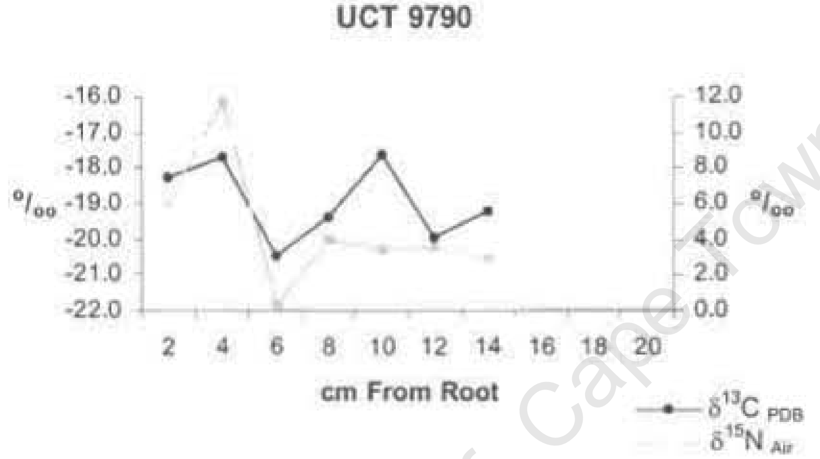


Figure 5.17 – Line graphs of $\delta^{13}C$ (left axis) and $\delta^{15}N$ (right axis) values obtained from serial analysis of a hair strand, sampled in 2cm increments, from a Waterberg baboon displaying an unusually high $\delta^{15}N$ fluctuation. The most recent growth is at the hair root (furthest left on the x-axis), with the oldest growth at the tip of the hair (further right along the x-axis).

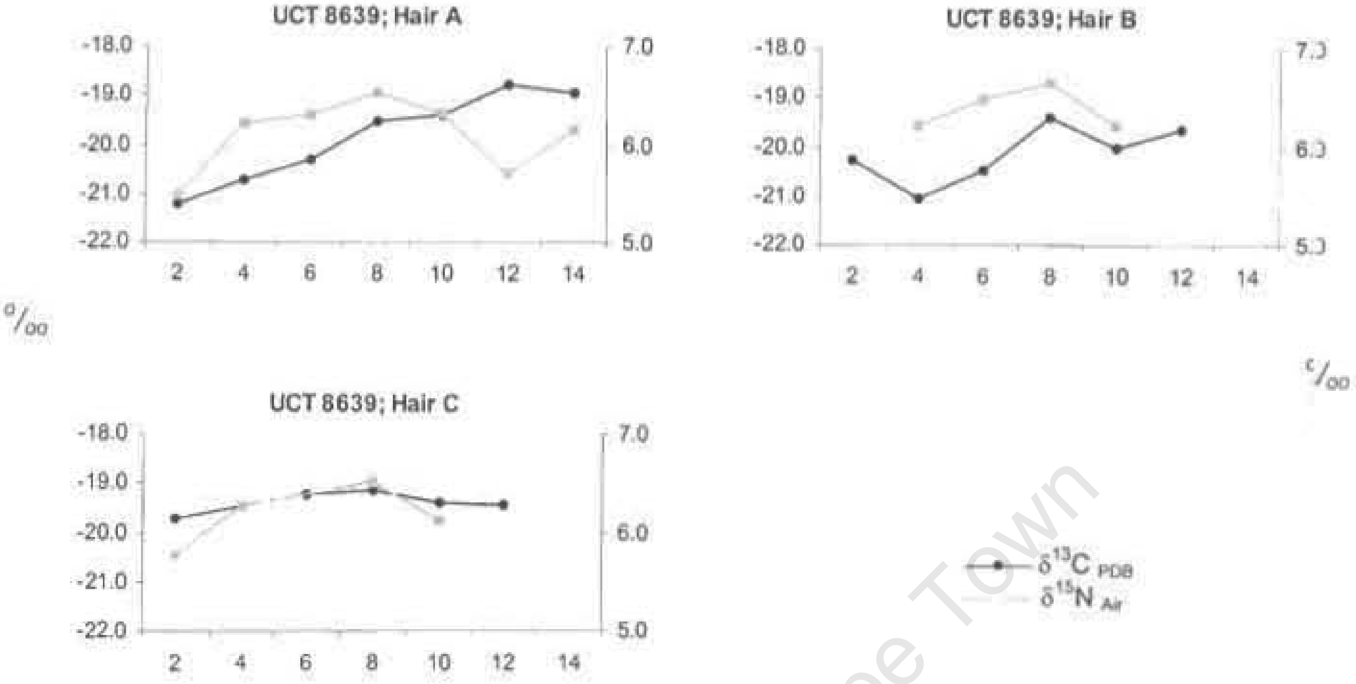


Figure 5.18 – Line graphs of $\delta^{13}C$ (left axis) and $\delta^{15}N$ (right axis) values obtained from serial analysis of 3 baboon hair strands of the same individual from the Kruger Park, sampled in 2cm increments. The most recent growth is at the hair roots (furthest left on the x-axis of each plot), with the oldest growth at the tip of the hairs (further right along the x-axes).

5.4. Bone Collagen, Tooth Dentine Collagen, and Tooth Enamel

5.4.1. Dentine Collagen

Intra-individual variability of $\delta^{13}C$ and $\delta^{15}N$ values in baboon tooth dentine was lower than that observed in hair (Figs. 5.19 to 5.21). End-member $\delta^{13}C$ values for collagen are higher than those for hair, due to the diet-collagen fractionation factor being 4.5 to 5°/oo (e.g. Ambrose & Norr, 1993).

$\delta^{13}C$ values fluctuated by amounts of only 2°/oo within individuals, generally ranging from about –21 to -19°/oo. $\delta^{15}N$ values were relatively high, between 8 and 9°/oo, but seldom varied by more than 1°/oo within an individual. The low isotopic variation is somewhat surprising, since the time period covered by serial analysis of molar tooth rows, in accordance with apposition rates, suggests that several years of ecological information are evinced in the data. One has to consider that the period represented by necessarily crude sampling may be longer than that covered by hair sections. Low variability in dentine serial analyses is thus probably attributable to crude sampling of dentine sections of ~1mm in diameter, creating overlap in the growth lines sampled, thereby decreasing variability of isotopic series.

The cyclical trends observed in hairs are absent from dentine series, owing primarily to the lack of variability in $\delta^{15}N$ values within individual animals. Teeth data do, however, indicate that baboons did change their diets through time. Shifts in $\delta^{13}C$ values from the earliest forming tooth (M1) to the most recently formed tooth (M3) were not in the same direction for all individuals, suggesting that an animal's age does not affect the ratio of C_3 to C_4 items consumed.

It is concluded here that serial analysis of $\delta^{13}C$ in tooth dentine collagen offer some insights into baboon ecological variability, but these results heavily underestimate dietary fluctuations as compared to faeces, and even hair. $\delta^{15}N$ values in tooth dentine are even less variable than are $\delta^{13}C$ values, indicating a slower turnover rate of body pool nitrogen than for carbon. Thus serial analysis of $\delta^{15}N$ in teeth is not at all informative about ecological variability.

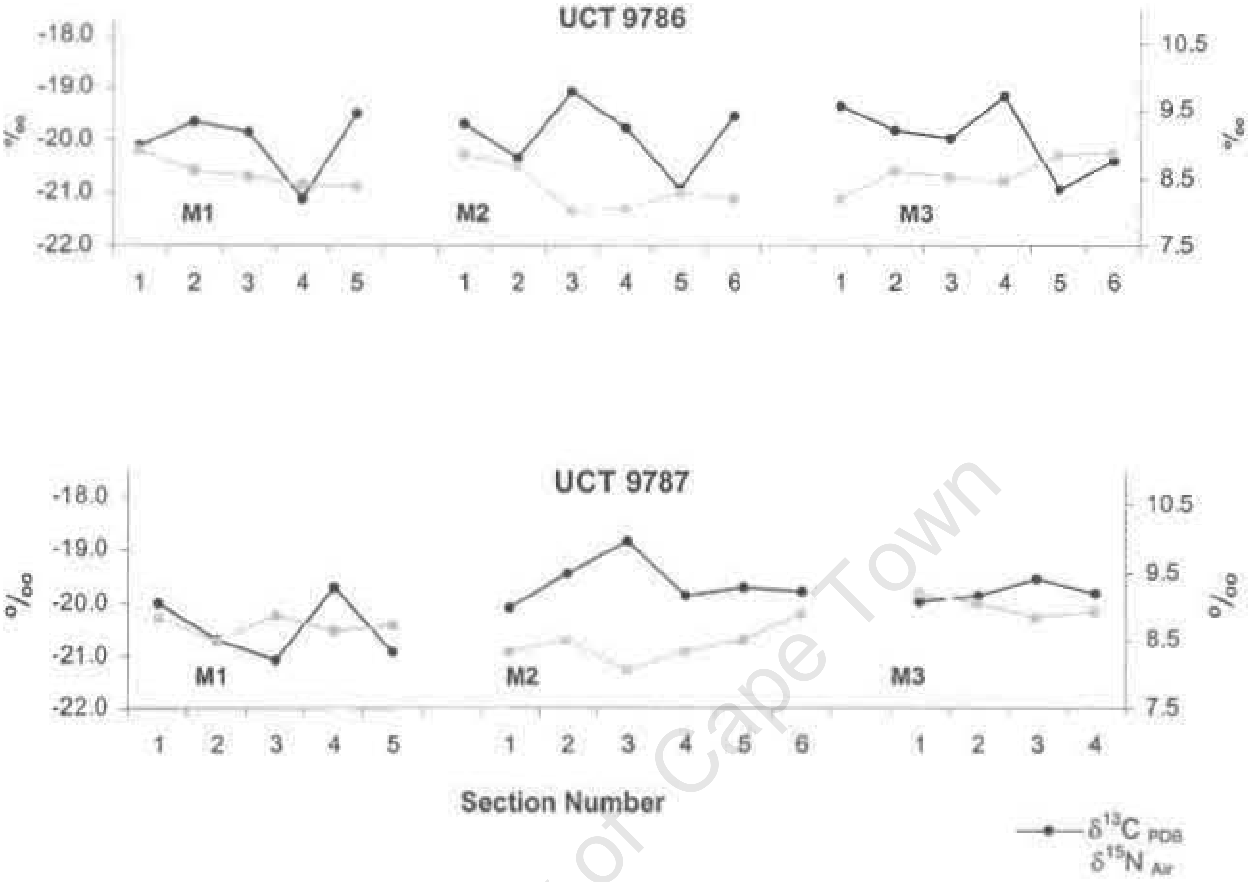


Figure 5.19 – Line graphs showing $\delta^{13}C$ (left axis) and $\delta^{15}N$ (right axis) fluctuations observed in serial analysis of dentine collagen of molar teeth (0.5mm increments, starting immediately below the dentino-enamel junction and progressing towards the root tip) from baboons collected in Zoetfontein that died in 2001.

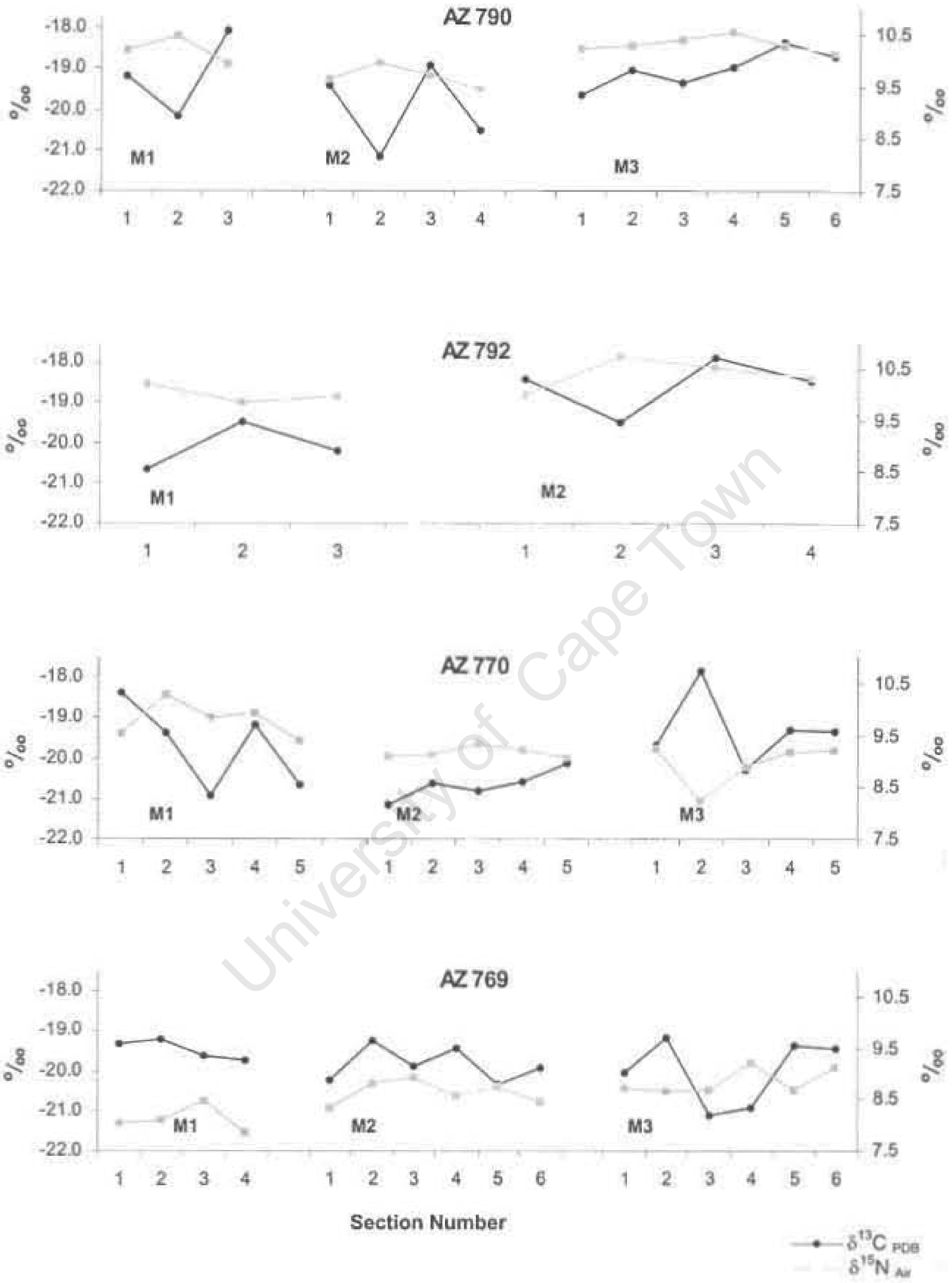


Figure 5.20 – Line graphs showing δ^{13}C (left axis) and δ^{15}N (right axis) fluctuations observed in serial analysis of dentine collagen of molar teeth (0.5mm increments, starting immediately below the dentino-enamel junction and progressing towards the root tip) from baboons collected in Ellisras that died in 1986.

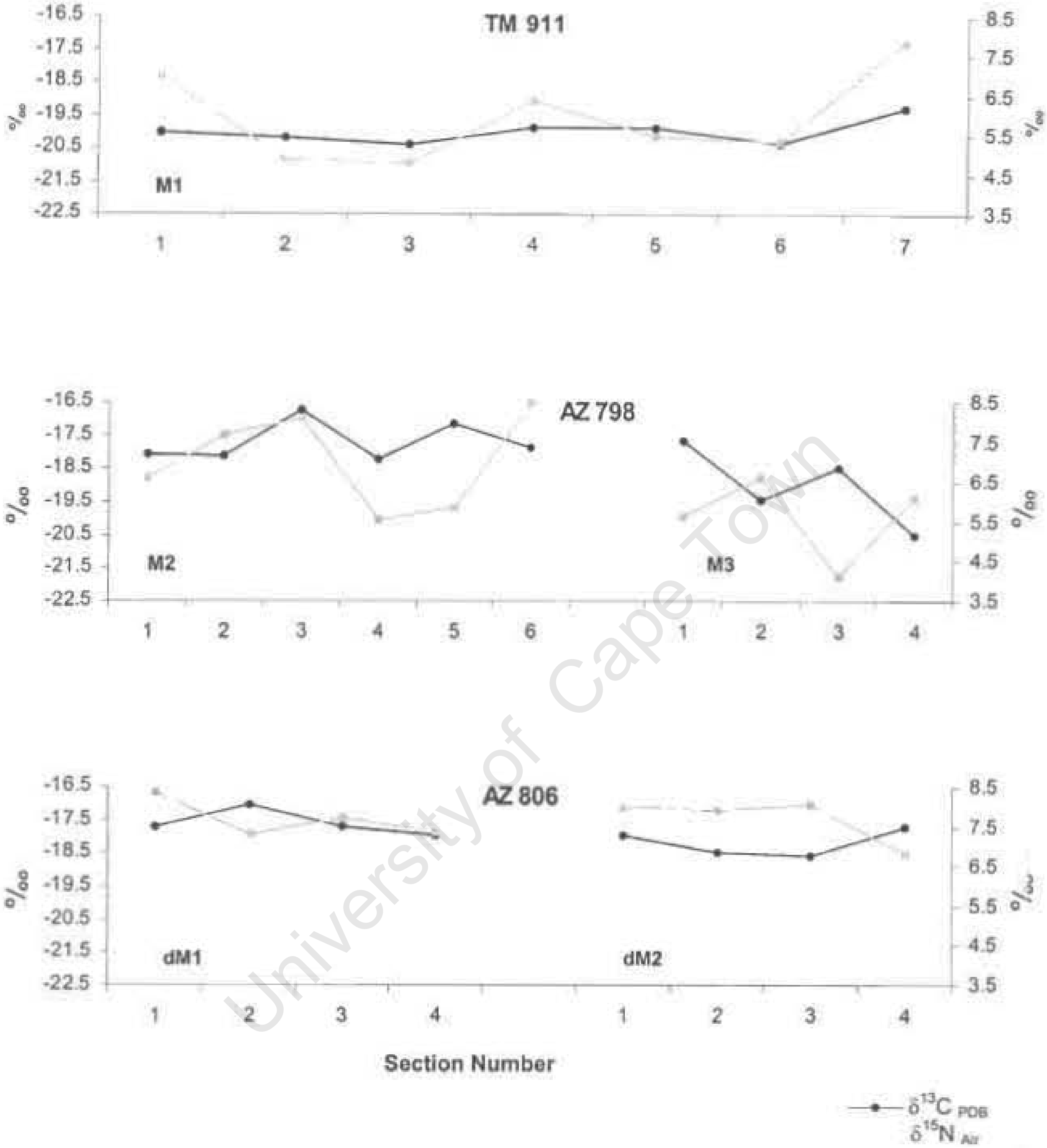


Figure 5.21 – Line graphs showing $\delta^{13}C$ (left axis) and $\delta^{15}N$ (right axis) fluctuations observed in serial analysis of dentine collagen of molar teeth (0.5mm increments, starting immediately below the dentino-enamel junction and progressing towards the root tip) from baboons collected in the lowveld that died in 1986 (death of TM 911 was 1926).

Historical Comparison

A comparison of $\delta^{13}C$ values obtained from different teeth of different individuals revealed information about dietary variability over a relatively long time period. Fig. 5.22 presents results comparing the calculated percentage dietary C_3, as observed in $\delta^{13}C$ values of the various teeth, and whole bone collagen, of individuals from the Waterberg and from Blydepoort, which is situated in a similar lowveld habitat as occurs in Kruger Park.

Bone and dentine collagen from Zoetfontein specimens reflected similar dietary habits as inferred from faecal $\delta^{13}C$ values, being roughly 90% C_3-based. In contrast with results obtained from Kruger Park faeces, the Blydepoort baboons apparently consumed less C_3 (~70 to 85%) than did those from the Waterberg region (Ellisras: ~80 to 100%). Since the museum specimens lived almost two decades ago (and TM 911 lived in the very early 1900's), the most plausible explanation is that baboon diets have changed in response to habitat shifts.

The reclamation of agricultural land for wildlife conservation during the 1990's appears to have provided the Waterberg baboons with the opportunity to feed on savanna-based resources that had previously been deteriorated in the region. As suggested by data from the Blydepoort specimens, the lowveld habitat previously offered a significant proportion of consumable savanna-based resources to baboons. Modern faecal $\delta^{13}C$ values indicate that in Kruger Park, these resources have become depleted, or are largely ignored by the baboons of today. Factors including bush encroachment and increased consumption of human food items may have contributed to the dietary shift in the lowveld habitats.

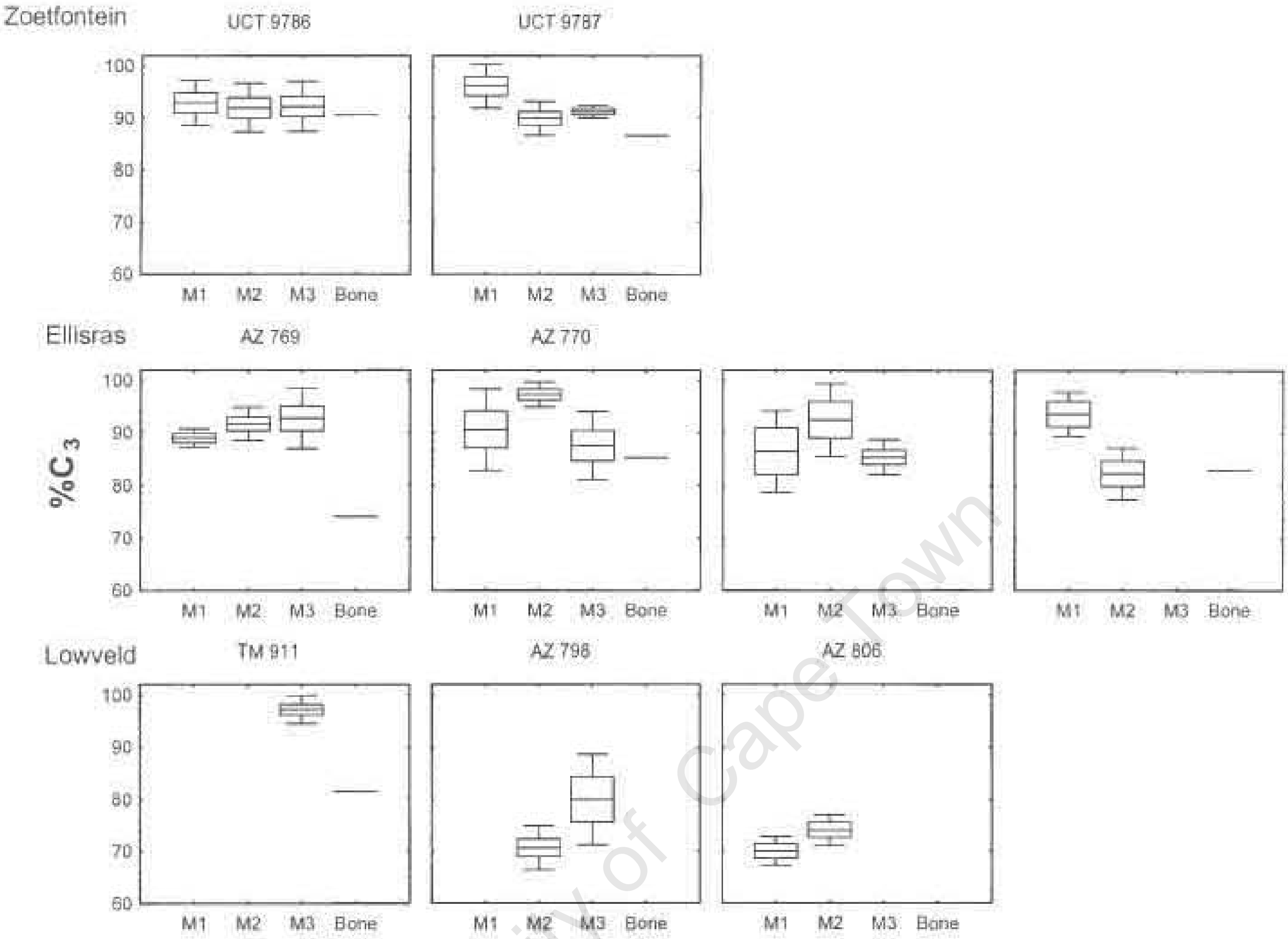


Figure 5.22 – Box plots with means and standard deviations showing fluctuations in the percentage of C_3-based foods in the diets of individual baboons as reflected by $\delta^{13}C$ values of bone collagen and serial sampling of dentine collagen from those individuals from the Lowveld, Ellisras, and Zoetfontein.

5.4.2. Tooth Enamel

Tooth enamel carbonate from all molar teeth available was analyzed for $\delta^{13}C$ and $\delta^{18}O$ values (see Appendix IV), in order to provide a more direct comparison with data from fossil material. The data obtained represents the entire enamel surface of each tooth, as this was necessary to remove sufficient sample for isotopic measurements.

$\delta^{13}C$ and $\delta^{18}O$ values in specimens from the lowveld and from the Waterberg were both randomly distributed, with no spatial or temporal patterns being evident. $\delta^{13}C$ values from tooth enamel carbonate did not display great variability, ranging from ~ -13.5 to –10.0‰. Given the diet-enamel carbonate fractionation factor for $\delta^{13}C$ of ~12.5 to 13‰ (e.g. Lee-Thorp *et al.*, 1989b), these values suggest a diet ranging between ~100 and 80% C_3.

$\delta^{18}O$ values were highly variable, between ~ +3.0 and –3.0‰, being consistent with $\delta^{18}O$ values for other mammal species previously analyzed from Morea Estate, also situated in the Limpopo Province, South Africa (Sponheimer & Lee-Thorp, 2001). No consistent difference was found in $\delta^{18}O$ values between specimens from the Waterberg and those from the lowveld. This is surprising, as the two study areas are approximately 600km apart, from east to west. The result suggests that climatic differences between the two regions do not affect, even indirectly, baboon tissue oxygen isotopes, as would be expected (e.g. Smith, 2003, pers. comm.). No other mammal species' tooth enamel was analyzed, and hence it is impossible to draw conclusions about the effects of such factors as differential water sources and body size on baboon $\delta^{18}O$ values.

Plotting enamel carbonate $\delta^{13}C$ and $\delta^{18}O$ values for different teeth (M1, M2, and M3) of each individual sampled, also revealed no discernible patterns. Nevertheless, these results are directly comparable with results from fossil primate tooth enamel, and are used here to assist with interpretations of ecological behaviour in Pleistocene cercopithecoids.

5.5. Comparison of Results from Different Tissues

Different tissues differed in the type and scale of ecological information each provided. Table 5.5 presents a comparison between $\delta^{13}C$ values and calculated percentage dietary C_3 from each tissue. Because calculations of percentage dietary C_3 incorporated published diet-tissue fractionation factors, this comparison is more appropriately represented in Fig. 5.23, indicating differences in dietary variability as reflected in each type of material.

Table 5.5. Comparison of $\delta^{13}C$ values and dietary variability between baboon tissues

				$\delta^{13}C$				Est. %C_3			
Region	**Tissue**	***n* (Inds)**	***n* (Samples)**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Waterberg	Bone collagen	5	5	-18.8	0.8	-19.7	-17.4	83.9	6.2	74.2	90.7
	Dentine collagen	6	103	-19.8	0.9	-22.9	-17.6	91.3	5.9	75.2	100.0
	Enamel carbonate	6	16	-11.9	0.8	-13.2	-10.3	92.1	5.3	80.6	100.0
	Hair	9	66	-19.0	1.0	-21.2	-16.6	72.8	6.8	56.0	88.3
	Faeces (September)	126	126	-21.7	2.0	-25.4	-16.5	69.3	14.2	33.7	95.6
	Faeces (January)	59	59	-21.2	1.6	-25.2	-17.6	53.3	12.5	25.8	84.2
	Faeces Pooled	185	185	-21.5	1.9	-25.4	-16.5	64.2	15.5	25.8	95.6
Lowveld	Bone collagen	2	2	-18.3	1.3	-19.3	-17.4	75.1	9.0	68.8	81.5
	Dentine collagen	4	36	-19.0	1.2	-22.1	-16.7	78.1	7.8	63.8	100.0
	Enamel carbonate	4	8	-11.7	0.9	-12.9	-10.3	84.3	6.4	74.6	92.7
Kruger Park	Hair	1	18	-19.8	0.7	-21.2	-18.8	75.0	5.0	67.7	84.8
	Faeces (June)	50	50	-25.1	0.8	-27.2	-23.5	85.0	5.6	74.3	99.5
	Faeces (January)	36	36	-26.3	1.2	-28.3	-21.9	92.1	7.9	61.0	100.0
	Faeces Pooled	86	86	-25.6	1.2	-28.3	-21.9	88.0	7.5	61.0	100.0

In both the Waterberg and the Kruger Park, faeces exhibited the greatest degree of dietary variation. This result is not surprising, since faeces represent diet in the order of only a few days. Data from hair in the Waterberg also suggested a reasonable amount of variation in baboon diets through time. Dentine collagen from Kruger Park specimens displayed a similar amount of dietary variability as faeces from the same area. Some of this can be attributed to the extended time scale provided by the specimens from where samples were obtained. Bone collagen and enamel carbonate give no indication of dietary variability across time in baboons. Dentine collagen would probably have yielded a similar result, had specimens been obtained from the same time period. These results demonstrate that skeletal tissues, although providing longer-term dietary averages, underestimate dietary variability, even in serial analysis.

The large number of faecal samples analyzed does not wholly account for the greater variability observed in faecal isotopic values, since a large number of hair and dentine collagen samples were obtained by serial analysis. Greater variability would probably not have been observed in hair, bone, and tooth material, respectively, had the number of individuals sampled been increased, given the attenuation time required for tissue growth to reach equilibrium with an animal's diet. Faeces seem to be the most appropriate material for dietary studies of modern fauna living in wild situations, providing the most accurate reflection of true ecological variability within taxa in any one environment. However, for maximum resolution, these require continuous collection.

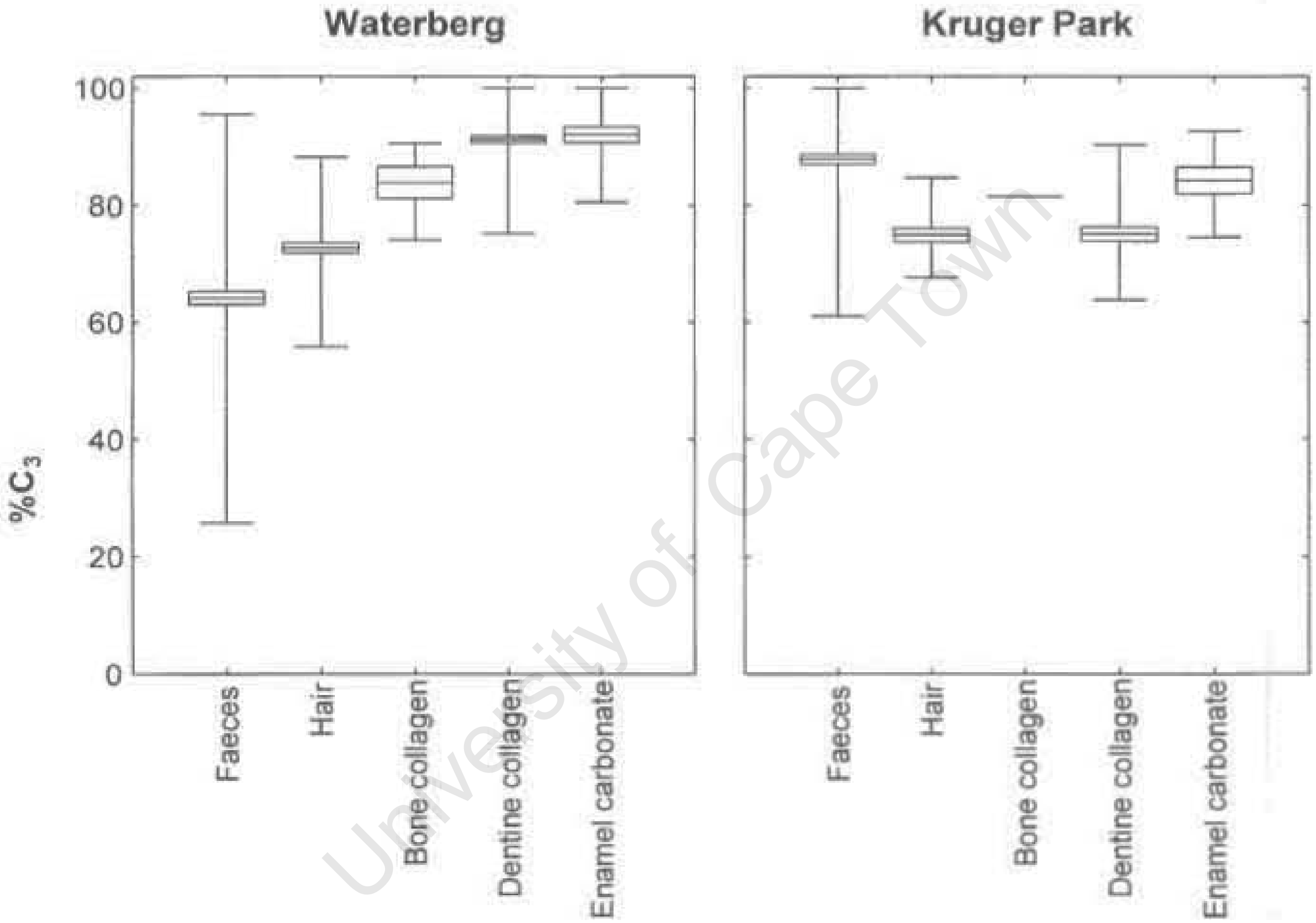


Figure 5.23 – Box plots with means and maximum - minimum bars showing the range of dietary information (%C$_3$) obtained from stable carbon isotope analysis of different baboon tissues

5.6. Cercopithecoids of the South African Pleistocene

A summary of δ^{13}C and δ^{18}O values obtained from fossil primate tooth enamel carbonate is presented in Table 5.6. As discussed in chapter 4, a large number of specimens yielded poor results for δ^{13}C analysis, and more so in their δ^{18}O values, likely due to the presence of glue. An entire list of these results is displayed in Appendix V. Specimens that yielded poor results are omitted from the results in Table 5.6.

Specimens SKX 2800 (identified as *Papio (Dinopithecus) ingens*) and SK 24615 (identified as *Parapapio jonesi*) showed δ^{13}C values more consistent with values expected for *Theropithecus oswaldi* (see Lee-Thorp, 1989a) or *Cercopithecoides williamsi* (see Luyt, 2001). Specimens SKX 2800 and SK 24615 are not included in the following discussion due to the likely taxonomic confusion.

Table 5.6. Mean δ^{13}C and δ^{18}O values for newly sampled fossil primate taxa from Swartkrans Members 1 and 2.

		δ^{13}C			δ^{18}O		
Taxon	**Member**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**
Cercopithecoides williamsi	M1/2	3	-11.2	3.5	2	-2.3	2.2
Theropithecus oswaldi	M1	5	-2.6	1.6	4	-6.4	0.4
Theropithecus oswaldi	M2	1	-1.1	-	-	-	-
Parapapio jonesi	M1/2	4	-8.2	1.4	2	-3.2	0.7
Papio (Dinopithecus) ingens	M1	4	-9.2	1.1	3	-3.5	0.5
Papio robinsoni	M1	4	-7.4	1.0	-	-	-
Papio robinsoni	M2	3	-8.4	1.7	-	-	-

Apart from specimens that yielded poor results, fossil primates exhibited δ^{13}C values within the C_3 and C_4 "end-member" range observed in previously published data for browsers and grazers from Swartkrans (Lee-Thorp *et al.*, 1989a; Lee-Thorp & van der Merwe, 1993). Hence, all primate taxa utilized a mixture of both C_3- and C_4-based resources. None of these taxa had tooth enamel carbonate δ^{13}C values similar to modern baboons, which are more depleted in ^{13}C. Taking into account the depletion of ^{13}C in atmospheric CO_2 during the twentieth century (e.g. Marino & McElroy, 1991), the diet of *C. williamsi* most closely resembles that of modern baboons. However, faecal and hair data of modern baboons suggests greater utilization of ^{13}C-enriched resources than does enamel carbonate, and thus it is more likely that *Papio robinsoni* and at least some members of the genus *Parapapio* had feeding ecologies akin to modern baboons.

Cercopithecoides williamsi (considered to be a colobine monkey, e.g. Delson, 1992) had $\delta^{13}C$ values indicating a ^{13}C-depleted diet, although one specimen had a $\delta^{13}C$ value of $-7.2^{0}/_{00}$, reflecting a high utilization of C_4-based resources by this individual. *Theropithecus oswaldi* from both Members 1 and 2 had $\delta^{13}C$ values indicating a grass-based diet of between roughly 80 and 100% C_4. The remaining fossil baboons had $\delta^{13}C$ values that were taxonomically indistinct, with the ranges overlapping in all cases. *Parapapio jonesi* had similar $\delta^{13}C$ values to *Papio robinsoni* from Member 2. *Papio robinsoni* from Member 1 were slightly more enriched in ^{13}C, but not clearly different from Member 2 specimens. *Papio (Dinopithecus) ingens* had the most depleted mean $\delta^{13}C$ values of all baboon taxa, but again the range of values overlapped with both *Papio robinsoni* and *Parapapio jonesi*.

The most negative $\delta^{18}O$ values were observed in *Theropithecus oswaldi*. This may reflect greater reliance on drinking water by this taxon than other primate species (e.g. Sponheimer & Lee-Thorp, 2001), which would be expected for a predominantly grazing mammal. *Cercopithecoides williamsi* had the highest $\delta^{18}O$ values, while the baboons *Parapapio jonesi* and *Papio robinsoni* had $\delta^{18}O$ values intermediate between that of *T. oswaldi* and *C. williamsi*.

Previously published data for some Pleistocene cercopithecoids from the Sterkfontein Valley (Lee-Thorp *et al*., 1989a; Lee-Thorp & van der Merwe, 1993; Luyt, 2001) are summarized in Table 5.7. $\delta^{18}O$ values for some of these specimens are presented by Lee-Thorp (2002), but these were obtained using earlier, incompatible pretreatment methods and are therefore not included here. Specimens analyzed by Luyt (2001) only include those from Sterkfontein Member 4, since the specimens she analyzed from Member 5 were not identified to genus level.

A similar distribution of $\delta^{13}C$ values in *Cercopithecoides williamsi* is reported by Luyt (2001) as is observed in the current data, with some individuals being far more ^{13}C-enriched than others. Hence, it may be concluded that *C. williamsi* specimens cluster into two dietary groupings: those with a C_4-dominated diet (combined $n = 3$), and those whose diets were heavily C_3-based (combined $n = 5$). This may be due to misidentification of specimens, the presence of more than one species of *Cercopithecoides* in South African

Pleistocene deposits, or sex and age related dietary differences between individuals. The latter seems highly unlikely, however, given the large isotopic difference between the two groups, and the lack of the sex and age distinction in modern *Papio ursinus*.

Table 5.7. Previously published mean $\delta^{13}C$ and $\delta^{18}O$ values for fossil primate taxa from Swartkrans Members 1 and 2 (from Lee-Thorp *et al.*, 1989a and Lee-Thorp & van der Merwe, 1993), and from Sterkfontein Member 4 (from Luyt, 2001).

Taxon	Locality	*n*	Mean	SD	*n*	Mean	SD	Literature Source
Papio robinsoni	Swartkrans	5	-11.2	0.9	-	-	-	Lee-Thorp *et al.*, 1989a
Theropithecus oswaldi	Swartkrans	5	-2.1	2.0	-	-	-	Lee-Thorp *et al.*, 1989a
Papio (Dinopithecus) ingens	Swartkrans	3	-10.6	0.5	-	-	-	Lee-Thorp & van der Merwe, 1993
Parapapio jonesi	Swartkrans	2	-11.2	2.4	-	-	-	Lee-Thorp & van der Merwe, 1994
Cercopithecoides williamsi	Sterkfontein	5	-9.3	4.1	4	0.4	1.9	Luyt (2001)
Parapapio broomi	Sterkfontein	5	-8.1	2.4	3	-1.9	1.4	Luyt (2001)
Parapapio jonesi	Sterkfontein	2	-8.4	1.5	2	-2.1	0.6	Luyt (2001)
Parapapio whitei	Sterkfontein	3	-10.3	2.3	2	-1.1	2.7	Luyt (2001)

Mean $\delta^{13}C$ values for *Theropithecus oswaldi* published in Lee-Thorp *et al.* (1989a) correspond well to values from current specimens. $\delta^{13}C$ values of *Papio robinsoni* appear to form two isotopically distinct groups. Newly analyzed specimens are between 3 and 4‰ enriched in ^{13}C compared to those presented by Lee-Thorp *et al.* (1989a). Difficulties due to differences between earlier pretreatment methods and those followed in the current study can be ruled out here. Luyt (2001) and Van der Merwe *et al.* (2003) showed that the effect of these different pretreatment methods minimally influence $\delta^{13}C$ values. Secondly, the range of $\delta^{13}C$ values in newly analyzed specimens of *T. oswaldi* did not differ consistently with previously reported values, nor did those of other primate taxa. Therefore, it is concluded that analytical error has not played a significant role in observed variability of *P. robinsoni* $\delta^{13}C$ values. If indeed only one species is represented, it appears that *P. robinsoni* had an extremely variable diet, most closely resembling the diet of modern baboons. Caution should be noted here, however, since there is likelihood that misidentification of isolated teeth occurred. In the current study, samples were taken mostly from isolated teeth, whereas at least some specimens reported on by Lee-Thorp *et al.* (1989a) were from maxillary or mandibular fragments.

Lee-Thorp & van der Merwe (1993) presented $\delta^{13}C$ values for *Papio (Dinopithecus) ingens* of less than $-10^{o}/_{oo}$, and suggested that the diet of this baboon was among the most ^{13}C-depleted of all Swartkrans fauna. This is in keeping with the idea that *P. (D.) ingens* was a large, probably folivorous animal. However, the new data clearly indicates that this baboon utilized more savanna-based resources than previously suggested, having $\delta^{13}C$ values greater than that observed in the more ^{13}C-depleted specimens of both *C. williamsi* and *Parapapio* spp.

$\delta^{13}C$ values of some specimens of *Parapapio* spp. reflect a mixed diet, crudely estimated to have been about 50% C_3- and 50% C_4-based (see Appendix V). Others had $\delta^{13}C$ values indicating greater reliance on a C_3-based diet. A similar isotopic split is evident in results for this genus published by Lee-Thorp & van der Merwe (1993) and Luyt (2001). These results suggest that at least two species of *Parapapio* did indeed co-exist in the South African Pleistocene. Difficulties and problems associated with previous species identifications, often based only on isolated teeth, are further illustrated here.

It is also possible that the observed isotopic distinction of the two groups of *Parapapio* may be because specimens are in fact separated by a time scale of several thousand years. Such a time period might involve changes in the landscapes, in turn leading to dietary differences within the genus. At this stage, however, there is very little other evidence to support the presence of a chronocline within specimens of *Parapapio* excavated in the Sterkfontein Valley (Brain, 1981).

A comparison of Table 5.6 and 5.7 indicates that chronological differences in $\delta^{13}C$ values are small, but that primate $\delta^{18}O$ values are somewhat different at Swartkrans Members 1 and 2 compared to the slightly older deposits of Sterkfontein Member 4. *Cercopithecoides williamsi* were more enriched in ^{18}O in Sterkfontein than Swartkrans, as were specimens of *Parapapio* spp. These observations likely reflect climatic differences between these habitats during different stages of the Pleistocene. Previously, isotopic data has been used to suggest habitat differences between Sterkfontein Members 4 and 5 (Luyt, 2001).

CHAPTER 6

DISCUSSION

This chapter presents an interpretation of modern baboon and extinct cercopithecoid feeding ecology as indicated by results described in chapter 5. The first section deals with the primary focus of this dissertation, presenting an interpretation of variability in dietary ecology of modern baboons. This includes a discussion of differences in the type of food items that baboons consumed in the study areas, the extent of dietary variability observed, and the degree to which diet selectivity plays a role in baboon foraging. Interpretation of faecal $\delta^{15}N$ values is not clear, and these results are discussed separately.

In the second section, the dietary behaviour, as reflected by isotopic data, of South African Pleistocene cercopithecoid taxa is discussed. The chapter also presents a possible model by which early hominid behavioural ecology can be compared against the dietary ecology of modern and fossil baboons.

The conclusion includes an overview of the scope and findings of this project.

6.1. Inter- and Intra-habitat Ecological Variability of Modern Baboons

6.1.1. Resource Utilization

Baboon diets in the Waterberg differ from those in Kruger Park, with those in the Waterberg consuming a greater proportion (~30 to 50%) of ^{13}C-enriched food items. In Kruger Park, ^{13}C-enriched foods, such as grasses, accounted for only 10 to 20% of baboon diets. Nevertheless, inter- and intra-habitat patterns in faecal percentage nitrogen (crude protein content) show that baboons obtain diets of equally high quality in both of these areas (between 2 and 3.5%). These results indicate that baboons are adaptive feeders, changing their diet to suit their immediate environment, but they are selective in that they consistently maintain a high level of dietary quality. It has previously been reported that baboons are well equipped to adapt their feeding behaviour in order to obtain maximum nutritional benefit from their immediate environment (Norton *et al.*, 1987). The absence of dietary differences in other mammal species between the two study areas further illustrates the flexibility of baboons in comparison to other species.

If one considers that resource availability is believed to place fundamental constraints on baboon feeding behaviour (Barton & Whiten, 1994), then the 4‰ enrichment of ^{13}C in baboon diets in the Waterberg as compared to Kruger Park is well within expectations. Baboons in the Waterberg had diets that were more enriched in ^{13}C than those in Kruger Park. At first glance, it might appear that the Waterberg baboons rely heavily on C_4 grasses. A strongly graminivorous diet in *Papio* spp. has previously been reported for baboons living in East African grasslands (DeVore & Hall, 1965). However, the only habitat included in the current study that would offer a comparably high abundance of palatable grass species, as found in East Africa, is the basaltic plains in the eastern parts of Kruger Park, such as at Lower Sabie and the Salitje River. In none of these areas, however, did baboons select for a grass-rich diet. In the Waterberg, where fewer palatable grasses are available, one has to consider that the ^{13}C-enriched portion of baboon diets constitutes several items other than grasses.

One explanation is that baboons in the Waterberg are dependant on fruits as a dietary resource to a greater extent than are those living in Kruger Park. This suggestion is based on the observation that fruits are 2 to 3‰ more enriched in ^{13}C compared to other plant parts. Fruiting trees and forbs are just as available in Kruger Park as in the Waterberg, so if this is the case, then a high degree of dietary selectivity is evident. Norton *et al.* (1987) reported that baboons living in less variable environments displayed highly selective feeding routines. Fruits may account for some of the ^{13}C-enriched portion of baboon diets in the Waterberg, but these are not sufficient to explain the basic Waterberg/Kruger difference.

Earlier studies have shown that *Euphorbia ingens* can be an important dietary item to baboons (Lock, 1972; Barton *et al.*, 1993). Baboons are also well known to consume plants that are toxic to humans (Hamilton III *et al.*, 1978; Hamilton III, 1985). Waterberg CAM plants all had $\delta^{13}C$ values indistinguishable from that of C_4 grasses. In Welgevonden, baboons were observed to feed on *E. ingens*, and faecal samples from around this feeding site displayed a significantly ^{13}C-enriched signal. Taken together, these observations suggest that the ^{13}C-enrichment of baboon diets in Welgevonden is primarily due to feeding on CAM photosynthesizing succulent plants.

Succulents occur in low densities in the Waterberg, but appear to be specifically sought by some baboon populations living there. The nutritional value of such dietary items is unclear. Hamilton III (1985) proposed that utilization of toxic plants by baboons is an adaptation to nutritional deficiencies in available forage. Barton *et al.* (1993) analyzed two *E. ingens* specimens for chemical constituents including total fibre, lipids, and phenolics. These plants were high in fibre and in phenolics (including digestion-inhibiting tannins). Those analyzed in this study did not have a particularly high crude protein content. Hence, if dietary items such as *E. ingens* are indeed of nutritional benefit, it could be related to trace elements or other micronutrients. It may even be possible that baboons utilize these plants for medicinal purposes. Chimpanzees (*Pan troglodytes*) have been reported to feed on certain plants for medicinal purposes (e.g. Takasaki & Hunt, 1987).

Another explanation could be that baboons in the Waterberg utilize succulents as a means of obtaining water, given that succulents do have high water content. In the Namib Desert baboons were observed to feed on fruits of *Ficus* spp. and *Salvadora persica* in times of drought (Brain, 1988). On Welgevonden, however, water is freely available in the form of seasonal rivers and perennial water from artificial boreholes, and hence it is unlikely that baboons should turn to such poisonous, thorny plants as *E. ingens* as a water source in this region.

Although baboon faeces from Zoetfontein have a higher mean $\delta^{13}C$ value (~-23‰) than do baboons from Kruger Park (~-25‰), the Zoetfontein baboons do not have diets that are as ^{13}C-enriched as do the Welgevonden baboons (~-21‰). Hence the Zoetfontein population does not seem to supplement their diets with significant proportions of succulents. It has already been suggested that farms surrounding Zoetfontein probably affect baboon feeding habits in this area, by providing them with the opportunity to feed on high quality fruits and other C_3 crop plants (see Chapter 5). The same is not true for Welgevonden, supporting the idea that succulents are utilized as a nutritional supplement of some sort.

In Kruger, baboons feed on human foods, especially those living near the tourist rest camps (Mills, 2002, pers. comm.; personal observation). Consumption of human foods would be expected to contribute to a greater degree of variability in the carbon isotopic composition of their diets. Contributions of human food items are not observed in faecal $\delta^{13}C$ values, nor do these suggest that in different microhabitats in Kruger, diets vary in terms of the ratio of C_3- to C_4-based foods consumed. Baboons throughout Kruger Park consumed diets based mostly on C_3 forage, with only about 10 to 15% of the composition of their diets being grass- or CAM-based. Even in open grassland habitats, such as the basaltic plains around Lower Sabie and the Salitje River, baboons concentrated on C_3-based resources. These likely included trees such as *Acacia* spp., *Ficus* spp., *Sclerocarya birrea* subsp. *caffra*, and the forb layer, present in these habitats.

The results indicate that baboons living in Kruger Park, an area of diverse resource availability, rely very little on items such as grasses (and insects that feed on grasses), and focus their foraging attentions on leaves, fruits, and bark of trees and forbs. Observations of Moolman & Breytenbach (1976) and Barton *et al.* (1993) also reported minimal grass consumption by South African baboons, in the Loskop Dam area and Drakensberg, respectively. In areas with a lesser diversity of high-quality resources, such as in the Waterberg, baboons appear to supplement their diets with succulent plants rather than grasses.

6.1.2. Dietary Variability and Diet Selectivity

Intra-habitat dietary variability was small compared to that observed between the two study areas. Thackeray *et al.* (1996) noted a similar phenomenon in the isotopic composition of baboon bone collagen, even though they analyzed a very small number of samples from each region. These observations suggest that, although baboons are ecologically adaptive animals, feeding on different staple items in different habitats (e.g. Byrne *et al.*, 1993; this study), they are nevertheless highly selective feeders. It has previously been reported that within any one environment, baboons exhibit such selectivity, choosing food items of high nutritional quality (DeVore & Hall, 1965; Norton *et al.*, 1987; Whiten *et al.*, 1991; Barton *et al.*, 1993).

Variability in baboon faecal $\delta^{13}C$ values was lower across Kruger Park habitats than in the Waterberg, even though there is more vegetational heterogeneity and a wider diversity of available resources in Kruger. The low dietary variability observed amongst Kruger populations suggests that diet selectivity is intensive in Kruger Park. The Kruger situation is not dissimilar to that of Mikumi, Tanzania, where a wide diversity of plant resources are available as forage, but baboons fed on less than 25% of the available plant species throughout a five-year period (Norton *et al.*, 1987).

Baboons in the Waterberg, where the vegetational landscape is largely homogenous, are perhaps forced to be more resourceful. This would account for why the Waterberg baboons supplement their diets with items such as succulents, and other resources, in order to meet their nutritional requirements. In terms of dietary quality, Waterberg mammals generally had lower levels of protein in their diets than did Kruger mammals. This is probably due to the soil nutrient content and relative homogeneity of the Waterberg vegetation as compared to Kruger Park. In contrast with grazers, browsers, and impala, however, baboons did not exhibit differences in the quality of their diets between the respective areas, again indicating the importance of selective foraging to these primates.

Results show that savanna baboons select diets of similar protein content in a number of different landscapes. This observation supports earlier suggestions that baboons will obtain maximum nutritional gain in any particular environment (DeVore & Hall, 1965; Norton *et al.*, 1987; Whiten *et al.*, 1991; Barton *et al.*, 1993). Baboon faeces were among the most proteinaceous of all mammals in the Waterberg and in Kruger Park, and can thus be said to be more selective feeders than ungulates.

6.1.3. Seasonality

From faecal $\delta^{13}C$ and $\delta^{15}N$ data, and percentage nitrogen of faeces from both study areas, no significant seasonal differences were observed. This result, however, may be compromised by unusually low rainfall during the study period, diminishing seasonal differences in available resources. However, seasonal fluctuations in impala diets were evident (at least in the Waterberg), as were changes in plant and other mammal faecal $\delta^{15}N$ values and protein content. These temporal fluctuations did not affect the ratio of C_3 to C_4/CAM plants utilized by baboons. Thus, baboons in any circumstance consistently chose items that best suited their nutritional requirements.

A more continuous sampling technique using serial analysis of hair, and dentine collagen, evinced a great deal of dietary variability within individual baboons. This variability was probably underestimated, a result of slow diet-tissue equilibration times (e.g. Jones *et al.*, 1981; Balasse *et al.*, 2001). At present, positing an accurate time frame on these serially sampled materials is almost impossible, due to variability in growth rates (see Inagaki & Nigi, 1988 for hair growth rates, and Molnar *et al.*, 1981 and Phillips-Conroy &

Jolly, 1988 for dental development). Nonetheless, the utility of such analysis in tracing animal diets through time is clearly evident.

Serial analysis of hair strands indicated that, at least in the Waterberg, an individual's diet may fluctuate by as much as 4‰ in carbon isotopic composition throughout a year. Results from faeces showed less seasonal dietary variability for baboons. The reason for this apparent discordance probably lies in the timing of faecal collections, samples representing only small parts of two seasons. Faeces were not collected over the entire year, but had faecal sampling taken place at higher resolution, say monthly, an extended variability in $\delta^{13}C$ values would likely have been observed.

Intra-individual dietary variability as observed in hair, and to a lesser extent dentine collagen, $\delta^{13}C$ values, signifies almost the same amount of variability as observed in faeces for the whole Waterberg population. This result suggests that all individuals living in an area exhibit similar dietary habits.

Anderson (1982) predicted that southern African baboons should display dietary fluctuations in response to seasonal changes in climate and habitat conditions. $\delta^{13}C$ and $\delta^{15}N$ peaks along serial transects of each hair appear to be more prolonged than would be expected if the isotopic composition of baboon diets were related to seasonal changes. The implication here is that temporal fluctuations in baboon diet selectivity may simply follow shifts in resource availability, or other changes in local conditions.

6.1.4. $\delta^{15}N$ in Faeces

Baboon faeces were consistently depleted in ^{15}N ($\delta^{15}N$ = ~3 to 5‰) compared to those of other mammal species ($\delta^{15}N$ = ~3 to 7‰ in herbivores, and ~7 to 10‰ in carnivores). Following the conventional trophic level explanation of nitrogen isotope fractionation, it could be argued that low faecal $\delta^{15}N$ values are due to South African savanna-dwelling baboons feeding almost entirely on plant material. Baboons often exhibited even lower $\delta^{15}N$ values than pure herbivores, including grazers (which were low in June and September) and browsers (having lowest faecal $\delta^{15}N$ in January). One possibility is that low faecal $\delta^{15}N$ values reflect omnivory. Kelly (2000) found that amongst terrestrial mammals, omnivores had the lowest tissue $\delta^{15}N$ values. However, invertebrates are relatively scarce in the Waterberg (Burger, 2002, pers. comm.), and are thus unlikely to contribute significantly to the diets of baboons living there. Clearly, an alternative explanation is required.

Ambrose (1986) suggested that low baboon $\delta^{15}N$ values are due to a high consumption of ^{15}N-depleted nitrogen-fixing plants, such as *Acacia* spp and other leguminous plants. This is not a satisfactory explanation because such plants are not consistently depleted in ^{15}N compared to other plants (e.g. Muzuka, 1999; Robinson, 2001; this study).

Succulents generally have higher $\delta^{15}N$ values than other plants (Koch *et al.*, 1991; Muzuka, 1999; this study), but baboon faeces were rarely ^{15}N-enriched. The most positive $\delta^{15}N$ values were indeed found in samples from the *Euphorbia* feeding site (Nalana), but also in Motswedi, Zoetfontein, and throughout Kruger Park. Faecal $\delta^{15}N$ values did not correlate well with rainfall and water availability, or with dietary protein.

If the diets of baboons are ^{15}N-depleted, then it appears that the only resource that could underlie this is underground storage organs of geophytes. The single specimen from the Waterberg was extremely depleted in ^{15}N ($\delta^{15}N = -3.8‰$). Daegling & Grine (1999) analyzed dental microwear patterns of some specimens from Ellisras, and concluded that utilization of subterranean food items in this area is high. More samples of this resource are required if it is to be shown that geophytes are consistently depleted in ^{15}N than other plants, and in any case, low $\delta^{15}N$ values were not observed in the few geophyte samples from Kruger Park.

It should also be noted that dietary $\delta^{15}N$ values do not necessarily correlate well with faecal values, as protein metabolism likely results in preferential retention or excretion of either of the stable isotopes of nitrogen. Hair (between 5 and 7‰) and tooth dentine collagen (between 8 and 9‰) both had higher $\delta^{15}N$ values than did baboon faeces, which could suggest a preferential retention of ^{15}N within the body nitrogen pool. Sponheimer *et al.* (2003d), however, argued that adult mammals do not preferentially retain or excrete either of the stable isotopes of nitrogen, as urea and faecal excretion leads to a steady state of nitrogen influx and efflux.

The $\delta^{15}N$ values observed in baboon faeces were strongly significantly higher ($p<0.0003$) in areas of Kruger Park where they were more likely to include greater amounts of human food items into their diet. Feeding on human foods probably occurred in relatively small amounts, as evidenced by faecal $\delta^{13}C$ values, but it appears that even a small amount of intake of these items might influence baboon faecal $\delta^{15}N$ values. If that is the case, it may provide some clues as to the type of information reflected by faecal $\delta^{15}N$. Man-made foods are more readily digestible than natural products, and this could contribute to $\delta^{15}N$ variability in body tissues and excreta. The hypothesis of nitrogen isotopic fractionation in mammals as a function of nitrogen efflux in faeces and urine, suggested by Sponheimer *et al.* (2003a), can probably be further refined by an examination of the relative digestibility of consumed foods.

Digestive anatomy and physiology may play a role in nitrogen isotope fractionation by different mammals (Sponheimer *et al.*, 2003a). To this end, further information on nitrogen sources and metabolism, and nitrogen isotope fractionation by primates, is required in order to resolve the information born in baboon faecal (and other body tissue) $\delta^{15}N$ values.

6.2. The South African Pleistocene Cercopithecoidea

Dietary habits of extinct cercopithecoids from the South African Pleistocene deposits are far from resolved, but significant insights into resource utilization by several taxa has been gained.

Two distinct groups of *Cercopithecoides williamsi*, the colobine monkey, are evident in the results. The first group consists of individuals with a C_4-dominated diet ($\delta^{13}C \sim -7^{o}/_{oo}$), supporting previous suggestions that this monkey was a terrestrial feeder (Delson, 1992), but a second group, with an almost 100% reliance on C_3-based resources, is also observed. The latter suggests a dietary behaviour more comparable with modern colobines. It is unclear whether there is more than one species present, or that misidentification of samples is at the root of this distinction. It is possible that isolated teeth of another taxon have been misidentified as *C. williamsi*.

Existence of more than one species of *Cercopithecoides*, or subspecies, in the South African Pleistocene, has been suggested previously, with authors having previously recognized *C. molletti* in addition to *C. williamsi* from Swartkrans. However, Freedman (1976) supported a chronocline if different forms of *Cercopithecoides* from these deposits are recognized. It is unlikely that the diet of this genus would change so radically over the relatively short time span he suggests. It is far more likely that some of the specimens identified as *C. williamsi* (likely the more ^{13}C-depleted individuals) actually belong to another taxon. In any event, at least some *Cercopithecoides* were primarily grass feeders that included a small amount of browse into their diets. This is important, because it suggests that these monkeys, and possibly other African Plio-Pleistocene colobines, were probably more commonly associated with open habitats, rather than closed woodlands. Previously, colobines in the African Plio-Pleistocene fossil record (specifically East African *Paracolobus*) have been used as indicators of closed woodland habitats (WoldeGabriel *et al.*, 1994; Leakey *et al.*, 1995), but such environmental reconstructions now require re-consideration.

Amongst the fossil baboons analyzed, only *Theropithecus oswaldi* had a consistently ^{13}C-enriched (between –1 and -5‰), probably graminivorous, diet, which is consistent with the results obtained by Lee-Thorp *et al.* (1989a) and the diet of modern gelada baboons (Jolly, 1970).

Specimens classified as *Parapapio* and *Papio* had similar δ^{13}C patterns. Both groups contain individuals that utilized savanna-based resources, including *Papio (Dinopithecus) ingens*. Dietary variability within *Papio robinsoni* was extremely high. Disparity between current and previous methods of sample pretreatment can at best only provide a partial explanation here. Some of the newly analyzed specimens may be isolated teeth that have been misidentified as *P. robinsoni*, whereas at least some of those reported on by Lee-Thorp *et al.* (1989a) were from jaw fragments.

Across the genus *Parapapio*, two dietary groupings are observed, with enamel δ^{13}C values averaging around –8 and -10‰, respectively. These groupings do not correspond well with taxonomic assignments of *Parapapio* spp. The absence of such bimodality in modern baboon diets rules out the possibility of sex and age related dietary differences. It is more likely that the results indicate the presence of at least two species of *Parapapio*, even though three species are currently recognized from the deposits at Swartkrans and Sterkfontein (Freedman, 1976).

Carter (2001) concluded that δ^{18}O values in primate skeletal material were most useful in differentiating vertical ecological niches of sympatric forest primate species. Unfortunately, too few reliable δ^{18}O results were obtained from fossil primates to test whether any similar separation patterns occurred in extinct taxa. *T. oswaldi* had the lowest carbonate δ^{18}O values (man = -6.4 ± 0.4‰), which might indicate reliance on drinking water rather than leaf water or other water bound in their food, high utilization of underground storage organs, or even some faunivory (Sponheimer & Lee-Thorp, 1999a &

2001). Lee-Thorp (2001) found that the large-bodied *P. (D.) ingens* had higher $\delta^{18}O$ values than *P. robinsoni*. Form the analysis presented here, it appears that *P. (D.) ingens* was, if anything, more depleted in ^{18}O compared to *Parapapio* spp. and *P. robinsoni*. Further analysis may reveal more consistent trends, thus stable light isotopes may help to clarify feeding niche separation amongst fossil cercopithecoids.

While the results indicate some differentiation in resource utilization by sympatric primate taxa, a great deal of dietary overlap is evident between genera and species. In modern African savanna ecosystems, such cercopithecoid sympatry does not exist, and one struggles to imagine how sympatric cercopithecoids would have co-existed in savanna environments of the Pleistocene in the absence of distinct dietary differences. It remains, however, that sample sizes, especially for oxygen isotopes, are still small. Possible misidentification of isolated teeth probably confounds many of the patterns observed.

In comparing the results of $\delta^{13}C$ analysis of fossil primate taxa with those from modern baboon enamel, it becomes evident that all taxa from the South African Pleistocene utilized savanna-based resources to a greater extent than do modern chacmas. Lee-Thorp *et al.* (1989a) and Thackeray *et al.* (1996) presented some results for modern chacma baboons indicating greater utilization of grasses. As discussed above, however, the current study holds that grasses are not an important component of the diets of modern South African savanna baboons. The observation of ^{13}C-enrichment in fossil taxa compared to modern baboons holds for the entire tooth row of the modern individuals sampled, i.e. molars 1, 2, and 3 of the modern specimens are all ^{13}C-depleted compared to fossil taxa. The difference persists even when the twentieth century ^{13}C-depletion of atmospheric CO_2 is taken into account. Hence the dietary difference observed between modern baboons and fossil taxa is not merely an artifact of dietary differences that may have occurred at different stages of life (represented by the different teeth analyzed). Given current observations, fossil primate taxa may have included grasses into their diets to a greater extent than modern baboons, as well as consuming varying proportions of fruits, CAM plants, and grass-feeding insects, which would contribute to enriched enamel $\delta^{13}C$ values.

6.3. Implications for Early Hominid Palaeoecology

Jolly (1970) first suggested that papionin ecology might be analogous with early hominid behaviour. This early attempt favoured gelada baboons (*Theropithecus gelada*), which are graminivorous. Early hominids do not appear to have had a diet predominated by C_4-grasses (e.g. Lee-Thorp *et al*., 1994), as do modern *T. gelada*. More recently, Jolly (2001) has made a strong case for *Papio* baboons being the most suitable extant primate on which to base models of early hominid differentiation. Based on stable light isotope evidence, Sponheimer & Lee-Thorp (2003) suggested that early hominid diets are not comparable with the diets of chimpanzees, but that hominids and baboons might share similar dietary behaviours.

Van der Merwe *et al*. (2003) argued specimens of *Australopithecus africanus* display greater variability in $\delta^{13}C$ values than do modern chacma baboons. The results of this study have shown that a great deal of variability *does* exist in modern baboon diets. Moreover, such variability also existed in the feeding habits of Pleistocene baboons, especially in the case of *Papio robinsoni*, *Parapapio* spp., and *Theropithecus oswaldi*. In addition, it must be noted that the specimens of *A. africanus* referred to by van der Merwe *et al*. (2003) were taken from a huge time range of more than one million years.

Jolly's (1970, 2001) main point is that expectations of *directly comparable* results between baboons and hominids are not the issue. Using baboons as an analogue means that this group of primates can offer insights into the adaptations displayed by early hominids if similar lines of evidence are examined (Jolly, 1970).

Despite their generalist behaviour, baboons have been shown to be highly selective feeders (e.g. Norton *et al*., 1987; this study). It is reasonable to assume that hominids, themselves being primates, could have displayed a similar adaptation to savanna environments in the Pleistocene. The case for intense selectivity of high quality foods by hominids in order to obtain sufficient energy for their enlarged brains is already strong (e.g. Milton, 1999; Leonard, 2002). Thus, even though diets might have varied considerably between individuals, early hominids were likely to have been selective feeders, choosing foods of high nutritional value. The high variability in $\delta^{13}C$ values in early hominid specimens (e.g. van der Merwe *et al*., 2003; Sponheimer & Lee-Thorp, 2003) merely indicates that the range of food items considered 'appropriate' by hominids such as *A. africanus* would have constituted a wide diversity of resources.

Hominids from the South African Pleistocene have $\delta^{13}C$ values suggesting that they consumed at least some C_4-based foods (Sponheimer & Lee-Thorp, 1999b; Lee-Thorp *et al*., 2003; Sponheimer & Lee-Thorp, 2003; van der Merwe *et al*., 2003). Sponheimer &

Lee-Thorp (2003) considered sedges, grasses, animal matter, or an as yet unidentified resource as being responsible for the ^{13}C-enriched component of hominid diets, and concluded that current evidence does not support the case for sedges and grasses. In the current study, it has been observed that savanna primates, such as baboons, may supplement their diets with CAM photosynthesizing succulent plants, even in habitats where this resource is relatively scarce. Thus, one cannot disregard the significance that succulents such as *Euphorbia ingens*, or more likely the highly medicinal and more abundant *Aloe* spp., may have had for hominids foraging selectively in early savanna environments.

Utilization of succulents would not account for the broader spread in hominid than in baboon δ^{13}Cvalues. There appears to be a dietary item that was important to early hominids, but is consumed in insignificant proportions by baboons. The case for omnivory in early hominids, probably chiefly grassland termite species and other invertebrates (e.g. Sponheimer & Lee-Thorp, 2003) remains.

Baboon diets can become primarily insect-dominated when this resource becomes available (e.g. Hamilton III, 1986; Brain, 1990), a propensity that was very likely shared by early hominids evolving in similar habitats to that of baboons. It is not known whether succulents such as *E. ingens*, that is toxic to modern humans, was toxic and hence unavailable to hominids in the Pleistocene. If this was the case, however, then early hominids could not have supplemented their diets with this resource, unlike the Waterberg baboons. Thus, early hominids may rather have relied on exploitation of an omnivorous propensity in order to sustain their nutritional requirements.

These results are inconclusive, but they do indicate where baboon ecology can provide pointers for modeling early hominid behavioural adaptations, and where it cannot.

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Appendix I A. Data for Plants from the Waterberg, Collected in September 2002.

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9882	WP119	*Acacia karroo*	Bark	Acacia Loop	-27.4	-2.7	38.4	0.6
9882	WP117	*Acacia karroo*	Leaves	Acacia Loop	-26.6	1.0	46.7	3.9
9882	WP118	*Acacia karroo*	Leaves	Acacia Loop	-27.2	-4.6	47.2	3.2
9899	ZP011	*Acacia mellifera*	Bark	Zoetfontein	-22.9	2.4	46.3	1.4
9899	ZP012	*Acacia mellifera*	Fruit	Zoetfontein	-22.8	4.4	49.5	0.7
9899	ZP008	*Acacia mellifera*	Leaves	Zoetfontein	-25.2	4.4	45.8	1.6
9899	ZP009	*Acacia mellifera*	Leaves	Zoetfontein	-24.9	4.1	48.0	1.6
9899	ZP010	*Acacia mellifera*	Leaves	Zoetfontein	-23.6	3.7	7.0	1.2
9875	WP102	*Agave* sp.	Leaves	Nalana	-8.9	5.7	39.7	1.4
9876	WP104	*Agave* sp.	Roots	Nalana	-11.9	13.3	49.0	0.7
9902	ZP024	*Aristida congesta*	Leaves	Zoetfontein	-10.9	-3.9	53.7	0.5
9902	ZP023	*Aristida congesta*	Roots	Zoetfontein	-11.5	2.4	39.7	0.5
9902	ZP025	*Aristida congesta*	Seeds	Zoetfontein	-10.7	2.3	65.9	1.0
9862	WP062	*Aristida* sp.	Leaves	Bushman's Painting	-10.0	3.6	60.3	1.0
9862	WP061	*Aristida* sp.	Roots	Bushman's Painting	-10.6	3.1	47.4	0.9
9862	WP063	*Aristida* sp.	Seeds	Bushman's Painting	-10.9	2.1	57.9	0.9
9851	WP032	*Aristida* sp.	Leaves	Motswedi	-9.7	2.7	59.8	0.8
9851	WP031	*Aristida* sp.	Roots	Motswedi	-14.3	1.2	8.8	0.3
9851	WP033	*Aristida* sp.	Seeds	Motswedi	-11.0	2.5	58.5	0.9
9909	ZP047	*Centropodia glauca*	Leaves	Zoetfontein	-10.5	3.3	60.3	0.9
9910	ZP050	*Centropodia glauca*	Leaves	Zoetfontein	-11.0	3.3	66.0	1.1
9909	ZP046	*Centropodia glauca*	Roots	Zoetfontein	-10.1	4.6	59.1	1.0
9910	ZP049	*Centropodia glauca*	Roots	Zoetfontein	-10.9	3.2	67.6	0.8
9909	ZP048	*Centropodia glauca*	Seeds	Zoetfontein	-10.5	4.0	64.2	1.3
9910	ZP051	*Centropodia glauca*	Seeds	Zoetfontein	-11.2	2.4	65.7	1.1
9928	ZP104	*Combretum apiculatum*	Bark	Zoetfontein	-20.2	1.7	45.4	0.6
9928	ZP105	*Combretum apiculatum*	Fruit	Zoetfontein	-24.6	4.4	6.3	0.7
9928	ZP101	*Combretum apiculatum*	Leaves	Zoetfontein	-24.6	5.8	43.4	1.8
9928	ZP102	*Combretum apiculatum*	Leaves	Zoetfontein	-22.9	6.6	48.6	1.7
9928	ZP103	*Combretum apiculatum*	Leaves	Zoetfontein	-23.5	6.4	48.6	1.6
9845	WP017	*Combretum zeyheri*	Bark	Keg and Fig	-23.9	1.0	42.7	0.6
9845	WP014	*Combretum zeyheri*	Leaves	Keg and Fig	-24.9	5.6	33.3	1.6
9845	WP015	*Combretum zeyheri*	Leaves	Keg and Fig	-24.0	2.4	50.9	1.2
9845	WP016	*Combretum zeyheri*	Leaves	Keg and Fig	-25.0	4.6	50.2	1.5
9845	WP018	*Combretum zeyheri*	Roots	Keg and Fig	-23.3	1.4	41.6	0.6
9868	WP081	*Cyperus textilis*	Roots	Mziki	-27.6	20.7	38.9	0.7
9868	WP080	*Cyperus textilis*	Stem	Mziki	-27.7	24.4	43.8	1.1
9841	WP008	*Cyperus textilis*	Stem	Keg and Fig	-24.6	3.9	55.4	0.6
9842	WP009	*Cyperus textilis*	Stem	Keg and Fig	-25.0	3.7	43.9	0.3
9855	WP044	*Diplorhynchus condylocarpon*	Bark	Motswedi	-20.0	2.5	30.6	1.3
9855	WP041	*Diplorhynchus condylocarpon*	Leaves	Motswedi	-25.4	4.0	44.0	1.0
9855	WP042	*Diplorhynchus condylocarpon*	Leaves	Motswedi	-23.2	2.1	49.6	1.0
9855	WP043	*Diplorhynchus condylocarpon*	Leaves	Motswedi	-24.0	3.6	30.8	0.8

Appendix I A / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9849	WP028	*Diplorhynchus condylocarpon*	Bark	Keg and Fig	-22.5	1.6	26.4	0.6
9849	WP025	*Diplorhynchus condylocarpon*	Leaves	Keg and Fig	-26.2	2.9	33.8	1.0
9849	WP026	*Diplorhynchus condylocarpon*	Leaves	Keg and Fig	-25.1	4.6	49.6	1.0
9849	WP027	*Diplorhynchus condylocarpon*	Leaves	Keg and Fig	-22.8	4.7	34.4	1.0
9929	ZP109	*Diplorhynchus condylocarpon*	Bark	Zoetfontein	-21.4	2.9	38.1	0.9
9929	ZP106	*Diplorhynchus condylocarpon*	Leaves	Zoetfontein	-22.9	3.2	45.5	1.4
9929	ZP107	*Diplorhynchus condylocarpon*	Leaves	Zoetfontein	-22.2	2.0	45.2	1.6
9929	ZP108	*Diplorhynchus condylocarpon*	Leaves	Zoetfontein	-21.6	-0.6	7.1	0.9
9857	WP048	*Englerophytum magalismontanum*	Bark	Motswedi	-23.8	0.2	47.0	1.2
9857	WP047	*Englerophytum magalismontanum*	Leaves	Motswedi	-25.8	1.2	47.8	1.1
9924	ZP092	*Enteropogon monostachyus*	Leaves	Zoetfontein	-14.4	1.2	42.9	0.8
9924	ZP091	*Enteropogon monostachyus*	Roots	Zoetfontein	-11.8	1.3	59.5	1.3
9924	ZP093	*Enteropogon monostachyus*	Seeds	Zoetfontein	-12.6	3.1	63.5	2.0
9861	WP060	*Eragrostis* sp.	Leaves	Bushman's Painting	-10.8	1.9	57.8	0.7
9861	WP059	*Eragrostis* sp.	Roots	Bushman's Painting	-11.5	3.0	48.4	1.3
9852	WP035	*Eragrostis* sp.	Leaves	Motswedi	-10.9	3.5	64.8	1.1
9852	WP036	*Eragrostis* sp.	Seeds	Motswedi	-10.3	5.1	57.9	0.7
9917	ZP071	*Eragrostis* sp.	Leaves	Zoetfontein	-10.4	3.2	67.4	0.7
9923	ZP089	*Eragrostis* sp.	Leaves	Zoetfontein	-10.2	2.2	70.1	0.7
9917	ZP070	*Eragrostis* sp.	Roots	Zoetfontein	-13.0	2.6	8.3	0.2
9923	ZP088	*Eragrostis* sp.	Roots	Zoetfontein	-13.9	4.1	8.4	0.4
9917	ZP072	*Eragrostis* sp.	Seeds	Zoetfontein	-11.6	4.8	59.6	1.1
9923	ZP090	*Eragrostis* sp.	Seeds	Zoetfontein	-10.9	3.3	56.7	0.8
9874	WP101	*Euphorbia ingens*	Leaves	Nalana	-12.7	7.2	44.8	1.5
9848	WP024	*Faurea saligna*	Bark	Keg and Fig	-25.2	0.6	33.6	0.4
9848	WP023	*Faurea saligna*	Leaves	Keg and Fig	-25.9	2.6	47.9	0.8
9907	ZP039	*Ficus* sp.	Bark	Zoetfontein	-23.9	6.4	41.8	0.9
9907	ZP040	*Ficus* sp.	Fruit	Zoetfontein	-23.1	11.3	40.9	1.6
9907	ZP036	*Ficus* sp.	Leaves	Zoetfontein	-23.9	10.6	43.0	1.3
9907	ZP037	*Ficus* sp.	Leaves	Zoetfontein	-25.6	9.6	39.3	1.6
9907	ZP038	*Ficus* sp.	Leaves	Zoetfontein	-26.4	8.6	28.4	0.8
9898	ZP007	Forb	Whole	Zoetfontein	-25.6	3.9	47.7	0.9
9919	ZP074	Forb	Whole	Zoetfontein	-25.1	5.3	43.3	1.3
9911	ZP052	Forb	Whole	Zoetfontein	-24.7	4.0	42.5	1.8
9912	ZP053	Forb	Whole	Zoetfontein	-25.3	4.2	19.8	0.7
9925	ZP094	Forb	Whole	Zoetfontein	-24.8	2.9	42.5	1.6
9913	ZP057	*Grewia bicolor*	Bark	Zoetfontein	-26.6	4.9	6.4	0.8
9913	ZP054	*Grewia bicolor*	Leaves	Zoetfontein	-27.0	6.2	45.3	2.2
9913	ZP055	*Grewia bicolor*	Leaves	Zoetfontein	-27.5	6.9	46.0	1.9
9913	ZP056	*Grewia bicolor*	Leaves	Zoetfontein	-27.1	6.7	42.6	2.0
9870	WP089	*Grewia flavescens*	Bark	Mziki	-27.5	0.9	46.5	0.7
9870	WP090	*Grewia flavescens*	Fruit	Mziki	-23.0	5.8	46.2	0.9
9870	WP086	*Grewia flavescens*	Leaves	Mziki	-26.4	5.8	47.6	1.8

Appendix I A / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9870	WP087	*Grewia flavescens*	Leaves	Mziki	-25.8	5.8	48.7	1.5
9870	WP088	*Grewia flavescens*	Leaves	Mziki	-27.8	5.0	49.2	1.8
9863	WP065	*Grewia occidentalis*	Bark	Bushman's Painting	-26.8	-1.1	31.6	0.9
9863	WP066	*Grewia occidentalis*	Fruit	Bushman's Painting	-24.7	2.9	46.5	1.0
9863	WP064	*Grewia occidentalis*	Leaves	Bushman's Painting	-27.2	4.9	45.9	1.5
9914	ZP061	*Grewia occidentalis*	Bark	Zoetfontein	-24.7	-0.2	45.8	0.5
9927	ZP099	*Grewia occidentalis*	Bark	Zoetfontein	-24.9	4.9	43.3	1.0
9914	ZP062	*Grewia occidentalis*	Fruit	Zoetfontein	-24.8	4.7	45.7	1.0
9927	ZP100	*Grewia occidentalis*	Fruit	Zoetfontein	-26.2	3.2	40.3	0.7
9914	ZP058	*Grewia occidentalis*	Leaves	Zoetfontein	-26.2	5.2	46.6	1.6
9914	ZP059	*Grewia occidentalis*	Leaves	Zoetfontein	-26.7	3.7	6.7	1.2
9914	ZP060	*Grewia occidentalis*	Leaves	Zoetfontein	-26.1	6.5	43.9	1.9
9927	ZP096	*Grewia occidentalis*	Leaves	Zoetfontein	-27.8	4.8	6.4	1.4
9927	ZP097	*Grewia occidentalis*	Leaves	Zoetfontein	-28.2	5.1	53.9	2.3
9927	ZP098	*Grewia occidentalis*	Leaves	Zoetfontein	-27.1	4.4	6.4	1.3
9879	WP111	*Heteropogon contortus*	Leaves	Acacia Loop	-9.6	0.4	65.8	1.0
9879	WP110	*Heteropogon contortus*	Roots	Acacia Loop	-10.1	0.5	67.8	1.1
9879	WP112	*Heteropogon contortus*	Seeds	Acacia Loop	-9.4	-0.2	64.6	0.8
9853	WP037	*Indigofera* sp.	Leaves	Motswedi	-24.3	4.2	42.1	1.5
9843	WP010	*Indigofera* sp.	Leaves	Keg and Fig	-25.8	-0.4	30.6	1.5
9867	WP078	*Miscanthus junceus*	Leaves	Mziki	-9.6	7.5	62.5	1.0
9867	WP079	*Miscanthus junceus*	Seeds	Mziki	-8.9	4.0	75.9	1.2
9864	WP070	*Ozoroa paniculosa*	Bark	Bushman's Painting	-26.8	0.7	13.0	0.3
9864	WP067	*Ozoroa paniculosa*	Leaves	Bushman's Painting	-22.4	3.6	62.7	1.2
9864	WP068	*Ozoroa paniculosa*	Leaves	Bushman's Painting	-25.9	8.2	55.0	1.1
9864	WP069	*Ozoroa paniculosa*	Leaves	Bushman's Painting	-24.9	7.5	53.7	1.3
9839	WP006	*Panicum maximum*	Leaves	Keg and Fig	-10.3	2.6	59.1	0.6
9839	WP005	*Panicum maximum*	Roots	Keg and Fig	-10.2	1.7	66.4	0.9
9906	ZP034	*Peltophorum africanum*	Bark	Zoetfontein	-23.0	0.3	6.6	0.6
9906	ZP035	*Peltophorum africanum*	Fruit	Zoetfontein	-24.5	2.9	6.6	0.7
9906	ZP031	*Peltophorum africanum*	Leaves	Zoetfontein	-25.3	5.4	47.5	1.3
9906	ZP032	*Peltophorum africanum*	Leaves	Zoetfontein	-24.6	6.0	6.9	0.9
9906	ZP033	*Peltophorum africanum*	Leaves	Zoetfontein	-25.0	4.0	7.0	0.8
9859	WP057	*Pseudolachnostylis maprouneifolia*	Bark	Motswedi	-25.4	2.1	38.2	0.6
9859	WP054	*Pseudolachnostylis maprouneifolia*	Leaves	Motswedi	-25.4	4.1	46.0	1.2
9859	WP055	*Pseudolachnostylis maprouneifolia*	Leaves	Motswedi	-24.8	5.5	48.4	1.2
9859	WP056	*Pseudolachnostylis maprouneifolia*	Leaves	Motswedi	-26.4	4.7	47.4	1.3
9871	WP094	*Pterocarpus rotundifolius*	Bark	Mziki	-25.6	-3.9	46.7	1.1
9871	WP091	*Pterocarpus rotundifolius*	Leaves	Mziki	-28.4	0.9	56.3	1.2
9871	WP093	*Pterocarpus rotundifolius*	Leaves	Mziki	-27.4	-1.4	49.3	0.9
9860	WP058	*Strychnos pungens*	Leaves	Motswedi	-25.6	2.8	60.4	1.6
9869	WP085	*Syzygium cordatum*	Bark	Mziki	-23.7	5.1	41.7	0.4
9869	WP082	*Syzygium cordatum*	Leaves	Mziki	-26.8	5.3	38.8	0.9

Appendix I A / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9869	WP083	*Syzygium cordatum*	Leaves	Mziki	-25.9	4.1	50.1	1.2
9869	WP084	*Syzygium cordatum*	Leaves	Mziki	-24.2	4.3	49.9	1.2
9900	ZP016	*Terminalia sericea*	Bark	Zoetfontein	-23.7	0.4	42.2	0.4
9900	ZP017	*Terminalia sericea*	Fruit	Zoetfontein	-23.7	4.1	44.4	1.3
9900	ZP013	*Terminalia sericea*	Leaves	Zoetfontein	-24.9	2.5	45.2	0.8
9900	ZP014	*Terminalia sericea*	Leaves	Zoetfontein	-24.1	2.9	46.4	0.8
9900	ZP015	*Terminalia sericea*	Leaves	Zoetfontein	-24.7	2.2	46.4	0.5
9854	WP039	*Xerophyta retinurvus*	Leaves	Motswedi	-25.0	2.1	48.2	1.8
9854	WP040	*Xerophyta retinurvus*	Stem	Motswedi	-23.7	-1.4	48.3	0.3
9865	WP074	*Ximenia caffra*	Bark	Bushman's Painting	-28.7	0.2	36.6	0.7
9865	WP071	*Ximenia caffra*	Leaves	Bushman's Painting	-27.4	2.3	50.7	1.3
9865	WP072	*Ximenia caffra*	Leaves	Bushman's Painting	-27.9	3.7	34.0	1.3
9865	WP073	*Ximenia caffra*	Leaves	Bushman's Painting	-27.8	3.9	50.9	1.1
9915	ZP066	*Ximenia caffra*	Bark	Zoetfontein	-25.1	0.7	45.4	1.0
9915	ZP063	*Ximenia caffra*	Leaves	Zoetfontein	-28.2	3.5	49.3	1.5
9915	ZP064	*Ximenia caffra*	Leaves	Zoetfontein	-28.2	3.8	51.3	1.1
9915	ZP065	*Ximenia caffra*	Leaves	Zoetfontein	-27.4	3.7	53.5	1.3
9883	WP120	*Ziziphus mucronata*	Leaves	Acacia Loop	-26.0	0.4	45.8	1.2
9883	WP121	*Ziziphus mucronata*	Leaves	Acacia Loop	-25.3	1.3	44.6	1.0

Appendix I B. Data for Plants from the Waterberg, Collected in January 2003.

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10166	WP123	*Acacia erubescens*	Leaves	Bushman's Painting	-27.1	9.4	59.7	4.0
10185	WP160	*Aristida congesta*	Leaves	Motswedi	-13.2	4.4	45.6	1.0
10185	WP159	*Aristida congesta*	Roots	Motswedi	-12.6	2.4	53.3	0.6
10185	WP161	*Aristida congesta*	Seeds	Motswedi	-12.5	3.3	43.6	0.9
10167	WP125	*Aristida* sp.	Leaves	Bushman's Painting	-14.5	5.1	48.1	1.3
10168	WP128	*Aristida* sp.	Leaves	Bushman's Painting	-13.6	5.6	58.0	0.9
10167	WP124	*Aristida* sp.	Roots	Bushman's Painting	-13.6	3.5	52.7	0.6
10168	WP127	*Aristida* sp.	Roots	Bushman's Painting	-12.9	2.9	56.7	0.8
10167	WP126	*Aristida* sp.	Seeds	Bushman's Painting	-13.0	4.8	45.4	1.1
10168	WP129	*Aristida* sp.	Seeds	Bushman's Painting	-12.7	5.2	45.4	1.3
10186	WP163	*Burkea africana*	Bark	Motswedi	-26.4	0.5	53.9	1.4
10186	WP162	*Burkea africana*	Leaves	Motswedi	-27.2	3.4	54.8	1.7
10169	WP130	*Combretum apiculatum*	Leaves	Bushman's Painting	-25.4	2.8	62.3	1.8
10187	WP165	*Combretum molle*	Bark	Motswedi	-25.8	2.6	48.3	0.7
10187	WP164	*Combretum molle*	Leaves	Motswedi	-26.0	7.3	58.5	1.7
10194	WP178	*Cyperus textilis*	Stem	Keg and Fig	-27.3	8.3	56.8	0.9
10194	WP179	*Cyperus textilis*	Stem	Keg and Fig	-11.8	3.9	45.1	0.6
10176	WP142	*Dichrostachys cinerea*	Bark	Mziki	-24.1	3.7	47.6	0.7
10176	WP141	*Dichrostachys cinerea*	Leaves	Mziki	-26.0	5.8	65.4	3.0
10188	WP167	*Digitaria eriantha*	Leaves	Motswedi	-13.0	7.2	54.4	1.6
10188	WP166	*Digitaria eriantha*	Roots	Motswedi	-15.4	3.7	45.3	0.7
10188	WP168	*Digitaria eriantha*	Seeds	Motswedi	-12.9	3.7	57.3	1.4
10189	WP170	*Diplorhynchus condylocarpon*	Bark	Motswedi	-25.2	2.9	47.1	0.8
10189	WP169	*Diplorhynchus condylocarpon*	Leaves	Motswedi	-25.7	4.0	63.1	1.7
10177	WP143	*Englerophytum magalismontanum*	Leaves	Mziki	-26.6	1.8	62.6	1.1
10190	WP172	*Englerophytum magalismontanum*	Bark	Motswedi	-25.6	2.3	61.7	1.4
10190	WP171	*Englerophytum magalismontanum*	Leaves	Motswedi	-26.5	1.2	65.8	1.5
10178	WP145	*Eragrostis superba*	Leaves	Mziki	-15.5	3.5	44.6	0.9
10179	WP148	*Euclea crispa*	Bark	Mziki	-28.2	1.5	48.3	0.6
10179	WP147	*Euclea crispa*	Leaves	Mziki	-27.6	-0.1	71.2	1.6
10195	WP181	*Euphorbia ingens*	Leaves	Nalana	-14.7	4.8	44.6	0.6
10180	WP158	Forb	Whole	Mziki	-26.4	5.0	46.1	1.1
10165	WP122	Geophyte	Leaves	Random	-27.2	-3.8	66.2	0.6
10170	WP132	*Grewia occidentalis*	Fruit	Bushman's Painting	-25.3	5.3	45.8	1.7
10171	WP134	*Grewia occidentalis*	Fruit	Bushman's Painting	-25.0	13.5	69.3	1.2
10170	WP131	*Grewia occidentalis*	Leaves	Bushman's Painting	-26.9	4.2	68.3	3.4
10171	WP133	*Grewia occidentalis*	Leaves	Bushman's Painting	-25.5	13.4	60.1	3.2
10172	WP135	*Indigofera* sp.	Whole	Bushman's Painting	-27.6	0.2	70.8	3.3
10181	WP149	*Indigofera* sp.	Whole	Mziki	-29.8	1.8	69.7	2.4
10191	WP173	*Indigofera* sp.	Whole	Motswedi	-26.0	5.5	47.0	1.9
10182	WP156	*Miscanthus junceus*	Leaves	Mziki	-12.1	6.9	65.5	0.8
10182	WP157	*Miscanthus junceus*	Seeds	Mziki	-12.5	5.6	47.7	1.0
10192	WP174	*Pelaea caliminalos*	Whole	Motswedi	-28.6	3.2	57.4	2.2

Appendix I B / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10183	WP151	*Pterocarpus rotundifolius*	Bark	Mziki	-27.7	3.4	47.8	0.8
10183	WP150	*Pterocarpus rotundifolius*	Leaves	Mziki	-27.8	2.2	70.4	3.0
10173	WP136	*Solanum* sp.	Whole	Bushman's Painting	-27.4	7.0	65.3	3.5
10184	WP154	*Syzygium cordatum*	Bark	Mziki	-25.8	-1.3	52.9	0.5
10184	WP153	*Syzygium cordatum*	Leaves	Mziki	-26.4	3.3	64.1	1.3
10193	WP176	*Vitex mombassae*	Bark	Motswedi	-23.6	5.0	61.2	1.3
10193	WP175	*Vitex mombassae*	Leaves	Motswedi	-27.2	7.4	58.5	1.9
10174	WP138	*Ximenia caffra*	Bark	Bushman's Painting	-29.0	1.9	51.3	0.9
10174	WP137	*Ximenia caffra*	Leaves	Bushman's Painting	-29.2	7.3	69.4	1.7
10175	WP140	*Ziziphus mucronata*	Leaves	Bushman's Painting	-27.5	2.5	64.7	3.4

Appendix I C. Data for Plants from the Kruger National Park, Collected in June 2002.

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
8978	KP216	*Acacia exuvialis*	Leaves	Renosterkoppies	-26.8	4.8	44.8	1.4
8979	KP217	*Acacia exuvialis*	Leaves	Renosterkoppies	-29.6	-1.3	46.7	0.9
9021	KP311	*Acacia nigrescens*	Leaves	Hlanganzwane	-28.3	12.2	49.7	2.0
9022	KP312	*Acacia nigrescens*	Leaves	Hlanganzwane	-28.5	2.3	45.5	2.1
9023	KP313	*Acacia nigrescens*	Leaves	Hlanganzwane	-28.7	2.2	44.6	1.8
8940	KP386	*Acacia nigrescens*	Leaves	N'watimvambu R	-25.9	1.6	44.1	1.4
8940	KP387	*Acacia nigrescens*	Bark	N'watimvambu R	-25.6	0.1	49.2	0.9
8943	KP393	*Acacia nigrescens*	Bark	N'watimvambu R	-24.4	0.2	49.3	0.7
9082	KP023	*Acacia tortilis*	Leaves	Crocodile River	-26.9	-0.1	56.9	1.6
9083	KP024	*Acacia tortilis*	Leaves	Crocodile River	-29.2	0.3	44.7	2.4
9085	KP026	*Acacia tortilis*	Leaves	Crocodile River	-27.3	-0.4	45.2	1.8
8966	KP430	*Aristida adscensionis*	Whole	N'watimvambu R	-10.0	1.2	45.7	0.4
8967	KP431	*Aristida adscensionis*	Whole	N'watimvambu R	-11.6	1.6	45.3	0.3
9008	KP252	*Aristida adscensionis*	No Roots	Renosterkoppies	-12.6	3.8	41.1	0.4
9008-9011	KP253	*Aristida adscensionis*	Roots	Renosterkoppies	-13.0	3.5	36.5	0.4
8971	KP209	*Balanites maughamii*	Leaves	Renosterkoppies	-25.5	8.8	42.1	2.0
8972	KP210	*Balanites maughamii*	Leaves	Renosterkoppies	-25.5	7.8	42.2	1.8
9047	KP343	*Bolusanthus speciosus*	Leaves	Hlanganzwane	-26.1	0.2	48.5	1.4
9048	KP344	*Bolusanthus speciosus*	Leaves	Hlanganzwane	-25.1	1.4	47.4	2.4
9049	KP345	*Bolusanthus speciosus*	Leaves	Hlanganzwane	-25.8	1.0	44.1	1.6
9123	KP067	*Bothriochloa* sp.	No Roots	Crocodile River	-12.0	0.2	54.3	0.3
9123-9124	KP068	*Bothriochloa* sp.	Roots	Crocodile River	-12.2	0.7	39.4	0.6
9124	KP069	*Bothriochloa* sp.	No Roots	Crocodile River	-11.6	0.6	54.9	0.4
9061	KP361	*Bothriochloa* sp.	No Roots	Hlanganzwane	-9.0	1.7	44.1	0.3
9061-9062	KP362	*Bothriochloa* sp.	Roots	Hlanganzwane	-9.4	0.7	46.9	0.7
8964	KP427	*Bothriochloa* sp.	No Roots	N'watimvambu R	-10.8	1.9	45.8	0.3
8964-8965	KP428	*Bothriochloa* sp.	Roots	N'watimvambu R	-13.3	1.9	11.8	0.3
9002	KP241	*Chloris virgata*	No Roots	Renosterkoppies	-13.4	4.9	41.4	0.5
9002	KP242	*Chloris virgata*	Roots	Renosterkoppies	-13.1	4.0	42.2	0.5
8928	KP367	*Combretum apiculatum*	Leaves	N'watimvambu R	-24.8	3.4	45.7	1.4
8929	KP369	*Combretum apiculatum*	Leaves	N'watimvambu R	-25.6	4.4	45.4	1.2
8929	KP370	*Combretum apiculatum*	Bark	N'watimvambu R	-24.8	1.7	42.6	0.8
9041	KP336	*Combretum hereroense*	Leaves	Hlanganzwane	-27.4	5.2	58.5	1.3
9036	KP331	*Combretum imberbe*	Leaves	Hlanganzwane	-28.7	4.5	49.2	1.0
9077	KP017	*Dichrostachys cinerea*	Leaves	Crocodile River	-27.4	-0.5	53.7	1.4
9079	KP019	*Dichrostachys cinerea*	Leaves	Crocodile River	-27.3	3.2	54.3	1.6
9081	KP022	*Dichrostachys cinerea*	Leaves	Crocodile River	-27.4	0.5	47.8	1.6
8936	KP380	*Dichrostachys cinerea*	Leaves	N'watimvambu R	-23.5	2.2	49.8	2.2
8936	KP381	*Dichrostachys cinerea*	Bark	N'watimvambu R	-24.8	0.6	45.7	0.9
8938	KP382	*Dichrostachys cinerea*	Leaves	N'watimvambu R	-22.3	1.5	48.4	2.3
8938	KP383	*Dichrostachys cinerea*	Bark	N'watimvambu R	-23.8	0.4	46.4	1.1
8974	KP212	*Dichrostachys cinerea*	Leaves	Renosterkoppies	-27.6	1.6	40.3	1.1
8976	KP214	*Dichrostachys cinerea*	Leaves	Renosterkoppies	-26.1	2.0	44.4	1.4

Appendix I C / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9087	KP028	*Diospyros mespiliformis*	Leaves	Crocodile River	-27.3	2.4	51.9	1.6
9088	KP029	*Diospyros mespiliformis*	Leaves	Crocodile River	-27.3	2.2	49.2	1.0
9089	KP030	*Diospyros mespiliformis*	Leaves	Crocodile River	-28.7	1.2	50.6	1.2
8970	KP435	*Eragrostis macrostachys*	Whole	N'watimvambu R	-12.9	2.6	48.1	0.9
9060	KP360	*Eragrostis* sp.	No Roots	Hlanganzwane	-9.6	1.4	46.1	0.3
9016-9018	KP263	*Eragrostis* sp.	Roots	Renosterkoppies	-12.9	3.6	35.1	0.4
9017	KP264	*Eragrostis* sp.	No Roots	Renosterkoppies	-12.9	4.1	40.5	0.5
9118	KP061	*Eragrostis superba*	No Roots	Crocodile River	-12.5	0.6	52.8	0.4
9119	KP062	*Eragrostis superba*	No Roots	Crocodile River	-13.0	0.3	42.4	0.3
9058	KP357	*Eragrostis superba*	No Roots	Hlanganzwane	-9.7	3.3	45.1	0.4
9058-9059	KP358	*Eragrostis superba*	Roots	Hlanganzwane	-12.3	2.2	8.4	0.3
8962	KP425	*Eragrostis superba*	No Roots	N'watimvambu R	-11.5	3.0	45.9	0.5
8963	KP426	*Eragrostis superba*	No Roots	N'watimvambu R	-10.1	2.9	45.5	0.5
9066	KP005	*Euclea divinorum*	Leaves	Crocodile River	-28.3	-0.2	50.3	0.9
9067	KP006	*Euclea divinorum*	Leaves	Crocodile River	-29.3	0.1	50.5	1.2
9037	KP332	*Euclea divinorum*	Leaves	Hlanganzwane	-20.4	7.0	8.6	2.9
9038	KP333	*Euclea divinorum*	Leaves	Hlanganzwane	-27.4	2.7	53.6	0.9
9100	KP043	Forb	Whole	Crocodile River	-26.3	0.6	51.7	0.9
9033	KP326	Forb	No Roots	Hlanganzwane	-26.8	2.9	50.9	1.8
9034	KP327	Forb	No Roots	Hlanganzwane	-26.3	5.5	45.0	1.2
8950	KP406	Forb	Stems	N'watimvambu R	-26.3	4.6	46.7	1.1
8951	KP407	Forb	Leaves	N'watimvambu R	-27.5	7.4	44.2	2.3
8953	KP412	Forb	Whole	N'watimvambu R	-10.3	0.9	45.4	0.4
8989	KP228	Forb	Whole	Renosterkoppies	-26.3	5.9	43.0	0.8
8991	KP230	Forb	Whole	Renosterkoppies	-26.2	4.4	40.2	0.5
8996	KP235	Forb	Leaves	Renosterkoppies	-27.0	5.6	40.8	1.2
8997	KP236	Forb	Leaves	Renosterkoppies	-27.4	5.6	41.2	1.1
9068	KP007	*Grewia* sp.	Leaves	Crocodile River	-28.0	7.2	43.6	1.2
9069	KP008	*Grewia* sp.	Leaves	Crocodile River	-28.1	3.6	50.2	1.4
9072	KP012	*Grewia* sp.	Bark	Crocodile River	-26.3	2.5	45.2	1.0
8946	KP398	*Grewia* sp.	Leaves	N'watimvambu R	-26.7	3.6	48.2	1.4
8946	KP399	*Grewia* sp.	Bark	N'watimvambu R	-26.0	2.8	44.7	0.7
8947	KP400	*Grewia* sp.	Fruit	N'watimvambu R	-23.5	1.9	46.6	0.5
8947	KP401	*Grewia* sp.	Leaves	N'watimvambu R	-29.9	3.1	96.2	2.4
8947	KP402	*Grewia* sp.	Bark	N'watimvambu R	-29.1	-5.8	1.0	0.0
8982	KP220	*Grewia* sp.	Leaves	Renosterkoppies	-27.1	5.6	45.6	0.8
8982	KP221	*Grewia* sp.	Fruit	Renosterkoppies	-24.5	5.8	44.0	0.6
9073	KP013	*Gymnosporia* sp.	Leaves	Crocodile River	-28.5	1.5	44.8	0.9
9074	KP014	*Gymnosporia* sp.	Leaves	Crocodile River	-28.2	2.2	41.9	0.9
9027	KP317	*Gymnosporia* sp.	Leaves	Hlanganzwane	-27.4	3.0	49.0	1.0
9027	KP318	*Gymnosporia* sp.	Bark	Hlanganzwane	-25.1	2.0	50.4	0.6
9028	KP319	*Gymnosporia* sp.	Leaves	Hlanganzwane	-25.7	2.1	49.0	1.0
9128	KP073	*Heteropogon contortus*	No Roots	Crocodile River	-12.6	0.9	40.2	0.3

Appendix I C / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9128-9130	KP074	*Heteropogon contortus*	Roots	Crocodile River	-12.1	0.8	39.2	0.5
8952	KP409	*Heteropogon contortus*	Whole	N'watimvambu R	-10.2	0.6	42.9	0.4
8992	KP231	Legume Forb	Whole	Renosterkoppies	-23.9	0.5	44.4	1.0
8993	KP232	Legume Forb	Whole	Renosterkoppies	-24.3	0.0	44.2	0.6
8994	KP233	Legume Forb	Fruit	Renosterkoppies	-22.8	2.4	43.8	1.5
9063	KP001	*Lonchocarpus capassa*	Leaves	Crocodile River	-26.9	2.7	46.0	2.3
9024	KP314	*Lonchocarpus capassa*	Leaves	Hlanganzwane	-26.3	5.2	44.9	2.2
9025	KP315	*Lonchocarpus capassa*	Leaves	Hlanganzwane	-27.8	1.7	41.0	2.1
8934	KP377	*Lonchocarpus capassa*	Leaves	N'watimvambu R	-24.1	2.1	45.2	2.1
8934	KP378	*Lonchocarpus capassa*	Bark	N'watimvambu R	-24.7	0.7	44.3	0.8
9001	KP240	*Opuntia* sp.	Fleshy	Renosterkoppies	-12.5	5.4	40.5	0.4
9042	KP337	*Ozoroa* sp.	Leaves	Hlanganzwane	-27.1	3.4	45.1	1.8
9125	KP070	*Panicum coloratum*	No Roots	Crocodile River	-12.6	1.1	57.9	0.4
9126	KP071	*Panicum coloratum*	Whole	Crocodile River	-12.4	0.1	54.5	0.4
9057	KP356	*Panicum coloratum*	No Roots	Hlanganzwane	-11.5	2.4	48.5	0.3
8957	KP419	*Panicum coloratum*	No Roots	N'watimvambu R	-11.8	1.5	28.3	0.3
8957-8959	KP420	*Panicum coloratum*	Roots	N'watimvambu R	-11.6	3.7	29.1	0.7
9003	KP243	*Panicum coloratum*	No Roots	Renosterkoppies	-14.9	5.2	41.1	0.5
9003	KP244	*Panicum coloratum*	Seeds	Renosterkoppies	-12.5	7.0	42.5	1.3
9003-9004	KP245	*Panicum coloratum*	Roots	Renosterkoppies	-13.1	3.9	40.5	0.6
9121	KP065	*Panicum maximum*	No Roots	Crocodile River	-12.4	0.3	55.7	0.7
9122	KP066	*Panicum maximum*	No Roots	Crocodile River	-12.8	0.9	44.8	0.7
9056	KP354	*Panicum maximum*	No Roots	Hlanganzwane	-9.8	0.2	43.0	0.5
9056	KP355	*Panicum maximum*	Roots	Hlanganzwane	-9.9	1.3	39.7	0.7
8955	KP414	*Panicum maximum*	No Roots	N'watimvambu R	-10.7	2.7	32.3	0.7
8955	KP415	*Panicum maximum*	Seeds	N'watimvambu R	-11.1	2.4	44.2	2.1
8955-8956	KP418	*Panicum maximum*	Roots	N'watimvambu R	-12.5	1.4	21.6	0.5
9005	KP247	*Panicum maximum*	No Roots	Renosterkoppies	-12.9	4.2	40.9	0.5
9005-9007	KP248	*Panicum maximum*	Roots	Renosterkoppies	-12.3	4.1	39.7	0.5
9007	KP251	*Panicum maximum*	Seeds	Renosterkoppies	-12.4	7.3	41.7	1.3
9131	KP077	*Phragmites australis*	Stems	Crocodile River	-25.9	5.3	50.2	0.3
9131	KP078	*Phragmites australis*	Leaves	Crocodile River	-25.7	8.7	44.1	1.1
9132	KP079	*Phragmites australis*	Stems	Crocodile River	-25.3	1.6	48.5	0.2
9132	KP080	*Phragmites australis*	Seeds	Crocodile River	-23.8	3.8	45.2	0.8
9132	KP081	*Phragmites australis*	Roots	Crocodile River	-23.5	5.1	46.7	0.7
9134	KP086	Sedge	Stems	Crocodile River	-27.7	7.7	40.9	0.3
9134	KP087	Sedge	Roots	Crocodile River	-26.3	4.5	40.2	0.2
9134	KP088	Sedge	Leaves	Crocodile River	-28.1	8.4	45.9	0.6
9135	KP089	Sedge	Stems	Crocodile River	-11.3	5.2	47.8	0.4
9135	KP090	Sedge	Seeds	Crocodile River	-12.1	5.9	50.1	1.0
9135	KP091	Sedge	Roots	Crocodile River	-12.8	4.5	15.2	0.3
9055	KP353	*Setaria* sp.	No Roots	Hlanganzwane	-8.7	2.0	38.9	0.3
9104-9107	KP047	*Solanum* sp.	Leaves	Crocodile River	-27.7	-0.6	45.2	1.1

Appendix I C / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9043	KP338	*Solanum* sp.	Leaves	Hlanganzwane	-26.0	1.1	43.2	0.8
9043	KP339	*Solanum* sp.	Roots	Hlanganzwane	-25.5	0.7	38.5	0.9
9043	KP340	*Solanum* sp.	Stems	Hlanganzwane	-26.7	0.8	43.3	0.7
9044	KP341	*Solanum* sp.	Roots	Hlanganzwane	-25.0	0.1	39.8	0.5
9045-9046	KP342	*Solanum* sp.	Leaves	Hlanganzwane	-25.1	2.7	43.4	1.8
8948	KP403	*Solanum* sp.	Stems	N'watimvambu R	-25.5	2.5	47.5	1.0
8949	KP404	*Solanum* sp.	No Roots	N'watimvambu R	-26.8	2.0	46.4	1.1
8987	KP226	*Solanum* sp.	Leaves	Renosterkoppies	-25.9	7.8	43.4	1.3
8988	KP227	*Solanum* sp.	Leaves	Renosterkoppies	-28.0	6.7	42.9	1.5
8930	KP371	*Spirostachys africana*	Leaves	N'watimvambu R	-24.7	2.3	43.6	1.1
8930	KP372	*Spirostachys africana*	Bark	N'watimvambu R	-24.7	1.4	44.4	1.1
9113	KP054	*Sporobolus* sp.	No Roots	Crocodile River	-12.5	3.1	44.7	0.6
9113-9114	KP055	*Sporobolus* sp.	Roots	Crocodile River	-13.1	1.8	47.9	0.6
9115	KP057	*Themeda triandra*	No Roots	Crocodile River	-12.2	0.2	43.3	0.3
9115-9117	KP058	*Themeda triandra*	Roots	Crocodile River	-12.7	0.4	35.8	0.5
9052-9054	KP350	*Themeda triandra*	Roots	Hlanganzwane	-9.2	2.4	40.5	0.7
9054	KP352	*Themeda triandra*	No Roots	Hlanganzwane	-9.4	1.3	43.2	0.3
8969	KP433	*Themeda triandra*	No Roots	N'watimvambu R	-11.5	1.6	47.6	0.4
8969	KP434	*Themeda triandra*	Roots	N'watimvambu R	-10.9	2.2	46.7	0.7
9110-9112	KP051	*Urochloa mossambicensis*	Roots	Crocodile River	-12.2	0.3	36.5	0.9
9112	KP053	*Urochloa mossambicensis*	No Roots	Crocodile River	-12.4	0.8	45.6	0.5
9050	KP346	*Urochloa mossambicensis*	No Roots	Hlanganzwane	-9.3	0.7	39.7	0.5
9050-9051	KP347	*Urochloa mossambicensis*	Roots	Hlanganzwane	-9.9	2.5	44.1	1.0
9013	KP258	*Urochloa mossambicensis*	No Roots	Renosterkoppies	-12.2	4.5	40.4	0.7
9013-9015	KP259	*Urochloa mossambicensis*	Roots	Renosterkoppies	-11.8	5.4	40.0	0.5
9064	KP003	*Ziziphus mucronata*	Leaves	Crocodile River	-24.7	3.5	53.3	1.7
9065	KP004	*Ziziphus mucronata*	Leaves	Crocodile River	-25.4	1.1	51.3	1.7
8935	KP379	*Ziziphus mucronata*	Bark	N'watimvambu R	-23.8	3.0	46.4	0.4
8981	KP219	*Ziziphus mucronata*	Leaves	Renosterkoppies	-26.0	4.7	43.8	0.9

Appendix I D. Data for Plants from the Kruger National Park, Collected in January 2003.

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10533	KP460	*Acacia nigrescens*	Leaves	Hlanganzwane	-27.7	2.7	40.4	1.9
10656	KP609	*Acacia nigrescens*	Leaves	N'watimvambu R	-28.2	2.1	45.0	2.1
10658	KP611	*Acacia nigrescens*	Leaves	N'watimvambu R	-28.9	2.7	44.8	1.8
10579	KP517	*Acacia nilotica*	Leaves	Crocodile River	-26.5	1.7	50.4	2.3
10534	KP461	*Acacia robusta*	Leaves	Hlanganzwane	-26.6	1.5	48.8	2.2
10535	KP462	*Acacia robusta*	Leaves	Hlanganzwane	-26.1	2.8	55.5	2.3
10659	KP612	*Acacia tortilis*	Leaves	N'watimvambu R	-27.5	2.8	48.1	2.5
10642	KP586	*Aristida adscensionis*	No Roots	N'watimvambu R	-12.1	2.4	42.6	0.8
10642	KP587	*Aristida adscensionis*	Roots	N'watimvambu R	-12.7	1.9	39.9	0.7
10606	KP546	*Aristida adscensionis*	No Roots	Renosterkoppies	-12.3	5.0	42.5	0.8
106505-10606	KP547	*Aristida adscensionis*	Roots	Renosterkoppies	-12.7	5.0	45.7	1.0
10519	KP443	*Aristida* sp.	No Roots	Hlanganzwane	-14.4	2.4	42.0	0.8
10519-10521	KP446	*Aristida* sp.	Roots	Hlanganzwane	-13.1	1.5	30.1	0.6
10620	KP564	*Balanites maughamii*	Leaves	Renosterkoppies	-26.5	10.5	42.9	3.2
10537	KP464	*Bolusanthus speciosus*	Leaves	Hlanganzwane	-21.5	0.5	47.5	2.4
10538	KP465	*Bolusanthus speciosus*	Leaves	Hlanganzwane	-22.6	4.6	45.0	2.0
10554	KP482	*Cenchrus ciliaris*	No Roots	Crocodile River	-12.3	2.3	42.8	0.8
10556	KP484	*Cenchrus ciliaris*	Whole	Crocodile River	-11.9	2.9	41.9	0.8
10557	KP485	*Chloris pycnothrix*	No Roots	Crocodile River	-12.4	1.6	41.5	0.7
10558	KP486	*Chloris pycnothrix*	Whole	Crocodile River	-13.3	6.1	36.8	0.8
10522	KP447	*Chloris virgata*	Whole	Hlanganzwane	-14.1	3.3	39.7	2.1
10523	KP448	*Chloris virgata*	Whole	Hlanganzwane	-14.3	4.1	41.5	2.0
10609	KP550	*Chloris virgata*	No Roots	Renosterkoppies	-12.4	8.0	39.6	0.8
10607-10609	KP551	*Chloris virgata*	Roots	Renosterkoppies	-12.6	10.0	36.2	1.1
10660	KP613	*Combretum apiculatum*	Leaves	N'watimvambu R	-26.1	4.9	49.3	1.5
10661	KP614	*Combretum apiculatum*	Seeds	N'watimvambu R	-23.7	4.8	45.2	1.3
10662	KP615	*Combretum apiculatum*	Leaves	N'watimvambu R	-25.8	4.7	55.0	1.7
10663	KP617	*Combretum apiculatum*	Seeds	N'watimvambu R	-25.0	1.9	52.0	1.4
10539	KP466	*Combretum imberbe*	Leaves	Hlanganzwane	-25.9	4.2	45.1	1.3
10540	KP467	*Combretum imberbe*	Leaves	Hlanganzwane	-26.7	3.8	48.6	1.8
10576	KP510	*Cyperus textilis*	Leaves	Crocodile River	-28.0	9.5	39.9	1.5
10576	KP511	*Cyperus textilis*	Stems	Crocodile River	-27.9	7.0	42.8	0.8
10576	KP512	*Cyperus textilis*	Roots	Crocodile River	-14.8	4.5	33.0	0.6
10577	KP513	*Cyperus textilis*	Leaves	Crocodile River	-27.0	7.8	42.1	1.3
10577	KP514	*Cyperus textilis*	Stems	Crocodile River	-26.7	4.3	37.4	0.5
10577	KP515	*Cyperus textilis*	Roots	Crocodile River	-26.2	4.7	30.1	0.7
10580	KP518	*Dichrostachys cinerea*	Leaves	Crocodile River	-27.9	3.3	48.5	2.1
10582	KP520	*Dichrostachys cinerea*	Leaves	Crocodile River	-25.9	3.5	54.8	2.7
10666	KP620	*Dichrostachys cinerea*	Leaves	N'watimvambu R	-26.3	2.1	46.2	2.7
10622	KP566	*Dichrostachys cinerea*	Leaves	Renosterkoppies	-27.0	1.6	48.1	2.4
10623	KP567	*Dichrostachys cinerea*	Leaves	Renosterkoppies	-25.5	4.7	49.2	2.5
10643	KP588	*Digitaria eriantha*	Leaves	N'watimvambu R	-11.5	2.8	34.6	1.0
10645	KP590	*Digitaria eriantha*	Leaves	N'watimvambu R	-11.6	4.0	48.1	1.7

Appendix I D / continued

UCT #	Sample ID	Species	Part	Collection Site	δ^{13}C	δ^{15}N	%C	%N
10643-10645	KP591	*Digitaria eriantha*	Seeds	N'watimvambu R	-10.8	2.7	44.4	1.4
10643-10645	KP592	*Digitaria eriantha*	Roots	N'watimvambu R	-11.7	1.9	39.8	0.6
10584	KP522	*Diospyros mespiliformis*	Leaves	Crocodile River	-26.8	4.3	47.6	1.2
10585	KP523	*Diospyros mespiliformis*	Leaves	Crocodile River	-27.8	1.8	48.4	1.1
10586	KP524	*Ehretia obtusifolia*	Leaves	Crocodile River	-25.2	2.4	49.0	1.6
10587	KP525	*Ehretia obtusifolia*	Leaves	Crocodile River	-26.8	3.8	47.6	2.4
10646	KP593	*Eragrostis* sp.	Leaves	N'watimvambu R	-12.8	5.3	41.5	0.9
10646-10648	KP596	*Eragrostis* sp.	Seeds	N'watimvambu R	-12.0	5.0	49.5	1.0
10647-10648	KP597	*Eragrostis* sp.	Roots	N'watimvambu R	-13.1	3.4	34.8	0.5
10611	KP553	*Eragrostis* sp.	No Roots	Renosterkoppies	-12.3	6.7	42.0	1.1
10612	KP554	*Eragrostis* sp.	No Roots	Renosterkoppies	-13.7	7.6	34.8	1.5
10560	KP488	*Eragrostis superba*	No Roots	Crocodile River	-12.7	0.2	44.2	0.8
10561	KP489	*Eragrostis superba*	Whole	Crocodile River	-12.7	1.2	42.8	0.8
10525	KP450	*Eragrostis superba*	No Roots	Hlanganzwane	-14.3	3.0	44.3	1.4
10524-10526	KP452	*Eragrostis superba*	Roots	Hlanganzwane	-14.3	2.6	20.5	0.4
10588	KP526	*Euclea divinorum*	Leaves	Crocodile River	-27.2	0.8	50.0	1.1
10541	KP468	*Euclea divinorum*	Leaves	Hlanganzwane	-28.9	2.7	48.3	1.0
10548	KP475	Forb	No Roots	Crocodile River	-26.8	4.3	46.7	3.7
10549	KP476	Forb	No Roots	Crocodile River	-25.9	3.0	51.3	2.9
10550	KP477	Forb	Whole	Crocodile River	-26.4	4.0	43.4	2.4
10514	KP438	Forb	No Roots	Hlanganzwane	-26.5	4.4	41.2	1.5
10515	KP439	Forb	No Roots	Hlanganzwane	-26.4	4.8	39.9	1.5
10516	KP440	Forb	Whole	Hlanganzwane	-25.3	3.8	43.6	2.1
10630	KP574	Forb	Leaves	N'watimvambu R	-27.3	4.5	42.0	2.0
10633	KP577	Forb	No Roots	N'watimvambu R	-28.4	3.3	43.0	1.1
10596	KP534	Forb	Whole	Renosterkoppies	-27.1	9.2	41.4	2.1
10597	KP535	Forb	No Roots	Renosterkoppies	-26.8	8.2	37.3	1.6
10552	KP480	Geophyte	Leaves	Crocodile River	-26.5	4.8	43.4	4.4
10553	KP481	Geophyte	Bulbs	Crocodile River	-26.1	3.9	37.2	1.5
10589	KP527	*Grewia monticola*	Leaves	Crocodile River	-26.5	3.8	46.1	2.1
10590	KP528	*Grewia monticola*	Leaves	Crocodile River	-28.4	4.1	44.8	2.0
10667	KP621	*Grewia* sp.	Leaves	N'watimvambu R	-28.9	4.6	42.5	1.8
10668	KP622	*Grewia* sp.	Leaves	N'watimvambu R	-27.3	5.5	38.9	3.0
10626	KP570	*Grewia* sp.	Leaves	Renosterkoppies	-27.2	10.1	45.7	2.7
10627	KP571	*Grewia* sp.	Leaves	Renosterkoppies	-26.4	6.7	41.4	2.2
10591	KP529	*Gymnosporia* sp.	Leaves	Crocodile River	-26.5	1.9	45.4	0.9
10542	KP469	*Gymnosporia* sp.	Leaves	Hlanganzwane	-26.7	3.8	49.9	1.9
10543	KP470	*Gymnosporia* sp.	Leaves	Hlanganzwane	-27.5	2.8	50.6	1.2
10563	KP491	*Heteropogon contortus*	No Roots	Crocodile River	-12.5	1.5	43.4	0.5
10564	KP492	*Heteropogon contortus*	No Roots	Crocodile River	-13.1	2.1	44.0	0.6
10634	KP578	Legume Forb	Leaves	N'watimvambu R	-23.2	4.2	49.3	2.4
10636	KP580	Legume Forb	Whole	N'watimvambu R	-25.6	0.9	44.5	1.7
10600	KP538	Legume Forb	Leaves	Renosterkoppies	-25.8	6.1	43.8	3.7
10601	KP539	Legume Forb	Leaves	Renosterkoppies	-25.4	3.4	36.3	3.8

Appendix I D / continued

UCT #	Sample ID	Species	Part	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10544	KP471	*Lonchocarpus capassa*	Leaves	Hlanganzwane	-25.4	3.3	45.6	2.0
10545	KP472	*Lonchocarpus capassa*	Leaves	Hlanganzwane	-24.0	1.2	45.8	2.7
10649	KP598	*Melinis repens*	No Roots	N'watimvambu R	-12.3	4.2	43.4	1.2
10527	KP453	*Panicum coloratum*	Whole	Hlanganzwane	-13.8	2.1	43.6	1.1
10528	KP454	*Panicum coloratum*	Whole	Hlanganzwane	-12.5	2.6	40.4	0.9
10650	KP599	*Panicum coloratum*	Whole	N'watimvambu R	-12.1	4.5	41.0	1.2
10651	KP600	*Panicum coloratum*	No Roots	N'watimvambu R	-12.3	4.1	43.4	1.3
10652	KP601	*Panicum coloratum*	Leaves	N'watimvambu R	-11.7	4.9	43.6	1.1
10652	KP602	*Panicum coloratum*	Seeds	N'watimvambu R	-12.2	4.6	42.2	1.1
10615	KP557	*Panicum coloratum*	No Roots	Renosterkoppies	-12.0	5.8	41.3	0.8
10615	KP558	*Panicum coloratum*	Seeds	Renosterkoppies	-11.9	5.9	44.7	1.1
10613-10615	KP559	*Panicum coloratum*	Roots	Renosterkoppies	-13.0	5.7	40.7	0.9
10565	KP493	*Panicum maximum*	Leaves	Crocodile River	-12.8	3.6	41.4	1.1
10566	KP494	*Panicum maximum*	No Roots	Crocodile River	-12.5	2.9	42.9	0.4
10567	KP495	*Panicum maximum*	Leaves	Crocodile River	-12.9	4.5	39.5	1.2
10565-10567	KP496	*Panicum maximum*	Roots	Crocodile River	-12.0	2.5	43.7	0.8
10567	KP498	*Panicum maximum*	Seeds	Crocodile River	-12.4	3.1	42.3	2.9
10529	KP455	*Panicum maximum*	Whole	Hlanganzwane	-12.7	3.7	47.1	1.6
10572	KP503	*Phragmites australis*	Leaves	Crocodile River	-27.4	8.1	42.6	1.5
10572	KP504	*Phragmites australis*	Stems	Crocodile River	-27.0	4.6	45.6	0.3
10573	KP505	*Phragmites australis*	Leaves	Crocodile River	-27.1	7.7	41.8	1.4
10573	KP506	*Phragmites australis*	Stems	Crocodile River	-27.1	4.2	49.8	0.7
10573	KP507	*Phragmites australis*	Roots	Crocodile River	-26.1	6.3	42.2	0.8
10568	KP499	*Schmidtia pappophoroides*	No Roots	Crocodile River	-12.4	1.5	40.9	0.7
10592	KP530	*Securinega virosa*	Leaves	Crocodile River	-26.4	3.8	45.5	1.6
10551	KP478	*Solanum* sp.	Whole	Crocodile River	-28.1	2.5	40.0	1.4
10551	KP479	*Solanum* sp.	Fruit	Crocodile River	-26.1	2.2	54.6	1.9
10639	KP583	*Solanum* sp.	Leaves	N'watimvambu R	-26.8	4.1	44.8	2.9
10640	KP584	*Solanum* sp.	Roots	N'watimvambu R	-26.3	2.4	42.1	0.9
10602	KP540	*Solanum* sp.	No Roots	Renosterkoppies	-27.5	6.8	41.2	2.7
10603	KP541	*Solanum* sp.	Leaves	Renosterkoppies	-27.6	9.6	42.4	3.4
10603	KP542	*Solanum* sp.	Roots	Renosterkoppies	-26.8	7.0	47.0	1.2
10603	KP543	*Solanum* sp.	Stems	Renosterkoppies	-28.4	6.4	42.8	1.1
10670	KP624	*Spirostachys africana*	Leaves	N'watimvambu R	-24.9	3.8	41.9	1.9
10671	KP625	*Spirostachys africana*	Leaves	N'watimvambu R	-25.3	5.3	42.5	1.7
10571	KP502	*Themeda triandra*	Whole	Crocodile River	-12.0	2.5	49.0	0.8
10532	KP458	*Themeda triandra*	No Roots	Hlanganzwane	-12.9	3.1	42.0	1.0
10531-10532	KP459	*Themeda triandra*	Roots	Hlanganzwane	-11.5	2.3	39.1	0.9
10616	KP560	*Urochloa mossambicensis*	No Roots	Renosterkoppies	-13.5	6.3	38.5	1.1
10617	KP561	*Urochloa mossambicensis*	Whole	Renosterkoppies	-12.6	6.2	39.8	1.3
10594	KP532	*Ziziphus mucronata*	Leaves	Crocodile River	-25.8	2.8	43.2	1.7
10595	KP533	*Ziziphus mucronata*	Leaves	Crocodile River	-27.8	4.1	42.0	2.5
10628	KP572	*Ziziphus mucronata*	Leaves	Renosterkoppies	-25.4	7.6	45.2	2.4
10629	KP573	*Ziziphus mucronata*	Leaves	Renosterkoppies	-24.9	8.5	44.5	2.9

Appendix II A. Data for Mammal Faeces from the Waterberg, Collected In September 2002.

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9542	WF003	*Aepyceros melampus*	Keg and Fig	-21.9	4.4	43.5	1.3
9543	WF004	*Aepyceros melampus*	Keg and Fig	-13.9	3.7	45.2	1.1
9556	WF001	*Aepyceros melampus*	Motswedi	-24.2	6.4	44.2	1.7
9557	WF002	*Aepyceros melampus*	Motswedi	-22.4	6.0	45.3	1.6
9717	ZF001	*Aepyceros melampus*	Zoetfontein	-22.1	4.7	40.2	1.4
9718	ZF002	*Aepyceros melampus*	Zoetfontein	-21.3	5.9	44.7	1.4
9735	ZF003	*Aepyceros melampus*	Zoetfontein	-24.3	5.9	45.6	1.5
9736	ZF004	*Aepyceros melampus*	Zoetfontein	-25.0	5.7	45.7	1.5
9749	ZF005	*Aepyceros melampus*	Zoetfontein	-16.0	4.7	40.0	1.1
9750	ZF006	*Aepyceros melampus*	Zoetfontein	-16.1	4.8	42.5	1.1
9536	WF007	*Ceratotherium simum*	Keg and Fig	-14.5	3.5	43.3	0.8
9546	WF005	*Ceratotherium simum*	Motswedi	-14.7	4.7	37.4	1.1
9547	WF006	*Ceratotherium simum*	Motswedi	-14.1	5.8	33.7	0.9
9567	WF008	*Connochaetes taurinus*	Bushman's Painting	-13.6	4.6	49.1	1.4
9568	WF009	*Connochaetes taurinus*	Bushman's Painting	-13.8	4.4	46.5	1.1
9569	WF010	*Connochaetes taurinus*	Bushman's Painting	-13.8	4.8	48.1	1.2
9570	WF011	*Connochaetes taurinus*	Bushman's Painting	-13.7	4.6	48.6	1.1
9538	WF012	*Connochaetes taurinus*	Keg and Fig	-14.4	3.8	43.4	0.9
9706	ZF007	*Connochaetes taurinus*	Zoetfontein	-14.6	6.3	40.0	0.9
9712	ZF008	*Connochaetes taurinus*	Zoetfontein	-13.9	4.8	42.8	0.8
9755	ZF009	*Connochaetes taurinus*	Zoetfontein	-14.9	5.5	47.3	1.0
9738	ZF010	*Connochaetes taurinus*	Zoetfontein	-13.7	4.6	41.5	0.7
9744	ZF011	*Connochaetes taurinus*	Zoetfontein	-14.1	4.8	48.7	0.9
9746	ZF012	*Connochaetes taurinus*	Zoetfontein	-15.6	4.9	49.4	0.9
9747	ZF013	*Connochaetes taurinus*	Zoetfontein	-13.9	4.4	45.0	0.7
9748	ZF014	*Connochaetes taurinus*	Zoetfontein	-14.6	5.3	45.3	1.0
9777	ZF015	*Connochaetes taurinus*	Zoetfontein	-14.5	4.5	43.1	0.9
9779	ZF016	*Connochaetes taurinus*	Zoetfontein	-15.2	4.5	45.9	0.9
9562	WF013	*Equus burchellii*	Bushman's Painting	-13.9	3.2	47.0	0.8
9563	WF014	*Equus burchellii*	Bushman's Painting	-14.4	2.9	46.6	0.9
9531	WF018	*Equus burchellii*	Keg and Fig	-13.3	6.2	33.9	1.0
9532	WF019	*Equus burchellii*	Keg and Fig	-13.3	5.0	34.1	0.8
9548	WF015	*Equus burchellii*	Motswedi	-13.5	4.2	44.0	1.3
9549	WF016	*Equus burchellii*	Motswedi	-15.5	4.2	47.3	0.8
9550	WF017	*Equus burchellii*	Motswedi	-14.5	4.2	40.7	0.8
9708	ZF017	*Equus burchellii*	Zoetfontein	-14.5	3.9	46.3	0.8
9709	ZF018	*Equus burchellii*	Zoetfontein	-14.8	3.5	46.7	0.8
9710	ZF019	*Equus burchellii*	Zoetfontein	-13.8	3.8	43.5	0.8
9724	ZF020	*Equus burchellii*	Zoetfontein	-13.7	5.3	45.3	0.9
9725	ZF021	*Equus burchellii*	Zoetfontein	-13.7	3.8	48.3	0.9
9739	ZF022	*Equus burchellii*	Zoetfontein	-13.8	3.6	46.1	0.7
9740	ZF023	*Equus burchellii*	Zoetfontein	-13.9	3.9	48.0	0.7
9771	ZF024	*Equus burchellii*	Zoetfontein	-14.0	3.9	44.3	0.8

Appendix II A / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9772	ZF025	*Equus burchellii*	Zoetfontein	-14.3	3.6	46.2	0.8
9773	ZF026	*Equus burchellii*	Zoetfontein	-14.0	3.3	44.9	0.8
9774	ZF027	*Equus burchellii*	Zoetfontein	-14.1	4.2	48.5	0.8
9551	WF020	*Giraffa camelopardalis*	Motswedi	-25.7	4.7	50.0	1.9
9552	WF021	*Giraffa camelopardalis*	Motswedi	-26.2	4.6	47.6	1.7
9553	WF022	*Giraffa camelopardalis*	Motswedi	-25.6	5.2	47.8	1.9
9554	WF023	*Giraffa camelopardalis*	Motswedi	-25.4	6.4	47.6	1.8
9545	WF028	*Hyaena brunnea*	Keg and Fig	-17.6	6.7	4.0	0.5
9559	WF025	*Hyaena brunnea*	Motswedi	-13.3	6.5	6.1	0.7
9560	WF026	*Hyaena brunnea*	Motswedi	-14.7	6.8	6.1	0.7
9561	WF027	*Hyaena brunnea*	Motswedi	-12.9	6.8	5.3	0.7
9585	WF024	*Hyaena brunnea*	Mziki	-18.8	7.2	9.9	1.2
9783	ZF029	*Hyaena brunnea*	Zoetfontein	-17.3	8.7	6.8	1.8
9784	ZF030	*Hyaena brunnea*	Zoetfontein	-16.5	8.7	7.5	0.9
9544	WF030	*Hystrix africaeaustralis*	Keg and Fig	-24.7	3.9	43.4	2.1
9558	WF029	*Hystrix africaeaustralis*	Motswedi	-23.6	4.6	38.8	1.8
9720	ZF031	*Hystrix africaeaustralis*	Zoetfontein	-25.6	5.2	41.5	1.8
9737	ZF032	*Hystrix africaeaustralis*	Zoetfontein	-25.2	5.2	33.5	1.8
9753	ZF033	*Hystrix africaeaustralis*	Zoetfontein	-23.5	5.2	39.8	1.9
9754	ZF034	*Hystrix africaeaustralis*	Zoetfontein	-23.6	5.5	40.2	2.1
9782	ZF035	*Hystrix africaeaustralis*	Zoetfontein	-23.1	5.9	36.7	2.0
9565	WF031	*Kobus ellipsiprymnus*	Bushman's Painting	-14.0	4.2	48.1	1.3
9721	ZF036	Mongoose	Zoetfontein	-21.7	5.1	33.6	5.5
9734	ZF037	*Oreotragus oreotragus*	Zoetfontein	-24.6	5.9	42.5	1.8
9766	ZF038	*Oreotragus oreotragus*	Zoetfontein	-25.8	5.5	46.5	1.6
9711	ZF039	*Oryx gazella*	Zoetfontein	-15.3	3.3	49.5	1.1
9728	ZF040	*Oryx gazella*	Zoetfontein	-13.8	5.0	44.5	0.8
9760	ZF041	*Oryx gazella*	Zoetfontein	-13.8	5.0	49.5	0.8
9743	ZF042	*Oryx gazella*	Zoetfontein	-14.7	4.7	47.4	1.0
9785	ZF043	*Panthera pardus*	Zoetfontein	-17.4	8.4	38.8	6.6
9480	WF132	*Papio ursinus*	Bushman's Painting	-19.9	3.5	74.4	3.1
9481	WF133	*Papio ursinus*	Bushman's Painting	-19.0	3.3	77.3	3.4
9482	WF134	*Papio ursinus*	Bushman's Painting	-19.6	3.7	72.0	3.0
9483	WF135	*Papio ursinus*	Bushman's Painting	-20.6	3.7	75.6	4.4
9484	WF136	*Papio ursinus*	Bushman's Painting	-21.1	3.7	69.6	3.7
9485	WF137	*Papio ursinus*	Bushman's Painting	-21.4	3.5	64.6	3.5
9486	WF138	*Papio ursinus*	Bushman's Painting	-19.5	2.8	78.5	2.5
9487	WF139	*Papio ursinus*	Bushman's Painting	-18.0	2.9	74.1	2.6
9488	WF140	*Papio ursinus*	Bushman's Painting	-21.6	3.8	71.6	3.7
9489	WF141	*Papio ursinus*	Bushman's Painting	-19.6	3.0	75.7	2.1
9490	WF142	*Papio ursinus*	Bushman's Painting	-20.1	3.5	75.2	3.3
9491	WF143	*Papio ursinus*	Bushman's Painting	-20.4	3.2	68.8	3.5
9492	WF144	*Papio ursinus*	Bushman's Painting	-20.0	2.8	70.6	2.9

Appendix II A / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9493	WF145	*Papio ursinus*	Bushman's Painting	-18.6	3.4	72.9	2.3
9494	WF146	*Papio ursinus*	Bushman's Painting	-19.0	3.6	70.4	2.9
9495	WF147	*Papio ursinus*	Bushman's Painting	-19.2	2.7	63.6	3.8
9496	WF148	*Papio ursinus*	Bushman's Painting	-21.6	3.1	62.9	4.2
9497	WF149	*Papio ursinus*	Bushman's Painting	-19.4	3.0	68.2	3.1
9498	WF150	*Papio ursinus*	Bushman's Painting	-19.1	3.0	71.5	3.5
9499	WF151	*Papio ursinus*	Bushman's Painting	-20.0	4.2	73.3	2.3
9500	WF152	*Papio ursinus*	Bushman's Painting	-20.2	3.6	77.3	3.3
9501	WF153	*Papio ursinus*	Bushman's Painting	-19.7	3.6	70.6	3.8
9502	WF154	*Papio ursinus*	Bushman's Painting	-20.1	4.3	72.2	3.7
9503	WF155	*Papio ursinus*	Bushman's Painting	-18.3	2.9	64.5	3.2
9504	WF156	*Papio ursinus*	Bushman's Painting	-20.0	3.3	65.4	3.2
9475	WF177	*Papio ursinus*	Motswedi	-19.9	3.4	49.2	2.2
9476	WF178	*Papio ursinus*	Motswedi	-20.3	3.4	65.0	2.6
9477	WF179	*Papio ursinus*	Motswedi	-22.7	1.8	57.2	2.5
9478	WF180	*Papio ursinus*	Motswedi	-22.6	7.5	63.0	4.6
9479	WF181	*Papio ursinus*	Motswedi	-21.7	4.8	49.7	2.0
9505	WF157	*Papio ursinus*	Mziki	-21.0	2.2	67.0	2.9
9506	WF158	*Papio ursinus*	Mziki	-23.2	2.5	76.0	2.9
9507	WF159	*Papio ursinus*	Mziki	-22.5	2.8	75.1	3.3
9508	WF160	*Papio ursinus*	Mziki	-23.4	3.9	45.1	2.0
9509	WF161	*Papio ursinus*	Mziki	-22.2	2.7	75.0	3.1
9510	WF162	*Papio ursinus*	Mziki	-25.4	3.7	58.2	2.2
9511	WF163	*Papio ursinus*	Mziki	-21.0	3.0	77.0	2.3
9512	WF164	*Papio ursinus*	Mziki	-21.7	3.1	54.1	2.3
9513	WF165	*Papio ursinus*	Mziki	-19.8	3.1	73.7	2.5
9514	WF166	*Papio ursinus*	Mziki	-19.6	3.3	43.5	1.5
9515	WF167	*Papio ursinus*	Mziki	-19.6	2.6	68.6	3.0
9516	WF168	*Papio ursinus*	Mziki	-19.2	2.3	57.7	1.5
9517	WF169	*Papio ursinus*	Mziki	-20.1	2.4	56.0	1.7
9518	WF170	*Papio ursinus*	Mziki	-21.3	2.4	62.6	2.1
9519	WF171	*Papio ursinus*	Mziki	-23.2	2.2	79.9	2.6
9520	WF172	*Papio ursinus*	Mziki	-21.6	2.5	50.3	2.5
9521	WF173	*Papio ursinus*	Mziki	-22.2	2.5	57.0	2.3
9522	WF174	*Papio ursinus*	Mziki	-21.2	7.6	70.0	4.8
9523	WF175	*Papio ursinus*	Mziki	-21.0	2.3	50.6	1.8
9524	WF176	*Papio ursinus*	Mziki	-21.3	2.6	56.7	2.2
9525	WF182	*Papio ursinus*	Nalana	-18.2	4.2	58.8	2.4
9526	WF183	*Papio ursinus*	Nalana	-18.6	3.1	59.1	2.0
9527	WF184	*Papio ursinus*	Nalana	-17.0	4.8	57.4	2.1
9528	WF185	*Papio ursinus*	Nalana	-22.1	3.2	69.9	2.8
9529	WF186	*Papio ursinus*	Nalana	-18.1	6.4	65.0	3.1
9530	WF187	*Papio ursinus*	Nalana	-16.5	6.7	68.0	2.0

Appendix II A / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9455	WF188	*Papio ursinus*	Tshetshepi	-19.5	7.4	73.7	2.5
9456	WF189	*Papio ursinus*	Tshetshepi	-22.0	7.4	77.3	2.0
9457	WF190	*Papio ursinus*	Tshetshepi	-21.2	3.7	51.5	2.0
9458	WF191	*Papio ursinus*	Tshetshepi	-21.0	3.8	42.0	1.9
9459	WF192	*Papio ursinus*	Tshetshepi	-20.3	3.6	48.0	1.9
9460	WF193	*Papio ursinus*	Tshetshepi	-21.2	3.7	75.6	2.2
9461	WF194	*Papio ursinus*	Tshetshepi	-18.4	3.5	65.7	1.9
9462	WF195	*Papio ursinus*	Tshetshepi	-20.5	4.2	74.3	2.0
9463	WF196	*Papio ursinus*	Tshetshepi	-19.0	3.6	65.3	1.6
9464	WF197	*Papio ursinus*	Tshetshepi	-21.3	3.4	65.2	1.6
9465	WF198	*Papio ursinus*	Tshetshepi	-24.0	4.1	67.8	1.7
9466	WF199	*Papio ursinus*	Tshetshepi	-19.5	4.1	63.4	2.0
9467	WF200	*Papio ursinus*	Tshetshepi	-20.8	3.6	68.7	2.0
9468	WF201	*Papio ursinus*	Tshetshepi	-23.7	4.1	68.2	2.3
9469	WF202	*Papio ursinus*	Tshetshepi	-21.4	3.5	71.1	2.3
9470	WF203	*Papio ursinus*	Tshetshepi	-22.3	4.0	51.8	2.3
9471	WF204	*Papio ursinus*	Tshetshepi	-21.2	3.5	52.4	2.0
9472	WF205	*Papio ursinus*	Tshetshepi	-21.1	3.6	46.8	2.0
9473	WF206	*Papio ursinus*	Tshetshepi	-20.6	3.6	47.8	1.7
9474	WF207	*Papio ursinus*	Tshetshepi	-20.9	4.1	47.7	2.1
9586	ZF044	*Papio ursinus*	Zoetfontein	-24.1	2.7	57.8	3.9
9587	ZF045	*Papio ursinus*	Zoetfontein	-22.5	3.5	66.8	3.0
9588	ZF046	*Papio ursinus*	Zoetfontein	-25.1	4.2	70.1	4.3
9589	ZF047	*Papio ursinus*	Zoetfontein	-24.3	3.9	66.6	3.1
9590	ZF048	*Papio ursinus*	Zoetfontein	-22.3	2.9	75.5	4.2
9614	ZF049	*Papio ursinus*	Zoetfontein	-23.6	3.8	51.7	3.1
9615	ZF050	*Papio ursinus*	Zoetfontein	-23.2	4.5	50.1	2.5
9616	ZF051	*Papio ursinus*	Zoetfontein	-24.4	4.6	54.9	3.1
9617	ZF052	*Papio ursinus*	Zoetfontein	-20.1	4.4	53.1	2.4
9618	ZF053	*Papio ursinus*	Zoetfontein	-22.2	4.0	50.8	3.4
9621	ZF054	*Papio ursinus*	Zoetfontein	-22.3	3.8	42.3	2.6
9622	ZF055	*Papio ursinus*	Zoetfontein	-23.1	4.2	48.8	3.1
9623	ZF056	*Papio ursinus*	Zoetfontein	-22.0	3.7	50.7	2.9
9624	ZF057	*Papio ursinus*	Zoetfontein	-23.7	4.2	51.9	2.9
9625	ZF058	*Papio ursinus*	Zoetfontein	-23.2	3.6	51.3	3.6
9626	ZF059	*Papio ursinus*	Zoetfontein	-23.0	4.1	53.7	3.4
9627	ZF060	*Papio ursinus*	Zoetfontein	-23.5	2.0	46.1	3.3
9628	ZF061	*Papio ursinus*	Zoetfontein	-22.5	2.4	45.7	3.5
9629	ZF062	*Papio ursinus*	Zoetfontein	-24.0	5.2	52.6	3.4
9630	ZF063	*Papio ursinus*	Zoetfontein	-25.2	3.5	48.6	3.0
9642	ZF064	*Papio ursinus*	Zoetfontein	-20.6	4.9	49.8	2.1
9643	ZF065	*Papio ursinus*	Zoetfontein	-24.2	6.9	43.9	1.7
9644	ZF066	*Papio ursinus*	Zoetfontein	-24.6	4.6	51.2	2.8
9645	ZF067	*Papio ursinus*	Zoetfontein	-22.9	5.0	49.8	2.6

Appendix II A / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9646	ZF068	*Papio ursinus*	Zoetfontein	-23.0	3.6	43.9	2.7
9647	ZF069	*Papio ursinus*	Zoetfontein	-24.6	5.4	36.4	2.2
9648	ZF070	*Papio ursinus*	Zoetfontein	-23.9	5.5	49.3	2.2
9649	ZF071	*Papio ursinus*	Zoetfontein	-24.4	5.2	37.6	1.8
9650	ZF072	*Papio ursinus*	Zoetfontein	-24.5	5.5	34.0	2.2
9651	ZF073	*Papio ursinus*	Zoetfontein	-24.4	4.9	52.0	2.5
9661	ZF074	*Papio ursinus*	Zoetfontein	-24.7	5.8	53.2	1.5
9662	ZF075	*Papio ursinus*	Zoetfontein	-23.9	4.9	54.7	2.2
9663	ZF076	*Papio ursinus*	Zoetfontein	-23.8	5.3	54.6	2.7
9664	ZF077	*Papio ursinus*	Zoetfontein	-23.0	4.6	52.1	3.4
9665	ZF078	*Papio ursinus*	Zoetfontein	-23.6	4.9	51.8	2.6
9666	ZF079	*Papio ursinus*	Zoetfontein	-23.5	4.4	51.7	2.7
9667	ZF080	*Papio ursinus*	Zoetfontein	-24.6	5.6	55.8	2.7
9668	ZF081	*Papio ursinus*	Zoetfontein	-21.9	5.4	52.0	2.2
9669	ZF082	*Papio ursinus*	Zoetfontein	-24.1	5.1	44.1	2.6
9670	ZF083	*Papio ursinus*	Zoetfontein	-24.7	4.6	49.2	3.3
9686	ZF084	*Papio ursinus*	Zoetfontein	-23.6	5.7	53.3	2.1
9687	ZF085	*Papio ursinus*	Zoetfontein	-21.7	3.9	47.4	2.7
9688	ZF086	*Papio ursinus*	Zoetfontein	-21.0	3.9	74.8	2.1
9689	ZF087	*Papio ursinus*	Zoetfontein	-23.8	3.7	64.3	3.5
9690	ZF088	*Papio ursinus*	Zoetfontein	-23.2	3.9	74.4	4.0
9691	ZF089	*Papio ursinus*	Zoetfontein	-19.4	4.4	70.3	2.3
9692	ZF090	*Papio ursinus*	Zoetfontein	-23.3	5.3	72.9	3.9
9693	ZF091	*Papio ursinus*	Zoetfontein	-23.3	4.4	70.4	3.8
9694	ZF092	*Papio ursinus*	Zoetfontein	-23.3	4.2	69.6	2.8
9695	ZF093	*Papio ursinus*	Zoetfontein	-23.0	3.5	68.9	4.0
9726	ZF094	*Phacochoerus aethiopicus*	Zoetfontein	-13.4	4.2	44.9	1.1
9727	ZF095	*Phacochoerus aethiopicus*	Zoetfontein	-12.6	3.7	44.3	0.9
9583	WF208	*Potamochoerus porcus*	Mziki	-19.7	3.7	29.4	1.2
9584	WF209	*Potamochoerus porcus*	Mziki	-19.8	3.9	45.9	2.0
9564	WF210	*Syncerus caffer*	Bushman's Painting	-14.3	3.8	46.8	1.0
9534	WF211	*Syncerus caffer*	Keg and Fig	-14.9	3.8	45.4	1.1
9535	WF212	*Syncerus caffer*	Keg and Fig	-15.3	3.6	45.9	1.1
9580	WF213	*Tragelaphus scriptus*	Mziki	-26.7	4.1	48.2	2.0
9537	WF214	*Tragelaphus strepsiceros*	Keg and Fig	-26.6	3.6	49.0	1.6
9539	WF215	*Tragelaphus strepsiceros*	Keg and Fig	-26.8	3.6	52.8	2.0
9540	WF216	*Tragelaphus strepsiceros*	Keg and Fig	-27.1	4.0	53.9	2.1
9707	ZF098	*Tragelaphus strepsiceros*	Zoetfontein	-25.9	5.0	50.0	1.8
9713	ZF099	*Tragelaphus strepsiceros*	Zoetfontein	-25.6	5.0	42.7	1.7
9714	ZF100	*Tragelaphus strepsiceros*	Zoetfontein	-24.6	5.2	44.5	2.3
9715	ZF101	*Tragelaphus strepsiceros*	Zoetfontein	-25.2	5.3	50.8	2.0
9716	ZF102	*Tragelaphus strepsiceros*	Zoetfontein	-26.1	5.6	44.1	1.8
9722	ZF103	*Tragelaphus strepsiceros*	Zoetfontein	-23.5	5.7	47.3	1.8

Appendix II A / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
9723	ZF104	*Tragelaphus strepsiceros*	Zoetfontein	-24.4	5.5	46.6	1.6
9745	ZF105	*Tragelaphus strepsiceros*	Zoetfontein	-25.8	5.4	48.1	1.6
9776	ZF106	*Tragelaphus strepsiceros*	Zoetfontein	-25.6	5.6	50.6	1.8
9778	ZF107	*Tragelaphus strepsiceros*	Zoetfontein	-24.4	6.2	49.4	1.9
9780	ZF108	*Tragelaphus strepsiceros*	Zoetfontein	-26.4	5.5	47.7	1.7
9781	ZF109	*Tragelaphus strepsiceros*	Zoetfontein	-25.5	5.6	47.9	1.9

Appendix II B. Data for Mammal Faeces from the Waterberg, Collected in January 2003.

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10197	WF218	*Aepyceros melampus*	Keg and Fig	-17.2	5.3	42.1	1.4
10198	WF219	*Aepyceros melampus*	Middle Dam	-17.1	6.0	44.4	1.9
10199	WF220	*Aepyceros melampus*	Middle Dam	-14.0	4.7	42.5	1.2
10196	WF217	*Aepyceros melampus*	Random	-15.6	6.6	43.6	1.7
10200	WF221	*Alcelaphus buselaphus*	Random	-14.5	6.3	44.5	1.2
10201	WF222	*Ceratotherium simum*	Random	-14.7	4.7	32.4	0.9
10202	WF223	*Connochaetes taurinus*	Keg and Fig	-15.5	6.7	38.9	1.7
10203	WF224	*Connochaetes taurinus*	Middle Dam	-13.8	4.3	41.2	1.1
10322	WF349	*Connochaetes taurinus*	Random	-15.0	5.3	42.5	1.0
10323	WF350	*Connochaetes taurinus*	Random	-16.3	5.5	39.9	1.3
10205	WF226	*Equus burchellii*	Bushman's Painting	-13.5	4.3	43.9	0.7
10206	WF227	*Equus burchellii*	Mziki	-12.3	4.7	39.5	0.8
10204	WF225	*Equus burchellii*	Random	-13.3	4.6	41.2	0.9
10212	WF233	*Giraffa camelopardalis*	Motswedi	-25.2	5.7	51.9	1.9
10207	WF228	*Giraffa camelopardalis*	Random	-26.8	3.6	46.9	2.5
10208	WF229	*Giraffa camelopardalis*	Random	-26.4	4.6	47.1	1.9
10209	WF230	*Giraffa camelopardalis*	Random	-26.3	4.4	49.9	2.0
10211	WF232	*Giraffa camelopardalis*	Random	-26.1	4.7	50.9	2.6
10210	WF231	*Kobus ellipsiprymnus*	Random	-14.4	4.6	45.3	1.0
10252	WF278	Mongoose	Random	-16.7	6.6	13.0	2.0
10253	WF279	*Papio ursinus*	Bushman's Painting	-22.1	4.7	36.0	2.4
10254	WF280	*Papio ursinus*	Bushman's Painting	-22.7	3.9	46.1	1.9
10255	WF281	*Papio ursinus*	Bushman's Painting	-20.2	3.9	39.4	2.1
10256	WF282	*Papio ursinus*	Bushman's Painting	-18.5	5.2	33.9	2.0
10257	WF283	*Papio ursinus*	Bushman's Painting	-21.5	3.0	47.2	2.2
10258	WF284	*Papio ursinus*	Bushman's Painting	-17.6	3.7	44.9	1.8
10259	WF285	*Papio ursinus*	Bushman's Painting	-21.0	3.7	46.2	2.3
10260	WF286	*Papio ursinus*	Bushman's Painting	-20.8	5.1	40.4	2.1
10261	WF287	*Papio ursinus*	Bushman's Painting	-19.7	4.1	44.6	2.4
10262	WF288	*Papio ursinus*	Bushman's Painting	-21.7	3.7	46.3	3.5
10263	WF289	*Papio ursinus*	Bushman's Painting	-20.2	4.1	46.8	2.5
10264	WF290	*Papio ursinus*	Bushman's Painting	-20.3	3.6	44.6	2.1
10265	WF291	*Papio ursinus*	Bushman's Painting	-22.2	3.1	50.7	2.1
10266	WF292	*Papio ursinus*	Bushman's Painting	-22.4	4.6	44.8	2.2
10267	WF293	*Papio ursinus*	Bushman's Painting	-25.2	3.8	49.4	2.8
10268	WF294	*Papio ursinus*	Bushman's Painting	-19.9	4.0	41.6	2.8
10269	WF295	*Papio ursinus*	Bushman's Painting	-17.7	3.7	45.4	2.2
10270	WF296	*Papio ursinus*	Bushman's Painting	-21.7	3.9	39.8	2.1
10271	WF297	*Papio ursinus*	Bushman's Painting	-21.5	3.4	45.1	2.5
10272	WF298	*Papio ursinus*	Bushman's Painting	-22.4	3.0	43.5	2.7
10273	WF299	*Papio ursinus*	Mziki	-21.0	4.8	40.6	2.6
10274	WF300	*Papio ursinus*	Mziki	-22.8	4.3	47.9	2.7
10275	WF301	*Papio ursinus*	Mziki	-20.8	5.1	34.2	2.1

Appendix II B / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10276	WF302	*Papio ursinus*	Mziki	-20.6	4.3	42.8	2.3
10277	WF303	*Papio ursinus*	Mziki	-19.2	5.8	39.1	2.1
10278	WF304	*Papio ursinus*	Mziki	-20.4	4.1	41.9	2.1
10279	WF305	*Papio ursinus*	Mziki	-23.0	3.7	50.2	2.5
10280	WF306	*Papio ursinus*	Mziki	-20.3	3.5	48.8	2.1
10281	WF307	*Papio ursinus*	Mziki	-22.8	5.0	42.5	3.1
10282	WF308	*Papio ursinus*	Mziki	-20.7	3.6	44.7	2.5
10283	WF309	*Papio ursinus*	Mziki	-23.9	4.4	45.5	2.8
10284	WF310	*Papio ursinus*	Mziki	-21.2	3.8	43.5	2.0
10285	WF311	*Papio ursinus*	Mziki	-19.4	3.8	43.3	2.1
10286	WF312	*Papio ursinus*	Mziki	-23.5	4.0	49.3	2.7
10287	WF313	*Papio ursinus*	Mziki	-19.9	3.7	48.6	2.3
10288	WF314	*Papio ursinus*	Mziki	-23.2	4.6	45.4	2.9
10289	WF315	*Papio ursinus*	Mziki	-20.5	4.6	40.3	2.1
10290	WF316	*Papio ursinus*	Mziki	-21.0	3.6	41.4	2.5
10291	WF317	*Papio ursinus*	Mziki	-21.4	5.6	33.9	2.4
10292	WF318	*Papio ursinus*	Mziki	-21.2	3.9	42.6	2.2
10293	WF319	*Papio ursinus*	Tshetshepi	-20.8	3.9	42.8	2.5
10294	WF320	*Papio ursinus*	Tshetshepi	-20.1	3.7	43.9	1.9
10295	WF321	*Papio ursinus*	Tshetshepi	-19.6	3.4	44.8	1.9
10296	WF322	*Papio ursinus*	Tshetshepi	-23.9	3.8	44.9	2.6
10297	WF323	*Papio ursinus*	Tshetshepi	-21.1	3.6	41.8	2.9
10298	WF324	*Papio ursinus*	Tshetshepi	-20.1	4.0	44.2	1.6
10299	WF325	*Papio ursinus*	Tshetshepi	-21.6	2.9	44.4	2.0
10300	WF326	*Papio ursinus*	Tshetshepi	-22.8	3.8	43.0	2.4
10301	WF327	*Papio ursinus*	Tshetshepi	-20.7	4.6	44.7	1.2
10302	WF328	*Papio ursinus*	Tshetshepi	-23.3	5.4	43.2	4.0
10303	WF329	*Papio ursinus*	Tshetshepi	-23.9	2.9	47.8	2.5
10304	WF330	*Papio ursinus*	Tshetshepi	-22.1	3.2	45.8	2.3
10305	WF331	*Papio ursinus*	Tshetshepi	-19.1	2.2	42.8	1.9
10306	WF332	*Papio ursinus*	Tshetshepi	-20.3	3.6	45.0	2.0
10307	WF334	*Papio ursinus*	Tshetshepi	-19.3	2.6	38.8	2.4
10308	WF335	*Papio ursinus*	Tshetshepi	-24.4	4.9	41.5	3.3
10309	WF336	*Papio ursinus*	Tshetshepi	-19.0	3.6	45.9	1.5
10310	WF337	*Papio ursinus*	Tshetshepi	-21.8	3.4	42.0	2.0
10311	WF338	*Papio ursinus*	Tshetshepi	-19.6	3.0	41.2	2.2
10312	WF339	*Potamochoerus porcus*	S48	-24.5	3.7	43.3	2.0
10316	WF343	*Syncerus cafer*	Mziki	-15.8	5.2	43.0	1.1
10314	WF341	*Syncerus cafer*	Random	-14.5	6.5	38.6	1.3
10315	WF342	*Syncerus cafer*	Random	-15.2	5.7	43.3	1.4
10317	WF344	*Taurotragus oryx*	Random	-26.8	5.9	45.0	2.1
10318	WF345	*Taurotragus oryx*	Random	-26.8	4.8	44.3	2.1
10319	WF346	*Taurotragus oryx*	Random	-26.9	6.0	43.4	1.9

Appendix II B / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10320	WF347	*Taurotragus oryx*	Random	-27.2	6.3	47.7	2.1
10321	WF348	*Tragelaphus strepsiceros*	Random	-26.9	4.7	48.3	2.5
10324	WF351	*Tragelaphus strepsiceros*	Random	-26.3	5.1	48.1	2.5

Appendix II C. Data for Mammal Faeces from the Kruger National Park, Collected in June 2002.

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
8592	KF089	*Aepyceros melampus*	Crocodile River	-23.9	3.5	65.7	2.5
8593	KF090	*Aepyceros melampus*	Crocodile River	-18.0	2.8	58.5	2.0
8594	KF091	*Aepyceros melampus*	Crocodile River	-23.0	2.8	62.3	2.5
8595	KF092	*Aepyceros melampus*	Crocodile River	-22.9	3.3	57.6	2.4
8586	KF083	*Giraffa camelopardalis*	Crocodile River	-26.4	3.1	60.0	2.7
8587	KF084	*Giraffa camelopardalis*	Crocodile River	-26.6	5.1	67.4	3.1
8588	KF085	*Giraffa camelopardalis*	Crocodile River	-27.2	3.8	70.9	3.0
8589	KF086	*Phacochoerus aethiopicus*	Crocodile River	-14.6	2.6	50.5	1.6
8590	KF087	*Phacochoerus aethiopicus*	Crocodile River	-14.5	3.5	48.2	1.3
8591	KF088	*Phacochoerus aethiopicus*	Crocodile River	-13.9	3.3	48.1	1.5
8596	KF093	*Syncerus caffer*	Crocodile River	-14.3	2.6	54.4	1.3
8597	KF094	*Syncerus caffer*	Crocodile River	-15.1	4.3	56.2	1.3
8598	KF095	*Syncerus caffer*	Crocodile River	-14.5	2.2	61.2	1.1
8599	KF096	*Syncerus caffer*	Crocodile River	-14.5	2.5	59.2	1.3
8600	KF097	*Syncerus caffer*	Crocodile River	-14.6	1.9	59.6	1.1
8561	KF058	*Aepyceros melampus*	Hlanganzwane	-17.9	3.6	55.7	1.6
8562	KF059	*Aepyceros melampus*	Hlanganzwane	-16.4	4.4	53.1	1.4
8563	KF060	*Aepyceros melampus*	Hlanganzwane	-16.7	4.7	58.1	1.4
8564	KF061	*Aepyceros melampus*	Hlanganzwane	-20.0	3.9	57.7	1.8
8565	KF062	*Aepyceros melampus*	Hlanganzwane	-17.2	3.7	56.7	1.5
8572	KF069	*Equus burchellii*	Hlanganzwane	-13.7	2.8	51.9	0.8
8573	KF070	*Equus burchellii*	Hlanganzwane	-14.3	2.5	18.5	0.5
8554	KF051	*Giraffa camelopardalis*	Hlanganzwane	-28.0	3.5	59.5	2.7
8555	KF052	*Giraffa camelopardalis*	Hlanganzwane	-27.5	2.5	60.2	2.6
8556	KF053	*Giraffa camelopardalis*	Hlanganzwane	-27.9	3.5	65.2	3.0
8707	KF201	*Giraffa camelopardalis*	Hlanganzwane	-27.6	3.1	66.1	2.3
8575	KF072	*Phacochoerus aethiopicus*	Hlanganzwane	-13.5	4.5	48.6	1.5
8576	KF073	*Phacochoerus aethiopicus*	Hlanganzwane	-14.3	4.9	40.9	1.3
8577	KF074	*Phacochoerus aethiopicus*	Hlanganzwane	-14.2	5.0	51.1	1.6
8578	KF075	*Phacochoerus aethiopicus*	Hlanganzwane	-13.7	4.8	50.5	1.5
8557	KF054	*Syncerus caffer*	Hlanganzwane	-14.2	3.2	49.5	1.3
8558	KF055	*Syncerus caffer*	Hlanganzwane	-14.5	3.1	53.5	1.2
8559	KF056	*Syncerus caffer*	Hlanganzwane	-14.5	3.7	54.5	1.3
8560	KF057	*Syncerus caffer*	Hlanganzwane	-14.2	3.6	52.9	1.2
8569	KF066	*Syncerus caffer*	Hlanganzwane	-14.7	3.3	55.9	1.1
8522	KF019	*Papio ursinus*	L Sabie Bridge	-23.5	4.3	13.3	2.9
8523	KF020	*Papio ursinus*	L Sabie Bridge	-23.6	5.5	12.3	2.4
8524	KF021	*Papio ursinus*	L Sabie Bridge	-24.5	4.8	12.2	2.6
8525	KF022	*Papio ursinus*	L Sabie Bridge	-25.1	5.4	12.7	3.2
8526	KF023	*Papio ursinus*	L Sabie Bridge	-23.6	5.1	12.5	2.8
8649	KF143	*Equus burchellii*	Maroela Loop	-14.0	0.7	55.9	1.1
8650	KF144	*Equus burchellii*	Maroela Loop	-14.1	3.4	61.1	1.3

Appendix II C / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
8642	KF136	*Panthera leo*	Maroela Loop	-15.9	9.0	50.1	8.3
8643	KF137	*Panthera leo*	Maroela Loop	-19.5	7.3	38.9	3.6
8644	KF138	*Panthera leo*	Maroela Loop	-15.0	8.5	50.8	7.9
8645	KF139	*Panthera leo*	Maroela Loop	-17.7	9.0	23.9	2.6
8646	KF140	*Panthera leo*	Maroela Loop	-16.2	9.4	30.3	9.3
8647	KF141	*Panthera leo*	Maroela Loop	-17.9	10.2	70.8	8.1
8634	KF131	*Aepyceros melampus*	N'watimvambu R	-21.1	6.3	62.6	2.3
8635	KF132	*Aepyceros melampus*	N'watimvambu R	-20.1	6.9	71.3	2.5
8636	KF133	*Connochaetes taurinus*	N'watimvambu R	-13.9	4.5	61.8	1.5
8637	KF134	*Connochaetes taurinus*	N'watimvambu R	-13.8	4.9	59.4	1.7
8616	KF113	*Aepyceros melampus*	Renosterkoppies	-20.3	6.0	58.7	2.5
8617	KF114	*Aepyceros melampus*	Renosterkoppies	-16.8	6.5	56.8	2.2
8618	KF115	*Aepyceros melampus*	Renosterkoppies	-17.0	6.8	54.8	2.3
8619	KF116	*Aepyceros melampus*	Renosterkoppies	-18.4	6.6	59.6	2.2
8620	KF117	*Aepyceros melampus*	Renosterkoppies	-18.5	7.1	56.7	2.4
8621	KF118	*Aepyceros melampus*	Renosterkoppies	-18.9	7.1	59.3	2.0
8622	KF119	*Aepyceros melampus*	Renosterkoppies	-19.0	7.0	56.0	2.1
8623	KF120	*Aepyceros melampus*	Renosterkoppies	-20.0	5.9	59.8	1.9
8624	KF121	*Aepyceros melampus*	Renosterkoppies	-19.6	6.5	55.9	1.8
8625	KF122	*Aepyceros melampus*	Renosterkoppies	-16.5	6.0	60.5	2.0
8609	KF106	*Connochaetes taurinus*	Renosterkoppies	-15.3	5.6	58.6	1.3
8610	KF107	*Connochaetes taurinus*	Renosterkoppies	-14.4	7.6	51.5	1.6
8611	KF108	*Connochaetes taurinus*	Renosterkoppies	-15.3	5.7	55.8	1.3
8613	KF110	*Connochaetes taurinus*	Renosterkoppies	-14.1	8.0	52.3	1.4
8614	KF111	*Connochaetes taurinus*	Renosterkoppies	-14.1	6.5	55.4	1.4
8615	KF112	*Connochaetes taurinus*	Renosterkoppies	-13.8	8.2	53.3	1.9
8626	KF123	*Connochaetes taurinus*	Renosterkoppies	-13.8	7.9	51.9	1.5
8633	KF130	*Connochaetes taurinus*	Renosterkoppies	-14.5	7.9	51.7	1.5
8605	KF102	*Equus burchellii*	Renosterkoppies	-13.5	3.2	64.6	1.1
8606	KF103	*Equus burchellii*	Renosterkoppies	-13.7	6.9	51.7	1.3
8607	KF104	*Equus burchellii*	Renosterkoppies	-13.7	4.3	58.6	1.2
8608	KF105	*Equus burchellii*	Renosterkoppies	-14.7	5.0	57.0	1.0
8604	KF101	*Syncerus caffer*	Renosterkoppies	-14.3	7.0	47.0	1.2
8612	KF109	*Tragelaphus strepsiceros*	Renosterkoppies	-26.8	6.4	67.5	3.3
8627	KF124	*Tragelaphus strepsiceros*	Renosterkoppies	-26.5	6.1	69.3	4.1
8628	KF125	*Tragelaphus strepsiceros*	Renosterkoppies	-26.2	5.6	72.2	2.8
8629	KF126	*Tragelaphus strepsiceros*	Renosterkoppies	-25.8	7.6	64.1	2.5
8630	KF127	*Tragelaphus strepsiceros*	Renosterkoppies	-26.8	6.5	64.9	3.4
8631	KF128	*Tragelaphus strepsiceros*	Renosterkoppies	-26.6	5.8	63.8	3.5
8632	KF129	*Tragelaphus strepsiceros*	Renosterkoppies	-27.4	4.4	71.6	3.2
8504	KF001	*Papio ursinus*	Sabie-Skukuza	-25.8	5.2	41.9	2.1
8505	KF002	*Papio ursinus*	Sabie-Skukuza	-26.2	4.2	44.8	2.4
8506	KF003	*Papio ursinus*	Sabie-Skukuza	-24.8	4.2	45.3	2.4

Appendix II C / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
8507	KF004	*Papio ursinus*	Sabie-Skukuza	-25.2	5.0	46.5	2.7
8508	KF005	*Papio ursinus*	Sabie-Skukuza	-25.9	4.1	44.4	2.4
8509	KF006	*Papio ursinus*	Sabie-Skukuza	-24.2	5.2	44.0	2.3
8510	KF007	*Papio ursinus*	Sabie-Skukuza	-26.1	5.4	43.1	2.8
8511	KF008	*Papio ursinus*	Sabie-Skukuza	-25.7	6.0	45.7	2.2
8512	KF009	*Papio ursinus*	Sabie-Skukuza	-25.2	5.0	13.5	1.8
8513	KF010	*Papio ursinus*	Sabie-Skukuza	-24.8	4.5	44.2	2.9
8514	KF011	*Papio ursinus*	Sabie-Skukuza	-26.4	4.5	13.2	1.7
8515	KF012	*Papio ursinus*	Sabie-Skukuza	-24.6	3.6	12.0	3.1
8516	KF013	*Papio ursinus*	Sabie-Skukuza	-26.9	4.6	14.8	1.9
8517	KF014	*Papio ursinus*	Sabie-Skukuza	-25.6	4.3	13.2	1.7
8518	KF015	*Papio ursinus*	Sabie-Skukuza	-24.6	3.9	12.8	2.8
8519	KF016	*Papio ursinus*	Sabie-Skukuza	-26.1	5.4	13.3	1.8
8520	KF017	*Papio ursinus*	Sabie-Skukuza	-25.4	5.6	14.2	2.0
8521	KF018	*Papio ursinus*	Sabie-Skukuza	-25.1	5.6	14.6	1.6
8533	KF030	*Papio ursinus*	Sabie-Skukuza	-25.7	4.0	48.1	2.6
8534	KF031	*Papio ursinus*	Sabie-Skukuza	-27.2	5.7	44.7	1.8
8535	KF032	*Papio ursinus*	Sabie-Skukuza	-25.5	5.0	49.0	2.6
8536	KF033	*Papio ursinus*	Sabie-Skukuza	-25.9	4.2	51.4	3.0
8537	KF034	*Papio ursinus*	Sabie-Skukuza	-25.9	4.2	36.8	2.0
8538	KF035	*Papio ursinus*	Sabie-Skukuza	-25.5	4.0	45.2	3.2
8539	KF036	*Papio ursinus*	Sabie-Skukuza	-25.1	4.4	49.9	2.6
8540	KF037	*Papio ursinus*	Sabie-Skukuza	-25.1	4.8	42.7	2.2
8541	KF038	*Papio ursinus*	Sabie-Skukuza	-24.8	3.4	48.5	3.8
8542	KF039	*Papio ursinus*	Sabie-Skukuza	-24.6	5.6	49.1	2.8
8543	KF040	*Papio ursinus*	Sabie-Skukuza	-24.4	5.9	50.7	3.4
8544	KF041	*Papio ursinus*	Sabie-Skukuza	-24.7	4.8	46.7	3.1
8651	KF145	*Equus burchellii*	Salitje	-14.1	3.0	54.9	1.2
8652	KF146	*Equus burchellii*	Salitje	-13.2	1.9	58.7	1.2
8659	KF153	*Syncerus caffer*	Salitje	-15.0	4.4	56.5	2.1
8660	KF154	*Syncerus caffer*	Salitje	-14.6	3.6	60.4	1.9
8661	KF155	*Syncerus caffer*	Salitje	-16.1	2.4	38.1	1.1
8662	KF156	*Syncerus caffer*	Salitje	-15.0	2.6	56.8	1.3
8527	KF024	*Papio ursinus*	Salitje River	-24.1	3.6	12.3	2.5
8528	KF025	*Papio ursinus*	Salitje River	-25.9	4.1	13.3	2.5
8529	KF026	*Papio ursinus*	Salitje River	-24.2	3.6	13.4	2.3
8530	KF027	*Papio ursinus*	Salitje River	-25.6	2.9	13.4	3.9
8531	KF028	*Papio ursinus*	Salitje River	-25.0	2.4	12.1	3.6
8532	KF029	*Papio ursinus*	Salitje River	-25.3	2.3	47.3	3.4
8545	KF042	*Papio ursinus*	Stolsnek	-24.4	2.2	50.6	2.3
8546	KF043	*Papio ursinus*	Stolsnek	-24.2	2.7	48.4	3.2
8547	KF044	*Papio ursinus*	Stolsnek	-25.1	1.3	22.3	0.9
8548	KF045	*Papio ursinus*	Stolsnek	-25.4	2.0	51.4	2.0

Appendix II C / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
8549	KF046	*Papio ursinus*	Stolsnek	-24.5	2.7	47.7	3.4
8550	KF047	*Papio ursinus*	Stolsnek	-25.3	3.2	47.2	2.3
8551	KF048	*Papio ursinus*	Stolsnek	-23.8	2.3	49.5	3.7
8552	KF049	*Papio ursinus*	Stolsnek	-24.8	2.3	49.3	2.5
8638	KF135	*Papio ursinus*	Stolsnek	-24.2	2.9	50.3	3.3

Appendix II D. Data for Mammal Faeces from the Kruger National Park, Collected in January 2003.

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10342	KF298	*Aepyceros melampus*	Crocodile River	-21.1	4.6	42.3	1.3
10343	KF299	*Aepyceros melampus*	Crocodile River	-22.9	3.0	45.4	2.0
10344	KF300	*Aepyceros melampus*	Crocodile River	-23.2	3.1	48.8	3.2
10345	KF301	*Aepyceros melampus*	Crocodile River	-22.7	3.6	45.3	1.9
10346	KF302	*Aepyceros melampus*	Crocodile River	-21.6	3.8	48.9	1.8
10347	KF303	*Aepyceros melampus*	Crocodile River	-21.7	1.3	62.8	2.1
10348	KF304	*Equus burchellii*	Crocodile River	-16.3	4.3	42.1	0.8
10349	KF305	*Equus burchellii*	Crocodile River	-15.7	2.9	54.0	1.2
10350	KF306	*Giraffa camelopardalis*	Crocodile River	-28.7	4.2	52.4	3.5
10351	KF307	*Kobus ellipsiprymnus*	Crocodile River	-15.5	4.6	40.3	0.7
10353	KF309	*Kobus ellipsiprymnus*	Crocodile River	-15.6	4.6	53.9	1.3
10354	KF310	*Kobus ellipsiprymnus*	Crocodile River	-16.0	6.0	52.6	1.3
10355	KF311	*Kobus ellipsiprymnus*	Crocodile River	-17.4	7.5	54.7	2.7
10357	KF313	*Phacochoerus aethiopicus*	Crocodile River	-15.0	5.8	31.4	0.7
10358	KF314	*Syncerus caffer*	Crocodile River	-15.2	2.6	48.4	1.1
10359	KF315	*Syncerus caffer*	Crocodile River	-16.6	8.0	54.7	1.6
10360	KF316	*Syncerus caffer*	Crocodile River	-15.3	5.0	49.2	2.7
10361	KF317	*Syncerus caffer*	Crocodile River	-16.7	9.7	49.1	2.7
10362	KF318	*Syncerus caffer*	Crocodile River	-16.7	7.0	48.6	1.9
10325	KF281	*Aepyceros melampus*	Hlanganzwane	-16.8	6.7	49.7	3.6
10326	KF282	*Aepyceros melampus*	Hlanganzwane	-17.3	5.5	42.6	1.5
10327	KF283	*Aepyceros melampus*	Hlanganzwane	-14.2	6.5	59.9	2.4
10328	KF284	*Aepyceros melampus*	Hlanganzwane	-20.4	4.1	60.0	2.0
10329	KF285	*Aepyceros melampus*	Hlanganzwane	-19.9	4.6	41.2	2.0
10332	KF288	*Equus burchellii*	Hlanganzwane	-15.1	3.0	57.4	0.8
10333	KF289	*Equus burchellii*	Hlanganzwane	-14.1	6.6	49.7	3.7
10334	KF290	*Equus burchellii*	Hlanganzwane	-15.2	4.5	39.7	0.6
10335	KF291	*Equus burchellii*	Hlanganzwane	-15.4	2.3	38.9	0.6
10336	KF292	*Giraffa camelopardalis*	Hlanganzwane	-25.7	3.7	30.1	1.5
10337	KF293	*Giraffa camelopardalis*	Hlanganzwane	-28.1	3.3	43.8	2.3
10338	KF294	*Giraffa camelopardalis*	Hlanganzwane	-27.5	3.2	50.1	2.2
10339	KF295	*Giraffa camelopardalis*	Hlanganzwane	-27.0	2.9	61.3	3.1
10340	KF296	*Giraffa camelopardalis*	Hlanganzwane	-27.3	3.5	49.5	2.5
10330	KF286	*Tragelaphus strepsiceros*	Hlanganzwane	-28.0	3.1	48.0	3.7
10503	KF465	*Papio ursinus*	L Sabie Bridge	-26.2	3.9	43.3	3.0
10504	KF466	*Papio ursinus*	L Sabie Bridge	-25.1	6.3	39.2	3.0
10505	KF467	*Papio ursinus*	L Sabie Bridge	-25.6	5.9	47.7	5.4
10506	KF468	*Papio ursinus*	L Sabie Bridge	-24.7	6.0	46.7	3.2
10507	KF469	*Papio ursinus*	L Sabie Bridge	-25.0	6.6	67.8	3.5
10508	KF470	*Papio ursinus*	L Sabie Bridge	-26.0	5.0	69.6	3.4
10509	KF471	*Papio ursinus*	L Sabie Bridge	-26.6	2.8	42.6	4.2
10510	KF472	*Papio ursinus*	L Sabie Bridge	-25.0	5.2	37.1	3.4
10511	KF473	*Papio ursinus*	L Sabie Bridge	-25.3	5.8	52.5	7.1

Appendix II D / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10512	KF474	*Papio ursinus*	L Sabie Bridge	-25.4	6.8	48.4	3.3
10374	KF330	*Aepyceros melampus*	N'watimvambu R	-26.9	6.7	65.7	3.1
10375	KF331	*Aepyceros melampus*	N'watimvambu R	-20.0	7.9	56.1	2.1
10376	KF332	*Aepyceros melampus*	N'watimvambu R	-20.9	6.7	62.1	2.3
10377	KF333	*Aepyceros melampus*	N'watimvambu R	-20.8	8.2	42.8	2.0
10378	KF334	*Aepyceros melampus*	N'watimvambu R	-19.3	7.2	42.7	1.9
10379	KF335	*Aepyceros melampus*	N'watimvambu R	-20.1	6.5	50.5	2.6
10399	KF355	*Aepyceros melampus*	N'watimvambu R	-19.7	6.5	48.1	2.3
10381	KF337	*Giraffa camelopardalis*	N'watimvambu R	-26.9	5.5	51.1	2.0
10382	KF338	*Giraffa camelopardalis*	N'watimvambu R	-26.9	5.6	51.6	2.1
10383	KF339	*Giraffa camelopardalis*	N'watimvambu R	-27.0	7.4	62.9	3.1
10384	KF340	*Giraffa camelopardalis*	N'watimvambu R	-27.0	5.4	55.7	2.1
10385	KF341	*Giraffa camelopardalis*	N'watimvambu R	-26.4	6.3	50.9	2.4
10363	KF319	*Aepyceros melampus*	Renosterkoppies	-14.2	7.2	39.0	1.6
10364	KF320	*Aepyceros melampus*	Renosterkoppies	-18.0	11.7	46.8	3.0
10365	KF321	*Aepyceros melampus*	Renosterkoppies	-19.1	10.5	52.3	2.3
10366	KF322	*Aepyceros melampus*	Renosterkoppies	-15.7	7.9	42.3	1.5
10367	KF323	*Aepyceros melampus*	Renosterkoppies	-17.8	9.2	55.6	2.3
10368	KF324	*Connochaetes taurinus*	Renosterkoppies	-15.0	11.3	47.4	2.6
10370	KF326	*Equus burchellii*	Renosterkoppies	-14.7	6.1	45.2	1.5
10371	KF327	*Equus burchellii*	Renosterkoppies	-15.0	6.1	33.6	1.0
10372	KF328	*Equus burchellii*	Renosterkoppies	-14.9	9.8	49.9	3.1
10464	KF434	*Papio ursinus*	Sabie-Skukuza	-26.3	7.4	66.1	3.4
10465	KF435	*Papio ursinus*	Sabie-Skukuza	-25.1	5.3	46.1	2.7
10466	KF436	*Papio ursinus*	Sabie-Skukuza	-26.6	5.9	44.1	3.2
10467	KF437	*Papio ursinus*	Sabie-Skukuza	-25.9	6.7	53.5	4.8
10468	KF438	*Papio ursinus*	Sabie-Skukuza	-26.8	4.5	42.5	3.0
10469	KF439	*Papio ursinus*	Sabie-Skukuza	-26.0	4.7	48.1	2.2
10470	KF440	*Papio ursinus*	Sabie-Skukuza	-26.5	5.6	64.6	2.9
10471	KF441	*Papio ursinus*	Sabie-Skukuza	-26.1	4.4	47.1	2.8
10472	KF442	*Papio ursinus*	Sabie-Skukuza	-26.0	4.3	49.5	2.6
10473	KF443	*Papio ursinus*	Sabie-Skukuza	-26.4	6.6	52.8	5.1
10474	KF444	*Papio ursinus*	Sabie-Skukuza	-26.3	5.4	51.9	4.8
10475	KF445	*Papio ursinus*	Sabie-Skukuza	-26.7	4.4	53.8	2.7
10476	KF420	*Papio ursinus*	Steve Hamilton	-27.6	4.5	46.4	2.3
10477	KF421	*Papio ursinus*	Steve Hamilton	-27.5	5.6	66.9	2.9
10478	KF422	*Papio ursinus*	Steve Hamilton	-27.9	4.9	53.2	2.6
10479	KF423	*Papio ursinus*	Steve Hamilton	-26.9	8.3	52.2	8.7
10480	KF424	*Papio ursinus*	Steve Hamilton	-28.0	5.8	48.4	4.5
10481	KF425	*Papio ursinus*	Steve Hamilton	-28.3	4.2	45.6	1.8
10482	KF426	*Papio ursinus*	Steve Hamilton	-27.7	4.8	42.9	2.4
10483	KF427	*Papio ursinus*	Steve Hamilton	-28.0	4.2	50.7	2.0

Appendix II D / continued

UCT #	Sample ID	Species	Collection Site	$\delta^{13}C$	$\delta^{15}N$	%C	%N
10484	KF428	*Papio ursinus*	Steve Hamilton	-26.0	6.3	53.5	4.5
10485	KF429	*Papio ursinus*	Steve Hamilton	-21.9	6.0	37.7	2.8
10486	KF430	*Papio ursinus*	Steve Hamilton	-26.2	6.3	68.0	4.9
10487	KF431	*Papio ursinus*	Steve Hamilton	-27.3	4.4	44.7	2.3
10488	KF432	*Papio ursinus*	Steve Hamilton	-27.7	4.8	43.5	2.3
10489	KF433	*Papio ursinus*	Steve Hamilton	-27.7	4.5	38.9	2.7

Appendix III. Data for Serial Analysis of Baboon Hairs

UCT No.	Region	Hair No.	Sample	cm From Root	Length (mm)	$\delta^{13}C_{PDB}$	$\delta^{15}N_{Air}$	C/N
8639	Kruger Park	A	1	2	140	-21.2	5.5	3.7
		A	2	4	140	-20.7	6.2	3.1
		A	3	6	140	-20.3	6.3	3.2
		A	4	8	140	-19.5	6.5	3.4
		A	5	10	140	-19.4	6.3	3.3
		A	6	12	140	-18.8	5.7	3.3
		A	7	14	140	-19.0	6.2	3.2
		B	1	2	120	-20.3		
		B	2	4	120	-21.0	6.2	3.5
		B	3	6	120	-20.5	6.5	3.2
		B	4	8	120	-19.4	6.6	3.1
		B	5	10	120	-20.0	6.2	3.0
		B	6	12	120	-19.6		3.2
		C	1	2	120	-19.7	5.8	2.9
		C	2	4	120		6.3	3.4
		C	3	6	120	-19.2		
		C	4	8	120	-19.2	6.5	3.4
		C	5	10	120	-19.4	6.1	3.2
		C	6	12	120	-19.4		
9789	Welgevonden		1	2	168	-17.7	4.9	2.9
			2	4	168	-19.2	5.4	3.7
			3	6	168	-19.4	5.1	3.1
			4	8	168	-20.7	5.5	3.0
			5	10	168	-19.1	5.4	2.8
			6	12	168	-18.6	3.9	3.0
			7	14	168	-18.6	3.2	3.4
9790			1	2	159	-18.3	6.1	2.8
			2	4	159	-17.7	11.6	3.2
			3	6	159	-20.5	0.4	3.7
			4	8	159	-19.4	3.9	3.3
			5	10	159	-17.6	3.4	3.1
			6	12	159	-20.0	3.6	3.2
			7	14	159	-19.2	2.9	3.4
9791			1	2	169	-19.3	5.0	3.4
			2	4	169	-19.5	4.6	2.8
			3	6	169	-19.5	5.2	3.2
			4	8	169	-19.8	4.0	3.4
			5	10	169	-18.4	3.3	3.0
			6	12	169	-18.1	3.0	2.8
			7	14	169	-19.2	2.2	2.8

Appendix III / continued

UCT No.	Region	Hair No.	Sample	cm From Root	Length (mm)	$\delta^{13}C_{PDB}$	$\delta^{15}N_{Air}$	C/N
9793			1	2	224	-17.8	4.1	3.1
			2	4	224	-18.6	4.1	3.1
			3	6	224	-19.3	3.9	3.4
			4	8	224	-20.2	3.6	3.0
			5	10	224	-19.1	3.9	2.8
			6	12	224	-20.5	3.4	3.1
			7	14	224	-20.2	4.9	3.1
			8	16	224		4.9	
			9	18	224	-20.8	5.3	3.0
			10	20	224	-21.2	5.4	3.4
9794			1	2	216	-17.8	3.8	3.5
			2	4	216	-18.3	3.6	3.4
			3	6	216	-18.5	3.7	3.6
			4	8	216	-19.5	3.5	3.4
			5	10	216	-18.1	5.1	3.3
			6	12	216	-19.6	3.2	3.2
			7	14	216	-19.1	4.8	3.3
			8	16	216	-19.1	5.2	3.7
			9	18	216	-19.0	5.3	3.3
9795			1	2	149	-18.1	5.5	3.2
			2	4	149	-20.0	5.9	3.6
			3	6	149	-17.8	4.2	3.5
			4	8	149	-17.8	3.3	3.1
			5	10	149	-17.6	3.5	3.0
			6	12	149	-19.1	3.7	3.5
			7	14	149	-19.0	5.9	3.4
9797			1	2	196	-19.1	5.7	3.1
			2	4	196	-18.4	5.1	3.3
			3	6	196	-20.0	5.8	3.5
			4	8	196	-17.4	5.0	3.5
			5	10	196	-17.8	4.0	3.3
			6	12	196	-17.9	4.1	3.6
			7	14	196	-19.4	5.1	3.6
			8	16	196	-18.7	4.7	3.4
9798			1	2	141	-20.1	5.6	3.6
			2	4	141	-16.6	3.6	3.5
			3	6	141	-18.9	3.0	3.7
			4	8	141	-18.6	3.2	3.7
			5	10	141	-19.7	3.1	3.1
			6	12	141	-19.1	2.8	3.6
9799			1	2	141	-18.5	4.5	3.7
			2	4	141	-19.8	4.4	3.6
			3	6	141	-18.4	4.9	3.2
			4	8	141	-19.7	5.0	3.7
			5	10	141	-20.4	3.9	3.7
			6	12	141	-18.7	3.1	3.0

Appendix IV. Data for Dentine collagen Sequences, Bone collagen, and Enamel carbonate. Life history details for individuals are given in Table 5.5

				Collagen			Carbonate	
Specimen ID	**Tooth**	**Tissue**	**Increment**	**$\delta^{13}C$**	**$\delta^{15}N$**	**C/N**	**$\delta^{13}C$**	**$\delta^{18}O$**
UCT 9786	M1	Dentine	1	-20.1	8.9	3.7		
			2	-19.7	8.6	3.6		
			3	-19.9	8.5	3.5		
			4	-21.1	8.4	3.1		
			5	-19.5	8.4	3.6		
		Enamel					-12.0	0.2
	M2	Dentine	1	-19.7	8.9	3.4		
			2	-20.4	8.7	3.1		
			3	-19.1	8.0	3.2		
			4	-19.8	8.0	3.3		
			5	-20.9	8.3	3.6		
			6	-19.6	8.2	3.5		
		Enamel					-12.2	-3.0
	M3	Dentine	1	-19.3	8.2	3.3		
			2	-19.8	8.6	3.2		
			3	-20.0	8.5	3.3		
			4	-19.2	8.5	3.3		
			5	-20.9	8.9	3.4		
			6	-20.4	8.9	3.6		
		Enamel					-12.4	0.1
		Whole bone		-19.7	7.7			
UCT 9787	M1	Dentine	1	-20.0	8.8	3.2		
			2	-20.7	8.5	3.2		
			3	-21.1	8.9	3.3		
			4	-19.7	8.6	3.3		
			5	-20.9	8.7	3.5		
		Enamel					-13.1	1.2
	M2	Dentine	1	-20.1	8.3	3.2		
			2	-19.5	8.5	3.2		
			3	-18.8	8.1	3.3		
			4	-19.8	8.3	3.3		
			5	-19.7	8.5	3.2		
			6	-19.8	8.9	3.3		
		Enamel					-10.3	0.0
	M3	Dentine	1	-20.0	9.2	3.3		
			2	-19.9	9.0	3.4		
			3	-19.6	8.8	3.3		
			4	-19.8	8.9	3.5		
		Enamel					-11.9	-1.3
		Whole bone		-19.2	8.8			

Appendix IV / continued

				Collagen			Carbonate	
Specimen ID	Tooth	Tissue	Increment	$\delta^{13}C$	$\delta^{15}N$	C/N	$\delta^{13}C$	$\delta^{18}O$
AZ 769	M1	Dentine	1	-19.3	8.0	3.7		
			2	-19.2	8.1	3.4		
			3	-19.6	8.5	3.4		
			4	-19.7	7.8	3.3		
		Enamel					-12.1	-2.6
	M2	Dentine	1	-20.2	8.3	3.6		
			2	-19.2	8.8	3.5		
			3	-19.9	8.9	3.5		
			4	-19.4	8.6	3.2		
			5	-20.4	8.7	3.3		
			6	-19.9	8.4	3.3		
		Enamel					-11.3	-2.9
	M3	Dentine	1	-20.1	8.7	3.5		
			2	-19.2	8.7	3.4		
			3	-21.1	8.7	3.2		
			4	-20.9	9.2	3.4		
			5	-19.4	8.7	3.2		
			6	-19.5	9.1	3.7		
		Enamel					-12.4	-2.2
		Whole bone		-17.4	9.6	3.4		
AZ 770	M1	Dentine	1	-18.4	9.5	3.4		
			2	-19.4	10.3	3.1		
			3	-20.9	9.8	3.4		
			4	-19.2	9.9	3.2		
			5	-20.7	9.4	3.4		
	M2	Dentine	1	-21.2	9.1	3.3		
			2	-20.6	9.1	3.3		
			3	-20.8	9.3	3.7		
			4	-20.6	9.2	3.5		
			5	-20.1	9.1	3.1		
		Enamel					-10.7	-2.2
	M3	Dentine	1	-19.7	9.2	3.6		
			2	-17.9	8.2	3.4		
			3	-20.3	8.9	3.2		
			4	-19.3	9.2	3.4		
			5	-19.3	9.2	3.3		
		Enamel					-12.1	0.1
		Whole bone		-19.0	9.4	3.2		

Appendix IV / continued

				Collagen			Carbonate	
Specimen ID	Tooth	Tissue	Increment	$\delta^{13}C$	$\delta^{15}N$	C/N	$\delta^{13}C$	$\delta^{18}O$
AZ 790	M1	Dentine	1	-19.2	10.2	3.6		
			2	-20.2	10.5	3.6		
			3	-18.1	9.9	3.4		
		Enamel					-11.2	0.3
	M2	Dentine	1	-19.4	9.6	3.5		
			2	-21.2	10.0	3.4		
			3	-18.9	9.7	3.4		
			4	-20.5	9.5	3.7		
		Enamel					-12.3	0.5
	M3	Dentine	1	-19.6	10.2	3.7		
			2	-19.0	10.3	3.6		
			3	-19.3	10.4	3.5		
			4	-18.9	10.5	3.7		
			5	-18.3	10.3	3.6		
			6	-18.7	10.1	3.7		
		Enamel					-11.8	-1.5
AZ 792	M1	Dentine	1	-20.6	10.2	3.4		
			2	-19.5	9.8	3.7		
			3	-20.2	10.0	3.4		
		Enamel					-13.2	2.6
	M2	Dentine	1	-18.4	10.0	3.4		
			2	-19.5	10.7	3.3		
			3	-17.9	10.5	3.3		
			4	-18.4	10.3	3.6		
		Enamel					-11.8	0.4
		Whole bone		-18.6	10.4	3.8		
TM 911	M3	Dentine	1	-20.1	7.0	3.3		
			2	-20.2	4.9	3.3		
			3	-20.4	4.8	3.3		
			4	-19.9	6.4	3.1		
			5	-19.9	5.5	3.1		
			6	-20.3	5.4	3.4		
			7	-19.3	7.9	3.1		
		Enamel					-12.3	1.1
		Whole bone		-19.3	6.2	3.1		

Appendix IV / continued

				Collagen			Carbonate	
Specimen ID	Tooth	Tissue	Increment	$\delta^{13}C$	$\delta^{15}N$	C/N	$\delta^{13}C$	$\delta^{18}O$
AZ 798	M2	Dentine	1	-18.1	6.6	3.1		
			2	-18.2	7.7	3.3		
			3	-16.7	8.1	3.2		
			4	-18.2	5.5	3.7		
			5	-17.2	5.8	3.3		
			6	-17.9	8.4	3.3		
		Enamel					-11.4	-2.6
	M3	Dentine	1	-17.7	5.6	3.2		
			2	-19.5	6.6	3.7		
			3	-18.5	4.1	3.6		
			4	-20.5	6.1	3.0		
		Enamel					-11.5	-0.9
AZ 797	M1	Dentine	1	-19.8	6.2	4.0		
			2	-20.1	6.7	4.6		
			3	-20.4	3.9	5.7		
			4	-22.1	6.5	7.1		
		Enamel					-12.9	-0.5
	M2	Dentine	1	-19.7	5.5	4.8		
			2	-19.7	8.2	4.5		
			3	-19.5	7.0	4.4		
			4	-19.4	7.3	4.5		
			5	-20.3	7.3	4.5		
		Enamel					-11.2	-0.9
	M3	Dentine	1	-17.8	7.4	3.2		
			2	-18.7	7.9	3.7		
		Enamel					-12.8	-3.1
		Whole bone		-17.4	7.8	2.9		
AZ 806	dM1	Dentine	1	-17.7	8.3	3.1		
			2	-17.0	7.3	2.9		
			3	-17.7	7.7	3.3		
			4	-18.0	7.3	3.1		
		Enamel					-10.3	-1.0
	dM2	Dentine	1	-18.0	8.0	3.0		
			2	-18.5	7.9	3.2		
			3	-18.6	8.0	2.8		
			4	-17.7	6.8	3.3		
		Enamel					-11.0	0.8

Appendix V. Data from tooth enamel carbonate of fossil specimens from Swartkrans Members 1 and 2.

UCT #	Sample ID	Taxon	Locality	Member	Tooth	$\delta^{13}C$	$\delta^{18}O$
11128	SK 412	*Cercopithecoides williamsi*	Swartkrans	M1/2	M2	-13.7	-0.7
11127	SK 551	*Cercopithecoides williamsi*	Swartkrans	M1/2	M2	-12.8	-3.8
11129	SK 579	*Cercopithecoides williamsi*	Swartkrans	M1/2	M?	-7.2	-11.4 #
11124	SK 2170	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M?	-8.4	-7.9 #
11123	SK 404	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M3	-8.3	-3.1
11115	SK 428	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M3	-6.3 #	-8.8 #
11116	SK 455	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M3	-9.5	-3.4
11119	SK 492	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M2/M3	-10.6	-4.0
11121	SK 548	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M2	-12.8 #	-13.4 #
11122	SK 574	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M3	-12.5 #	-21.7 #
11117	SK 585	*Papio (Dinopithecus) ingens*	Swartkrans	M1	M2/M3	-13.5 #	-22.7 #
11126	SKX 2800	*Papio (Dinopithecus) ingens ?*	Swartkrans	M2	M?	-0.8	-2.5
11125	SKX 2962	*Papio (Dinopithecus) ingens*	Swartkrans	M2	M?	-10.4 #	-5.6 #
11105	SK 419	*Papio robinsoni*	Swartkrans	M1	M2/M3	-6.5	-6.3 #
11106	SK 436	*Papio robinsoni*	Swartkrans	M1	M3	-6.6	-16.3 #
11107	SK 457	*Papio robinsoni*	Swartkrans	M1	M3	-8.2	-7.3 #
11108	SK 458	*Papio robinsoni*	Swartkrans	M1	M3	-8.2	-8.6 #
11112	SKX 1036	*Papio robinsoni*	Swartkrans	M2	M?	-6.8	-12.7 #
11113	SKX 1037	*Papio robinsoni*	Swartkrans	M2	M?	-8.3	-7.6 #
11114	SKX 12443	*Papio robinsoni*	Swartkrans	M2	M?	-10.1	-18.5 #
11136	SK 24615	*Parapapio jonesi ?*	Swartkrans	M1/2	M?	-3.5	-6.5
11138	SK 433	*Parapapio jonesi*	Swartkrans	M1/2	M?	-7.6	-3.7
11140	SK 442	*Parapapio jonesi*	Swartkrans	M1/2	M?	-7.3	-5.8 #
11139	SK 472	*Parapapio jonesi*	Swartkrans	M1/2	M?	-10.2	-10.5 #
11137	SK 588 B	*Parapapio jonesi*	Swartkrans	M1/2	M?	-7.5	-2.7
11131	SK 2181	*Theropithecus oswaldi*	Swartkrans	M1	M?	-2.6	-6.8
11133	SK 403	*Theropithecus oswaldi*	Swartkrans	M1	M2	-5.3	-6.4
11130	SK 491	*Theropithecus oswaldi*	Swartkrans	M1	M?	-1.6	-6.3
11134	SK 581	*Theropithecus oswaldi*	Swartkrans	M1	M?	-2.4	-9.7 #
11132	SK 597	*Theropithecus oswaldi*	Swartkrans	M1	M?	-1.3	-5.9
11135	SKX 616	*Theropithecus oswaldi*	Swartkrans	M2	M?	-1.1	-15.4 #

= Specimens yielding insufficient CO_2 gas, thus isotopic results considered to be unreliable