

Annals of Ivory:
Perspectives on African Elephant *Loxodonta africana* (Blumenbach
1797) Feeding Ecology from a Multi-Decadal Record

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Declaration

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

.....

Dedication

For Ethan (“Harbhajan”) and Jesse (“Akaikes”)

“...And as my mind begins to spread its wings, there’s no stopping curiosity”

(Jack Johnson)

Abstract

This thesis explores the dietary responses of African elephants (*Loxodonta africana*) to environmental change by testing the hypothesis that diet switching (from predominantly browse-based to more grass-rich diets) is driven by cyclical patterns of climate and habitat change in a southern African savanna. Elephants are thought to have substantial impacts on their environments, primarily because they consume large amounts of vegetation over sustained periods. However, the woody plant composition of their diet varies considerably across space and through time, so that in some instances they have been found to be almost pure grazers. Tracking these changes by traditional approaches (e.g. field observations) is difficult because of the geographical and temporal constraints inherent to these methods. Stable light isotope tracking of diet allows diet switching to be studied over multiple space/time scales. Here, I use stable isotope data from elephant faeces, tail hair, and ivory to record short- (monthly), medium- (seasonal to annual), and long-term (decadal) ecological variability, respectively, of elephant diets in the Kruger National Park, South Africa. Results from faeces collected at monthly resolution for one year confirm findings of a previous study (based on biannually-collected samples over two years) that elephants generally consume more grass in the more wooded habitats of the northern Kruger Park, but that there is a greater degree of seasonal diet switching in southern Kruger Park habitats. Moreover, diet changes also relate to changes in underlying bedrock across Kruger Park. Isotopic time-series produced by serial profiling of tail hairs confirm patterns observed in faeces. Long-term diet histories of individuals are derived from serial isotope sampling of ivory, yielding records that represent several decades of an animal's life, at sub-annual (seasonal) resolution. Overlaying individual ivory series in time produces the first, to my knowledge, multidecadal record of African elephant diet, dating from 1903 to 1993. Contrary to expectations, stable carbon, nitrogen, and oxygen isotope records from ivory do not correlate well with cyclical climate trends for the study region. Rather, pronounced diet shifts are observed during extreme climatic events (floods and droughts), and the greatest levels of intra- and inter-annual variability coincide with significant changes in park management policy during the 20th century, i.e. the introduction of water provision programs after the mid 1930s, and the onset of elephant population control in 1967. It is proposed that such direct intervention has played the biggest role in disturbance of elephant-plant equilibria during the 20th century, and further studies to improve our understanding of this phenomenon will be instrumental to development of appropriate management strategies for the 21st century.

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- Chapter 1 -

Introduction

The African elephant *Loxodonta africana* (Blumenbach 1797) is a keystone species that occurs throughout sub-Saharan Africa in environments ranging from savanna grasslands to woodlands, forests and even deserts (Sikes 1971; Owen-Smith 1988; Cumming et al. 1990; Hall-Martin 1992; Douglas-Hamilton & Michelmore 1996; Bossen 1998). Elephants are thought to have substantial impacts on their environments because, as megaherbivores (>1000 kg), they consume large amounts of vegetation (e.g. Laws et al. 1974; Caughley 1976; Owen-Smith 1988; Dublin et al. 1990; Dublin 1995; Cumming et al. 1997; Rutina et al. 2005; Makhabu et al. 2006; Mtui & Owen-Smith 2006). Exploitation of woody plants over sustained periods is predicted to significantly alter botanical composition, ecosystem functioning, and ultimately biodiversity (Caughley 1976; Dublin et al. 1990; Dublin 1995; Prins 1996; Van de Koppel & Prins 1998; Rutina et al. 2005). However, elephants are mixed-feeders that feed on both woody plants and grass, in proportions that can vary from one extreme to the other (e.g. Laws et al. 1974; Barnes 1982; Owen-Smith 1988; Dublin 1995; Cerling et al. 1999; Codron et al. 2006). Indeed, diet variations are so extreme that contention persists over whether they are primarily browsers or grazers (e.g. Wing & Buss 1970; Guy 1976; Norton-Griffiths 1979; Dublin 1995; Tanglely 1997; Cerling et al. 1999). It is therefore difficult to predict how their diets and subsequent impacts on vegetation will change in response to environmental fluctuations, over the short and long term.

Sustained pressure on woody vegetation can decrease the diversity of available browsing niches for sympatric species, impact on tree height, open up forest margins allowing fire to give grasses a competitive advantage over woody plants, or even lead to the conversion of woodlands to open grasslands (e.g. McCullagh 1969a; Laws 1970; Laws et al. 1974; Caughley 1976; Jachmann & Bell 1985; Dublin et al. 1990; Dublin 1995; Cumming et al. 1997; Ben-Shahar

1998). These changes may cause competitive exclusion of sympatric browsers and restrict habitat availability for small mammals, birds, and even insects (van Wyk & Fairall 1969; Laws 1970; Cumming et al. 1997; Johnson et al. 1999; Fritz et al. 2002). By contrast, the role of elephants in terrestrial foodwebs may also be facilitative, through plant hedging and coppicing that creates niches at lower feeding heights, and contributing to the establishment of closed habitats by promoting seed dispersal through their faeces (Chapman et al. 1992; Theuerkauf et al. 2000; Smallie & O'Connor 2000; Styles & Skinner 2000; Gillson & Lindsay 2002; Rutina et al. 2005; Makhabu et al. 2006). Much emphasis has therefore been placed on elephants as seminal agents for maintaining ecosystem dynamics, resilience, and instability (Caughley 1976; Dublin et al. 1990; Dublin 1995; Inamdar 1996; Gillson & Lindsay 2002; Rutina et al. 2005). Similarly, grazing and/or browsing megaherbivores were likely central to palaeoecosystems, contributing to dynamic savanna woodlands with a diverse mixture of different species of tree and grass, as have been identified from the pollen record (Owen-Smith 1988). Evidence from the South African Pleistocene fossil record indicates that megaherbivores were facilitative agents for many extinct browser and grazer species, presumably opening gaps for faster-growing, more palatable woody vegetation, and creating areas for colonization by low-growing pioneer grasses (Brink 1987; Owen-Smith 1987, 1988; Brink & Lee-Thorp 1992). The global disappearance of many megaherbivore species at the terminal Pleistocene has been implicated as one of the major causes underlying the extinction of numerous smaller species that followed (Owen-Smith 1987).

Caughley (1976) identified three main types of models used by earlier studies to describe elephant-landscape interactions, i.e. equilibrium, compression, and intrinsic eruption models. Equilibrium models hold that elephants are vital for maintaining woody vegetation in such a condition so as to be beneficial to other browser species (e.g. Darling 1960; Lawton & Gough 1970; Lawton 1971; *cf.* Owen-Smith 1987, 1988). According to this model, the elephant's role in the system also extends to seed dispersal, tree felling, waterhole creation, opening paths for animal movement, and soil ventilation. Compression models maintain that disequilibrium is

induced only by the compression of elephants into an area (e.g. Buechner & Dawkins 1961; Lamprey et al. 1967; Laws & Parker 1968; Watson & Bell 1969; Astle 1971; Field 1971). Forcing elephants into sanctuaries and cutting off migration routes is predicted to lead to increased and consistent pressure on local vegetation because the elephants cannot migrate/disperse from the area. This scenario has obvious implications for elephant conservation today, in relation to increasing human populations, the expansion of cultivation, and increased direct disturbances on the environment (e.g. Tchamba 1996; Hoare & du Toit 1999; O'Connell-Rodwell et al. 2000; Sitati et al. 2003; Zhang & Wang 2003; Chiyo et al. 2005; Lee & Graham 2006; Rode et al. 2006; van Aarde et al. 2006). Intrinsic eruption models predict that the origin of an “elephant problem” lies in the past, and is the result of significant disturbance(s), either in habitat or in elephant population density (e.g. culling, disease, poaching, human manipulation of environment), which displaces a previous equilibrium state (Laws 1970; Sikes 1971). For example, substantial increases in elephant numbers in southern and East Africa since the late 19th century are expected to have followed almost complete extirpation of certain sympatric ungulates by a panzootic of rinderpest between 1889 and 1896 (Caughley 1976).

Caughley (1976) also proposed an alternative model, the “limit cycle hypothesis”, which predicts eruptions of elephant populations followed by woodland clearance and elephant die-offs as necessary for habitat resilience, stability, and sustained biodiversity in the long term. Whereas all other models for the dynamics of elephant-tree interactions assume disturbance of a previous “primary state” equilibrium between elephants and woody vegetation, the limit cycle hypothesis maintains that there is no natural equilibrium between elephants and trees. The “natural” condition is envisaged as a cyclical relationship in which elephant densities increase while woody vegetation decreases and then elephants decline again when trees become too sparse. When elephant numbers decline, there is a resurgence of the tree layer, and with increasing tree cover the elephant numbers again begin to rise. This cyclicity is proposed as integral to the interactive relationship between elephants and trees, rather than a pathological displacement from a “natural

equilibrium” (except in cases where elephant or tree densities are artificially displaced from the cycle, in which case the cycle will re-establish itself only when the external forces causing the disruption are removed).

A revised variation of Caughley’s (1976) limit cycle hypothesis is presented by Van de Koppel & Prins (1998). They hypothesize that the interplay of competition and facilitation between small and large herbivores could explain savanna woodland-grassland transitions (and vice versa). In particular, they suggest that elephants suffer from competition for grasses with herbivores such as buffalo and impala *Aepyceros melampus*. The result is that elephants will over-exploit woody vegetation as an alternative to grasses, leading to conversion of woodland to grassland, and competitive dominance by grazers (Van de Koppel & Prins 1998; see also Dublin 1995 and Prins 1996). Some corroboration for models predicting woodland-grassland transitions as part of a natural cycle has recently been provided by Gillson & Lindsay (2002), who argued that alternations between woodland and grassland states are the ecological “norm”, rather than a fixed “climax” vegetation state in elephant habitats.

While all of the above offer reasonable explanations for specific cases, none can be unequivocally applied to all elephant populations across Africa, since similar conditions do not necessarily lead to similar outcomes in different places (Caughley 1976). Besides proportions of browse and grass consumed, other factors underlying elephant-induced habitat modifications are also highly variable. For instance, browsing and even breaking of trees does not necessarily lead to tree mortality, modification of tree morphology may either promote or reduce habitat heterogeneity, and the number of trees pushed over per day is not constant (e.g. Croze 1974; Guy 1976; Stokke & du Toit 2000; Midgley et al. 2005). Moreover, predictions focus largely on the outcomes of sustained pressure on local vegetation over the long term, but very little evidence for changes in elephant ecology over extended time periods exists (see Whyte et al. 2003). Despite these limitations to our knowledge base, the notion that, in high densities, elephants are pivotal for ecosystem function and biodiversity is very strong, be they viewed as landscape engineers,

competitors, or facilitators. Consequently, management of Africa's elephant populations is clouded with controversy regarding the need for (and methods used in) population control, effects of fencing, effects of elephants on agricultural activities and rural communities, and the ivory trade (Bell 1983; Walker et al. 1987; van Aarde et al. 1999; Whyte et al. 1999, 2003; O'Connell-Rodwell et al. 2000; Gillson & Lindsay 2002, 2003; reviewed in Owen-Smith et al. 2006). The persistence of debate has led to the establishment of several working groups to integrate knowledge and identify gaps (Owen-Smith et al. 2006). The one common theme that emerges is that existing evidence for the interplay between elephants, sympatric herbivore species, and vegetation change is inadequate, and that there is dire need for further, especially long term, studies of elephant-plant interactions to better understand their significance in savanna ecosystem functioning.

To understand elephant diet niches, and the factors that influence dietary variation, a wide range of spatial and temporal scales should be covered within the realms of a single study (Owen-Smith 1988). Stable isotope ecology is a technique ideally suited to spatio-temporal variability in diet, including through historical time (Tieszen et al. 1989; Koch et al. 1995; Dalerum & Angerbjörn 2005; Stevens et al. 2006). A preliminary study based on faeces from South Africa's Kruger National Park demonstrated the benefits of this technique for tracking short-term spatial and seasonal shifts in diet that are difficult to demonstrate using traditional approaches (Codron 2004; Codron et al. 2006). It is proposed here that extending this methodology to extract serial isotope profiles from ivory can address the paucity of long-term diet histories for this species. Elephant and other proboscidean tusks grow in ordered incremental layers throughout life (Schour & Hoffman 1939a; Klevezal' & Kleinenberg 1969; Koch et al. 1989; Raubenheimer 1993, 1999). Analysis of the stable isotopes of elements such as carbon, nitrogen, and oxygen along ivory growth trajectories can therefore capture lifetime records of diet and environmental change (Koch 1989; Koch et al. 1989; Hoppe 2000; Fisher 2001a; Fox et al. 2007). Serial isotope analyses of ivory carbonate have been successfully used to trace subtle diet

changes over the long term in response to season, climate, and migration, for mastodons *Mammut* sp., mammoths *Mammuthus* spp., gomphotheres, and modern Asian elephants *Elephas maximus* (Koch 1989; Koch & Hoppe 1996; Koch et al. 1998; Fox 2000; Hoppe 2000; Fisher 2001a; Fisher & Beld 2002; Fisher & Fox 2003; Fox et al. 2007). However, this approach has not yet been applied to ivory of modern African elephants.

1.1. Background to Stable Isotope Ecology

Principles

Stable isotope ecology is an empirical tool for studying diet selectivity and habitat utilization, and for detailing variations within these parameters. The technique is based on measurement of the relative abundances of naturally occurring stable isotopes in biological materials, which trace nutrient flow through foodwebs because they reflect (with some further fractionation) the isotopic signatures of the sources from which they are derived (DeNiro & Epstein 1978; Vogel 1978; Peterson & Fry 1987; Ehleringer & Rundel 1989; Post 2002). The stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$), nitrogen ($^{15}\text{N}/^{14}\text{N}$), and oxygen ($^{18}\text{O}/^{16}\text{O}$) are by convention expressed using delta (δ) notation, i.e. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{18}\text{O}$, respectively, in units per mil (‰), with reference to the standards Vienna PeeDee Belemnite (VPDB, for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) and atmospheric N_2 (for $\delta^{15}\text{N}$) from the equation:

$$\delta R = (R_{\text{sample}} / R_{\text{standard}} - 1) * 1000,$$

where R = the isotope ratio of element R ($^x\text{R} / ^y\text{R}$); y is the most abundant isotope.

One of the fundamental principles of stable isotope approaches to diet is the bimodal distribution of $\delta^{13}\text{C}$ values amongst terrestrial plants. Plants utilizing the C_3 photosynthetic pathway have a consistently lower $\delta^{13}\text{C}$ than those that use the C_4 photosynthetic pathway (Smith & Epstein 1971). In subtropical savannas, trees, shrubs, and forbs use the C_3 photosynthetic pathway, while almost all grasses are C_4 (Vogel et al. 1978). Animal $\delta^{13}\text{C}$ values record this

distinction, and thus reflect proportions of C₃ (browse) to C₄ (grass) biomass intake (Vogel 1978; Tieszen et al. 1979; Lee-Thorp & van der Merwe 1987; Cerling & Harris 1999). Animal $\delta^{15}\text{N}$ is influenced by a combination of variables, integrating ^{15}N -abundances in soils and plants, and varying with trophic level, ecophysiology, protein digestion and metabolism, and most importantly the quantity and biological value of dietary proteins (Schoeninger & DeNiro 1984; Sealy et al. 1987; Ambrose 1991; Sponheimer et al. 2003a; Robbins et al. 2005). Variations in the $\delta^{18}\text{O}$ of animal tissues reflect that of their drinking and food water, which in turn, reflect the $\delta^{18}\text{O}$ values of meteoric water, with further local environmental influences (Luz et al. 1984; Koch 1989; Sponheimer & Lee-Thorp 1999, 2001). Hence faunal $\delta^{18}\text{O}$ values (such as archived in bone or tooth mineral) can reflect climatic fluctuations such as season, rainfall, humidity, and temperature (Longinelli 1984; Luz & Kolodny 1985; Koch 1989; Koch et al. 1989; Kohn et al. 1996; Fox et al. 2007). A relationship between $\delta^{18}\text{O}$ and climate is expected to hold best for large, water-dependent animals (Bryant & Froelich 1995) such as elephants.

Stable isotope approaches offer insights over different time scales, depending on the type of material analyzed. Faeces provide information over the short term (several days), whereas body tissues integrate a signal over several months or years (Tieszen et al. 1979, 1983; Ambrose & Norr 1993; Sponheimer et al. 2003b; Codron, D. & Codron in press; Codron, D. et al. 2005a, 2007a, 2007b). Serial profiles of incrementally growing tissues such as hair and teeth yield diet chronologies within individuals at daily, monthly, and/or annual scales (Koch et al. 1995; Balasse et al. 2001; Ayliffe et al. 2004; Cerling et al. 2004, 2006, 2007; Sponheimer et al. 2006a). In continuously growing teeth such as proboscidean tusks, these records extend throughout an animal's life, i.e. up to 60 to 70 years (Koch 1989; Hoppe 2000; Fox et al. 2007). In this study, I use isotope profiles in elephant ivory to reconstruct long-term (20th century) changes in diet, at sub-annual resolution, in the Kruger National Park, South Africa.

Stable Isotope Records of Elephant Dietary Variation

A number of studies, based primarily on insights obtained from $\delta^{13}\text{C}$, testify to the extreme nature of elephant diet variations, and to the ability of this technique to record these variations (van der Merwe et al. 1988; Tieszen et al. 1989; Vogel et al. 1990a; Koch et al. 1995; Cerling et al. 1999, 2004, 2006, 2007; Seydack et al. 2000; Codron 2004; Codron et al. 2006). Many of these studies have yielded somewhat unexpected results. Data for faeces from Kruger Park showed huge dietary disparity between populations in northern and southern landscapes, demonstrating, somewhat counter-intuitively, that grass intake was higher in the more wooded landscapes of the northern regions than in the south (Codron 2004; Codron et al. 2006). Seydack et al. (2000) used elephant faecal $\delta^{13}\text{C}$ to investigate dietary changes in elephants translocated from Kruger Park to the coastal Knysna Forest in South Africa, and found that elephants did not change their diet to become more ^{13}C -depleted even though they had moved from savanna woodland to a rainforest habitat. $\delta^{13}\text{C}$ values in collagen extracted from elephant bone and tooth fragments revealed that elephants in Amboseli National Park, Kenya, ate less browse in the late 1980's than in the early 1970's (Koch et al. 1995). Within twenty years elephant diets had thus shifted from 75 to 40% browse in the same study area. Conversely, similar data for elephants in Tsavo National Park, Kenya, suggested they maintained relatively constant diets for fifty years, even though the region had undergone a transition from woodland to grassland over the same period (Tieszen et al. 1989).

Perhaps the best example of elephants' abilities to change their diets is evinced in $\delta^{13}\text{C}$ data from enamel carbonate of fossil elephants and other extinct proboscideans (Cerling et al. 1999). Following the Late Miocene proliferation of C_4 grasslands throughout African and other subtropical savannas, the diets of all proboscideans (excluding the deinotheres) rapidly shifted from being C_3 to C_4 based. Similar diet shifts around the same time have been documented for other ungulate herbivores, including equids, suids, and giraffids (Cerling et al. 1997, 2005). The

unexpected result for elephants, however, is that some time after 1 Ma., most reverted to a predominantly C₃ browsing diet (Cerling et al. 1999).

Isotope profiles in elephant ivory have the potential to go beyond the insights of previous studies because continuous, near-lifetime diet records can be reconstructed for individuals. Mammalian teeth are not remodeled after dentine deposition and/or enamel mineralization (e.g. Schour & Hoffman 1939a, 1939b; Gage et al. 1989), hence diet chronologies are preserved in the isotope composition of incremental tooth “layers” (Koch et al. 1989; Lee-Thorp et al. 1997; Cerling et al. 1997; Fisher & Fox 1998; Koch et al. 1998; Balasse et al. 2001; Fisher & Beld 2002; Passey & Cerling 2002; Boisserie et al. 2005). Ivory dentine exhibits paired dark and light annual growth bands (first-order incremental laminae), which have been associated with periods of slower (dry season) and faster (wet season) growth, respectively (Koch 1989; Koch et al. 1989; Fisher 2001a; Mol et al. 2001; Fisher & Beld 2002; Fisher & Fox 2003; Fisher et al. 2003; Fox et al. 2007). Paired annual light and dark bands each comprise pairs of smaller light and dark sub-units, or second-order incremental laminae, which have a weekly periodicity in Elephantidae and Gomphotheriidae (elephants and mammoths), and are biweekly in Mammutidae (mastodons) (Fisher 1987; Koch 1989; Koch et al. 1989; Fisher 2001a, 2001b; Mol et al. 2001). Third-order incremental laminae are identical to the daily incremental lines of von Ebner present in most mammalian teeth (Schour & Hoffman 1939a, 1939b; Yilmaz et al. 1977; Molnar et al. 1981; Koch 1989). Thus, approximately seven pairs (light and dark bands) of third-order increments are present within each second-order increment in modern elephant tusks, and 14 pairs in each second-order increment of mastodon tusks. Several studies have used serial isotopic analyses of ivory in fossil mastodons, mammoths, and gomphotheres to extract long-term diet records (from $\delta^{13}\text{C}$) at sub-annual resolution, in response to seasonality, climate (from $\delta^{18}\text{O}$) and even migration (using stable isotopes of strontium, $^{87}\text{Sr}/^{86}\text{Sr}$) (e.g. Koch 1989; Koch & Hoppe 1996; Koch et al. 1998; Fox 2000; Hoppe 2000; Fisher 2001a; Fisher & Beld 2002; Fisher & Fox 2003; Fox et al. 2007).

1.2. Thesis Objectives

This thesis studies long-term variations in elephant feeding ecology by testing the hypothesis that, in Kruger Park, proportions of browse to grass consumed changed in response to environmental (climate and habitat) changes that occurred through the 20th century. This hypothesis has direct implications for predicting responses of keystone species to present and past global change trajectories, and for conservation policy development in the 21st century. First, it is important to understand the factors that drive changes in proportions of browse:grass intake, because impacts on woody vegetation are expected to be greater under conditions of elevated browse consumption (Styles & Skinner 2000; Scholes et al. 2003). Second, if the primary hypothesis does not hold then the most important shifts in diet are likely to coincide with human activities. Specific predictions are:

- i) Grass intake increases (and browsing decreases) on a continuous gradient from south to north;
- ii) Diet changes from south to north reflect changes in the relative nutritional value of available grasses and the dominance of browse-deterring mopane *Colophospermum mopane* in the north;
- iii) 20th century diet changes follow the 18-20 year climatic cycle of temperate southern Africa, i.e. during wet periods elephants consumed more grass, and during dry periods they ate more browse; and
- iv) Elephant diets also responded to stochastic episodes, e.g. increased grass intake during extreme floods and decreased grazing during drought periods.

The study builds on my Masters study (Codron 2004), in which I used faeces to track differences in short term (dry versus wet season) diet shifts between elephants from northern and southern Kruger Park habitats. Results of the earlier study showed that elephants consumed more grass in certain woody habitats of Kruger Park (northern regions), i.e. proportions of browse:grass

consumed do not necessarily reflect local vegetation structure. Rather, their diets vary in response to other environmental factors, e.g. increased grass intake when the nutritional value of available grasses is high (preferential grazer model), or the quality of browse is inadequate (preferential browser model). Here, I expand the two-year biannual faeces dataset using samples collected over a third year from a wider variety of habitat types and a higher-resolution temporal series (monthly) to further test the preferential grazer versus preferential browser models. Faecal records are compared with serial isotope analyses of tail hairs, an approach which has been shown to yield sub-annual records of diet change (Cerling et al. 2004, 2006; Codron 2004). These data should provide clues about the environmental conditions that favour browsing and those that favour grazing, and faeces and tail hair records are therefore an important step towards understanding causes of change in elephant feeding ecology recorded over the long term. I then use serial isotope records extracted from the tusks of 16 individuals to reconstruct a 20th century history of diet change at sub-annual resolution. These data represent the first attempt to apply this approach to the diets of extant African elephants, and are the most complete historical record of African elephant diets to date.

The advantage to serial isotopic profiling is that diet records are continuous, whereas bulk methods (e.g. Tieszen et al. 1989; Koch et al. 1995) offer only “collapsed snapshots” in time. In elephant ivory, the scale of resolution is expected to be at least seasonal, and likely sub-seasonal. This means that records for different individuals, or different ivory sections within individuals, can potentially be cross-matched at points where they overlap in time. Dating of isotope records from ivory is achieved using Accelerator Mass Spectrometry (AMS) radiocarbon (¹⁴C) dating and counts of incremental bands (mainly weekly second-order laminae) from date of death and/or birth. Reliable estimates for dates represented within incremental bands facilitate high-resolution comparison of isotopic patterns and diet switches with seasonal, annual, and decadal environmental change records.

The use of African elephant ivory has implications for future palaeoecological studies that might apply a similar approach to proboscideans and other mammals with continuously growing teeth. Previous studies of fossil proboscidean tusks have focused largely on $\delta^{13}\text{C}$ data derived from analysis of the carbonate in the inorganic phase of ivory dentine (but see Rountrey et al. 2007). Here, I use data for both the collagen and carbonate phases of dentine. These two materials differ in turnover rate (the time taken for the isotopic signature of newly-deposited material to reflect diet changes) and because carbonate incorporates carbon assimilated from the whole diet, whereas collagen preferentially incorporates carbon from dietary protein (Tieszen et al. 1983; Lee-Thorp et al. 1989; Sukumar & Ramesh 1992; Ambrose & Norr 1993; Tieszen & Fagre 1993; Passey & Cerling 2002). It is predicted that carbonate and collagen trajectories will yield similar patterns, but that temporal resolution of diet shifts will vary between the two. In addition, environmental influences on abundances of isotopes of other elements are poorly understood because of the complex interaction of variables that influence them (e.g. Handley & Raven 1992; Sponheimer & Lee-Thorp 1999, 2001; Robinson 2001; Sponheimer et al. 2003a; Robbins et al. 2005; Codron, D. & Codron in press). Patterns of variation in $\delta^{15}\text{N}$ of ivory collagen and $\delta^{18}\text{O}$ of carbonate will be examined in relation to changes in both diet (proportions of browse:grass consumed) and climate (e.g. rainfall) so that these proxies can be applied to palaeoecological studies with greater confidence.

Kruger Park is an appropriate study area for this research because local geological, climatic, and vegetational heterogeneity offer resident herbivores a variety of habitats that lead to extensive variations in diet through space and time (du Toit 2003; Codron et al. 2006; Codron, D. et al. 2006). Kruger Park has a long history of elephant conservation and population management policies; the expanding present-day population forms the subject of much debate and controversy (Owen-Smith et al. 2006). The Kruger Park and surrounding areas form part of the temperate summer rainfall region of the South African interior, characterized by an 18-20 year

(approximating to a dry decade followed by a wet decade) quasi-periodic cyclical rainfall regime (Tyson & Dyer 1975; Venter et al. 2003). This rainfall pattern is expected to lead to changes in primary production, which may ultimately be a fundamental factor regulating elephant diet changes (*cf.* Coe et al. 1976). Further, the climatic, vegetational, and demographic history of Kruger Park and its animals is well described (reviewed in du Toit et al. 2003). This provides a constrained environmental framework for ecological studies, in terms of events such as floods and droughts, epizootics, changes in woody plant cover, river systems, and fluctuations in animal population size. Kruger Park also has a long management history, with regards to fencing, artificial water provision, fire management, etc. against which ecological changes can be further assessed.

1.3. Thesis Outline

In this chapter, I have outlined the motivation for, objectives of, approach followed, and significance of this study. The next chapter describes the study area (Kruger Park), its climate regime, geology, and habitat composition, its history, and the history of its elephant population. Chapter 3 presents results for stable isotope variations in Kruger Park vegetation, combining previously published data for the first two years (Codron et al. 2005) with new data for a third sampling year. Accurate diet reconstructions are dependant on our knowledge of variations in plants at the base of the food chain, because environmentally-driven variations in plant isotope compositions are recorded in the tissues of animals feeding on them. This chapter discusses the implications of variations in plant isotope signatures for reconstructing diet and environmental records from animal tissue. Chapter 4 uses data from Kruger Park elephant faeces and tail hairs to determine spatial and seasonal patterns of diet shifting in response to changes in geology, vegetational composition, plant nutrient composition, and rainfall. The chapter combines results for the first two years (Codron 2004; Codron et al. 2006), with higher-resolution spatial and

temporal (monthly) collections during a third study year, and the preferential grazer versus preferential browser models are discussed.

Chapters 5 and 6 focus on dietary information archived in elephant ivory. In Chapter 5, a review of ivory growth and morphometrics is presented, alongside results of microscopic techniques used in this thesis to study ivory growth. Previous studies using fossil proboscidean tusks revealed long-term chronological records of diet and environmental change at seasonal resolution (e.g. Koch 1989; Hoppe 2000; Fisher 2001a). Similar trajectories should be available in African elephant ivory for the 20th century, but this remains to be demonstrated. Tusks of different species grow at different rates, particularly the second-order laminae, which represent weekly growth intervals in gomphotheres, mammoths, and modern elephants, and bi-weekly growth intervals in mastodons (Fisher 1987; Koch 1989; Fox 2000; Fisher 2001a; Mol et al. 2001; Fisher et al. 2003). In this chapter, the prediction that records in modern elephant ivory yield similar temporal resolution to mammoths is assessed. Chapter 6 presents and describes stable isotope records of long-term diet and environmental change archived in ivory. The chapter includes a comparison between carbonate and collagen $\delta^{13}\text{C}$ records, and changes in $\delta^{15}\text{N}_{\text{collagen}}$ and $\delta^{18}\text{O}_{\text{carbonate}}$ in relation to climate records (rainfall, temperature) for the Kruger Park. The near-continuous chronology of changes in browse:grass consumption for the 20th century is evaluated against changes in climate, habitat, and management regime. Raw data used in Chapters 3, 4, and 6 are provided in Appendix I. Chapter 7 summarizes the main results of the study in relation to the predictions given above, and discusses implications for wildlife conservation and environmental science.

- Chapter 2 -

Study Area: Kruger National Park and its Elephants

The Kruger National Park is an important reserve for the conservation of biodiversity of African savanna ecosystems. Since its inception in 1898, Kruger Park has faced many natural changes and undergone numerous phases of management. Research and development of wildlife management policies is ongoing, and a thorough review of past, current, and future events and policies has recently been published in du Toit et al. (2003). This chapter provides an overview of the geological and climatic background, natural change and stochastic events, and a century of different management regimes in Kruger Park, emphasizing events in the history of its elephant populations.

2.1. Background to Study Area

2.1.1. Abiotic Component

Topography

Kruger Park is a semi-arid savanna reserve, forming part of the northeastern South African “lowveld”, the relatively low-lying (near coastal altitudes) land extending from the footslopes of the Drakensberg Great Escarpment in the west, towards the Mozambique coastal plain on the east (Venter et al. 2003). The Park is situated in the lowveld and currently covers an area of approximately 20 000 km², between the latitudes 22^o20’ and 25^o32’ south and longitudes 30^o53’ and 32^o02’ east (Fig. 2.1). The Limpopo and Mpumalanga provinces and several river systems (the Sigaas River in the far south, the Klein Letaba River in the central west, and the Luvuvhu and Limpopo Rivers in the north) constitute its western boundary.

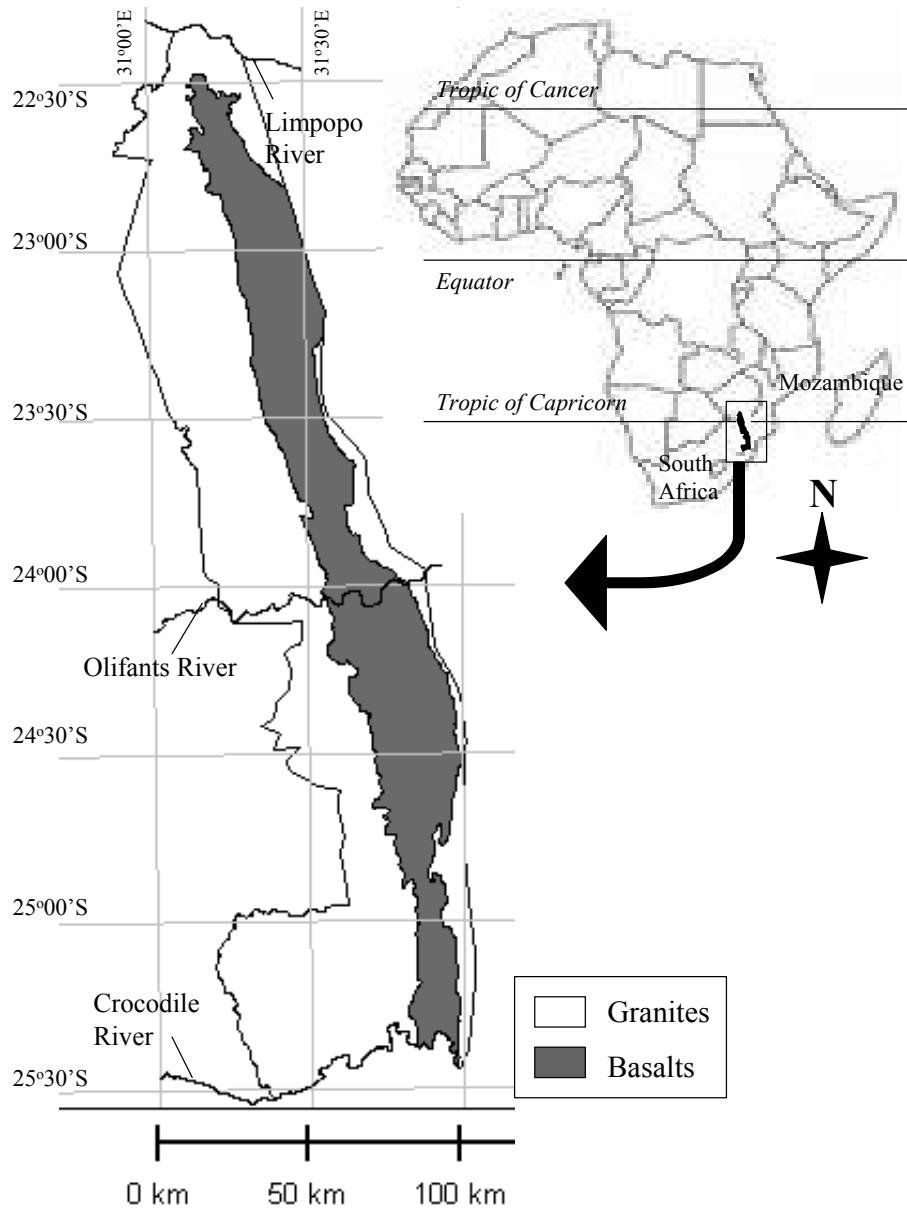


FIGURE 2.1 - Map of Kruger National Park, showing its geographical location within Africa, as well as the Rivers forming the northern and southern borders (Limpopo and Crocodile, respectively), the broad geological separation between the granites in the west and basalts in the east, and the centrally-located Olifants River separating northern *Colophospermum mopane* dominated landscapes from southern *Acacia/Combretum* savannas.

The eastern boundary is the Lebombo Mountain range, which also serves as the international boundary between South Africa and Mozambique. The northern and southern boundaries are delineated by the Limpopo and Crocodile Rivers, respectively (Fig. 2.1). The topography of the landscape is mainly flat (approximately 300-200 m above sea level), although it does peak at 835m above sea level in the southwest near Malelane.

Geology

The major geomorphologic events that led to the present soil configurations in Kruger Park and the rest of the lowveld have been described by several authors (e.g. King 1967; Venter & Bristow 1986; Moon & Dardis 1988; Venter 1990; summarized in Venter et al. 2003). The underlying geology has been categorized into 14 main categories. The most relevant geological characteristic for this study is that the lithological strike is north-south, so that the most common surface rock changes from granite in the west to basalt in the east (separated by a narrow strip of north-south sedimentary rock; Fig. 2.1.). Two major soil types are derived: sandy soils on the western granites and clay-rich soils on the eastern basalts (Venter et al. 2003).

Natural Surface Water Distribution

A total of 31 548 km of river flows across a wide range of geological and rainfall zones (O’Keeffe & Rogers 2003; Fig. 2.2a). The distribution and availability of natural surface water is dependent on underlying geology, with the western granites having a higher stream density than the eastern basalts (e.g. Gaylard et al. 2003; Rogers & O’Keeffe 2003). Surface water sources are categorized as riparian (i.e. perennial rivers) or savanna (springs, pans, and seasonally flooded drainage depressions, or “vleis”), according to associated vegetational composition and herbivore habitats (see Gaylard et al. 2003).

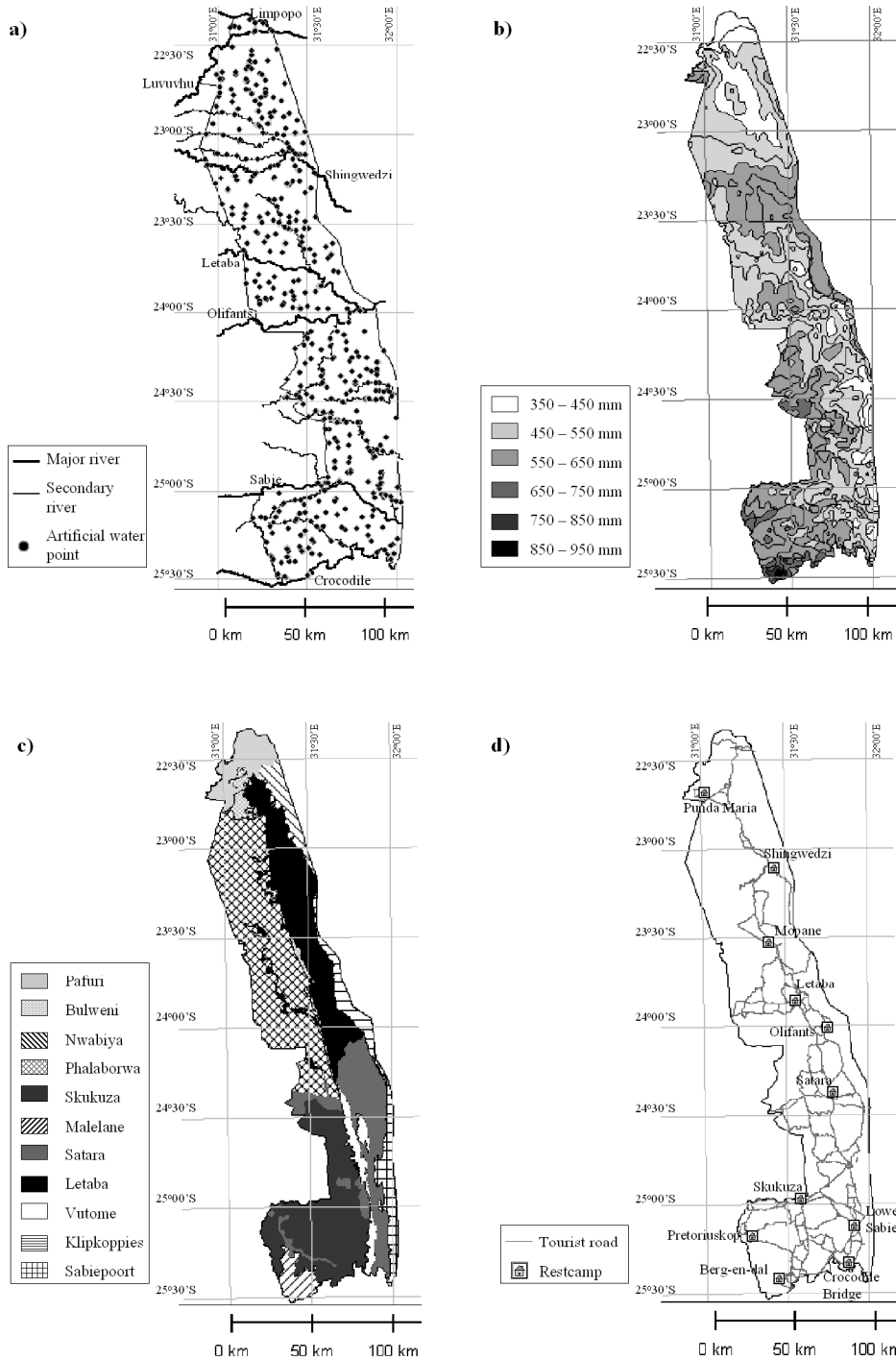


FIGURE 2.2. – Kruger Park maps showing a) distribution of major (perennial) rivers, secondary rivers, and artificial water points; b) spatial variation in mean annual rainfall; c) geological and vegetational Land Systems described by Venter et al. (2003); and d) the public road network and location of primary tourist camps.

Kruger Park is considered a semi-arid savanna (rainfall ~400-600 mm per annum), and owes its perennial rivers to the escarpment in the west, which receives an annual rainfall in excess of 2 000 mm (O’Keeffe & Rogers 2003). Seven major river systems traverse Kruger Park from the west and flow into Mozambique and the Indian Ocean in the east. These are, from north to south, the Limpopo, the Luvuvhu, the Shingwedzi, the Letaba (a tributary of the Olifants), the Olifants, the Sabie, and the Crocodile (Fig. 2.2a). Most of these have been modified over the last ~40 years by water abstraction, increased sediment input, and pollution; the Shingwedzi is no longer considered a perennial water source (O’Keeffe & Rogers 2003). Apart from these major river systems (~600 km), there are many ephemeral water sources or secondary rivers (>30 000 km) that flow across the Park, such as the Tsende, Bububu, Mphongolo, and Phugwane Rivers in the north, and the Timbavati, Nwaswitsontso, Nwanedzi, Mlondozi, Sand, and Sweni Rivers in the south (Gaylard et al. 2003; O’Keeffe & Rogers 2003).

Climate

Kruger Park lies within the southern African summer rainfall zone. Most of the precipitation is in the form of thunderstorms, falling during the wet season (summer) months from October to March, and peaking in November, December, and January (Venter & Gertenbach 1986; Venter et al. 2003; Figs 2.3a & b). Mean annual rainfall shows a decreasing trend from south to north and from west to east, varying from 700 mm per annum in Pretoriuskop in the southwest to 400 mm per annum in Pafuri in the northeast (Gertenbach 1980; Venter & Gertenbach 1986; Figs 2.2b & 2.3c). Higher altitude areas in the extreme northwest and southwest receive relatively high rainfall (>700 mm per annum). In spite of these details, the entire lowveld experiences a similar climate, and prolonged droughts affect the entire region (Venter et al. 2003). A time series of long-term annual rainfall shows no overall trend in rainfall, but coherent periods of above-average and below-average rainfall (rainfall “cycles”) are evident (Venter et al. 2003; Fig. 2.3d), as is the case for most of the

summer rainfall region (Tyson 1985). Rainfall cycles of 15-20 years have been identified, with 7-10 dry years being followed by a similar number of wet years (Tyson & Dyer 1975; Gertenbach 1980).

The lowveld has a sub-tropical climate, where the wet season months (October to March) are hot and humid, and the dry season months (April to September) are cold and dry (Venter & Gertenbach 1986). There is a slight spatial trend in temperature from cooler in the south (Skukuza mean annual max/min temperatures = 29.7°C and 13.7°C, respectively) to hotter in the north (Shingwedzi mean annual max/min temperatures = 30°C and 15.3°C, respectively) (Venter & Gertenbach 1986; Venter et al. 2003). Temperatures may reach 44°C or more in the wet season, but seldom fall below zero in the dry season.

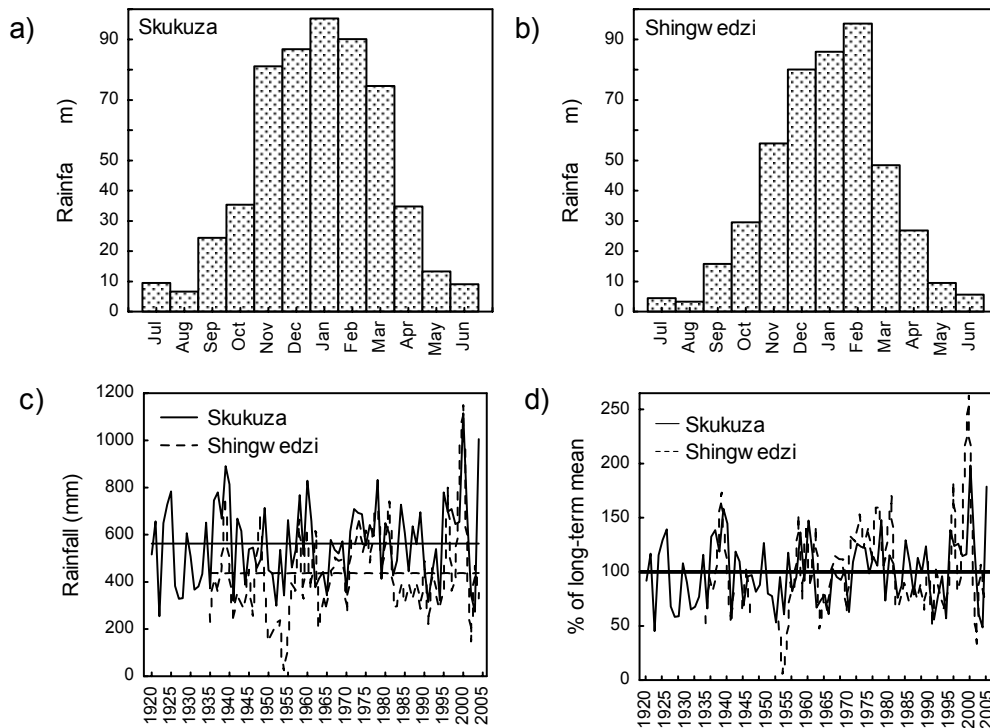


FIGURE 2.3. – Temporal variation in rainfall for Kruger Park, showing seasonal distribution of rain in a) southern (Skukuza), and b) northern (Shingwedzi) regions; c) changes in mean annual rainfall through the 20th century in the north and south with long-term mean displayed as horizontal lines; and d) changes in rainfall through the 20th century expressed as a percentage of the long-term mean to portray years of above and below average rainfall (100%, horizontal line). Data provided by the South African Weather Bureau and Nick Zambatis (Scientific Services, Skukuza, Kruger National Park).

2.1.2. Biotic Component

Land Systems and Vegetation Composition

The landscapes of Kruger Park are derived largely from the longitudinal granite/basalt division and a strong difference in vegetation between the northern (to the north of the Olifants River; see Fig. 2.1) and southern regions (reviewed in Scholes et al. 2003; Venter et al. 2003). Granite-based substrates give rise to more closed, wooded habitats, and basalts support open grasslands. In the north, mopane *Colophospermum mopane* is by far the most dominant tree species, but mopane is completely absent in the south where *Acacia* and *Combretum* spp. dominate. Thus, Kruger Park is divided into four major landscapes (northern and southern granites and basalts, respectively), which can be expected to support different ecosystems and foodwebs (Grant et al. 2002). The grass component differs between sandy, granitic soils associated with unpalatable species like *Aristida* spp., *Eragrostis* spp., and *Pogonarthria squarrosa*, compared with clayey, basalt-based soils which favour nutritious grasses such as *Panicum coloratum*, *Themeda triandra*, and *Urochloa mosambicensis* (e.g. Grant et al. 2002; Venter et al. 2003).

While useful for many purposes, the above description is a gross oversimplification of the diversity of landscapes and ecotypes found within Kruger Park; as many as 35 different ecotypes have been described (Gertenbach 1983). Venter (1990) developed a classification of 11 major land systems and 56 land types based on the geological and associated vegetational complexity of the region (Fig. 2.2c; reviewed in Venter et al. 2003). A brief overview of the land systems relevant to this study, i.e. areas where plants and elephant faeces were collected (see Chapters 3 and 4), follows (see Fig. 2.2c).

The Far North Study Area (Pafuri and Bulweni Land Systems)

Pafuri Land System – the Pafuri-Punda Maria region is a distinct, complex array of habitat types, soils, and associated geological formations. The landscape varies from rocky hills and gorges to lowland floodplains, with *Colophospermum mopane* woodland and forest, *Burkea africana* and

Pseudolachnostylis maprouneifolia broad-leaved “bushveld”, *Kirkia acuminata*, *Azelia quanzensis*, and *Combretum apiculatum* broad-leaved tree savanna, *Androstachys johnsonii* and *Croton pseudopulchellus* dry thicket and woodland, and *Acacia albida* and *Ficus sycomorus* river forest forming the most important plant communities.

Bulweni Land System – in the Punda Maria area paraduplex soils (sandy topsoil changing gradually into clay subsoil) dominate, and are characterized by *Colophospermum mopane*, which makes for a virtually monospecific closed woodland. The hilly areas of Punda Maria comprise mainly shallow soils and rocky outcrops, with deeper soils distributed sparsely in between (where *Burkea africana* may be present).

The Western Granites Study Area (Malelane, Skukuza, and Phalaborwa Land Systems)

The western regions of Kruger Park are underlain by granite rocks characterized by a variety of soil types (sand, clay, duplex soils, and mixed alluvial soils). Sandy areas in the southwest are dominated by dense deciduous broad-leaved bushveld, and characterized by *Combretum* spp. and *Terminalia sericea*. Along footslopes, small-leaved shrubveld with thorny trees, e.g. *Acacia gerrardii*, *A. nigrescens*, *Albizia harveyi*, and *Dichrostachys cinerea*, are prominent. Other species in these parts include *Euclea divinorum* and *Combretum hereroense*. Grass cover is sparse in drier years and medium to dense in wetter years, becoming denser and taller as the average annual rainfall increases towards the southwest (e.g. tall grasses such as *Hyperthelia dissoluta* and *Elyonurus argenteus* dominate the Pretoriuskop region, which has an annual rainfall exceeding 700mm). On crested areas grass cover is sparse, with *Pogonarthria squarrosa* and *Digitaria eriantha* dominating, while footslopes are characterised by denser and more palatable species such as *Themeda triandra* and *Panicum maximum* (Venter & Gertenbach 1986). Granitic regions in north comprise mainly *Colophospermum mopane* and *Combretum apiculatum* bushveld.

The Eastern Basalts Study Area (Satara, Letaba, and Vutome Land Systems)

Satara and Letaba Land Systems – weathering of igneous rock (mostly basalts) in these regions forms the clayey soils associated with the eastern half of Kruger Park. South of the Olifants River (the Satara land system) the area comprises mainly fine-leaved tree savanna/bushveld, and is characterized by *Acacia nigrescens*, *Dichrostachys cinerea*, and *Sclerocarya birrea*. North of the river (the Letaba land system), plains are dominated by *Colophospermum mopane* shrubveld and *Combretum imberbe* trees. Abundant grass cover is also prominent in this area under high rainfall conditions.

Vutome Land System – this land system is characterized by sodic duplex soils (sand or loam topsoil overlaying dispersed clay). In the areas underlain by Ecca shale, fine-leaved *Acacia welwitschii* and *Euclea divinorum* woodlands and thickets occur. Areas of sandy soils (derived from sandstone) are characterized by broad-leaved bushveld or tree savanna, with *Terminalia sericea* and *Combretum zeyheri* occurring.

Animal Species Composition

The heterogeneity of the abiotic component of Kruger Park at various spatial and temporal scales lends itself to an array of habitat types that support numerous faunal and floral species. Thus far, 147 mammals (Pienaar et al. 1987), 505 birds, 119 reptiles, 49 fish, 34 amphibians, 1 980 plants, and thousands of invertebrates have been identified (see Whyte 2001a). Mammals include 27 species of carnivore (e.g. lion *Panthera leo*, leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta*, and cheetah *Acinonyx jubatus*), numerous ungulate herbivores including African elephant, white rhinoceros *Ceratotherium simum*, black rhinoceros *Diceros bicornis*, Burchell's zebra *Equus burchellii*, hippopotamus *Hippopotamus amphibius*, giraffe, and 23 bovid species (e.g. buffalo, kudu *Tragelaphus strepsiceros*, impala, blue wildebeest *Connochaetes taurinus*, and waterbuck *Kobus ellipsiprymnus*), and five primate species (e.g. vervet monkey *Chlorocebus (=Cercopithecus) aethiops* and chacma baboon *Papio hamadryas*

ursinus). Approximate population sizes for mammals are provided by Whyte (2001a). For elephants, the 2005 census total was reported as 12 467 (Kruger elephant and buffalo census report 2005 provided by I. Whyte).

2.2. Natural Events

The effects of events such as droughts, floods, and disease on faunal and floral composition in Kruger Park are discussed in detail by several authors (e.g. Bengis et al. 2003; Pickett et al. 2003; Rogers and O’Keeffe 2003; Scholes et al. 2003; Venter et al. 2003). Three major floods (1925, 1996, and 2000) have occurred since the Park’s inception, while prolonged droughts were experienced during most of the 1940s, from the early 1960s to 1970s, and between 1981 and 1994 (see Figs 2.3c & d). The northern and southern regions of Kruger Park have generally experienced similar rainfall conditions, although the north is drier than the south overall (see Fig. 2.3c).

The Rinderpest epizootic that erupted in 1896 and decimated both wildlife and domestic stock just prior to the proclamation of the Sabi Game Reserve in 1898, contributed to local extinction of several species such as white rhinoceros (Carruthers 1995; Bengis et al. 2003). Extensive anthrax epidemics were recorded during 1959-1960, 1970, and 1990-1991 in the north, and in 1993 and 1999 in the central regions. Most mammals in Kruger Park are susceptible to anthrax, but species most severely affected are kudu and buffalo. Bovine tuberculosis (BTB) is an alien bacterial disease that entered Kruger Park during the 1950s (Bengis et al. 1996), and is maintained in the system mainly by buffalo, kudu and possibly warthog *Phacochoerus africanus*. BTB has not been detected in elephant, rhino, hippo, and zebra, and the long-term effects of this disease on sympatric animal populations are difficult to predict (Bengis et al. 2003).

2.3. Anthropogenic Influences

People have occupied the Kruger Park region intermittently for thousands of years (e.g. Cooke 1969; Plug 1982, 1989; Voigt 1983; Deacon & Deacon 1999). The early history of the region includes the Stone Age (Pleistocene to Holocene), the Iron Age (AD 200 to 1836), and the Colonial period (1836-1902) (Mabunda et al. 2003). This thesis is concerned mostly with the more recent events of the late Colonial period (towards the end of the 19th century), and the 20th and 21st centuries in Kruger Park. For events occurring between 1898 and 1926, Kruger Park is referred to as the Sabi Game Reserve. This was the initial game reserve proclaimed by Paul Kruger in 1898, including only the portion of the current area south of the Sabie River (see Mabunda et al. 2003). In 1903 the region between the Sabie and Olifants Rivers was appended to the Sabi Game Reserve, and the region between the Letaba and Levuvhu Rivers was proclaimed the Shingwitsi Game Reserve.

Management of the Sabi Game Reserve was initiated by the Park's first game warden, James Stevenson-Hamilton (appointed in 1902), who attempted to restore "some balance in the ecosystem" (Joubert 1986). From 1902 to 1926 the emphasis was on the protection and rebuilding of game populations, mainly by stopping hunting activities in the area. Wildlife management during this time also included controlled 'veld' burning, predator control, manipulation of herbivore populations (re-introduction and culling operations, excluding elephants), and establishment of tourist facilities and roads (post-1925) (see Joubert 1986). In 1924, government took over management, and under the National Parks Act (1926) the Sabi and Shingwitsi reserves were amalgamated and renamed "Kruger National Park" (see Mabunda et al. 2003). The new legislation allowed for a Board of Trustees to be appointed, and the era of exclusive power by the Park warden was over. The state undertook to pay for management and maintenance of the new national park, provided development was financed from tourist income.

Roads and Tourism

Up until 1926, no motor vehicles entered Kruger Park because no proper roads or bridges had been constructed (Freitag-Ronaldson & Foxcroft 2003). The Selati railway, pack donkeys, and horses were used for transport. In 1923 the South African Railways (SAR) also instituted a round-trip of the Lowveld for tourists that included a night stop at the Sabie Bridge in Skukuza (using the Selati railway). However, no over-night facilities were available and the tourists were confined to the train (Joubert 1986). The need for roads increased with an increase in tourism and management requirements. The first dirt tracks opened in 1928. The first road was tarred in 1961. Since then, the road network (including firebreaks, management roads, and airstrips) has expanded to ~8 000 km, with the most significant increases occurring between 1956 and 1970. The impacts of roads will, however, be species, ecosystem, and landscape specific, depending on road type and associated characteristics (Tshiguvho 2000). Tarred roads are considered to have the highest ecological impact (more so than firebreak roads or dirt roads). For example, they affect the abundance, distribution, colonization, and mortality rates of species (Tshiguvho 2000) due to road kills, road avoidance by animals because of noise, and barrier effects (separating populations may have demographic and genetic consequences) (Forman & Alexander 1998). Road impacts also include hydrological, erosion, sedimentation, and chemical effects, nutrient cycling, and invasion of alien plant species. These effects will have been most pronounced in southern Kruger Park, where tourism has always been concentrated (Freitag-Ronaldson & Foxcroft 2003; Fig. 2.2d).

Tourism is considered an economic stimulus, but carries with it impacts and environmental costs that inevitably lead to the degradation of the very resource around which it revolves (Joubert 1986; Braack & Marais 1997; Ferreira & Harmse 1999; Freitag-Ronaldson & Foxcroft 2003). Tourism, with its associated role as revenue generator, was established in Kruger Park in 1926. The Skukuza, Satara, and Pretoriuskop rest camps were established in 1928, following the opening of the Pretoriuskop section to tourists for day trips in 1927. Since 1926,

tourism has increased dramatically, with numbers reaching close to one million visitors per annum in 1997/8 (Freitag-Ronaldson & Foxcroft 2003).

The Technical Services Department (TSD) was established in 1958 to deal with proposed development of new, and improvement of existing, road networks and tourist amenities (see Fig. 2.2d). The TSD also completed the fencing of Kruger Park boundaries for disease and veterinary control purposes. The southern boundary along the Crocodile River was completed in 1959, the western boundary in 1961, the eastern boundary in 1976, and a short northern boundary in 1980 (Mabunda et al. 2003). In 1960/61 and 1967/68 the southwestern boundary underwent some changes that led to the excision of certain areas to the west (for provincial road construction), and in turn to a loss of biodiversity. The western boundary fence cut off large sections of wet season grazing areas and traditional dry season migration routes (from the east to the southwest) (Whyte & Joubert 1988), thus the fence was later moved (1994) to the outer boundary of neighboring private game reserves, regenerating some of the more natural movement routes for animals.

Over the years, apart from keeping domesticated livestock and humans out, and wild animals relatively protected against hunting and poaching, the boundary fence turned the Kruger Park into an ecological island for large mammals: it prevented migrating species from moving seasonally, thereby not allowing populations to escape natural pressures such as water scarcity, fire (and its effects on grazing), competition for food, disease epidemics, and local predation (Mabunda et al. 2003). The boundary fence also facilitated increases in population densities of large herbivores (e.g. elephant, buffalo, and hippo). Because these species were no longer exposed to hunting or poaching in surrounding areas, and because they could also not continue to migrate during the dry season, management expanded the network of artificial water sources, and established culling operations for the sake of conservation and maintenance of biodiversity (Pienaar 1970; Joubert 1986; Whyte 2001a; Gaylard et al. 2003).

Water and Fire Management

The water provision program, which has supplied Kruger Park with spatially and seasonally constant sources of surface water for about 70 years (i.e. >300 boreholes, dams, sluices, and weirs), used the heterogeneous availability of natural surface water as a template for superimposing artificial watering points. The principles were to stabilize existing natural water supplies, to provide additional artificial supplies to areas where natural water had existed previously, and to construct dams in areas where storage capacity was sufficient to guarantee water through periods of severe droughts (Pienaar 1970). It was also envisaged that certain boreholes could be shut down in rotation to minimize local overgrazing (Pienaar 1970), but this option has not as yet been applied (Gaylard et al. 2003). The start of the water provision program was marked by the installation of six boreholes after an extended dry period in 1933. Further major projects were completed in the 1950s and again in the 1960s. By 1995 a total of 365 boreholes and approximately 50 dams had been constructed (1933-1994). The highest density of artificial surface water points occur in the north of Kruger Park, followed by the central regions, while the lowest densities occur in the south and far north. On a broader spatial scale, artificial water points have drastically reduced the proportion of the Park that is in excess of 5 km from water during severe drought conditions (Gaylard et al. 2003; Fig. 2.2a).

There have been four major policies regarding fire management in Kruger Park (Table 2.1). First, it was avoided where possible, but later fire became an integral, somewhat inflexible component of management (van Wilgen et al. 2000, 2003). Fire management was characterized by a prescribed burning policy for 36 years (1956-1992). This burning policy was abandoned in 1992 for a number of reasons: unpalatable grass species became dominant as a result of the combined effects of excessive frequent burning and artificial water points (see Trollope et al. 1995); the number of large trees in Kruger Park were declining (see Trollope et al. 1998; Eckhardt et al. 2000); “ringburning” (where fires are ignited around the periphery of management blocks and allowed to burn towards the centre) does not simulate natural fires, which spread out in all directions from a point, allowing them to burn at a range of intensities as they spread.

Ringburning also traps animals and heterogeneity of vegetation decreases when burning on a fixed cycle over a long period (van Wilgen et al. 2000). A lightning fire approach was adopted in 1992, under which only fires started by lightning would be left to burn. However, the objectives of allowing a lightning-dominated fire regime to develop were hampered by accidental ignitions that forced management to adopt an integrated approach in 2002. This approach, which is ongoing, combines elements of patch mosaic, range condition, and lightning burns, allowing many of the non-planned ignitions to burn at managers' discretion, while some control may still be exerted by applying prescribed burns where the condition of the grass layer is perceived to require burning (van Wilgen et al. 1998, 2003).

Animal Population Management

Numerous introductions, reintroductions, and translocations (particularly of antelope species) have taken place in Kruger Park following improvement of wild animal capture and care techniques in the early 1960s. The last naturally occurring white rhino were seen in Kruger Park in 1896, and black rhino in 1936. Successful reintroduction of white rhino from KwaZulu-Natal commenced in 1961, followed by black rhino in 1972, and the process for the latter is still ongoing. Reintroduction of nyala *Tragelaphus angasii* from KwaZulu-Natal in 1980 was successful. Many other reintroductions have had limited success, e.g. eland *Taurotragus oryx*, tsessebe *Damaliscus lunatus*, Lichtenstein's hartebeest *Alcelaphus lichtensteinii*, roan antelope *Hippotragus equinus*, sable antelope *H. niger*, mountain reedbuck *Redunca fulvorufula*, grey rhebok *Pelea capreolus*, oribi *Ourebia ourebi*, suni *Neotragus moschatus*, red duiker *Cephalophus natalensis*, cheetah, and aardwolf *Proteles cristatus* (Freitag-Ronaldson & Foxcroft 2003).

Culling of various species was a regular occurrence during early management regimes, with the process being described as "pragmatic intervention" (Freitag-Ronaldson & Foxcroft 2003). Predators, considered "overabundant vermin" and a threat to human lives at the time, were

initially targeted, with control reaching its peak between 1911-1920, and between 1951-1960. Controlling predator numbers was also justified as a “conservation effort” in response to concerns about declining ungulate numbers. The aims and objectives of carnivore population control changed under the rule of different park wardens, officially ceasing in 1975 (Freitag-Ronaldson & Foxcroft 2003). The 1960s and 1980s were associated with the culling of large herbivore populations based on principles that large herbivores are limited by grazing and available water during droughts, and that high-density species may impact on habitat and compete with rarer species (Joubert 1986; Whyte 2001a; Whyte et al. 2003). In 1965/66 culling practices for elephant, zebra, hippopotamus, giraffe, buffalo, wildebeest, and impala were approved (Whyte 1985, 2001a; Whyte et al. 2003). After 1985 additional means of population reduction were employed, i.e. gaining financial return through the capture, sale, or donation of species (Whyte 2001a; Freitag-Ronaldson & Foxcroft 2003).

Animal populations have been vulnerable to poaching ever since the proclamation of the Sabi Game Reserve in 1898 (Carruthers 1995; Pollard et al. 2003). In 1903, Stevenson-Hamilton established the first anti-poaching unit. During the late 1970s and early 1980s organized rhino and elephant poaching had a significant impact on game populations. In recent times, poaching incidences have fluctuated, mainly as a result of increasing numbers of poor communities on Kruger Park’s borders and a high demand for rhino horn and elephant ivory. Contemporary anti-poaching operations are highly organized, and are logistically and financially well supported (Freitag-Ronaldson & Foxcroft 2003). Operations are proactive and play an important deflective role outside the Park’s borders, including strategies of informer networks, general education, and counterincentives.

2.4. Elephant Population History

Elephants were previously widely distributed throughout the southern African subregion (Douglas-Hamilton & Michelmore 1996; Plug & Badenhorst 2001). By the middle of the

nineteenth century, the growing human population increasingly excluded elephants from their natural range. Today, they are compressed into game reserves, national parks, and the more remote areas of Mozambique, Botswana, and Namibia (e.g. Laws 1970; Sikes 1971; Douglas-Hamilton & Michelmore 1996). Available evidence suggests that elephant population densities in the past were high in southern Africa and indeed the rest of the continent south of the Sahara (Douglas-Hamilton & Michelmore 1996). The history of elephant populations in Kruger Park and the rest of the lowveld have been described under four time frames, i.e. i) pre-European, ii) arrival of Europeans, iii) after proclamation as a game reserve in 1898, and iv) elephant management era (including elephant management and culling operations between 1967 and 1994) (Whyte et al. 2003). The first three are summarized in section 2.4.1 below, and the management era is discussed in section 2.4.2. The post-management era, i.e. population growth over the last 12 years, current elephant abundances, and the future of these animals in Kruger Park, is discussed in section 2.4.3.

2.4.1. From the Pre-European Era to Post-Proclamation as a Game Reserve in 1898

The scarcity of elephant skeletal remains from archaeological sites in Kruger Park (Plug 1984, 1989), the limited representation of elephants in Bushman (San) shelters with rock art (Cooke 1969), and the relatively high density of old baobab *Adansonia digitata* trees in the north underlie the argument that elephant abundances were historically low (Whyte 2001a; Whyte et al. 2003). However, as recognized by Whyte et al. (2003), these lines of evidence offer a poor reflection of historical elephant population demographics. For one, faunal remains, especially at Iron Age sites, are poorly protected from the elements and hence not well preserved (Voigt 1983). It is also unlikely that Iron Age communities, heavily reliant on domestic livestock and hunting of smaller animals such as impala (e.g. Voigt 1983), would have hunted elephants and collected elephant bone to any great degree. In cases where elephant remains comprised only ivory, these were usually in the form of chips and objects, and represent Iron Age ivory workshops, in which

case the ivory could have been introduced from elsewhere (Plug & Badenhorst 2001). Further, elephant tusks, unless they were carried away and processed, seldom survive in archaeological sites as they become brittle and flaky, and are easily disintegrated after death (J.S. Brink 2007 pers. comm.). Thus the scarcity of elephant bones at these sites is not necessarily an indication of low elephant numbers. Second, evidence from San rock art does not constitute a good argument for the inference of faunal representation in an area, because paintings only reflect species of special cultural or other significance, and therefore do not represent animal population trends (Dowson & Holliday 1989; Lewis-Williams & Dowson 1989; Ouzman 1995; Moodley 2002). Lastly, trees such as the baobab are a poor proxy for elephant populations. Today, high densities of baobabs occur in other African savannas in the presence of relatively large elephant populations. Whyte (2001a) further argued that baobabs in Kruger Park show only recent signs (<100 years old) of elephant damage, but elephants in the region may not have been utilizing and/or damaging these trees in earlier years, and it is possible that elephant-induced scratches on the bark do not persist over hundreds of years. Although extensive damage to baobabs during the 20th century has been recorded elsewhere, e.g. Tanzania, Kenya and Zimbabwe (e.g. Barnes 1980; Swanepoel & Swanepoel 1986; Swanepoel 1993), this can be expected to have been significantly less in times before elephants were geographically confined by fences.

Whyte (2001a) contended that because diaries of several European tradesmen and hunters who infiltrated the lowveld region by the mid-19th century do not mention elephant hunting (e.g. Selous 1881; Bryden 1903; Finaughty 1916; Preller 1917), they were therefore rare in the region. Yet Plug & Badenhorst (2001) claim that many diaries, notes, and numerous town and farm names referring to the animal, point to elephants as having been present in the lowveld and other parts of southern Africa. Vaughn Kirby (1896) noted that large herds of elephant were common in parts of the lowveld until ca. 1880 to 1890. Indeed, the Olifants River was so-named by travelers in 1725 because it was home to large elephant herds (Punt 1990). In sum, the evidence is incomplete, and our knowledge of historical elephant abundances in this region remains

debatable. Nonetheless, all sources agree that towards the end of the 19th century, elephants were very scarce or even extinct in the Kruger Park region. Poaching and the growth of the ivory trade (dating back to 850 AD) had begun to take its toll, threatening populations throughout Africa (Bryden 1903; Douglas-Hamilton & Michelmore 1996).

2.4.2. The Elephant Management Era (Population Control Between 1967 and 1994)

In the 19th century, the ivory trade had become a major factor affecting the continent-wide status of African elephants (see Douglas-Hamilton & Michelmore 1996). In the Kruger Park area, the few remaining elephants were shot to extinction between 1880 and 1896 (Whyte et al. 2003). Early colonial game laws in many countries put an end to the most obvious forms of commercial hunting for ivory, restricting offtake to controlled quotas for sport hunting. In many areas of southern, east, and central Africa elephant populations recovered in the first six decades of the 20th century (Percival 1924 in Douglas-Hamilton & Michelmore 1996; Pitman 1934; Spinage 1973; Laws et al. 1974; Lindeque 1988; Hall-Martin 1991; Douglas-Hamilton & Michelmore 1996). In the Kruger Park region, Stevenson-Hamilton (1905) first reported elephant sightings near the confluence of the Letaba and Olifants Rivers some years after proclamation of the Sabi Game Reserve. According to Whyte et al. (2003), elephants recolonized the Park from the Letaba region northwards between 1903 and 1945, and more slowly southwards, between 1903 and 1958.

Since the proclamation of the Sabi Game Reserve in 1898, elephant population densities increased at a mean intrinsic rate of 7.5% per annum. After completion of the eastern boundary fence in 1976, this rate decreased to 6.6%, suggesting that immigration of elephants from Mozambique likely contributed to the rapid increase in population numbers before 1976 (Whyte et al. 2003). In 1965, a symposium on overprotection convened by the National Parks Board of Trustees recommended that the elephant population should be maintained at 7 000 (estimated population size at the time), but accepting fluctuations between 6 000 and 8 500 (Joubert 1986; see also Whyte 2001a). This decision was based on the fact that management authorities (see Smuts 1974) felt

appropriate information regarding the full implications of the ecological role of elephants in ecosystems to be lacking, and therefore maintaining elephant abundances at their current (1965) levels seemed to be the most plausible option at the time. This recommendation was approved in 1966, and culling commenced in 1967 (Mills et al. 1996; Whyte et al. 2003). In all, 16 201 elephants were removed (through culling and/or translocation) from Kruger Park during the period 1966 to 1994 (Whyte 2001; and see Table 2.2.).

2.4.3. The Post-Management Era (1994 to present)

Apart from the healthy elephant populations in protected and confined areas such as the Kruger Park, this species has become locally extinct across much of its former range, especially in central and West Africa, largely because of hunting (for meat and ivory) and the conversion of habitats to crops and anthropogenic influences (Whyte et al. 2003). In 1989, in an effort to protect Africa's elephants, a ban was placed on international trade in elephant products, through listing of the African elephant in Appendix I of the Parties to the Convention on International Trade in Endangered Species (CITES) at Lausanne, Switzerland. In 1994, an animal rights group questioned the reasons for, and the ethical morality of culling. After a public debate the National Parks undertook to review of its management policy in 1995. They placed a moratorium on culling until the review process was completed. In 1999, a new policy for the management of Kruger Park's elephant population was put forward (Whyte et al. 1999; Whyte 2001a, 2001b), and is summarized here.

The New Elephant Management Policy

The "New Elephant Management Policy" was the result of many consultative debates between South African National Parks and a wide diversity of interested and affected parties (Whyte 2004). The primary objective of this policy was (and is) to maintain indigenous biodiversity. Kruger Park was divided into six zones, consisting of two botanical reserves in which elephants were to be maintained at medium densities, two low-impact zones where elephant densities were to be kept low

through management, and two high-impact zones where elephant densities were to be allowed to increase with no management interference. Management policies of the low-impact and high-impact zones were to be reversed once biodiversity-monitoring programmes suggested that acceptable thresholds of change have either been reached, or exceeded (Whyte et al. 1999; Whyte 2004).

However, the new management policy was never implemented, and the Park has subsequently been rezoned (Whyte 2004). The original zoning process was based on results of research on elephant clan movements, with the belief that zoning along natural clan boundaries will limit movement of elephants between zones once the policy is implemented. Nonetheless, the management policy put forward by Whyte et al. (1999) made no attempt to model expected population trends once the policy was implemented, or to determine the number of elephants that may have to be removed from the population (Whyte 2004). Although amendments to the new management policy have been proposed, its implementation is at a standstill.

Since 1994, a total of 763 elephants have been removed, mainly through translocation (see Table 2.2.). Still, elephant numbers have increased from 8 064 in 1995 to ~12 500 in 2005, with an influx of animals from neighbouring countries (Zimbabwe and Mozambique) likely contributing to the increase (Kruger elephant and buffalo census report 2005, provided by I. Whyte). The “transfrontier” park (Limpopo National Park) was established in 2001 by removal of part the eastern fence between Kruger Park and the adjacent protected area in Mozambique (Whyte 2001a). The fence between Kruger Park and the Sabie Sands Private Nature Reserve to the west was removed in 1993, resulting in the Sabie Sand population increasing from 60 to 913 by 2005 (IUCN 2006). Thus, with the inclusion of a section of Mozambique the numbers of existing elephants (~12 500) are thought not to be in excess (WESSA 2004). Nevertheless, there remains an increasing concern about the rapid rise in elephant numbers in Kruger Park, and the way to deal with this continues to be a controversial issue (see Owen-Smith et al. 2006).

Many debates have taken place in recent years, and issues regarding the need to control elephant numbers are constantly revisited (see Walker et al. 1987; Gillson & Lindsay 2002; van

Aarde et al. 1999, 2004; Havemann 2006; IUCN 2006; Owen-Smith et al. 2006). A recent review of articles on this subject shows that only 9% of studies conducted over a 44-year period support the perception that elephant impacts on their environment are sufficient to represent a potential threat to biodiversity (R.J. van Aarde 2005 pers. comm.). With the number of contrasting viewpoints (Pienaar et al. 1966; Whyte & Grobler 1998; Whyte et al. 1998; van Aarde et al. 1999, 2004; Fayrer-Hosken et al. 2000, 2001; Whyte 2001a, 2001b; Dublin & Niskanen 2003), and the extent of public controversy (e.g. WESSA 2004), the way forward is not clear. The only consistent outcome of discussions is that the dynamics of elephant-plant interactions is poorly understood and that further studies integrating multiple spatio-temporal scales (especially long term) are badly needed (Owen-Smith et al. 2006). This study aims to address these gaps, both over the short term and more importantly, reconstructing long term diet histories of Kruger Park elephants.

TABLE 2.1. – Different fire management approaches (1926-present) applied to vegetation in Kruger Park (from van Wilgen et al. 2003).

Time period	Fire Management Approach	Rationale for Approach
Fire avoidance		
1926-1947	Occasional, limited fires.	Provision of green grass for wildlife.
1948-1956	Prescribed burning stopped; Firebreaks established to assist with control of wildfire.	Concern about perceived negative effects of fire.
Prescribed burning policy		
1956-1980	Formal system of prescribed burning: once every 3 years on burn plots only.	Maintenance of ecosystem health
1981-1992	Rainfall and other specific objectives in local landscape considered with the intent of having more variable periods between fire, more seasonal variation.	Application of fires over a longer time period.
Lightning-fire approach		
1992-2001	Lightning fire, suppression of anthropogenic fires.	Simulation of natural conditions.
Integrated approach		
2002-present	Patch burns in certain areas and suppression of fires in others; all lightning fires tolerated.	Adaptive management: promote/maintain biodiversity.

TABLE 2.2. – Annual elephant census totals and culling quotas in Kruger Park for the period of 1903-2005, and numbers removed from the population (data derived from Whyte et al. 2003, and the 2005 census report for elephant and buffalo in Kruger Park).

Year	Census total	Culling quota	Total culled	Translocated animals			Total removed after census
				Juveniles	Family units	Adult bulls	
1903	0	-	-	-	-	-	-
1905	10	-	-	-	-	-	-
1908	25	-	-	-	-	-	-
1925	100	-	-	-	-	-	-
1931	135	-	-	-	-	-	-
1932	170	-	-	-	-	-	-
1933	200	-	-	-	-	-	-
1936	250	-	-	-	-	-	-
1937	400	-	-	-	-	-	-
1946	450	-	-	-	-	-	-
1947	560	-	-	-	-	-	-
1954	740	-	-	-	-	-	-
1957	1000	-	-	-	-	-	-
1960	1186	-	-	-	-	-	-
1962	1750	-	-	-	-	-	-
1964	2374	-	-	-	-	-	-
1966	No census	-	-	26	-	-	26
Culling operations initiated							
1967	6 586	650	355	-	-	-	355
1968	7 701	1 230	460	-	-	-	460
1969	8 312	1 408	1 160	-	-	-	1 160
1970	8 821	2 093	1 846	-	-	-	1 846
1971	7 916	889	602	-	-	-	602
1972	7 611	618	608	-	-	-	608
1973	7 965	738	732	-	-	-	732
1974	7 702	853	764	-	-	-	764
1975	7 408	601	567	-	-	-	567
1976	7 275	350	285	-	-	-	285
1977	7 715	663	544	26	-	-	570
1978	7 478	392	348	35	-	-	383
1979	-	380	322	48	-	-	370
1980	7 454	395	356	55	-	-	411
1981	7 343	71	16	0	-	-	16
1982	8 051	555	427	46	-	-	473
1983	8 678	2 229	1 290	66	-	-	1 356
1984	8 273	1 890	1 289	88	-	-	1 377
1985	6 887	369	268	101	-	-	369
1986	7 617	495	404	94	-	-	498
1987	6 898	305	245	59	-	-	304
1988	7 344	367	273	83	-	-	356
1989	7 468	367	281	85	-	-	366
1990	7 287	367	232	132	-	-	364
1991	7 470	367	218	140	-	-	358
1992	7 632	350	185	150	-	-	479
1993	7 834	577	308	74	8	-	390
1994	7 806	600	177	31	146	2	356
Culling operations ceased							
Sub-total (1966-1994)		20 169	14 562	1 339	154	2	16 201
1995	8 064	0	44	0	83	0	127
1996	8 320	0	18	0	169	6	193
1997	8 371	0	5	0	52	34	91
1998	8 869	0	0	0	12	34	46
1999	9 152	0	0	0	20	8	28
2000	8 356	0	0	0	16	18	34
2001	9 276	0	0	0	70	26	96
2002	10 459	0	0	0	65	19	84
2003	11 672	0	0	0	40	11	44
2004	11 454	0	0	0	0	0	0
2005	12 467	0	0	0	14	6	20
TOTAL	-	20 169	14 629	1 339	695	164	16 964

- Chapter 3 -

Background to Stable Isotope Ecology: Variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Vegetation

Stable isotope approaches to herbivore diet are founded on our knowledge of the isotope composition of plants at the base of the food chain. This chapter discusses the basis for carbon and nitrogen isotope fractionation in plants, and the ecophysiological and environmental factors that underlie variations in plant and animal isotope composition. I discuss the implications of stable light isotope data for vegetation from Kruger Park for reconstructing animal diets. I have added a third year to an existing two-year isotopic study of Kruger Park plants (Codron et al. 2005; included with this thesis as Appendix II), and explore whether the trends observed for the first two years persist in the third.

3.1. Introduction

Stable isotope ecology is widely applied to ecological, archaeological, and palaeoecological research (reviewed in Dalerum & Angerbjorn 2005; Thompson et al. 2005). The basis of this technique is that stable isotope ratios of elements such as carbon, nitrogen, and oxygen in biological materials undergo fractionation during the carbon, nitrogen and oxygen cycles, respectively, and during metabolic reactions, so that the relative abundances of these isotopes vary in a patterned way across ecosystems (Peterson & Fry 1987; Rundel et al. 1989). Once the isotope effects for various cycles and shifts are understood, this knowledge can be used as a basis for tracing carbon, nitrogen and other elemental cycles. For animal population science, isotopic tracing of nutrient flow through foodwebs allows for reconstructing complex diets and foodwebs (DeNiro & Epstein 1978; Vogel 1978; Peterson & Fry 1987; Ehleringer & Rundel 1989). It is therefore important to know how stable isotope compositions of sources at the base of

the food chain vary in response to environmental changes across space and time (Koch et al. 1991; Tieszen 1991; Heaton 1999; Post 2002; Cerling et al. 2003). For long-term and/or palaeoecological studies, however, this kind of information is seldom available, and improving the confidence of diet reconstructions requires that patterns observed in the food base over the short term are consistent through time, or at least that changes can be predicted.

Stable isotope-based foodweb reconstruction in terrestrial systems is dependant on our knowledge of isotopic abundances across different plant groups. In African savannas and other subtropical environments, $^{13}\text{C}/^{12}\text{C}$ ratios (denoted as $\delta^{13}\text{C}$) of C_3 - (dicotyledonous trees, shrubs, and forbs) and C_4 - (grass) photosynthesizing plants are distinct and the ranges do not overlap (Smith & Epstein 1971; Vogel et al. 1978). The mean $\delta^{13}\text{C}$ for C_3 plants is around -27.0‰, but this figure varies from \sim -34‰ to -20‰ because of physiological responses to the environment that influence CO_2 fixation rates and isotopic discrimination during photosynthesis. Factors including higher rainfall, water availability, greater canopy cover (reduced solar radiation), and intense recycling of atmospheric CO_2 in forests, are expected to contribute to relatively low $\delta^{13}\text{C}$ values in C_3 plants (e.g. Vogel 1980; Farquhar et al. 1982, 1988; Ehleringer & Cooper 1988; Tieszen 1991; van der Merwe & Medina 1991; Garten & Taylor 1992; Ehleringer 1993; Mole et al. 1994; O'Leary 1995; Stewart et al. 1995; Heaton 1999; Codron et al. 2005). Although typically less variable than C_3 plants (because CO_2 is fixed early on during photosynthesis), the $\delta^{13}\text{C}$ of C_4 plants also varies (from about -16 to -9‰, mean -12.5‰) in response to environmental changes (e.g. Vogel 1980; Farquhar et al. 1982, 1988; O'Leary 1988, 1995). In contrast to patterns of variation expected for C_3 vegetation, lower $\delta^{13}\text{C}$ values in C_4 occur with decreases in rainfall and water availability, and with increased exposure to solar radiation. More importantly, $\delta^{13}\text{C}$ values differ significantly depending on photosynthetic sub-type; NADP-ME (nicotinamide adenine dinucleotide phosphate-malic enzyme) plants are enriched by about 1.0 to 1.5‰ relative to NAD-ME (nicotinamide adenine dinucleotide-malic enzyme) and PCK (phosphoenolpyruvate

carboxykinase) plants, although their respective ranges may overlap (Hattersley 1982; Cerling & Harris 1999; Sage et al. 1999; Codron et al. 2005).

Plant $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) is related to that of its nitrogen (N) sources, which are derived mainly from the soil substrate. The $\delta^{15}\text{N}$ of the N sources represent the mean of the $\delta^{15}\text{N}$ values of all the potential N sources (which are all influenced by environmental factors), weighted by their availabilities (Robinson 2001). Thus, factors influencing soil $\delta^{15}\text{N}$ values such as geology, soil age, disturbance (e.g. soil erosion, fire), soil moisture content and rainfall, mineralization/nitrification potential, and sources of isotopically distinct nitrogen (N) should be reflected in plants (Stewart & Schmidt 1999; Robinson 2001; Schmidt & Stewart 2003). The $\delta^{15}\text{N}$ of plants do not, however, reflect that of the available N source directly (Robinson 2001; Schmidt & Stewart 2003). Plant $\delta^{15}\text{N}$ is influenced by several biological, physiological and environmental factors, including plant root depth, nitrogen assimilation (influenced by mycorrhizal root associations), nitrogen availability (in soil and air), geology, soil type, water stress and availability, and climate (Steele & Daniel 1978; Heaton 1987; Handley & Raven 1992; Handley et al. 1994; Muzuka 1999; Robinson 2001; Schmidt & Stewart 2003; Swap et al. 2004; Codron et al. 2005). Interpretations are further complicated by the complexity of the nitrogen cycle (e.g. process of nitrogen fixation and denitrification) relative to the carbon cycle, because there is a continuum in isotope compositions, and because plants often have access to (and can use either) oxidized or reduced N (Handley & Raven 1992). Despite the growing knowledge of $\delta^{15}\text{N}$ variations in plant communities, the causal determinants of ^{15}N natural abundances in natural systems are yet to be fully understood.

Carbon and nitrogen isotope variations in plants are recorded in the tissues of animals feeding on them, not only in terms of the well-known difference in $\delta^{13}\text{C}$ between C_3 - (browsers) and C_4 -feeders (grazers), but also within them (Vogel 1978; Tieszen et al. 1979; Lee-Thorp & van der Merwe 1987; Cerling & Harris 1999). For example, C_3 -feeders foraging on gallery forest

floors have more negative $\delta^{13}\text{C}$ than canopy feeders and animals foraging at forest margins or in more open savannas (Ambrose & DeNiro 1986; Carter 2001; Cerling et al. 2004b), and $\delta^{15}\text{N}$ values have been used to track patterns in resource use and niche partitioning (e.g. Schoeninger et al. 1999; Fisk et al. 2002; Urton & Hobson 2005; Cerling et al. 2006). C_4 -feeders also differ slightly in $\delta^{13}\text{C}$ depending on whether the primary grass type eaten is NADP or NAD/PCK (Cerling & Harris 1999; Cerling et al. 2003; Codron, D. & Codron in press). As our knowledge of isotopic variations in plants improves, so too will our ability to use stable isotope approaches to diet with greater confidence.

A previous two-year study of variations in plants from Kruger National Park, South Africa, revealed relatively small variations in plant isotope composition (particularly in $\delta^{13}\text{C}$), even though Kruger Park comprises an array of habitats differing in climate regime, geology, and vegetation (Codron 2004; Codron et al. 2005). The implication is that large-scale plant isotopic variations, predicted from comparisons across environments as different as tropical rainforests and deserts, are not evident within a single savanna environment. Hence the potential impact of plant isotope variability on diet studies at seasonal, and perhaps inter-annual scales has been in many instances over-stated. Nevertheless, the Kruger Park study did yield some patterns which have led to improved accuracy of diet-source isotope mixing models, including subtle changes in $\delta^{13}\text{C}$ across different microhabitats, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences between multiple C_3 (leaves, fruit, sedges) and C_4 (NADP, NAD, and PCK grasses) food types (Codron et al. 2006; Codron, D. et al. 2006; Codron, D. & Codron in press). The primary aim of this chapter is to determine whether previously reported trends are consistent, based on the addition of data for a third study year. Differences between plant food groups, and patterns of spatial and seasonal variation, are compared within and between each year of the three years, allowing for details of annual changes. Inclusion of three years of data also allows for more rigorous statistical exploration of the potential effects of climatic factors (rainfall, temperature) on plant isotope composition.

3.1.1. Methodological Background

Photosynthesis and Carbon Isotope Distributions among Terrestrial Plants

The bimodal distribution of $\delta^{13}\text{C}$ values among terrestrial plants is ascribed to differences in anatomical and physiological photosynthetic characteristics of C_3 versus C_4 plants (Smith & Epstein 1971; Vogel 1980; Farquhar et al. 1982; O'Leary 1988, 1993, 1995). During photosynthesis, photosynthetic processes discriminate, to varying degrees, against ^{13}C incorporated in the CO_2 that is absorbed via stomata. The magnitude of this discrimination differs greatly between C_3 and C_4 plants, due mainly to the activity of different enzymes involved in carboxylation (fixation of absorbed atmospheric CO_2). In C_3 plants, ^{13}C discrimination by the enzyme *ribulose biphosphate carboxylase* (Rubisco), which converts absorbed CO_2 into phosphoglyceric acid (PGA) consisting of three carbon atoms, is in the order of $\sim 29\text{‰}$ (Vogel 1980; Farquhar et al. 1982; O'Leary 1988). In C_4 plants, the enzyme *phosphoenolpyruvate carboxylase* (PEP), discriminates against ^{13}C to a much smaller degree ($\sim 2\text{‰}$), accounting for the consistently higher $\delta^{13}\text{C}$ values of C_4 versus C_3 plants. Other processes that influence carbon isotopic distributions between and amongst C_3 and C_4 plants include rates of diffusion, dissolution, and stomatal responses to environmental changes.

Farquhar et al. (1982) recognized a positive relationship between $\delta^{13}\text{C}_{\text{plants}}$ with CO_2 concentrations in intercellular leaf spaces. This relationship, which describes changes in photosynthetic discrimination (F) against ^{13}C is modeled as

$$F = [a + (b - a) C_i/C_a - d] \quad (\text{Equation 1}),$$

where a is the discrimination effect due to diffusion (4.4‰), b the discrimination due to carboxylation ($\sim 29\text{‰}$ in C_3 plants), d the minimal effect that respiration, liquid-phase diffusion, carbon export and other factors have on isotope exchange, and C_i/C_a is the ratio of absorbed CO_2

concentration in the intercellular space to the ambient atmospheric CO₂ concentration (Farquhar et al. 1982; O'Leary 1993).

In C₃ plants, external CO₂ is transported through the stomata and into the internal gas space. The internal CO₂ then dissolves in the cell sap and diffuses to the chloroplast where carboxylation occurs. The most significant fractionation (~29‰) occurs during the carboxylation (CO₂-fixation) of absorbed atmospheric CO₂ (Vogel 1980; O'Leary 1988). The carboxylation step is irreversible, hence subsequent steps (diffusion and dissolution), although resulting in some ¹³C discrimination, are not as important in determining the overall isotope fractionation (O'Leary 1988). In most instances, *d* is negligible, and for most plants C_i is about one half of C_a, so that the net result of Equation 1 is that discrimination against ¹³C in CO₂ fixed from the atmosphere (which has a δ¹³C of -8.0‰, but see below) leads to δ¹³C values in C₃ plants of around -27.0‰ (Vogel 1978; Farquhar et al. 1982; O'Leary 1988).

Changes to C_i, or more specifically C_i/C_a, describe the most important variations in δ¹³C within C₃ plants. Under conditions of elevated stomatal conductance and [CO₂]_{atm} absorption, C_i increases so that *F* increases and δ¹³C values decrease. For example, stomatal activity tends to increase in wet/moist conditions, as plants attempt to maximize water loss relative to uptake, resulting ultimately in ¹³C-depleted plant tissues (O'Leary 1988; Farquhar et al. 1989; Tieszen 1991). In more arid conditions, stomatal closure increases as plants attempt to limit water loss, leading to lower C_i/C_a ratios. These trends likely underlie the negative relationship sometimes observed between C₃ plant δ¹³C with rainfall, such as has been reported for plants from areas where mean annual rainfall ranges between 350mm and 1700mm (Stewart et al. 1995), and similarly why plants from desert and semi-desert environments tend to have very high δ¹³C values (up to -20 ‰; Ehleringer & Cooper 1988; Ehleringer 1993). Variations in C₃ plant δ¹³C are, however, not only sensitive to changes along a moisture gradient, but also to variations in atmospheric CO₂ concentrations (van der Merwe & Medina 1989, 1991; Feng & Epstein 1995),

solar radiation (Farquhar et al. 1989), temperature and altitude (Tieszen 1991). For example, enzymatic activity and C_i/C_a , and hence F , decrease when ambient temperatures deviate from the optimum for a given species, or with altitude due to air pressure effects (Tieszen 1991). The so-called “canopy effect”, whereby C_3 plants growing in dense canopy forests become so ^{13}C -depleted that $\delta^{13}\text{C}$ values as low as -37‰ have been recorded, is attributed largely to reduced C_i in response to low levels of solar radiation (Farquhar et al. 1989). According to this hypothesis, ^{13}C -depletion under closed canopy conditions is due to more complete expression of discrimination by Rubisco, while under high light conditions (such as the tops of trees) the discrimination is smaller due to kinetic effects. An alternative, possibly complementary, explanation, is that recycling of ^{13}C -depleted source CO_2 from forest soils is responsible for the canopy effect (Vogel 1980; van der Merwe & Medina 1989, 1991).

C_4 photosynthesis occurs in plants with a specialized leaf anatomy in which the vascular bundles are surrounded by a prominent concentric arrangement of mesophyll cells containing a large number of chloroplasts, described as Kranz anatomy (from the German word for wreath (*kranz*); Laetsch 1974; Salisbury & Ross 1992). In these plants, an additional reaction takes place prior to Rubisco converting CO_2 to PGA (Smith & Epstein 1971; Vogel 1980; O’Leary 1988, 1993). CO_2 initially enters the leaf through the stomata and is taken up by the enzyme PEP *carboxylase* in the mesophyll cells. Here the absorbed CO_2 is converted either into aspartate or malate, before being transported to the bundle sheath cells where it is converted to a four-carbon compound, oxaloacetic acid (OAA). The isotopic fractionation that occurs during carboxylation by PEP in C_4 plants is irreversible (as it is with Rubisco in C_3 plants). Since PEP discriminates against ^{13}C far less heavily ($\sim 2\text{‰}$) than does Rubisco (29‰), C_4 plants have higher $\delta^{13}\text{C}$ values than C_3 plants (-12.5‰ on average).

C_4 plants effectively concentrate absorbed CO_2 as an initial step (carboxylation by PEP), and although Rubisco is also involved in C_4 photosynthesis later on, further fractionation is

limited by the preceding effect of PEP (Vogel 1980; Farquhar et al. 1982; O'Leary 1988). Thus C₄ plants are consistently enriched in ¹³C relative to C₃ plants, and the variation within C₄ plants is limited (Smith & Epstein 1971; Vogel 1980; Farquhar et al. 1982, 1989; O'Leary 1988). The major source of carbon isotopic variations is ascribed to alternative photosynthetic sub-pathways. The C₄ photosynthetic sub-pathways are represented by three enzymatic sub-types, i.e. NADP-ME, NAD-ME, and PCK, which discriminate differently against ¹³C during carboxylation, resulting in small (~0.5 to 1.5‰) but significant variations in δ¹³C (Hattersley 1982; Cerling & Harris 1999; Sage et al. 1999; Codron et al. 2005). NADP grasses, more common in mesic environments, tend to be ¹³C-enriched relative to NAD and PCK grasses which generally occur in xeric habitats (Cerling & Harris 1999).

C₃ photosynthesis is the oldest and most dominant pathway followed by plants, occurring in 90% of all living taxa (Sage 2005). Most predictions are that C₄ plants originated between ~23 and 30 Ma., but the timing of C₄ origins remains controversial and the evolutionary steps that led to biochemical and anatomical modifications from C₃ to C₄ photosynthesis are poorly known (Kellogg 1999; Hibberd & Quick 2002; Keeley & Rundel 2003; Segalen et al. 2006). It is clear that a rapid radiation of C₄ photosynthesis occurred during the Late Miocene and/or Early Pliocene (~4 to 7 Ma.), documented by shifts in carbon isotope values of soil carbonates, faunal tooth enamel, and ratite eggshells (Quade et al. 1989; Cerling et al. 1993, 1997b, 2005; Morgan et al. 1994; Ehleringer et al. 1997; Segalen et al. 2006). Cerling et al. (1997b) hypothesized that the late Miocene C₄ expansion resulted from declining atmospheric CO₂ levels. Their proposal was based on models of photosynthetic quantum yield at different temperatures and atmospheric CO₂ concentration, on the ocean/atmosphere equilibrium model of Berner (1994), and the known efficiency of C₄ plants to capture CO₂ under low atmospheric [CO₂] conditions. Indeed, C₄ plants are known to tolerate arid conditions, and high radiation and warm temperatures in the growing season primarily control the distribution of C₄ grasses (Vogel et al. 1978; Ehleringer et al. 1997). However, two later studies revealed no evidence for a

significant drop in $[\text{CO}_2]_{\text{atm}}$ around the Mio-/Pliocene boundary (Pagani et al 1999; Pearson & Palmer 2000), and C_4 expansions have been demonstrated in the Namib region at $[\text{CO}_2]_{\text{atm}}$ levels below Cerling et al.'s (1997b) predicted thresholds (Segalen et al. 2006). Keeley & Rundel (2003) offer an alternative scenario; that increasing seasonality was the major climatic stimulus for C_4 expansion. The Namib evidence partially supports the seasonality hypothesis (Segalen et al. 2006). Keeley & Rundel (2003) also suggest that “climatic changes in late Miocene altered disturbance regimes, in particular the incidence of fires, which today are often associated with maintenance of C_4 grasslands”, although this hypothesis remains largely unexplored. Interactions between herbivores and the expanding grasslands may also have further promoted grassland proliferation (Retallack 2001). Evidently, climate, CO_2 , and disturbance are not mutually exclusive explanations, and all likely contributed to promote the expansion of C_4 grasslands. Perhaps the underlying problem is that much of our evidence for C_4 expansion is based on stages in which animals began incorporating C_4 foods into their diet; C_4 grasslands may simply have evolved independently and at different times.

Today, C_4 is most common amongst monocotyledonous plants, but occurs in at least 18 families of Angiosperms (in some 8 000 to 10 000 species) including several dicotyledonous taxa, and is thought to have evolved independently at least 31 times (Kellogg 1999; Sage et al. 1999; Hibberd & Quick 2002). The ability of plants to evolve C_4 traits is illustrated in some C_3 taxa (e.g. tobacco *Nicotiana* spp.) that exhibit characteristics of C_4 photosynthesis in certain plant organs (Hibberd & Quick 2002). Some plant species such as the grasses *Alloteropsis* spp. and some *Panicum* spp., may have both C_3 and C_4 representatives, or can switch pathways depending on whether environmental conditions favour C_3 or C_4 (Sage et al. 1999). Nevertheless, in African and other subtropical savannas (including Kruger Park), almost all dicotyledonous trees, shrubs, and forbs are C_3 , while grasses are overwhelmingly C_4 (Vogel et al. 1978; Cerling & Harris 1999; Ehleringer & Cerling 2001; Codron et al. 2005). Other monocots in these environments, for

Ehleringer & Cerling 2001; Codron et al. 2005). Other monocots in these environments, for example the Cyperaceae (sedges), comprise both C₃ and C₄ taxa (Stock et al. 2004; Codron et al. 2005).

Plants reflect changes in the concentration and carbon isotopic abundance of carbon dioxide in the atmosphere over the last century. Today, the $\delta^{13}\text{C}$ value of atmospheric CO₂ is close to -8‰ (Arens et al. 2000). However, ice core records show that in circa 1850 the $\delta^{13}\text{C}$ of atmospheric CO₂ was around -6.5‰, indicating a ~1.5‰ depletion in the ¹³CO₂ of the atmosphere over the last ~150 years (Friedli et al. 1986; Feng & Epstein 1995; Trudinger et al. 1999). Intensified changes in the concentrations of atmospheric CO₂ over last 50 years, especially that due to the burning of fossil fuels (e.g. Etheridge et al. 1996), have been tracked by actual measurements of the atmosphere (Keeling 1960, 1984; Pales & Keeling 1965; Keeling et al. 1976, 1982, 1995, 1996; Bacastow et al. 1985; Whorf & Keeling 1998; Keeling & Whorf 2005). Corresponding changes in $\delta^{13}\text{C}$ of both C₃ (Arens et al. 2000) and C₄ (Marino & McElroy 1991) plants through time have been documented. These effects are of particular importance for historical and palaeoecological studies, and researchers need to take into account that, in the past, C₃ and C₄ plant $\delta^{13}\text{C}$ would have been somewhat higher than at present (Lee-Thorp 2000; Long et al. 2005).

A third photosynthetic pathway, Crassulacean Acid Metabolism (CAM), is found in some plant groups (reviewed in Keeley & Rundel 2003). CAM concentrates CO₂ around Rubisco through the use of dual carboxylation pathways, first by CO₂ fixation with PEP and then by Rubisco. These two processes are separated temporally in the same tissue, with stomata opening at night to absorb and fix CO₂ (using PEP), and then storing it temporarily in the vacuole, primarily as malic acid. During the day, stomatal closure reduces water loss, but results in an internal carbon deficit, which is compensated for by decarboxylation of the malic acid (fixed CO₂) stores (Lüttge 2002). In many CAM species, dark fixation accounts for almost all of the

the primary role of CAM is in recycling of respiratory carbon (Osmond 1984). This gradient of CAM dependence for carbon uptake has led to the designation of species as being either obligate CAM or CAM-flexible (CAM-cycling species), and involves both a genetic component and phenotypic agility, which allows some species to change photosynthetic pathways in response to seasonal changes in their environment (Keeley & Rundel 2003).

CAM plants may have $\delta^{13}\text{C}$ values intermediate to those of C_3 and C_4 plants, generally ranging from -10‰ to -22‰, depending on ambient conditions and whether they are obligate CAM or CAM-flexible species. Carbon isotope analyses alone are unable to distinguish between C_4 plants and obligate CAM species, but morphological structure and phylogenetic relationships may be used to separate them (Vogel 1980; O’Leary 1988; Sage et al. 1999; Keeley & Rundel 2003). Carbon isotope ratios have been widely used in studies of obligate CAM plants to identify the relative proportions of CAM and C_3 metabolism used by plants (Rundel et al. 1999). However, CAM-flexible species resemble C_3 plants in their $\delta^{13}\text{C}$ composition (e.g. Rundel et al. 1999), and this method is therefore usually insufficient for distinguishing between these (Winter & Holtum 2002).

The vacuolar storage demands of CAM plants require an evolutionary coupling to succulent tissues, a linkage which is present in the majority of Cactaceae, Crassulaceae, succulent *Euphorbia*, and monocot genera such as *Agave* and *Aloe* (Keeley & Rundel 2003). In South Africa, CAM plants are confined largely to the Succulent Karoo (semi-arid desert), where a vast number of succulent CAM species belonging to the families Aizoaceae, Portulacaceae, Asteraceae, Crassulaceae, Zygophyllaceae, and Asphodelaceae have been documented (Cowling et al. 1999). However, carbon isotope studies have shown that apart from obligate CAM species, CAM-flexible and C_3 forms of metabolism are also represented among these succulent taxa (Vogel 1980; Rundel et al. 1999; Keeley & Rundel 2003). A prominent CAM genus is *Crassula* (Tolken 1977; Keeley 1998), of which the majority of the terrestrial species are CAM-obligate

(Tolken 1977; Keeley 1998), of which the majority of the terrestrial species are CAM-obligate perennials (Rundel et al. 1999) restricted mainly to the semi-desert regions of South Africa (Keeley & Rundel 2003). CAM plants generally occupy atypical conditions of extreme soil aridity, such as in shallow soils or on rocky outcrops. They commonly increase in species diversity and dominance along aridity gradients, and show a distinct interaction with temperature (Keeley & Rundel 2003). CAM plants tend to decline with decreases in temperature (Keeley and Keeley 1989) and at high latitudes (Nobel 1981). The occurrence of CAM also declines when nighttime temperatures are too high (Mooney et al. 1974). Because of their distribution, succulents seldom contribute significantly to plant-mammal foodwebs in African savanna environments such as the Kruger Park, and thus do not feature significantly in this thesis.

Nitrogen Isotope Distributions in the Herbivore Food Base

Plant $\delta^{15}\text{N}$ incorporates and reflects nitrogen isotope variations of the substrate on which they occur. However, the obvious complexities of soil nitrogen often confound interpretations of stable nitrogen isotope behaviour within these systems (Hopkins et al. 1998). Difficulties arise because ^{15}N discrimination in soils, which form the basis of any terrestrial system, takes place not only as a result of biological processes, but also of physical and chemical processes (Handley & Raven 1992). For example, soils in which the rates of nitrification (conversion of NH_4^+ to NO_3^-) and denitrification (conversion of NO_2^- to N_2O and N_2) are higher than the rate of decomposition have raised $\delta^{15}\text{N}$ values; biological fixation of atmospheric nitrogen contributes to ^{15}N -depleted soil; soil dryness and high temperatures may inhibit soil nitrogen fixation so that in hot and arid environments soil $\delta^{15}\text{N}$ values are often high; soils with a high clay content, and saline soils, also tend to be ^{15}N -enriched (Delwiche & Steyn 1970; Heaton 1987; Muzuka 1999; Schmidt & Stewart 2003). Fractionation effects that occur during biological denitrification processes in soils may be as large as 30%, and even larger (60%) in the case of N_2O production via nitrification

rare, at least within any one system, and $\delta^{15}\text{N}$ values in biological materials generally range between ~ -10 and $+20\%$.

Soil $\delta^{15}\text{N}$ is expressed in plants growing on these soils, with some further modifications at the plant level. Thus, plants growing in arid environments, on clay-based soils, or on saline soils, are expected to be relatively ^{15}N -enriched (Heaton 1987; Handley & Raven 1992; Muzuka 1999; Robinson 2001; Swap et al. 2004). Heterogeneity of $\delta^{15}\text{N}$ values within soil profiles has also been associated with depth, maturity, texture, and distribution of nitrates and ammonium (e.g. Ambrose 1991), and therefore plants that root at different depths, or prefer substrates of different particle size (e.g. clay soils versus sandy soils), may have different $\delta^{15}\text{N}$ values. Nitrogen-fixing plants (mostly legumes) often exhibit $\delta^{15}\text{N}$ values lower than that of non-nitrogen-fixing plants (mostly non-leguminous species) (Delwiche & Steyn 1970; Virginia & Delwiche 1982). However, this pattern is not always consistent (Koch et al. 1991; Handley et al. 1994; Muzuka 1999), and it appears that only those nitrogen-fixing plants that have mycorrhizal root associations are consistently ^{15}N -depleted (Schmidt & Stewart 2003; W. Stock 2003 pers. comm.). There is no consistent difference between C_3 and C_4 photosynthesizing plants, but reeds (*Phragmites* spp.), sedges (Cyperaceae), and CAM-photosynthesizing succulent plants are often associated with elevated $\delta^{15}\text{N}$ (Koch et al. 1991; Muzuka 1999; Codron et al. 2005). Overall, the controlling mechanisms for ^{15}N abundances in plants and ultimately variability in terrestrial foodwebs are poorly understood (Sealy et al. 1987; Ambrose 1991; Sponheimer et al. 2003a).

Discrimination of ^{13}C and ^{15}N in Herbivores

Reconstructing animal diets from stable isotope data requires knowledge of the magnitude of, and processes involved in, isotope discriminations that occur between diet and consumer tissue. Although the $\delta^{13}\text{C}$ of all the tissues in a herbivore's body consistently reflect the carbon isotope composition of the basic plant diet, isotopic values of different tissue types within

an individual varies (DeNiro & Epstein 1978, 1981; Vogel 1978; Tieszen et al. 1983; Lee-Thorp et al. 1989). This is because of differences in tissue composition and turnover time, secondary fractionation effects, and synthesis from different constituents of the diet. Diet-tissue ^{13}C -discriminations of 5.5‰ for bone collagen, 3.1‰ for hair, and 1.5‰ for muscle have been demonstrated for tissues synthesized primarily from the organic (protein) component of the diet, and -0.9‰ for faeces (representing largely the undigested part of the diet) (Ambrose & Norr 1993; Tieszen & Fagre 1993; Sponheimer et al. 2003b; Codron, D. et al. 2005a). For apatite carbonate in bone and tooth material, which is derived from a mix of all or most biochemical constituents of the diet, the ^{13}C diet-tissue discrimination is between 10 and 14‰ (laboratory feeding experiments versus field observations) (see Lee-Thorp et al. 1989; Ambrose & Norr 1993; Tieszen & Fagre 1993; Cerling & Harris 1999; Passey et al. 2005). Thus, in an environment where C_3 and C_4 plant $\delta^{13}\text{C}$ averages are -27‰ and -12.5‰, respectively, $\delta^{13}\text{C}$ in tooth enamel of a pure C_3 -feeder will be approximately -13‰, and hair from a pure C_4 -feeder will have a value around -9.4‰. In smaller animals such as rodents, diet-tissue discriminations appear to be slightly smaller, e.g. 4.5‰ for bone collagen and 0.5‰ for muscle (Tieszen et al. 1983; Ambrose & Norr 1993; Sponheimer et al. 2006b).

Animal $\delta^{15}\text{N}$ shows a stepwise ^{15}N -enrichment of 2 to 4 ‰ upwards along trophic levels of the food chain, in both terrestrial and aquatic ecosystems (Minagawa & Wada 1984; Schoeninger & DeNiro 1984; Peterson & Fry 1987; Sealy et al. 1987; Kelly 2000; Post 2002). The most likely mechanism for this is that animal $\delta^{15}\text{N}$ increases with dietary protein levels (Ambrose 1991; Sponheimer et al. 2003a), or rather the biological value of proteins consumed (i.e. the relative amounts of protein consumed that are available for metabolism; Robbins et al. 2005). However, the amplitude of trophic shifts is variable, and variations within trophic levels may even exceed differences between them. For example, a pattern of increasing animal $\delta^{15}\text{N}$ with increasing aridity has also been reported, as well as large differences between animals with

different dietary adaptations, water conservation strategies, and digestive physiologies (Sealy et al. 1987; Ambrose 1991).

Mass balance models to explain ^{15}N -abundance variations in mammals focus on excretion of ^{15}N -depleted urea compared with the isotopic signature of the N remaining in the body's nutrient pool (Ambrose & DeNiro 1986; Sealy et al. 1987; Ambrose 1991). Thus, animals excreting more concentrated urea, an adaptation to water conservation in mammals, would effectively retain N with higher $^{15}\text{N}/^{14}\text{N}$ ratios for tissue synthesis. The urea mass-balance model has been used to explain higher $\delta^{15}\text{N}$ values in drought tolerant versus water dependant species, and the negative correlation sometimes recorded for mammal $\delta^{15}\text{N}$ with rainfall (Heaton et al. 1986; Sealy et al. 1987; Ambrose 1991; Cormie & Schwarcz 1996). It has also been proposed that ruminants will have higher $\delta^{15}\text{N}$ than non-ruminants, due to recycling of urea during protein digestion, with the recycling of gut microbes from rumen-kidneys-rumen effectively adding internal trophic levels to the system (Sealy et al. 1987). However, the proposed patterns are not consistent; it has been shown that ^{15}N is not necessarily discriminated against during urea excretion (Sponheimer et al. 2003c), and N loss via faeces (which are ^{15}N -enriched relative to diet; see Steele & Daniel (1978)) may account for as much as 40% of N efflux and hence $^{15}\text{N}/^{14}\text{N}$ mass balance in mammals (Sponheimer et al. 2003a). Sponheimer et al. (2003a) proposed that, because N loss via urea increases on higher protein diets, mammal $\delta^{15}\text{N}$ increases with dietary protein levels, but with low dietary protein, N loss via faeces becomes more important and body tissue $\delta^{15}\text{N}$ decrease. This model seems to explain increases in $\delta^{15}\text{N}$ along trophic levels, negative correlations with rainfall in southern African systems (where %N of available vegetation often decreases with increases in rainfall due to loss of nutrients through soil leaching; see Tainton (1999)), and higher values in ruminants (which should consume higher protein diets than non-ruminants; *cf.* Duncan et al. (1990)). In sum, most authors concur that our understanding of ^{15}N -

abundance variations in mammals is poor, as is the case for $\delta^{15}\text{N}$ variations in biological systems in general.

The scale of information archived in data from different tissues is dependant on differences in the assimilation of dietary constituents, growth, and turnover rates. For example, bone is remodeled throughout life and hence offers an integrated near-lifetime average of dietary isotopic composition, teeth represent the period(s) of dentine and/or enamel accretion (i.e. are not subject to turnover and remodeling after formation), hair grows incrementally but is relatively short-lived compared to bone, and faeces reflect food intake over a few days prior to deposition (Jones et al. 1981; Tieszen et al. 1983; Butler 1984; Ericson 1985; Coates et al. 1991; Ambrose & Norr 1993; Sealy et al. 1995; Sponheimer et al. 2003b). Incremental tissues such as teeth and hair also archive chronological records of diet, if sampled in series (e.g. Koch 1989; Balasse et al. 2001; Cerling & Viehl 2004; Cerling et al. 2004a, 2006; Codron 2004). Incremental profiles are imperfect, however, because newly-formed tissues integrate a mixed signal of both a new diet and the body's nutrient pool (derived from previously consumed foods) (Balasse et al. 2001; Passey & Cerling 2002; Ayliffe et al. 2004). Thus, an equilibration period occurs before the new material reflects only the isotope composition of a new diet; in animals including cattle and horses the turnover for proteins like collagen and keratin (in hair and hoof) is predicted to be between two and four months (Balasse et al. 2001; Ayliffe et al. 2004; Zazzo et al. 2007).

Finally, the question arises as to how accurately faeces (which form a significant component of this thesis) reflect actual food intake, because they comprise mostly undigested plant remains. A number of controlled-feeding experiments have demonstrated consistency between diet and faecal $\delta^{13}\text{C}$ despite differences in the digestibility of different food types and differential digestive efficiencies across ungulate species (Jones et al. 1981; Coates et al. 1991; Hare et al. 1991; Sponheimer et al. 2003b; Codron, D. et al. 2005a; Codron, D. & Codron in press). While carbon in faeces is derived mainly from ingested foods, much of the nitrogen in herbivore faeces is derived

from the animal's body, in the form of sloughed endogenous material and gut microbes (Van Soest 1994). This factor may greatly influence interpretations of $\delta^{15}\text{N}$ trends in faeces (Sponheimer et al. 2003c).

Crude Protein Content (%N) of Plants and Faeces

Percent nitrogen (%N) is measured routinely alongside nitrogen isotopes during mass spectrometry. Percent N is a reflection of the crude protein content of plants, and in faeces provides a rough measure of dietary quality (e.g. Erasmus et al. 1978; Holecheck et al. 1982; Leslie & Starkey 1985; Grant et al. 2000). However, not all the N in plants is available to herbivores. Some proportion of plant N is bound within the cell wall, and available N is therefore influenced by the relative dry matter digestibility of plant cell walls (which increases with hemicellulose:lignin ratios) and the amount of N occurring as acid detergent insoluble nitrogen (Robbins 1993; Van Soest 1994; Hummel et al. 2006). Faecal %N as a proxy for diet quality is further complicated by consumption of plant material containing protein-precipitating compounds, such as condensed tannins, that lead to raised faecal nitrogen levels (Arman et al. 1975; Robbins et al. 1987), and the presence of non-dietary proteins in faeces derived from epithelial tissues and gut microbes (Van Soest 1994; see above). Nonetheless, the relationship between faecal and dietary %N is quite strong ($r^2 \sim 0.70$; Wrench et al. 1996), and %N is thus used in this thesis as an indicator of the relative nutritional value of the basic plant diet.

3.2. Materials and Methods

3.2.1. Sample Collection

The initial two-year study period was from June 2002 to February 2004 (Codron 2004; Codron et al. 2005, see Appendix II), and later extended to May 2005. Vegetation samples were collected to represent the dry months (April to September) and the wet months (October to March), with 86% of collections occurring in January, February, and June. Circular sampling

transects (<10 m diameter) were established over a diversity of landscape types in Kruger Park (Fig. 3.1). Twelve transects were used for the first two years of the study (Codron et al. 2005), and in 2004 one additional site, a montane woodland, was set up in the Punda Maria region (site 13), and a further three were established on the northern basalts (sites 14 to 16). Within each sampling transect, specimens were taken from the full array of plant taxa (between three and five samples per taxon), including trees, forbs, and grass, as well as reeds (*Phragmites australis*) and sedges (Cyperaceae), where available. Sampling included leaves, fruit, and bark of trees, but for forbs and grass in this study was focused on aerial parts (leaves and/or stems). Climate data for this study period are presented in Table 3.2, showing that the northern regions experienced mostly dry years (lower than the long-term mean), whereas the southern regions received relatively high rainfall during the second and third years of sampling.

3.2.2. Analytical Techniques

Each specimen was oven dried at 60°C for 24 hours and ground in a hammer mill through a 1 mm sieve into a homogenous powder. Powdered samples were combusted individually in an automated Elemental Analyzer (Carlo-Erba, Milan), and the resultant CO₂ and N₂ gases introduced to a Mass Spectrometer (MAT 252 or DELTA XP; Finnigan, Bremen) using a continuous flow-through inlet system. ¹³C/¹²C and ¹⁵N/¹⁴N ratios are presented in delta (δ) notation, by convention, in per mil (‰) relative to the VPDB and N₂ air standards, respectively. Standard deviations of repeated measurements of laboratory plant, protein, and chocolate standards were less than 0.1‰ for δ¹³C, and 0.3‰ for δ¹⁵N. This method also provided the elemental composition (%C and %N) by weight for each sample.

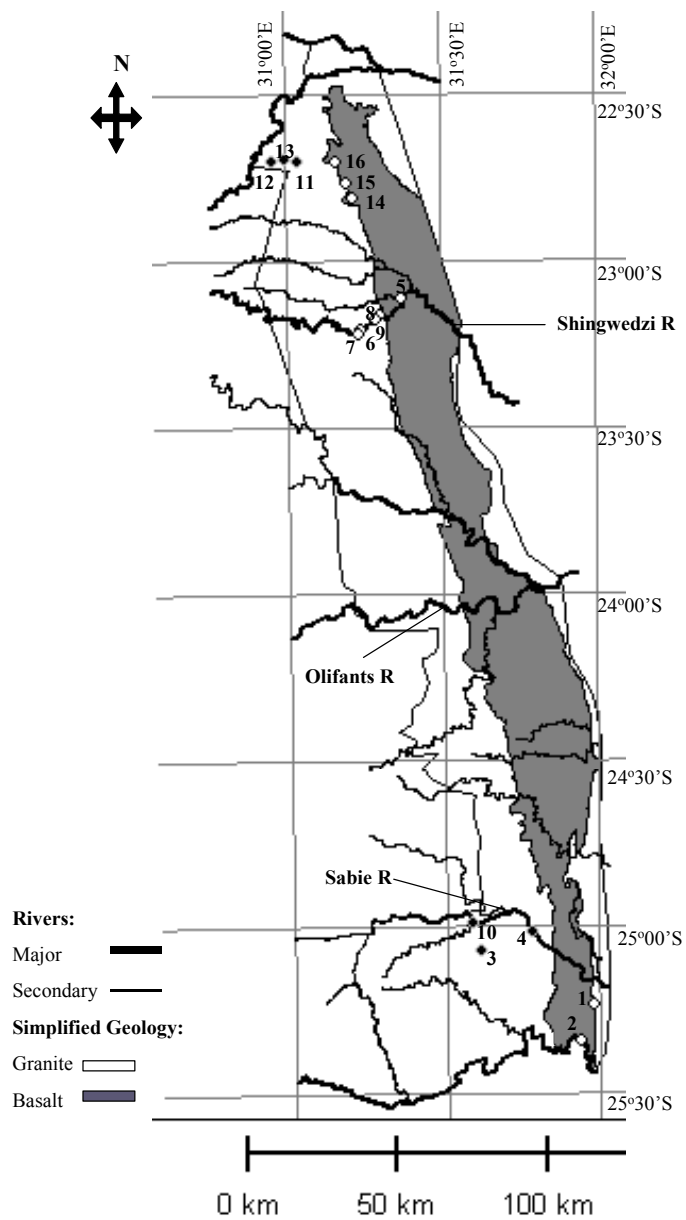


FIGURE 3.1. – Map of Kruger Park indicating location of plant sampling sites (1 to 16), showing northern and southern granite/basalt landscape divisions and the major river systems.

Data were categorized according to study year (year 1 = June 2002 and January 2003; year 2 = June 2003 and February 2004; year 3 = June 2004 to May 2005), season (dry season = April to September; wet season = October to March), and landscape (northern and southern granites and basalts, respectively, and Punda Maria). Although multiple sampling transects were established within each of the five major landscapes (see Table 3.1), plant isotopic variations within them were found to be non-significant ($P > 0.05$), and a similar result was found previously, with few exceptions (Codron 2004; Codron et al. 2005). At three northern sites, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of local vegetation deviated significantly from the overall plant mean (Codron et al. 2005), and these sites (site 6 = dry riverbed; site 8 = sodic patch; and site 9 = dense riparian woodland) are therefore treated here as distinct from the five major landscape types. Plant groups were subdivided into tree foliage, tree fruit, tree bark, forbs, and grass. Grasses were also grouped as NAD/PCK or NADP sub-types, based on taxonomic assignments provided by Sage et al. (1999). Results are presented as means \pm standard deviation (and graphically as means \pm 95% confidence limits), or simply as the magnitude of difference between data subsets. Comparisons between groups are carried out using analysis of variance (ANOVA) and Tukey's Honest Significant Difference (HSD) *post-hoc* test for significant differences between means (P -level 0.05). These tests are performed for changes from year-to-year, as well as within years to determine whether patterns of variation are consistent. Lastly, environmental controls on plant isotope composition are studied using linear regression models for correlations between stable isotope data with mean annual rainfall, maximum daily temperature (data supplied by the South African Weather Bureau), and plant %N.

3.3. Results

3.3.1. Plant $\delta^{13}\text{C}$ Variations

Mean $\delta^{13}\text{C}$ for C_3 vegetation from Kruger Park was $-26.6 \pm 1.5 \text{‰}$ ($n = 1\,375$) and for C_4 vegetation was $-12.7 \pm 1.2 \text{‰}$ ($n = 1\,038$), and their ranges do not overlap ($\text{C}_{3\text{maximum}} = -20.4\text{‰}$, $\text{C}_{4\text{minimum}} = -17.5\text{‰}$). $\delta^{13}\text{C}$ of C_3 trees and forbs did not change significantly from year to year (P ranges from 0.07 to 0.99; Table 3.3). Mean $\delta^{13}\text{C}$ of trees (including leaves, fruit, and bark) did decrease from year 2 to year 3 ($P < 0.01$), but the difference is too small to be meaningful for isotope studies (0.4 ‰). Higher $\delta^{13}\text{C}$ of tree fruit ($-25.4 \pm 1.4 \text{‰}$, $n = 41$) compared with leaves ($-26.7 \pm 1.4 \text{‰}$, $n = 1\,208$; $P < 0.0001$) persisted within all three years, although the magnitude of this difference changed from 2.3 ‰ in year 1 to 1.1 ‰ in years 2 and 3 (Fig. 3.2a). C_4 grass, by contrast, showed a substantial decrease (by 1.2 - 1.4 ‰) in mean $\delta^{13}\text{C}$ from years 1 and 2 to year 3 ($P < 0.0001$). Nonetheless, NAD and PCK grasses maintained lower mean $\delta^{13}\text{C}$ ($-12.9 \pm 1.0 \text{‰}$, $n = 671$) than NADP grasses ($-12.4 \pm 1.3 \text{‰}$, $n = 353$) within all three years ($P < 0.01$ in all cases), and the size of this difference remained relatively stable (between 0.5 and 0.7 ‰) (Fig. 3.2b).

Most reeds and sedges collected during year 3 had $\delta^{13}\text{C}$ values consistent with C_3 photosynthesis ($-25.7 \pm 0.9 \text{‰}$, $n = 11$, and $-26.5 \pm 1.1 \text{‰}$, $n = 24$, respectively; Table 3.3), consistent with previous predictions that the majority ($> 75\%$) of taxa occurring in Kruger Park and similar lowveld savannas in South Africa are C_3 (Stock et al. 2004; Codron et al. 2005). Only four out of 28 sedges sampled in year 3 were C_4 ($-12.5 \pm 0.9 \text{‰}$).

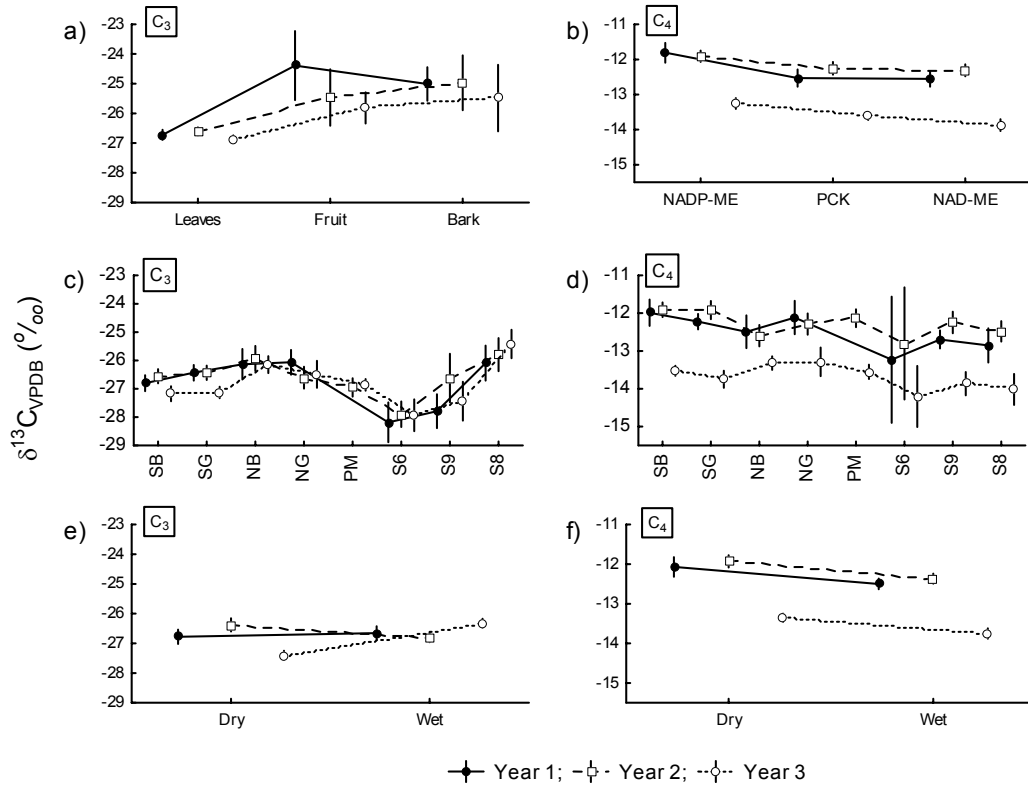


FIGURE 3.2. – Variations in the $\delta^{13}\text{C}$ composition of Kruger Park vegetation over the three-year study period, comparing differences across a) C_3 (trees and forbs) plant parts; b) C_4 grass photosynthetic sub-types; c) geographical origin of C_3 tree foliage and forbs; d) geographical origin of C_4 grasses (all sub-types); e and f) dry and wet seasons. Symbols depict means and bars \pm 95% confidence limits. Regional key: SB = southern basalts; SG = southern granites; NB = northern basalts; NG = northern granites; PM = Punda Maria; S6 = dry riverbed site 6; S9 = riparian site 9; S8 = sodic site 8. The dry season is represented by samples collected from April to September, and the wet season is from October to March.

Patterns of spatial variation in plant $\delta^{13}\text{C}$ were remarkably similar within each study year. For C_3 plants (tree foliage and forbs), no differences in $\delta^{13}\text{C}$ were recorded between the five major landscapes (northern and southern granites and basalts, and Punda Maria) (mean ranged

from -26.9 ± 1.1 ‰, $n = 152$ at Punda Maria to -26.1 ± 1.2 ‰, $n = 111$ on northern basalts; P ranged from 0.11 to 0.71; Fig. 3.2c). The only deviation occurred on northern basalts, where trees and forbs were slightly ^{13}C -enriched relative to plants from the other landscapes, but the difference was small (< 1.0 ‰) and significant only for year 3 ($P < 0.05$). However, $\delta^{13}\text{C}$ did change significantly at riverine sites, because C_3 plant $\delta^{13}\text{C}$ was 1.0 to 2.0 ‰ lower at the dry riverbed site (site 6 mean = -27.3 ± 1.4 ‰, $n = 52$) and dense riparian woodland (site 9 mean = -28.0 ± 1.5 ‰, $n = 84$) than other landscapes within each of the three years ($P < 0.05$). C_4 grass $\delta^{13}\text{C}$ (NADP, NAD and PCK combined) also varied minimally across landscapes (mean ranged from -13.3 ± 1.8 ‰, $n = 24$ at site 9 to -12.4 ± 1.2 ‰, $n = 106$ on northern granites), although during years 1 and 2 grasses from the southern landscapes were 0.4 to 0.8 ‰ higher in $\delta^{13}\text{C}$ compared with the northern regions ($P < 0.05$; Fig. 3.2d).

Seasonal (dry versus wet season) changes in plant $\delta^{13}\text{C}$ were surprisingly small. For C_3 tree foliage and forbs, the only significant change in $\delta^{13}\text{C}$ occurred during year 3, with an increase of 1.1 ‰ from the dry to the wet season, i.e. from -27.4 ± 1.3 , $n = 252$ to -26.3 ± 1.3 , $n = 257$ ($P < 0.0001$; Fig. 3.2e). In contrast, $\delta^{13}\text{C}$ of C_4 grasses always decreased from the dry to the wet season ($P < 0.0001$ within each year), but the change never exceeded 0.5 ‰ (Fig. 3.2f).

3.3.2. Plant $\delta^{15}\text{N}$ Variations

Mean $\delta^{15}\text{N}$ of C_3 vegetation was 4.3 ± 2.5 ‰ ($n = 1\,375$), and for C_4 plants was 3.3 ± 2.2 ‰ ($n = 1\,038$) ($F_{1,2411} = 89.199$, $P < 0.0001$). $\delta^{15}\text{N}$ varied widely, with reeds and sedges having consistently higher means (> 5.5 ‰) compared with other plants (< 4.5 ‰) ($P < 0.0001$; Table 3.3). Over the three years, mean $\delta^{15}\text{N}$ of forbs and grass remained relatively stable (P ranges from 0.73 to 0.99), but trees showed an increase from 3.4 ± 2.6 ‰ ($n = 237$) in year 1 to 4.3 ± 2.3 ‰ ($n = 301$) and 4.1 ± 2.2 ‰ ($n = 405$) in years 2 and 3, respectively ($P < 0.05$). Leaf $\delta^{15}\text{N}$ (4.2 ± 2.4 ‰, $n = 1208$) did not differ significantly from that of fruit (3.4 ± 1.7 ‰, $n = 41$; $P = 0.09$), but

$\delta^{15}\text{N}$ of bark was lower than both ($1.7 \pm 0.36 \text{ ‰}$, $n = 37$; $P < 0.01$; Fig. 3.3a). However, relatively low $\delta^{15}\text{N}$ of tree bark was only evident in years 1 and 3; in the second year bark was similar to that of leaves and fruit ($3.6 \pm 1.9 \text{ ‰}$, $n = 9$; $P = 0.98$).

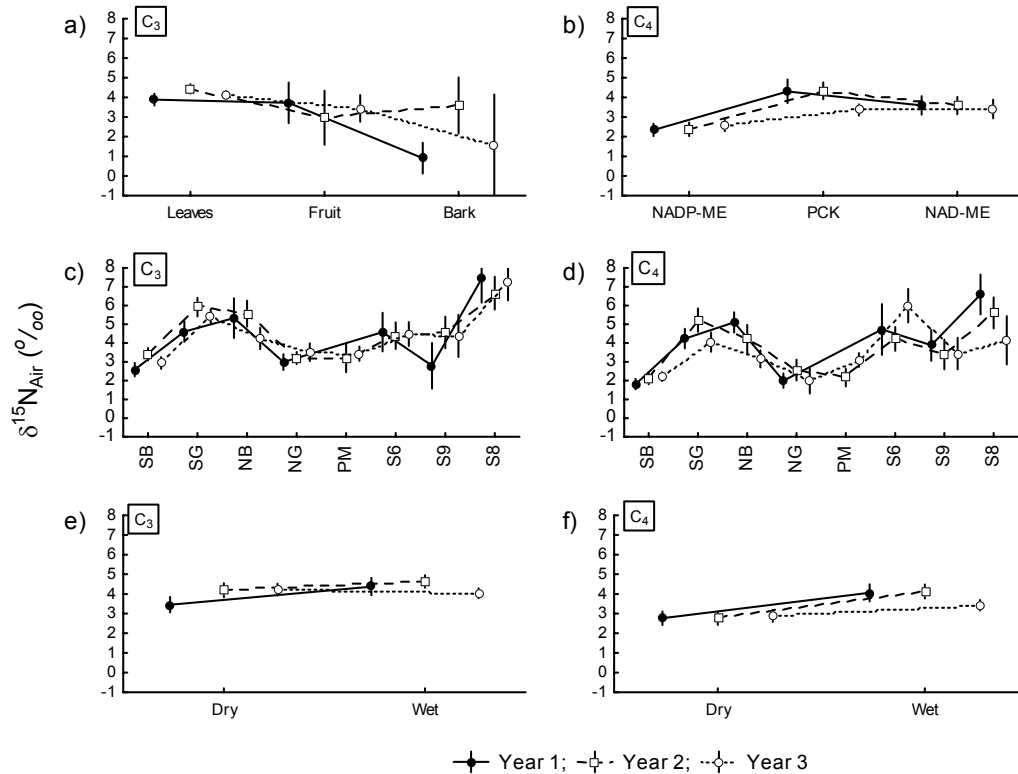


FIGURE 3.3. – Variations in the $\delta^{15}\text{N}$ composition of Kruger Park vegetation over the three-year study period, comparing differences across a) C_3 (trees and forbs) plant parts; b) C_4 grass photosynthetic sub-types; c) geographical origin of C_3 tree foliage and forbs; d) geographical origin of C_4 grasses (all sub-types); e and f) dry and wet seasons. Symbols depict means and bars \pm 95% confidence limits. Regional key: SB = southern basalts; SG = southern granites; NB = northern basalts; NG = northern granites; PM = Punda Maria; S6 = dry riverbed site 6; S9 = riparian site 9; S8 = sodic site 8. The dry season is represented by samples collected from April to September, and the wet season is from October to March.

For C₄ grasses, the previously reported lower δ¹⁵N of NADP grasses (mean = 2.5 ± 1.9 ‰, n = 353 compared with 3.7 ± 2.3 ‰, n = 671 for NAD/PCK types) continued throughout (*P* < 0.05 for all years), but a difference of 1.6 and 1.7 ‰ between NADP and NAD/PCK grass δ¹⁵N in years 1 and 2, respectively, decreased to 0.8 ‰ in year 3 (Fig. 3.3b).

C₃ and C₄ plant δ¹⁵N showed corresponding patterns of variation across landscapes, with means for C₃ plants (tree foliage and forbs) ranging from 3.0 ± 1.9 ‰, n = 346 on southern basalts to 7.1 ± 2.4 ‰, n = 69 at sodic site 8, and C₄ grasses ranging from 2.1 ± 1.5 ‰, n = 266 on southern basalts to 5.6 ± 2.4 ‰, n = 63 at sodic site 8 (Fig. 3.3c & d). δ¹⁵N of C₃ vegetation from southern basalts, northern granites, and Punda Maria was 1.6 to 2.7 ‰ lower than those from southern granite and northern basalt landscapes (*P* < 0.01 within each year). Similar variations of 1.0 to 3.3 ‰ were recorded for C₄ grasses from these landscapes (*P* < 0.01 for year 1, *P* < 0.05 for year 2, and *P* < 0.0001 for year 3). For both C₃ and C₄ plants, highest δ¹⁵N at sodic site 8 is significant for all cases (*P* < 0.0001). Seasonally, C₃ plant δ¹⁵N increased from 3.5 ± 2.6 ‰ (n = 165) in the dry season to 4.4 ± 2.6 ‰ (n = 145) in the wet season of year 1 (*P* < 0.01), but showed no significant change during years 2 (*P* = 0.45) and 3 (*P* = 0.96) (Fig. 3.3e). δ¹⁵N of C₄ grass always increased from dry to wet seasons, and the change is significant for years 1 (*P* < 0.0001) and 2 (*P* < 0.0001) entailing increases of 1.3 and 1.4 ‰, respectively, but not significant for year 3 (*P* = 0.10; Fig. 3.3f).

3.3.3. Plant Nitrogen Content

Plant %N followed the predicted trend for savanna vegetation of higher values in trees (mean = 2.1 ± 0.9 %, n = 943) and forbs (2.4 ± 1.3 %, n = 343) compared with grass (1.2 ± 0.60 %, n = 1024) ($F_{2,2309} = 391.613$, *P* < 0.0001; see e.g. Robbins 1993; Van Soest 1994; Meissner et al. 1999). All groups changed significantly from year-to-year, with the general trend being an increase from year 1 to years 2 and 3 (*P* < 0.01), although mean %N of forbs decreased from 2.9

$\pm 1.6\%$ ($n = 110$) in year 2 to $2.5 \pm 1.1\%$ ($n = 129$) in year 3 ($P < 0.05$; Table 3.3). C_3 plant leaves had higher %N ($2.2 \pm 1.0\%$, $n = 1\,208$) than fruit ($1.6 \pm 0.9\%$, $n = 41$) and bark ($1.1 \pm 0.7\%$, $n = 37$) ($P < 0.001$), but in year 3 bark %N was not significantly lower than that of leaves ($P = 0.09$; Fig. 3.4a).

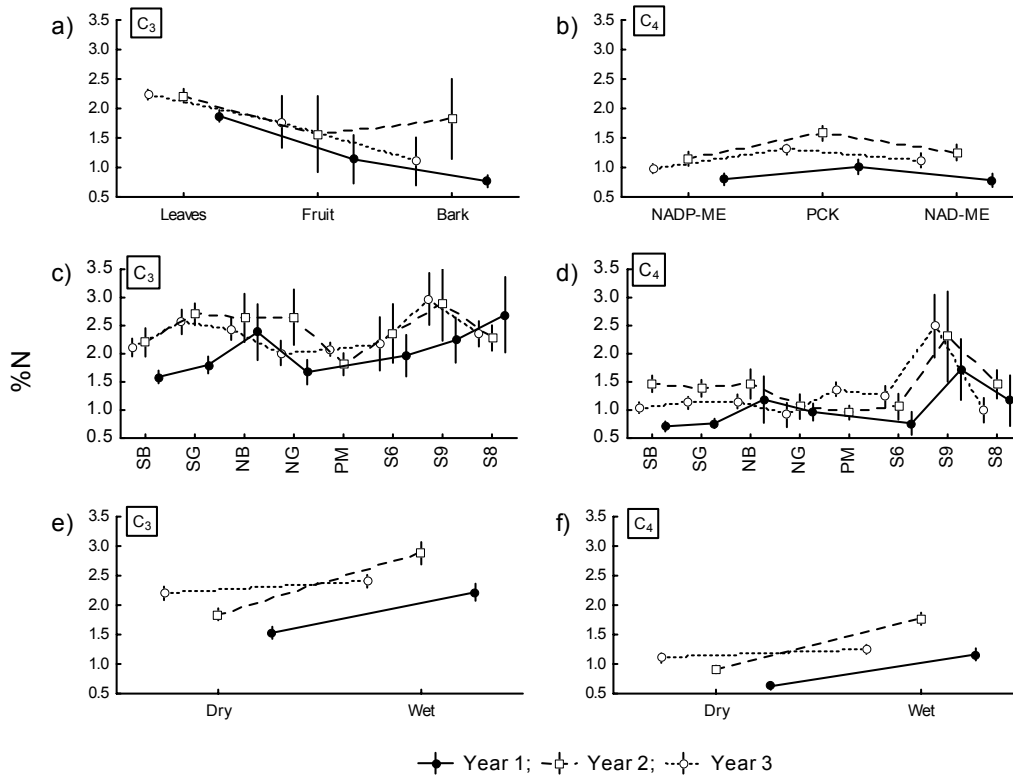


FIGURE 3.4. – Variations in %N of Kruger Park vegetation over the three-year study period, comparing differences across a) C_3 (trees and forbs) plant parts; b) C_4 grass photosynthetic sub-types; c) geographical origin of C_3 tree foliage and forbs; d) geographical origin of C_4 grasses (all sub-types); e and f) dry and wet seasons. Symbols depict means and bars $\pm 95\%$ confidence limits. Regional key: SB = southern basalts; SG = southern granites; NB = northern basalts; NG = northern granites; PM = Punda Maria; S6 = dry riverbed site 6; S9 = riparian site 9; S8 = sodic site 8. The dry season is represented by samples collected from April to September, and the wet season is from October to March.

Amongst C₄ grass, %N was slightly but significantly higher in NAD/PCK (1.2 ± 0.8 %, $n = 671$) than NADP types (1.0 ± 0.6 %, $n = 353$; $P < 0.0001$), and this difference increased from ~0.1 % in year 1 to ~0.3 % in years 2 and 3 (Fig. 3.4b). Percent N of C₃ vegetation (tree foliage and forbs) differed significantly across landscapes ($P < 0.0001$), being lowest on southern basalts (mean = 2.0 ± 1.1 %, $n = 346$) and highest at riparian site 9 (2.7 ± 1.5 %, $n = 84$; Fig. 3.4c). C₄ grass showed minimal variations in %N across regions ($P > 0.05$; means ranged from 1.0 ± 0.5 %, $n = 106$ on northern granites to 1.3 ± 0.7 %, $n = 63$ at sodic site 8), except that grasses from riparian site 9 had very high N content (2.2 ± 0.9 %, $n = 24$; $P < 0.0001$; Fig. 3.4d). Dry-to-wet season shifts in plant %N were substantial, C₃ plants (tree foliage and forbs) increasing from 1.9 ± 0.7 % ($n = 593$) to 2.5 ± 1.2 % ($n = 615$) ($P < 0.0001$; Fig. 3.4e), and C₄ plants from 0.9 ± 0.5 % ($n = 536$) to 1.4 ± 0.7 % ($n = 488$) ($P < 0.0001$; Fig. 3.4f), from the dry to the wet season. This pattern of seasonal increases persisted in all 3 years ($P < 0.05$ in all cases), following trends expected for southern African savanna vegetation (Meissner et al. 1999; Tainton 1999).

3.3.4. Relationships with Climate and %N

Linear regression models showed little correlation between plant carbon and nitrogen isotope composition with climatic (rainfall and maximum temperature) variations across the landscapes and study years (Fig. 3.5). The relationship between C₃ plant $\delta^{13}\text{C}$ (tree foliage and forbs) and rainfall is particularly weak ($R^2 = 0.00$, $P = 0.96$; Fig. 3.5a). Only C₄ grass $\delta^{13}\text{C}$ showed a significant correlation with rainfall, increasing with rainfall increases through space and time ($R^2 = 0.27$, $P < 0.05$; Fig. 3.5b). Plant $\delta^{15}\text{N}$ also varied minimally with the climate parameters, but significant correlations were recorded for the regressions of $\delta^{15}\text{N}$ with %N for both C₃ ($R^2 = 0.31$, $P < 0.01$; Fig. 3.5c) and C₄ vegetation ($R^2 = 0.23$, $P < 0.05$; Fig. 3.5d).

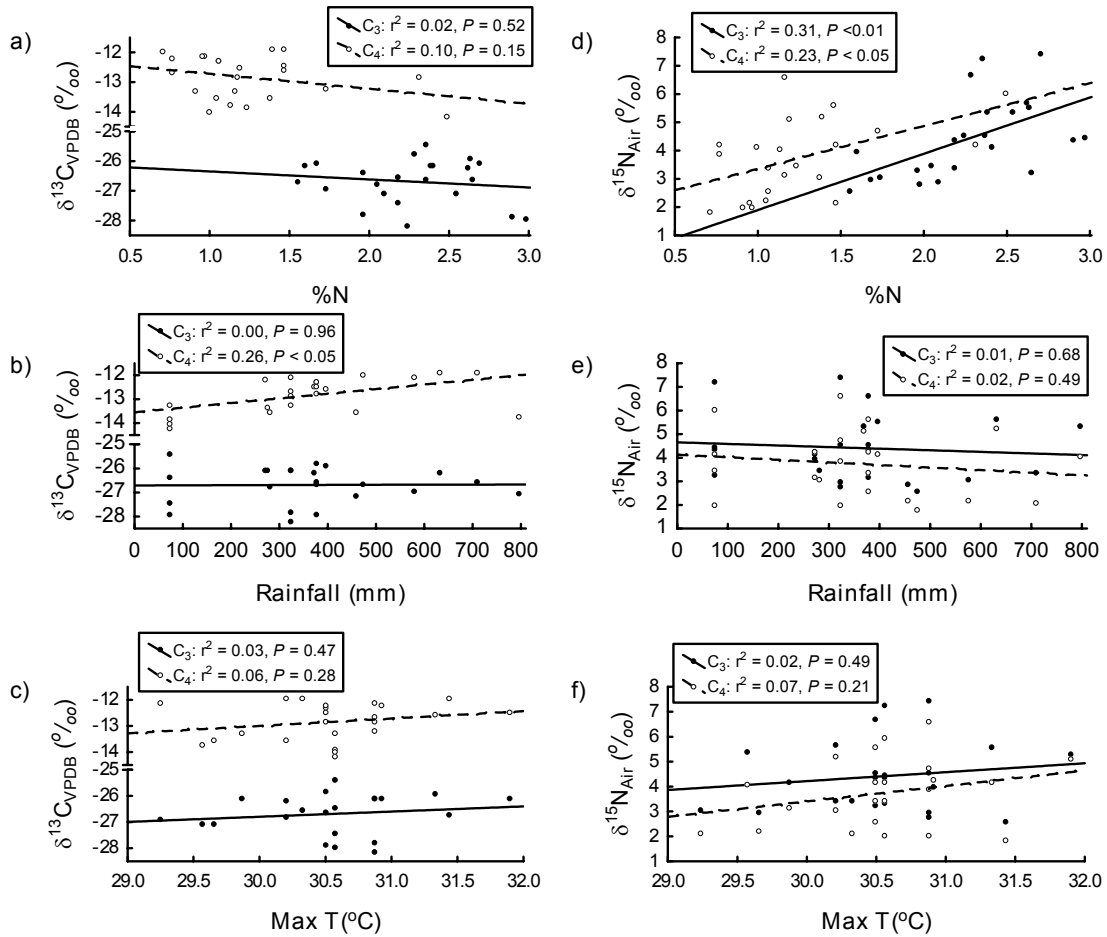


FIGURE 3.5. – Linear regression models for $\delta^{13}\text{C}$ (a-c) and $\delta^{15}\text{N}$ (d-f) of C_3 vegetation (tree foliage and forbs) and C_4 grass as functions of plant %N (a, d); rainfall (mm; b, e); and maximum daily temperature ($T^{\circ}\text{C}$; c, f). Symbols depict means region, season, and year.

3.4. Discussion

These results demonstrate patterns of variation consistent with those previously reported for the first two years of the study. Given the wide variety of climates and habitats represented by these data, there is no reason to believe that observed patterns would persist over longer time periods, e.g. a decadal shift in annual rainfall from 300 to 800mm would likely lead to similar patterns as observed in this spatially-explicit study. Also, compared with other studies, these

results cover a longer time period than has hitherto been obtained from other studies of modern vegetation. I will therefore be using these data as baseline information to compare elephant diets in different parts of Kruger Park, both in a modern and historical context.

The magnitude of variation in plant $\delta^{13}\text{C}$ observed here (up to $\sim 2\text{‰}$ for C_3 and up to $\sim 1\text{‰}$ for C_4 vegetation) is similar to data reported for temperate boreal systems (Heaton 1999) and central African rainforest (Cerling et al. 2004b), the latter consisting only of C_3 . Differences between these and other types of environments may indeed be greater (e.g. Farquhar et al. 1982; Ehleringer & Cooper 1988; van der Merwe & Medina 1989, 1991; O'Leary 1995), and this has prompted a degree of conservatism when approaching isotope-based palaeodiet studies. For example, in a study of herbivores from the middle Miocene of Fort Ternan, Kenya, Cerling et al. (1997a) presumed that tooth enamel $\delta^{13}\text{C}$ of pure C_3 -feeders may range anywhere between -20 and -8‰ which, based on a diet-enamel discrimination of $\sim 14\text{‰}$, correspond to a diet value of between -34 and -22‰ (i.e. the global $\delta^{13}\text{C}$ range for C_3 plants, notwithstanding the caveat that atmospheric CO_2 likely also changed in the past). Thus, any C_4 input into the diets of these herbivores could only be interpreted with certainty if tooth enamel $\delta^{13}\text{C}$ increased above -8‰ (diet value higher than -22‰). Results of the current study suggest that accepting such a wide range of variation for C_3 food sources is tenable only if there is good independent evidence to suggest that palaeoenvironments at a site changed in major ways, e.g. from deep forest to savanna, or from savanna to desert. While such environmental heterogeneity may have occurred at Fort Ternan during the Miocene, this is unlikely to be the case for most situations, especially for centennial or even millennial scale studies within a single study region. Most Plio-Pleistocene fossil localities were C_4 savannas in which environmental heterogeneity is unlikely to have exceeded that of modern-day places such as Kruger Park (see Vrba 1988; Reed 1997). The significance is that environments like Kruger Park vary extensively in terms of rainfall (300 to

700 mm), geology, habitat, and species composition (e.g. Naiman et al. 2003; Venter et al. 2003), yet carbon isotopic variations in vegetation remain small.

Patterns of carbon isotope variation that are likely more important for diet are the lower $\delta^{13}\text{C}$ of C_3 foliage compared with fruit, lower $\delta^{13}\text{C}$ of C_3 riverine vegetation compared with other habitat types, lower $\delta^{13}\text{C}$ (and higher $\delta^{15}\text{N}$) of NAD/PCK compared with NADP C_4 grasses (see also Cerling & Harris 1999; Cerling et al. 2003), and the 1‰ decline in C_4 grass $\delta^{13}\text{C}$ from years 1 and 2 to year 3 in this study. Relative ^{13}C -enrichment of C_3 fruit compared with foliage is consistent not only with findings from other modern African environments (Cerling et al. 2004b; Codron, D. et al. 2005b), but has also been reported for ancient environments, e.g. the ~25.8 Ma. Oligocene site Enspel Fossilagerstätte in Westerwald, Germany (Schweizer et al. 2006). The relatively low $\delta^{13}\text{C}$ observed for riverine C_3 vegetation is expected because, in C_3 plants, higher water availability leads to a greater degree of stomatal closure in foliage, resulting in decreased carboxylation rates and increased isotopic discrimination during photosynthesis (Tieszen 1991). By contrast, $\delta^{13}\text{C}$ of C_4 grasses collected during the third year appeared to decrease with increased water stress. Of the 415 grass specimens collected during the final year, 62% was taken from northern regions, which experienced very low rainfall between April 2004 and March 2006 (see Table 3.2). It has been shown previously that the $\delta^{13}\text{C}$ of C_4 plants decreases with increased water stress due to water leakage from the bundle sheath cells, possibly related to changes in recruitment and growth rate, and accelerated desiccation of annuals during drier periods (Buchmann et al. 1996). The shift in grasses observed here cannot be attributed to changes in proportions of NADP versus NAD/PCK taxa in the sample set, because similar proportions (31 to 39% NADP, 61 to 69% NAD/PCK) were collected in each year. Thus, these data support the observations of Buchmann et al. (1996), with the outcome that while C_3 plant $\delta^{13}\text{C}$ will tend to increase in response to water stress, the opposite should be true for C_4 plants. These results could have implications for diet studies, implying that within any one type of environment, changes in

$\delta^{13}\text{C}$ of ~ 1 to 2 ‰ in animals may not necessarily reflect diet shifts in terms of C_3/C_4 intake, but may be influenced by use of C_3 or C_4 plants growing in different habitats (e.g. riverine versus grassland), by drought conditions, or by diet changes at other scales (e.g. frugivory versus folivory; NAD/PCK versus NADP grass-feeding).

The poor correlation between C_3 plant isotope composition and rainfall was somewhat surprising, as several studies have demonstrated a relationship between plant water stress and isotope composition, where decreasing rainfall has been associated with increasing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in plants (Heaton 1987; Ehleringer & Cooper 1988; Tieszen 1991; Stewart et al. 1995). In this study such explanations appear to hold only for the riverine vegetation compared with the other habitat types. Effects of rainfall may have been obscured in regression models because of the relatively small variations in $\delta^{13}\text{C}$ through space and time. Only the $\delta^{13}\text{C}$ of C_4 grass showed a significant correlation with rainfall, i.e. increasing in higher rainfall situations, but this correlation is exaggerated by the drop in $\delta^{13}\text{C}$ with very low rainfall experienced in northern regions (~ 300 mm or less) during the third year. This finding supports the previous interpretation (Codron et al. 2005) that although rainfall may have some effect, influences are only substantial across a very diverse array of climate regimes, e.g. 300 to 2 000 mm mean annual rainfall (see Stewart et al. 1995). In a study of available data for the whole of southern Africa, including rainfall regimes ranging between 200 and >1 200 mm per annum, Swap et al. (2004) found only modest relationships between C_3 and C_4 plant $\delta^{13}\text{C}$ with rainfall. This, coupled with the limited seasonal variation observed for Kruger Park vegetation, implies a limited influence of rainfall on plant $\delta^{13}\text{C}$, but changes in water availability (e.g. riverine sites) may have a more direct effect.

Swap et al. (2004) also ascribe the relationship of plant $\delta^{15}\text{N}$ with rainfall to be a function of changes in plant nitrogen content. This observation is supported by data presented here, because while no relationship was recorded for $\delta^{15}\text{N}$ with rainfall, $\delta^{15}\text{N}$ of both C_3 and C_4 vegetation increased linearly with ‰N. The lack of fit with rainfall may appear surprising because

of the relationship often predicted for rainfall with primary productivity and ultimately plant %N (Coe et al. 1976; Acocks 1988; Boutton et al. 1988; Tainton 1999). However, as noted by Swap et al. (2004) (and Handley et al. (1994), who also found no relationship between plant $\delta^{15}\text{N}$ and rainfall in an East African savanna), these explanations oversimplify plant responses to the environment. Plant %N is known to vary with a range of parameters, including rainfall, water availability, frost, geological substrate, and root depth (e.g. Ellery et al. 1995; Tainton 1999). Increasing plant $\delta^{15}\text{N}$ with increased %N may be expected because changes to soil moisture content and water availability influence both N uptake and ^{15}N -discrimination (Handley et al. 1994). These authors demonstrated a spatial relationship between soil water supply and plant $\delta^{15}\text{N}$, and suggested that site water relations more strongly influence $\delta^{15}\text{N}$ signatures of soils and plants than the amount of rainfall. This complexity likely underlies the complexity of $\delta^{15}\text{N}$ variations within Kruger Park, for example the higher values recorded for southern granites than southern basalts compared with the reversed pattern in northern regions.

The relationship between plant %N and $\delta^{15}\text{N}$ also has implications for herbivores. There is by now good evidence that herbivore $\delta^{15}\text{N}$ increases with dietary protein content (%N) (Roth & Hobson 2000; Sponheimer et al. 2003a; Codron & Brink 2007), and coupled with similar trends in plants suggests ways for understanding ^{15}N -abundance variations in modern and past foodwebs.

3.5. Conclusion

Variations in the stable isotope composition of C_3 and C_4 vegetation provide the baseline for diet studies in modern and palaeoecological contexts. The results presented here are important for understanding the significance of changes in animal isotope composition within Kruger Park, and are used in subsequent chapters to provide isotopic control. This approach is predicted to enhance the accuracy of isotope-based diet reconstructions. Nonetheless, it remains that

variations within plants, especially in $\delta^{13}\text{C}$, are fairly small in Kruger Park. The limited effects of external environmental/climate fluctuations on plant $\delta^{13}\text{C}$ in the region implies that elephant (and other animal) $\delta^{13}\text{C}$ values can be expected to offer reliable records of diet, including in historical times for which no plant data are available.

TABLE 3.1. – Summary of Kruger Park Land Systems included in this study, based on descriptions in Venter et al. (2003), with associated plant sampling transects.

Land system	Geology	Topography	Annual rain	Vegetation	Sampling sites
Satara (southern basalts)	Volcanic rocks (basalts); red and dark clays	Flat plains	500-650 mm	Fine-leaved tree savanna (<i>Acacia</i> spp.); dense riverine bushveld with heterogeneous vegetation Composition	1-Open grassland 2-Open riparian woodland
Skukuza (southern granites)	Granitic rocks; sandy soils and duplex clay soils	Slightly undulating Plains	500-750 mm	Dense riverine bushveld, woodland and forest with heterogeneous vegetation Composition	3-Open shrubland 4-Closed woodland 10-Riverbed
Letaba (northern basalts)	Volcanic rocks (basalts); red and dark clays	Flat plains	450-500 mm	Broad-leaved shrubveld (mopane-dominated); dense riverine bushveld with heterogeneous vegetation composition	5-Open grassland 14-Open grassland 15-Wooded grassland 16-Grassland at waterhole
Phalaborwa (northern granites)	Granitic rocks; sandy soils and loam or duplex clay	Slightly to strongly undulating Plains	450-600 mm	Broad-leaved bushveld (mopane-dominated); dense riverine bushveld, woodland and forest with heterogeneous vegetation Composition	6-Dry riverbed 7-Open woodland 8-Sodic patch 9-Dense riparian woodland
Pafuri (Punda Maria)	Sedimentary and volcanic rocks; alluvial floodplains	Slightly to strongly undulating Plains	400-650 mm	Broad-leaved dry bushveld and mopane woodland; dense riverine woodland/ river forest with heterogeneous vegetation Composition	11-Open woodland 12-Dense, closed woodland 13-Montane woodland

TABLE 3.2. – Mean annual rainfall (mm) and average daily maximum temperatures ($^{\circ}\text{C}$) recorded for Kruger Park landscapes over the study period (including the full dry season for 2002, i.e. from April 2002, and ending at the end of the 2004/5 wet season, i.e. March 2005). Data are from the South African Weather Bureau and N. Zambatis (Scientific Services, Skukuza, Kruger National Park).

<i>Region</i>	Climate station and period for which data are available	Long-term Mean	Year 1 Apr02-Mar03	Year 2 Apr03-Mar04	Year 3 Apr04-Mar05
Rainfall (mm)					
<i>Far North</i>					
Punda Maria	Punda Maria (1981-2005)	539	360	577	280
<i>North</i>					
Granite	Sirheni (1991-2004)	502	324	377	72
Basalt	Shingwedzi (1935-2005)	424	370	394	274
<i>South</i>					
Granite	Skukuza (1920-2005)	555	270	630	796
Basalt	Lower Sabie (1969-2005)	583	474	707	457
Maximum T($^{\circ}\text{C}$)					
<i>Far North</i>					
Punda Maria	Punda Maria (1924-2005)	29.4	30.0	29.2	30.2
<i>North</i>					
Granite	Sirheni (1991-2004)	30.5	30.9	30.5	30.6
Basalt	Shingwedzi (1981-2004)	30.9	31.9	31.3	29.9
<i>South</i>					
Granite	Skukuza (1975-2004)	29.6	30.9	30.2	29.6
Basalt	Satara (1981-2004)	30.0	31.4	30.3	29.7

TABLE 3.3. – Stable carbon and nitrogen isotope composition, and percent nitrogen (%N), of tree leaves, forbs, grasses, reeds and sedges from Kruger Park (year 1 = June 2002 and January 2003; year 2 = June 2003 and February 2004; year 3 = June 2004 to May 2005). Data for June 2002 to February 2004 are from Codron et al. (2005).

Plant form	Year of study	n	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)		$\delta^{15}\text{N}_{\text{Air}}$ (‰)		%N	
			Mean	SD	Mean	SD	Mean	SD
Trees	Year 1	237	-26.5	1.7	3.4	2.6	1.7	0.8
	Year 2	301	-26.4	1.4	4.3	2.3	2.2	1.0
	Year 3	405	-26.8	1.4	4.1	2.2	2.2	0.9
	All	943	-26.6	1.5	4.0	2.4	2.1	0.9
Forbs	Year 1	104	-26.7	1.2	4.3	2.8	1.8	1.1
	Year 2	110	-26.9	1.3	4.5	2.7	2.9	1.6
	Year 3	129	-26.8	1.2	4.1	2.5	2.5	1.1
	All	343	-26.8	1.3	4.3	2.6	2.4	1.3
Grass	Year 1	254	-12.3	1.2	3.3	2.3	0.9	0.5
	Year 2	355	-12.1	1.0	3.4	2.4	1.3	0.7
	Year 3	415	-13.5	0.9	3.1	2.1	1.2	0.6
	All	1024	-12.7	1.2	3.3	2.2	1.2	0.6
C ₃ Reeds	Year 1	17	-26.7	1.4	7.2	1.0	1.5	0.6
	Year 2	11	-25.8	0.9	7.1	1.6	2.4	1.8
	Year 3	11	-25.7	0.9	8.1	1.3	2.1	1.2
	All	39	-26.2	1.2	7.4	1.3	1.9	1.2
C ₄ Reeds	Year 1	4	-13.0	3.0	5.7	1.0	1.6	0.7
	Year 2	0	-	-	-	-	-	-
	Year 3	0	-	-	-	-	-	-
	All	4	-13.0	3.0	5.7	1.0	1.6	0.7
C ₃ Sedges	Year 1	10	-27.8	1.2	7.4	2.2	1.4	0.6
	Year 2	16	-26.4	1.4	6.3	1.3	2.0	1.3
	Year 3	24	-26.5	1.1	6.4	2.3	1.7	0.8
	All	50	-26.7	1.3	6.6	2.0	1.7	1.0
C ₄ Sedges	Year 1	5	-11.4	0.6	4.8	0.9	0.7	0.3
	Year 2	1	-10.6	-	6.4	-	1.3	-
	Year 3	4	-12.5	0.9	6.4	1.3	1.1	0.2
	All	10	-11.8	0.9	5.6	1.3	0.9	0.3

n = number of samples; SD = ± 1 standard deviation

- Chapter 4 -

Short-term Geographical Variations in Elephant Diet from Stable Isotope Composition of Faeces and Tail Hair

This chapter focuses on elephant dietary variations over the short term, using isotopic results from faeces and tail hairs that represent a diversity of habitat and seasonal scales within Kruger Park. These data are augmented with data for changes in the nitrogen composition (reflecting crude protein) of local vegetation, faecal nitrogen content, and rainfall. The aim of the chapter is to explore the relationship between diet with habitat, season, rainfall, and plant nutritional composition, in order to facilitate interpretation of mechanisms underlying historical diet changes in later chapters.

4.1. Introduction

A prevailing theme in contemporary African savanna ecology is the so-called “elephant problem”, based on the premise that African elephants are keystone agents of ecosystem functioning and biodiversity (Laws 1970; Field 1971; Laws et al. 1974; Bell & Jachmann 1984; Caughley 1976; Owen-Smith 1987, 1988; Dublin et al. 1990; Ben-Shahar 1993, 1998; Wilson 1993; Dublin 1995; Bowland & Yeaton 1997; Cumming et al. 1997; Shoshani 1997, 1998; Van de Koppel & Prins 1998; Whyte 2001; Rutina et al. 2005). By contrast, it is becoming increasingly clear that empirical evidence for elephant-induced changes, particularly negative changes like habitat and biodiversity loss, seldom supports these assumptions (Owen-Smith et al. 2006). Such debates call for a more thorough understanding of the dynamics of elephant-plant

interactions if we are to improve our ability to understand and predict the implications of elephants for biodiversity.

The substantial impacts elephants are thought to have on their habitats is founded in beliefs that they habitually consume and destroy large amounts of woody vegetation. However, elephants are mixed-feeders capable of switching almost entirely along the browser-grazer continuum (Wing & Buss 1970; Williamson 1975; Field & Ross 1976; Guy 1976; Norton-Griffiths 1979; Short 1981; Jachmann & Bell 1985; Owen-Smith 1988; van der Merwe et al. 1988; Skinner & Smithers 1990; Dublin 1995; Cerling et al. 1999; De Boer et al. 2000; Seydack et al. 2000; Styles and Skinner 2000; Steyn & Stalmans 2001). This adaptive propensity allows elephants to survive in a wide variety of habitats, and likely facilitated their persistence through the climatic and environmental turbulence of the mid-Late Pleistocene, during times in which they are also predicted to have had significant outcomes for biodiversity (Osborn 1934; Coppens et al. 1978; Owen-Smith 1987, 1988; Douglas-Hamilton & Michelmore 1996; Shoshani 1997, 1998; Palombo & Ferretti 2005). Despite this, relatively little emphasis has been placed on browse/grass switching in this species. As a consequence, seemingly mundane questions about mechanisms including i) whether browse consumption is necessarily higher in more wooded areas; ii) the role of key tree species in homogeneous woodlands acting as browse-deterrents; iii) whether seasonal shifts to increased grass intake occur at the start, middle, or end of the rainy season, and iv) the role of changes in plant nutritional composition in food selection; and v) whether grass, browse, or a mix of these two food groups are the preferred diet, remain untested and unanswered (Field 1971; Wyatt & Eltringham 1974; Laws et al. 1974; Williamson 1975; Guy 1976; Barnes 1982; van der Merwe et al. 1988; Skinner & Smithers 1990; Dublin 1996; Bowland & Yeaton 1997; Babaasa 2000; Kennedy 2000; Seydack et al. 2000; Stokke & du Toit 2000; Styles & Skinner 2000; Holdo & McDowell 2004; Midgley et al. 2005; Codron et al. 2006; Mtui & Owen-Smith 2006; Shimane & Skarpe 2006).

Traditional approaches to elephant diet rely largely on direct observations (e.g. Bax & Sheldrick 1963; Short 1981; Barnes 1983; Viljoen 1989; Spinage 1994; Dublin 1995, 1996; Whyte 1996; Paley & Kerley 1998; Hiscocks 1999; Stokke & du Toit 2000; Holdo & McDowell 2004; Midgley et al. 2005) or analysis of stomach content and/or faeces (e.g. Bax & Sheldrick 1963; McCullagh 1969a, 1969b; Laws et al. 1974; De Boer et al. 2000). These approaches can provide reliable details about parameters such as plant species and plant parts utilized. However, field observations do not record actual biomass intake (see Cerling et al. 2003) and it is possible to misidentify certain plant foods eaten (Dublin 1995). Gut analysis requires extensive slaughter of individuals (e.g. Laws et al. 1974), and certain plant species can be difficult to identify once masticated, especially if studies are carried out during the dry season when many browse plants are leafless (Bax & Sheldrick 1963). Most importantly, traditional methods are time-consuming and therefore typically limited to single time periods, habitats, and even herds, hence results of separate studies are seldom comparable (Owen-Smith 1988). The upshot is that opinions vary as to how elephant diets vary in space according to changes in vegetation cover, plant nutrient content, water availability, geology, soil nutrient composition, rainfall, and season (Field 1971; Williamson 1975; Field & Ross 1976; Guy 1976; Short 1981; Barnes 1982; Western & Lindsay 1984; Owen-Smith 1988; Viljoen 1989; Dublin et al. 1990; Skinner & Smithers 1990; Koch et al. 1995; Cerling et al. 1999; Holds et al. 2002; Codron 2004; Mwangi et al. 2004; Codron et al. 2006; Mtui & Owen-Smith 2006).

Stable carbon and nitrogen isotope tools can overcome many of these constraints, because empirical records of diet change can be recorded over multiple scales (Peterson & Fry 1987; Post 2002; Dalerum & Angerbjörn 2005; Thompson et al. 2005). Stable carbon isotope ratios ($\delta^{13}\text{C}$) in savanna herbivore tissues reflect proportions of C_3 (browse) to C_4 (grass) consumed, and stable nitrogen isotope ratios ($\delta^{15}\text{N}$) reflect changes in trophic position, ecophysiology, and dietary protein (see Chapter 3; Vogel 1978; Tieszen et al. 1979; Lee-Thorp & van der Merwe 1987; Sealy et al. 1987; Ambrose 1991; Cerling & Harris 1999; Sponheimer et al. 2003a; Robbins et al.

2005). Stable isotope ecology lacks the detail associated with traditional approaches such as field observations, but the approach is well suited to spatio-temporal variability in diet. Faeces turn over within a few days and therefore record changes over the short term (Jones et al. 1981; Coates et al. 1991; Sponheimer et al. 2003a). Several experimental and field studies have demonstrated that, despite representing mostly the undigested portion of the diet, faeces provide a faithful record of dietary isotope composition (Jones et al. 1981; Coates et al. 1991; Hare et al. 1991; Sponheimer et al. 2003b; Codron, D. et al. 2005a, 2007a; Codron, D. & Codron in press). Hairs grow over several months or years, and because growth is incremental, isotope profiles along individual strands yield dietary time series (Ayliffe et al. 2004; Cerling et al. 2004a, 2006; Codron 2004).

The aim of this chapter is to determine, through use of stable isotope distributions in faeces, whether elephant diets change significantly across seasons and habitats even within a single savanna reserve (Kruger National Park, South Africa), and what environmental influences underlie these variations. An earlier study reported on differences in the stable carbon isotope composition between elephant faeces from the northern (north of the Olifants River) and southern regions of Kruger Park, and between two dry season (June 2002 and 2003) and two wet season months (January 2003 and February 2004) (Codron 2004; Codron et al. 2006). Results showed that %C₄ grass intake was significantly higher amongst northern Kruger Park elephants compared with their southern counterparts, at least during the dry season. It was hypothesized that the diets of elephants in northern Kruger Park habitats did not conform to predictions for reduced grass consumption in these more wooded areas because a) seasonal variability in available resources is low, limiting seasonal diet switches; and b) the maintenance of grass-rich diets was a mechanistic negative-feedback response to the homogeneity of available woody vegetation in the north, where a single tree species (*Colophospermum mopane*) predominates throughout. The current study aimed to increase the spatial and seasonal resolution of the previous investigation, thus includes

data from faeces representing eight landscapes within Kruger Park collected at monthly intervals over one complete seasonal cycle (1 year).

Two primary hypotheses are tested: 1) elephant diets change significantly across different habitats and seasons, based on the prediction that they consume relatively more C₄ grass in all northern habitats and/or during all wet season months; 2) dietary variations are a function of environmental changes, including shifts in grass availability (using rainfall data as a surrogate for productivity), grass nutritional quality, browse quality (using percent nitrogen content of available vegetation to estimate quality), and homogeneity of woody landscapes dominated by mopane. I also test hypotheses for ¹⁵N-abundance variations in faeces, including effects of climate, diet quality, and variations in ¹⁵N-content of available vegetation. Last, I provide stable isotope profiles from tail hairs of 20 individuals, to determine whether isotope records from body tissues substantiate records of short-term diet shifts recorded in faeces.

4.2. Materials and Methods

4.2.1. Materials

Elephant faeces were sampled at monthly intervals for one year (February 2004 to January 2005) from eight landscape types identified within Kruger Park (Fig. 4.1). These landscapes are northern basalts, northern granites, north central basalts, north central granites, south central basalts, south central granites, southern basalts, and southern granites. In the south, the Sabie River separates southern from south central landscapes, while the Mopane restcamp was used as the point of latitude dividing northern from north central sampling areas. Where possible, 10 individual faecal specimens were collected on each occasion per region, and only recently deposited, i.e. fresh or damp, faeces were collected so as to ensure that samples represented the appropriate month and were not contaminated by fungi, soil and insects (see Wrench et al. 1996). For comparison, but excluded from the statistical analyses described below, results for faeces collected in June 2002, January 2003, and June 2003 are presented, representing

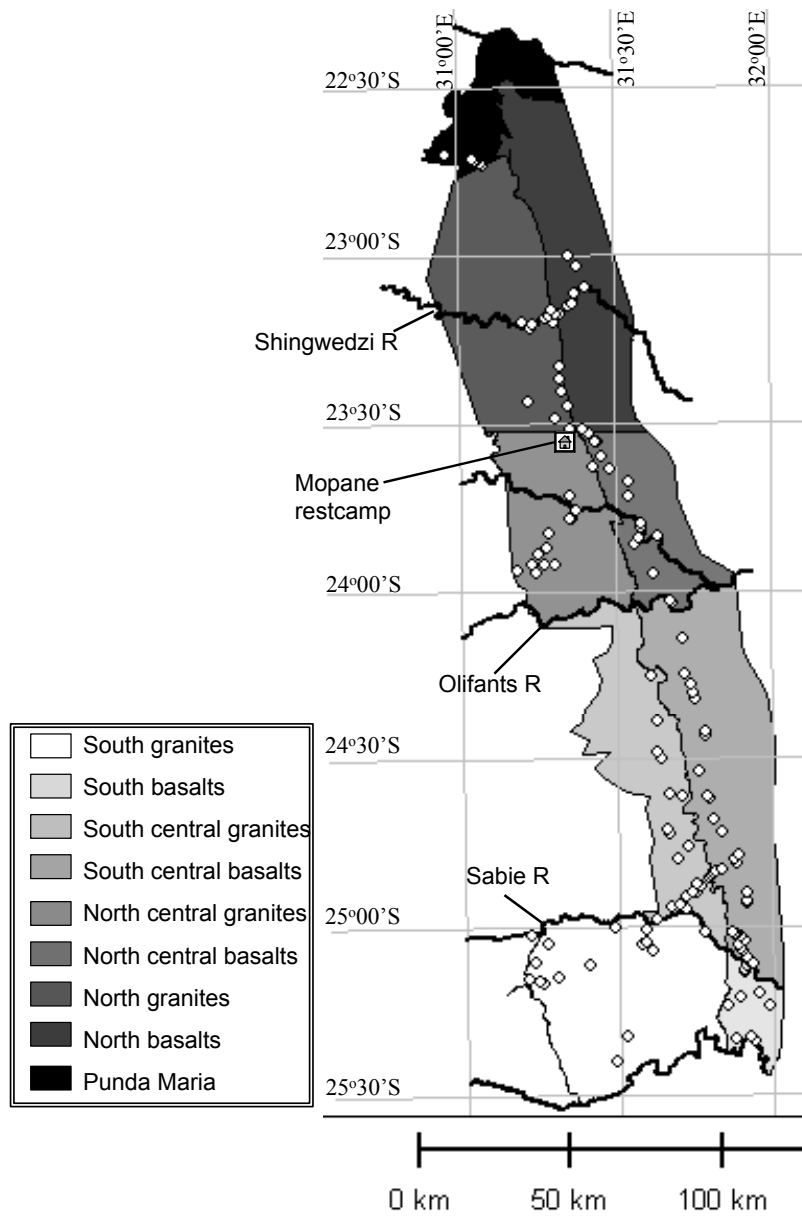


FIGURE 4.1. – Map of Kruger Park showing the nine habitat types included in this study, in relation to geology and the major river systems. Elephant faecal sampling sites are presented as white circles. The Mopane rest camp indicates the latitudinal separation between northern and north central habitats identified for this study.

previously published data (Codron et al. 2006) as well as a subset ($n = 17$) of specimens from Punda Maria, the densely wooded savanna in the far northern Kruger Park. Faeces were prepared for isotope analysis by oven-drying at 60°C for at least 24 hours, and then mill-ground through a 1 mm sieve into a homogeneous powder.

Tail hair strands from 19 individuals were provided by the Kruger Game Capture Unit. Hairs ranged from 80 to 290 mm in length, and the Game Capture Unit had recorded collection time for each specimen (day, month, year), sex, and age group. Age categories are based primarily on the sizes of the animals, which are used to estimate the development of a particular individual. That is, a calf is an animal that is still suckling, a juvenile is a weaned individual, a sub-adult is an animal approaching adult size but is not yet reproductively active, and an adult is a cow that has had a calf or a bull that is able to compete for females (P. Buss 2005 pers. comm.). In 2001, one hair of 430 mm had been obtained from an adult male elephant in the Lion Sands Game Reserve, a private reserve situated within the greater Sabie Sands Private Game Reserve (bordering Kruger Park on the southwest). Although isotope data from this specimen have been reported previously (Codron 2004), it is included in this chapter because it is the only sample available representing southern granite habitats.

Tail hairs were wiped with acetone to remove lipids and surface contaminants, and then sectioned at 10 mm intervals from the root towards the tip using a scalpel. Between 0.45 and 0.6 mg of material was removed from within each increment, ensuring that a distance of precisely 10 mm was maintained between samples. Sampling hairs at this resolution was deemed sufficient for purposes of examining seasonal shifts in diet; a previous experiment showed that higher resolution (i.e. 1 mm increments) represents too short a time frame for recording substantial diet shifts (see Codron 2004).

4.2.2. Analytical Techniques

The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, percent carbon (%C), and percent nitrogen (%N) of each faecal sample and tail hair sub-sample were measured by stable light isotope ratio mass spectrometry (SLIR-MS) following the same procedures as used for plants (see Chapter 3). Faecal %N of herbivores is a useful proxy for diet quality, roughly reflecting crude protein content of the diet (Holecheck et al. 1982; Leslie & Starkey 1985; Irwin et al. 1993; Grant et al. 1995, 2000; Wrench et al. 1997), even though anomalously high N content may occur when browse intake is high, due to protein-precipitation by condensed tannins (Arman et al. 1975; Robbins et al. 1987). The C/N ratio of intact biological proteins (such as keratin in hair) is expected to be between 2.9 and 3.6 (see DeNiro 1985 for bone proteins, i.e. collagen). C/N ratios of hair specimens analyzed for this study range from 3.1 to 3.5. Elephant diets were quantified by converting faecal $\delta^{13}\text{C}$ values to estimates of %C₄ grass intake using the following dual-mixing model (Post 2002; Cerling et al. 2003; Sponheimer et al. 2003d):

$$\%C_4 = (\delta^{13}\text{C}_{\text{C3 plants}} + \varepsilon - \delta^{13}\text{C}_{\text{faeces}}) / (\delta^{13}\text{C}_{\text{C3 plants}} - \delta^{13}\text{C}_{\text{C4 plants}})$$

where ε is the diet-consumer ^{13}C -discrimination, assumed here to be -0.9‰ for faeces (Sponheimer et al. 2003b; Codron, D. et al. 2005a). Each individual faeces sample was assigned a regional and temporally specific (year, month) $\delta^{13}\text{C}_{\text{C3 plant}}$ and $\delta^{13}\text{C}_{\text{C4 plant}}$ value, using mean $\delta^{13}\text{C}$ values of local vegetation (data from Chapter 3; see Table 4.1). Results are presented as means \pm 1 standard deviation.

The hypotheses for spatial and temporal variations in diet were tested using analysis of variance (ANOVA). A main effects ANOVA model of the effects “month” and “region” on faeces $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and %N was used, constituting a hierarchical within-effects design. Layering of these effects in the ANOVA model followed a months-within-regions design for the seasonal variation hypothesis, and a regions-within-months design for regional variations. Where multiple comparisons were necessary, Tukey’s *post hoc* HSD test was used. All tests were two-tailed, with significant *P*-level 0.05. In addition, differences in faecal $\delta^{13}\text{C}$ are only considered to be

significantly different if estimated %C₄ intake varied by 10% or more; this figure constitutes the maximum allowable error estimate in the mixing model used (see Codron, D. et al. 2005a).

In order to further characterize the spatial diversity of elephant diets, I used Principal Components Analysis (PCA) based on a data matrix of mean %C₄ intake in each region during the third year, treating the mean for each month as a separate variable (i.e. 12 variables). PCA is a multivariate, linear reduction model, which identifies directions of maximum variance in the data matrix, and projects data into lower-dimensionality space based on subsets (components) of variance (Bishop 1995). These components were interpreted here as groups (habitats) where elephant diet composition and diet variability were most similar.

The environmental response hypotheses were tested using regression models of environmental variables (rainfall as a partial surrogate for grass abundance; %N of available C₃ and C₄ vegetation; and variations in diet quality from faecal %N) on %C₄ in elephant diets. For $\delta^{15}\text{N}$, climate (rainfall and maximum daily temperature per month; data from the South African Weather Bureau), diet (%C₄ intake), diet quality (faecal %N), and available plant $\delta^{15}\text{N}$ (data from Codron et al. 2005), were tested as predictor variables. Visual inspection showed that some of these relationships appeared to be linear, but in several cases %C₄ intake appeared to increase curvilinearly with the environmental predictor variable, and some regressions on $\delta^{15}\text{N}$ also appeared to be non-linear (and negative). Thus, linear models were tested ($y = \alpha + Bx$), but also compared with non-linear alternatives. For regressions on %C₄ intake, I fitted an exponential model to the data, $y = \alpha.e^{(Bx)}$, as well as an asymptotic model $y = a-B\rho^x$, where $0 < \rho < 1$ (Patterson 1956). The hypothesis that elephant diets are, in part, a function of homogeneous woody plant distributions, was tested using multiple linear and non-linear regression models. This hypothesis predicts that elephant %C₄ grass intake will increase in mopane-dominated regions of Kruger Park (see Codron et al. 2006), and so an additive parameter ($+B_2M$), where M indicates presence (1) or absence (0) of mopane, was introduced in all linear and non-linear regression models. For regressions on $\delta^{15}\text{N}$, linear models are compared with a negative exponential decay model $y =$

$\alpha \cdot e^{(-Bx)}$. All variables included in the regression models were normalized from 0 to 1 following $(X_{\min} - X_i)/(X_{\min} - X_{\max})$ (Motulsky & Christopoulos 2003); for equal scaling, %C₄ intake was thus introduced in proportions (i.e. $X_i \cdot 10^{-2}$). Models were parameterised using initial values of 0.0001 for all parameters, estimated over 1 000 iterations (Gauss-Newton method).

Model selection, comparing fits between the different model types used, and to estimate which of the predictor variables had the strongest effect on faecal isotope distributions, was based on the second-order Akaike's Information Criterion (Burnham & Anderson 2001, 2002). AIC is a Kullback-Leibler information-theoretic approach to model selection, which are approaches based not on statistical significance but rather the likelihood that one of a set of hypotheses provides the best explanation for a studied phenomenon. AIC is computed from log-likelihood ratio, or the residual sum of squares, to compare the strength of support for each model in the candidate set. The second-order AIC_c also penalizes for the addition of parameters, thus offers an approach to parsimony, e.g. assessing whether additional parameters such as mopane improve model fits substantially enough to warrant inclusion of more complex expressions. Here, AIC_c was calculated from

$$AIC_c = n \log(\sigma^2) + 2K + \frac{2K(K+1)}{K-n-1}$$

where $\sigma^2 = SS_{\text{residuals}}/n$, n = number of observations, and K is the number of parameters plus the intercept. Models with the highest AIC_c will thus be the least well-supported amongst the candidate set. Indices for model selection are provided by ΔAIC_c and Akaike weights (w_i , the evidence ratio) as follows

$$\Delta AIC_{ci} = AIC_{ci} - \text{minimum } AIC_c, \text{ and}$$

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$$

where i represents the candidate model, R the whole set of models, and $r = 1$ the sum of all models to unity 1. Models with $\Delta AIC_{ci} < 2$ are considered strongly supported, weakly supported when $2 < \Delta AIC_{ci} < 10$, and are considered to have a very poor fit to the data if $\Delta AIC_{ci} > 10$. The evidence ratio indicates strength of evidence, i.e. the probability of a candidate model having the best fit amongst the whole set of models.

For tail hair profiles, a crude monthly growth rate for hairs of between 10.0 and 20.0 mm was assumed, based on data in Cerling et al. (2004a, 2006) for elephants from East Africa. A number of hairs were identified as being in the active (anagen) growth phase, by the presence of the internal root sheath at the base of the hair. In these cases, the most recent date represented in a series (the root) was taken as the month of collection, as all hairs were collected within the first eight days of the respective months. For hairs not in active growth, the month preceding that of collection was used as most recent. Temporal records of diet change recorded in hair profiles were then compared with monthly data from faeces using Spearman's Rank correlation coefficient for non-parametric data and small sample sizes. Isotope distributions between individual hairs were compared using two approaches: i) multiple non-parametric ANOVAs (Kruskal-Wallis H -test, P -level = 0.05); and ii) resampling/reshuffling procedures to compare random pairs of observations between individuals over 1 000 iterations (where the subject for a minimum difference was set at 0.5‰). Under the latter approach, individuals were considered to have significantly different isotopic distributions if the probability of a 0.5‰ difference over 1 000 iterations was 95% or greater. All analyses were conducted in STATISTICA 7.0 and 8.0 (StatSoft Inc.), except that the resampling approach to inter-individual hair comparisons was run in MS-Excel.

4.3. Results

4.3.1. Seasonal Diet Hypothesis

There were significant month-to-month changes in mean faecal $\delta^{13}\text{C}$ within all regions (Fig. 4.2; main effects ANOVA, $F_{11, 862} = 64.879$, $P < 0.0001$). These changes were sufficiently large to invoke diet switches through the seasonal cycle (main effects ANOVA on %C₄ in diet, $F_{11, 862} = 41.561$, $P < 0.0001$). Mean $\delta^{13}\text{C}$ shifted by magnitudes of between ~ 3 and 6‰ across different months within any one region (by 8‰ in the case of southern basalts), corresponding to diet switches of ~ 25 to $\sim 60\%$ (19 to 71% on southern basalts) C₄ grass consumption at different stages of the year.

The prevailing trend was that mean faecal $\delta^{13}\text{C}$ (and hence estimated %C₄ grass consumption) was significantly lower during the dry months of April to September compared to wet season months of October to March (Tukey's HSD $P < 0.001$ in all comparisons), except that means for October were not different compared to any of the dry season months ($P = 0.53$ to 0.99). Overall, mean %C₄ intake estimated for the dry season was $34\% \pm 13$ ($n = 408$) and for the wet season $48\% \pm 16$ ($n = 473$). In most instances, seasonal switches followed a gradual increase shortly after the onset of the wet season (November mean = $43\% \pm 14$ C₄ diet; $P < 0.001$) through to the very late wet season (March mean = $52\% \pm 15$ C₄ diet; $P < 0.0001$), before gradually returning to lower dry season levels. In the four southern regions, two grazing 'peaks' are evident in Fig. 4.2, with %C₄ grass intake reaching a maximum in December ($68\% \pm 16$ C₄ diet; $P < 0.0001$), decreasing by more than 10% in January and February ($P < 0.0001$), and then rising again in March ($57\% \pm 12$ C₄ diet; $P < 0.01$).

4.3.2. Regional Diet Hypothesis

Comparison of mean faecal $\delta^{13}\text{C}$ between the different regions revealed relatively small differences, from $-23.4\text{‰} \pm 2.5$ ($n = 108$) on southern granites to $-21.3\text{‰} \pm 2.1$ ($n = 132$) on northern basalts (Table 4.2). While there was a significant effect of "region" on $\delta^{13}\text{C}$ ($F_{7, 873} =$

12.247, $P < 0.0001$), the differences, at most, only indicate dietary differences of 10% C_4 intake across regions (34% on southern granites, 44% on northern basalts). This is in contrast to results

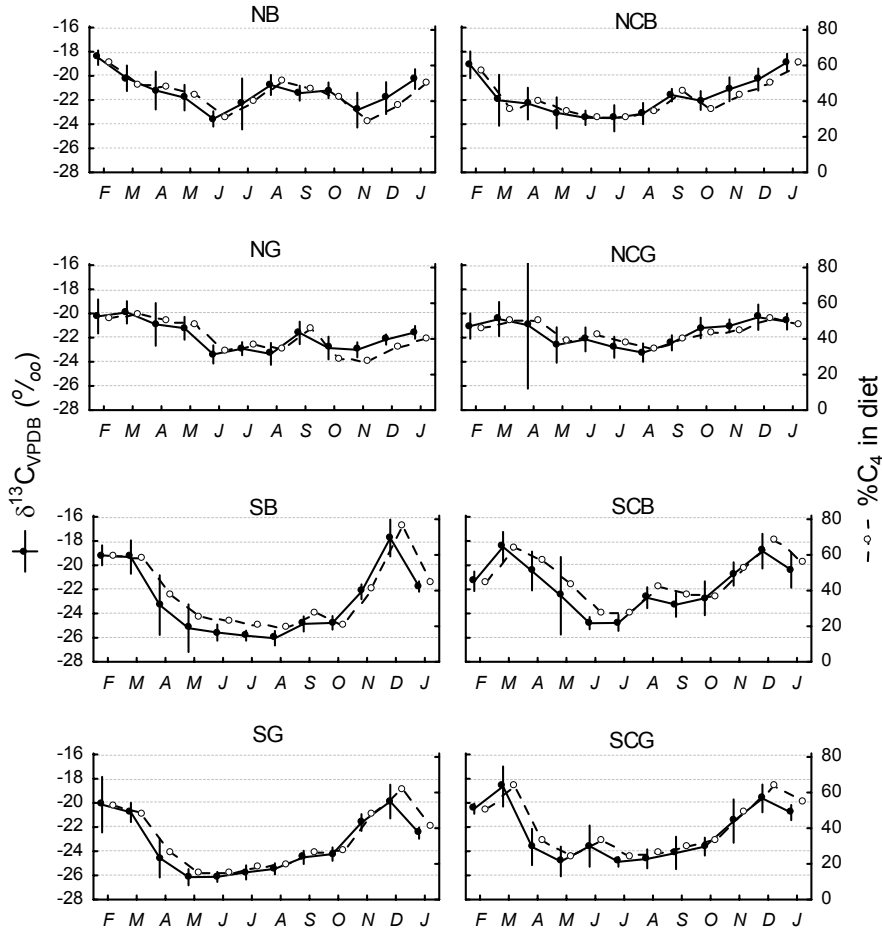


FIGURE 4.2. – Monthly changes in mean faecal $\delta^{13}C$ and $\%C_4$ in the diet of elephants from eight habitat types in Kruger Park, representing the period February 2004 to January 2005. NG = northern granites; NB = northern basalts; NCG = north central granites; NCB = north central basalts; SCG = south central granites; SCB = south central basalts; SG = southern granites; SB = southern basalts. Symbols are means and error bars $\pm 95\%$ confidence limits.

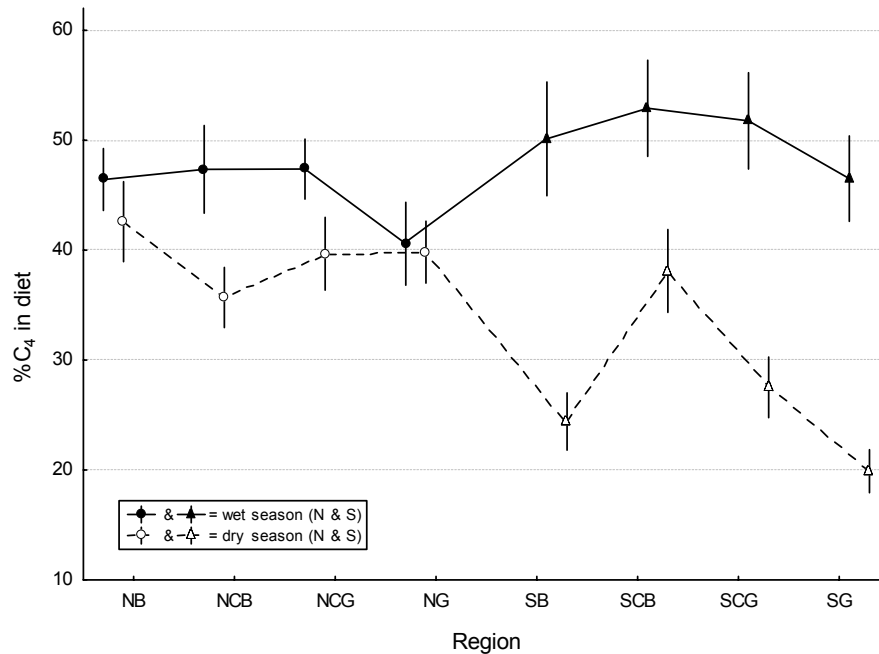


FIGURE 4.3. – Graphical illustration of seasonal effects on the north(N)-south(S) differences in Kruger Park elephant diets (%C₄ grass intake), as revealed by analysis of faecal $\delta^{13}\text{C}$ in different seasons. Data for all months are pooled into either dry season (April to September) or wet season groups (October to March). Symbols are means and error bars $\pm 95\%$ confidence limits.

of the earlier study (Codron et al. 2006), in which larger differences between northern and southern Kruger Park elephant diets were reported (see Table 4.2). However, in that study the difference only persisted for the dry season (June), and it was hypothesized that the main effect was a lack of seasonal variation in the north so that northern elephants did not significantly reduce %C₄ grass intake from the wet to the dry season. In the current study, the higher temporal resolution of data might dampen this effect, but it is clearly evident from Table 4.2 that northern elephants do show smaller diet switches than those in the south. The hierarchical design in the main effects ANOVA applied to current data support this assertion, with regional comparisons within each month of the study revealing a significant effect of “region” on faecal $\delta^{13}\text{C}$ ($F_{7, 862} =$

20.188, $P < 0.0001$). Moreover, it was found that the regional effect was not significant for all wet season months (Tukey's HSD $P = 0.32$ to 0.99 , except for southern basalts, $\sim 50\%$ C₄ intake, compared with northern granites, $\sim 40\%$ C₄ intake, $P < 0.05$). By contrast, elephants on southern granites ($20\% \pm 7$, $n = 51$), southern basalts ($24\% \pm 9$, $n = 53$), and south central granites ($28\% \pm 9$, $n = 45$) had lower overall %C₄ intake estimates than elephants from all of the northern regions, where means vary from $36\% \pm 10$ ($n = 5$) on north central basalts to $43\% \pm 15$ ($n = 64$) on northern basalts ($P < 0.001$ in all comparisons). On south central basalts, elephants appeared to maintain similar diets compared with their northern counterparts, even in the dry season months ($P = 0.40$ to 1.00), but consume significantly more C₄ grass than elephants in other southern regions (mean = $38\% \pm 13$, $n = 45$, $P < 0.01$). These seasonal effects on spatial differences in diet are presented for visualization in Fig. 4.3.

Thus, regional shifts in elephant diet, although small overall, are certainly manifest when the effects of seasonal variation are taken into account. For example, the coefficient of variation for %C₄ grass intake in the northern regions varies between 27 and 33%, whereas in the southern regions this figure is much higher at 32 to 54% (Table 4.2), providing support that variability in the north is limited. Indeed, the overall month-to-month range of variation in mean %C₄ intake for southern regions is 15 to 71%, and 27 to 61% in northern regions. The result is that while southern elephants (except those on south central basalts) consume much less C₄ grass than other sub-populations in the dry months, they also consume *more* C₄ grass than northern elephants during certain wet season months, especially during December, January and February when the differences are significant ($P < 0.01$ in all comparisons).

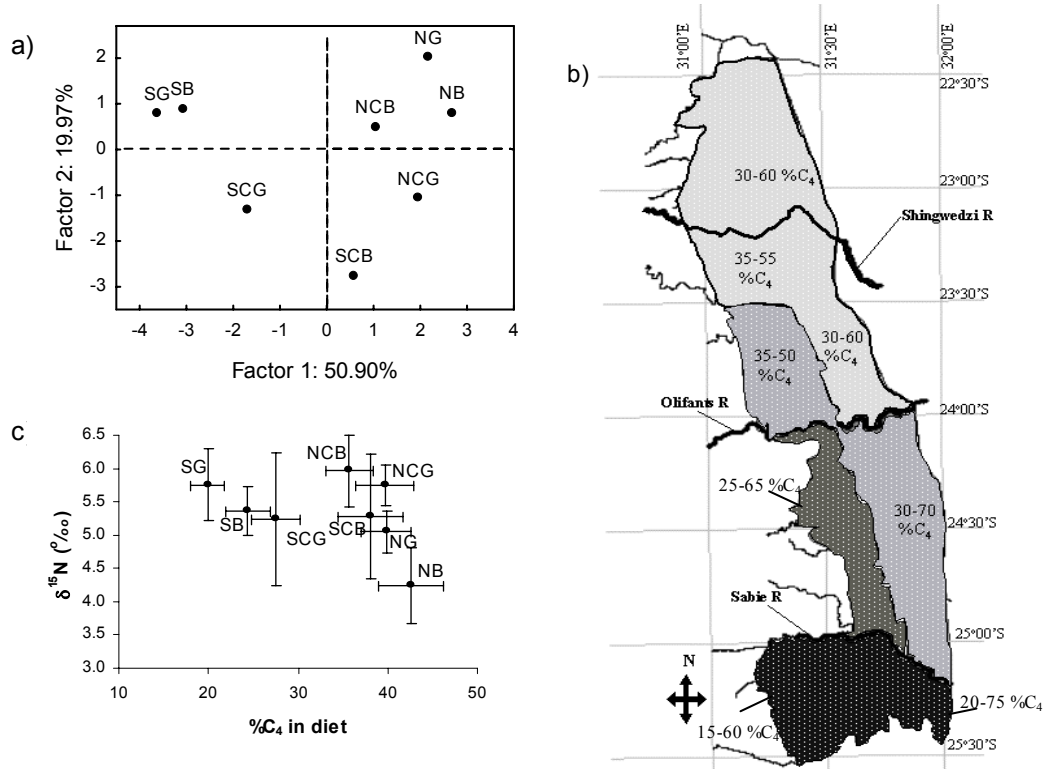


FIGURE 4.4. – Spatial characterization of Kruger Park elephant diets based on a, b) Principal Component Analysis (PCA) using monthly variations in %C₄ intake as a set of 12 variables, and c) bivariate analysis of %C₄ intake with faecal δ¹⁵N (dry season data only). Components/quadrants in (a) are used to distinguish different feeding ecologies and are represented in the map (b). Symbols in (a) and (c) depict means, bars in (c) are ±95% confidence limits.

The principal components analysis applied to these data accounted for not only dietary differences between regions, but also differences in monthly variations within them. Results revealed that the spatial complexity of elephant diets within Kruger Park can be summarized into four components, accounting for ~70 % of the total variation in these data (Figs 4.4a & b). Southern granites and southern basalts group together, seemingly because of the lower overall C₄

grass intake but more pronounced seasonal variation in diet (~15 to 75% C₄); elephants on south central granites had similarly low C₄ grass intake compared with southern granites and basalts, but can be distinguished on the basis of higher values for dry season months (24 to 33% compared with 15 to 27%); south central basalts, where elephants showed as high C₄ grass consumption (30 to 70%) as in northern regions (30 to 60%), groups with north central granites; and north central basalts, northern granites, and northern basalts cluster together likely because of consistently high C₄ grass consumption with limited variability through the seasonal cycle. A bivariate plot of mean %C₄ grass intake with faecal δ¹⁵N (see below) for each region (dry season months only) supports the results of the PCA (Fig. 4.4c): southern granites, southern basalts, and south central granites are distinct from the other regions in terms of %C₄ grass in diet ($P < 0.01$), while south central basalts are similar to northern habitats ($P = 0.86$ to 0.99). Northern basalts faeces have lower faecal δ¹⁵N compared with other regions ($P < 0.05$), and, as already discussed, also showed the highest C₄ grass contributions to diet with the least amount of seasonal change.

4.3.3. Environmental Responses Hypotheses

The C₄ grass component of elephant diets showed significant relationships with rainfall, %N content of available grass, and %N content of C₃ browse ($P < 0.001$ in all cases; Figs 4.5a to c). The best-fit regression models tested for each of these variables (i.e. lowest AIC_c; see Table 4.3) revealed the shape of these relationships to be positively asymptotic for rainfall ($R^2 = 0.32$), exponential for %N_{grass} ($R^2 = 0.29$), and linear for %N_{browse} ($R^2 = 0.11$). These results support hypotheses that increases in C₄ grass intake by elephants are a function of grass availability (in turn, a function of increased rainfall such as occurs during the rainy months and in higher rainfall regions of Kruger Park) and a selective process for higher quality grasses when these are available. However, because %C₄ grass intake also increased with %N_{browse}, the hypothesis that elephants select for C₃ browse under conditions of elevated browse quality is not supported. There was also a significant, positive, linear relationship of %C₄ intake with faecal %N ($R^2 =$

0.20, $P < 0.01$; Fig. 5d), indicating a tendency for elephants to select between grass or browse to maximize nutrient uptake (in terms of N gain).

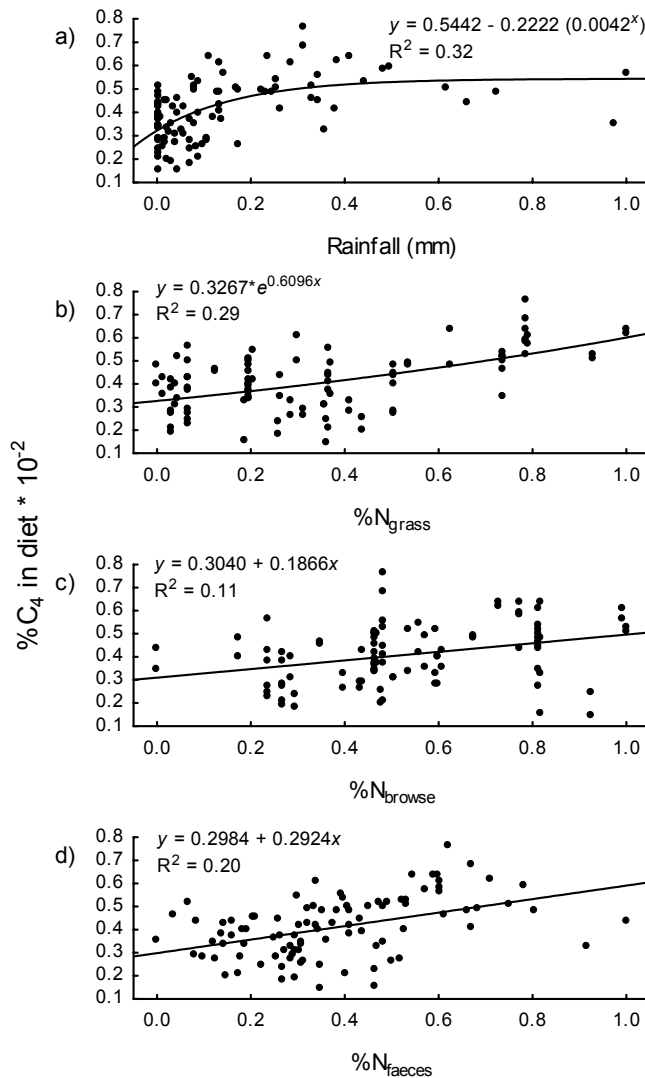


FIGURE 4.5. – Best-fit (see Table 4.3) regression models for variations in elephant C_4 consumption as a function of a) rainfall (used as a partial surrogate for grass abundance); b) grass nutritional value (%N); c) browse nutritional value (%N); and d) diet quality as indicated by %N of faeces. $\%C_4$ intake presented as proportions, and predictor variables were normalized from 0 to 1 for the regressions. Symbols are means per month per region. All models are significant at $P < 0.001$.

The regression models in Fig. 4.5 suggest that grass availability and nutritional value are more important predictors of elephant diet than effects related to browse availability. Yet when the effect of presence/absence of mopane was introduced to these models, a different pattern emerges. The most well-supported of all models tested in these analyses is one that describes elephant diets as an asymptotic function of rainfall and the presence/absence of mopane ($AIC_c = -374.08$, $\Delta AIC_c = 0.00$; Table 4.3). This model has a w_i of 0.90, implying a 90% probability that this model provides the most parsimonious (even after penalizing for the additional parameter) explanation for diet variations, at least amongst the models tested here, and is 30% more likely the best-fit model than the asymptotic response to rainfall alone ($w_i = 0.03$). No other model in the candidate set had a ΔAIC_c less than 2, but models for %N_{grass} as a dietary predictor do receive moderate support, with and without inclusion of the mopane expression ($\Delta AIC_c < 10$). Again, models for %N_{browse} as an important factor in elephant diets are poorly supported ($\Delta AIC_c > 26$).

4.3.4. ¹⁵N-Abundances in Faeces

Mean faecal $\delta^{15}N$ for the various regions and months generally ranged between ~ 4.0 and 6.0‰ (Table 4.2; Fig. 4.6a). There were significant effects of both “month” and “region” on ¹⁵N-distributions ($F_{11, 880} = 8.744$, $P < 0.0001$ and $F_{7, 880} = 5.047$, $P < 0.0001$, respectively), but post hoc comparisons revealed these to be primarily due to a significant increase from $\sim 4.0 - 5.5\text{‰}$ in most months to $6.6\text{‰} \pm 1.4$, $n = 80$, in July ($P < 0.001$ compared with all other months), and a relatively lower mean for northern basalts ($4.5\text{‰} \pm 1.8$, $n = 130$) compared with 5.0‰ or more in other regions ($P < 0.05$). No other significant differences between months or regions were found ($P = 0.08$ to 1.00), and in instances where month-to-month variations were apparent visually (Fig. 4.6a), there appeared to be no consistent pattern in terms of responses to environmental changes through the seasonal cycle.

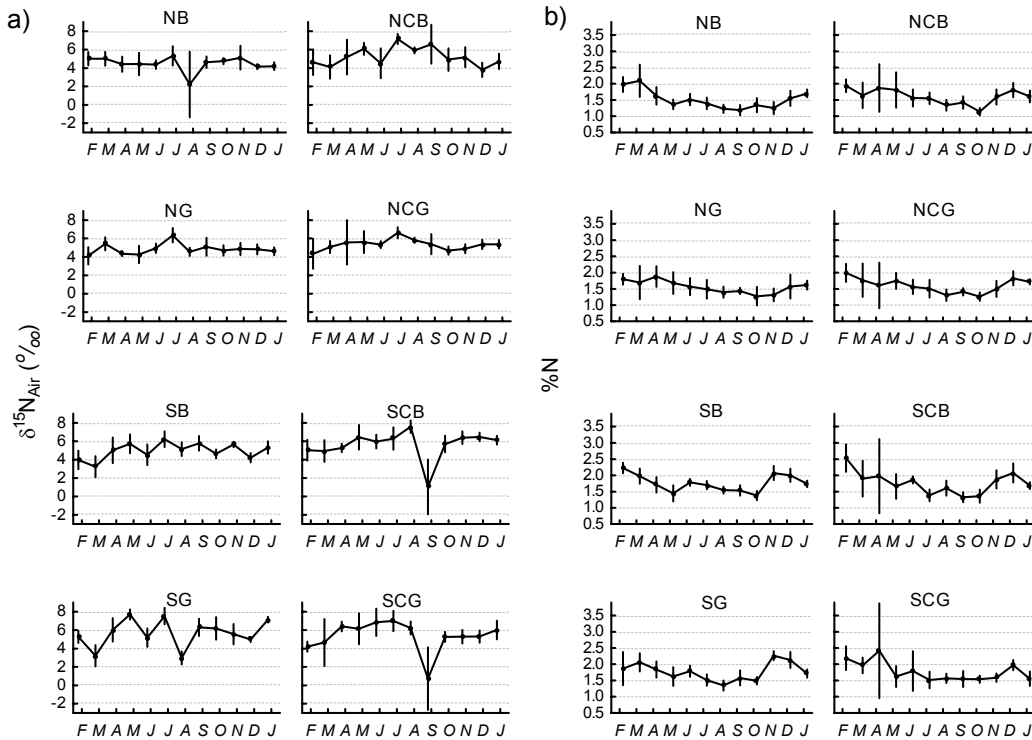


FIGURE 4.6. – Monthly changes in a) mean faecal $\delta^{15}\text{N}$; and b) faecal %N, of elephants from eight habitat types in Kruger Park, representing the period February 2004 to January 2005. NG = northern granites; NB = northern basalts; NCG = north central granites; NCB = north central basalts; SCG = south central granites; SCB = south central basalts; SG = southern granites; SB = southern basalts. Symbols are means and error bars $\pm 95\%$ confidence limits.

Faecal %N showed more substantial monthly, and regional, changes ($F_{11, 880} = 28.439$, $P < 0.0001$ and $F_{7, 880} = 10.097$, $P < 0.0001$, respectively; Fig. 4.6b). Changes through the seasonal cycle were large enough to imply significant changes in diet quality, from $1.3\% \pm 0.3$ ($n = 80$) in October, to $2.1\% \pm 0.4$ ($n = 83$) in February. Generally the trends corresponded more-or-less to changes in %C₄ grass consumption, faecal %N increasing at the onset of the wet season ($P < 0.01$ for October compared to previous months), but dropping in January ($P < 0.01$) before rising again in February ($P < 0.0001$), March ($P < 0.01$), and April ($P < 0.01$), and then decreasing through

the dry season months. These seasonal changes account for the significant, albeit weak, positive regression of faecal %N on %C₄ variations in elephant diet described earlier (Fig. 4.5d). Interestingly, whereas shifts between wet season months were abrupt and generally significant ($P < 0.05$), following the sharp decline in faecal %N after April there were no further significant changes through the dry season ($P = 0.35$ to 1.00). Only after October, i.e. in the early rainy season, did faecal %N show an abrupt increase from $1.3\% \pm 0.3$ to $1.7\% \pm 0.4$ in November ($P < 0.0001$). At a regional scale, faeces from southern regions had higher means than those from northern regions ($P < 0.01$), but the differences were small (means ranged from 1.7% to 1.8 in southern regions, and were 1.6 for all northern regions; Table 4.2).

At first glance, no significant effects of any of the five environmental variables (rainfall, temperature, %C₄ intake, faecal %N, and $\delta^{15}\text{N}$ of available vegetation) tested on faecal $\delta^{15}\text{N}$ variations were found (R^2 ranged from 0.0 to 0.05, P from 0.07 to 0.78). However, six groups were found to have means well below the average (3.2‰ or lower, when all other groups had means of 3.8‰ or higher), and had a high degree of residual variance from all of the regression lines (σ -level = 3). Removal of these samples, which were randomly scattered throughout the dataset (5 regions and 3 months were represented in these samples), from the analysis, revealed some interesting trends that could help explain functional mechanisms for variations in faecal ^{15}N -abundance in this species. In these analyses, both temperature ($R^2 = 0.16$, $P < 0.001$) and %C₄ in diet ($R^2 = 0.13$, $P < 0.001$) showed a significant, negative exponential regression on faecal $\delta^{15}\text{N}$ variations. Rainfall also had a negative effect on faecal $\delta^{15}\text{N}$ ($R^2 = 0.05$, $P < 0.05$), but model selection based on AIC_c revealed that the exponential decay model as a function of temperature (44% likelihood), and %C₄ in diet (10% likelihood), are most well-supported by these analyses (Table 4.3).

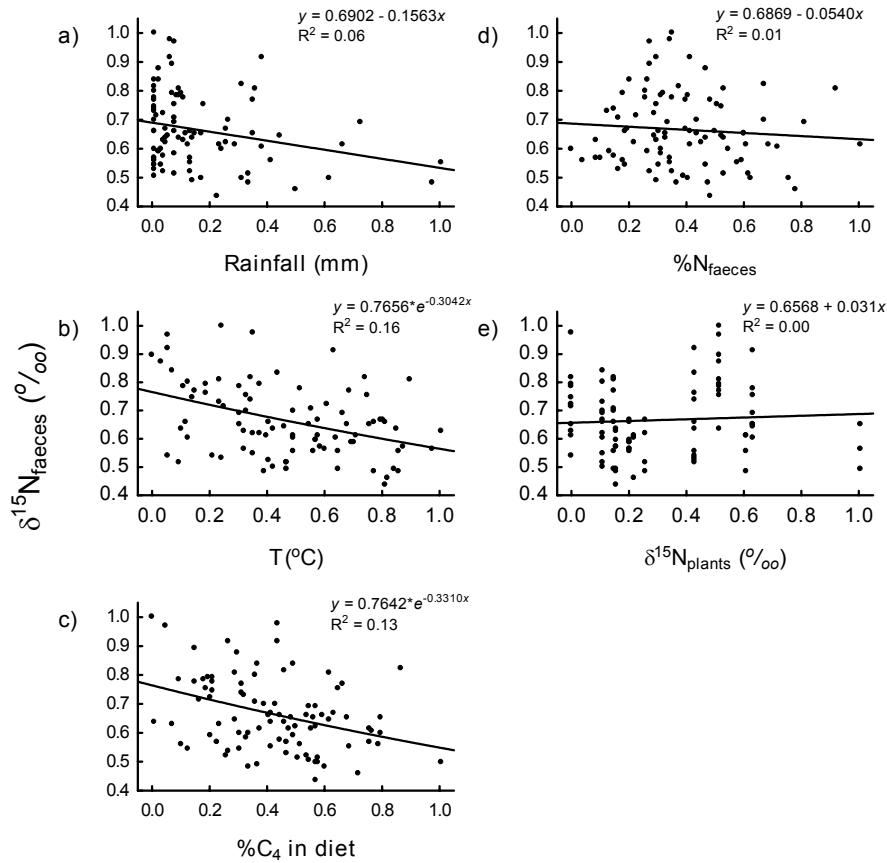


FIGURE 4.7. – Best-fit (see Table 4.3) regression models for variations in elephant faecal $\delta^{15}\text{N}$ as a function of a) rainfall; b) temperature; c) $\%C_4$ grass consumption; d) diet quality ($\%N$ of faeces); and e) variations in $\delta^{15}\text{N}$ of available vegetation. Symbols are means per month per region. Models exclude residual outliers at σ -level 3 ($n = 6$). Model a) is significant at $P < 0.001$; b) and c) have $P < 0.001$; d) $P = 0.44$; and e) $P = 0.58$.

4.3.5. Tail Hairs

Stable isotope profiles along tail hairs varied substantially within individuals, by as much as 3.3 to 7.9‰ for $\delta^{13}\text{C}$ (Fig. 4.8), and 0.8 to 6.6‰ for $\delta^{15}\text{N}$ (Fig. 4.9). While the majority of $\delta^{13}\text{C}$ observations fell within the range between -19 and -21‰, values as high as -16.0‰ were recorded, forming a C_4 grazing “peak” evident within each of the hairs analyzed. Thus, it appears that the chronological record archived in hairs record diet shifts through the seasonal cycle. This

assertion is supported by the fact that 15 of the 20 $\delta^{13}\text{C}_{\text{hair}}$ profiles corresponded well with monthly variations in mean $\delta^{13}\text{C}_{\text{faeces}}$ for represented regions (Spearman's R ranged from 0.62 to 0.90, $P < 0.05$ to < 0.001). In fact, in four of the five cases where the $\delta^{13}\text{C}_{\text{hair}}$ with $\delta^{13}\text{C}_{\text{faeces}}$ correlations were not significant, relatively high R values persisted (0.35 to 0.55), and the lack of statistical significance was probably due to the low number of observations for these individuals ($n = 9$ to 14).

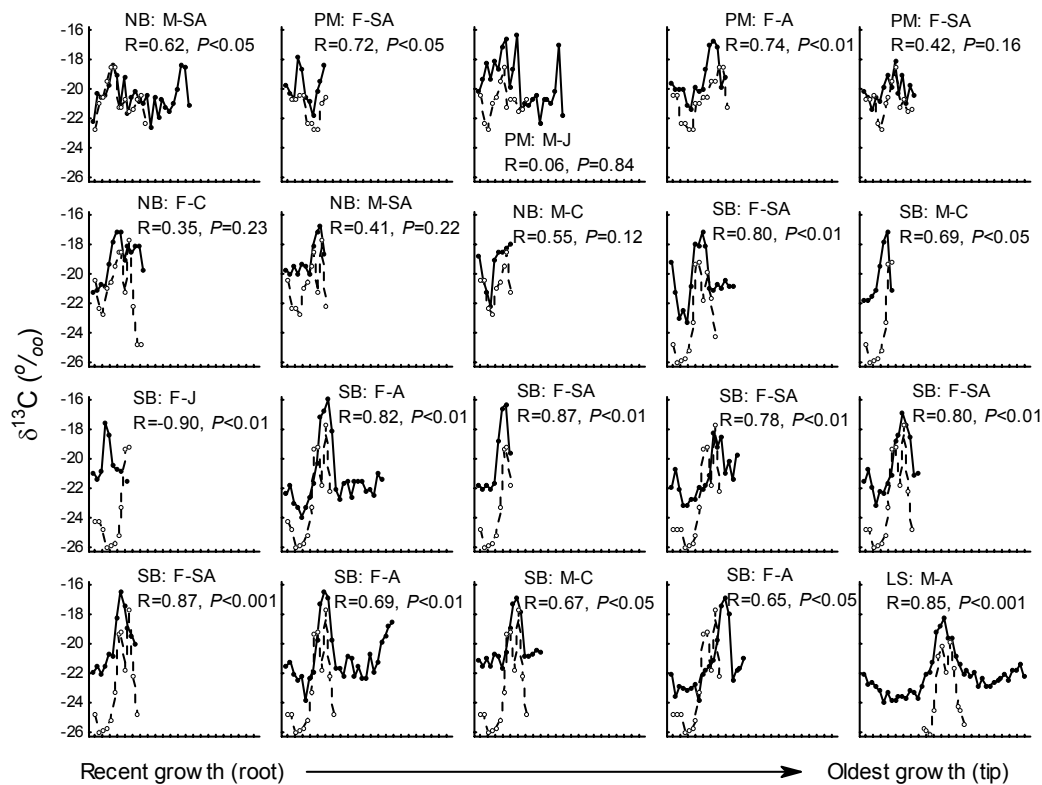


FIGURE 4.8. – $\delta^{13}\text{C}$ profiles along individual elephant tail hairs (solid circles, solid lines) sampled at 10 mm intervals from root to tip, compared with mean faecal $\delta^{13}\text{C}$ values (open circles)

By contrast, $\delta^{15}\text{N}_{\text{hair}}$ profiles for 19 of the 20 individuals samples did not correlate well with changes in $\delta^{15}\text{N}_{\text{faeces}}$ (R ranged from 0.02 to 0.54, $P = 0.13$ to 0.91), indicating that different mechanisms regulate ^{15}N -abundance variations in hairs compared with those in faeces.

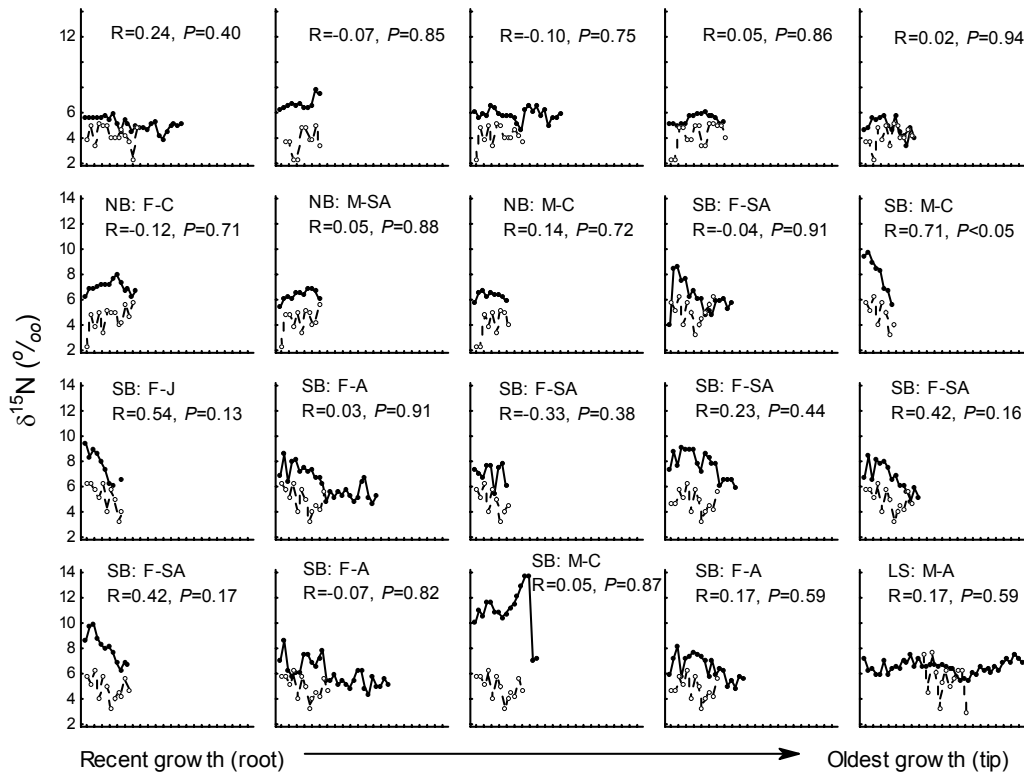


FIGURE 4.9. – $\delta^{15}\text{N}$ profiles along individual elephant tail hairs (solid circles, solid lines) sampled at 10 mm intervals from root to tip, compared with mean faecal $\delta^{13}\text{C}$ values (open circles, dotted lines) for each month. Hair and faeces profiles are compared using Spearman's Rank correlation co-efficient for non-parametric data distributions. Key: NB = northern basalts; SB = southern basalts; PM = Punda Maria, LS = Lion Sands Reserve; M = male; F = female; A = adult; SA = sub-adult; J = juvenile; C = calf.

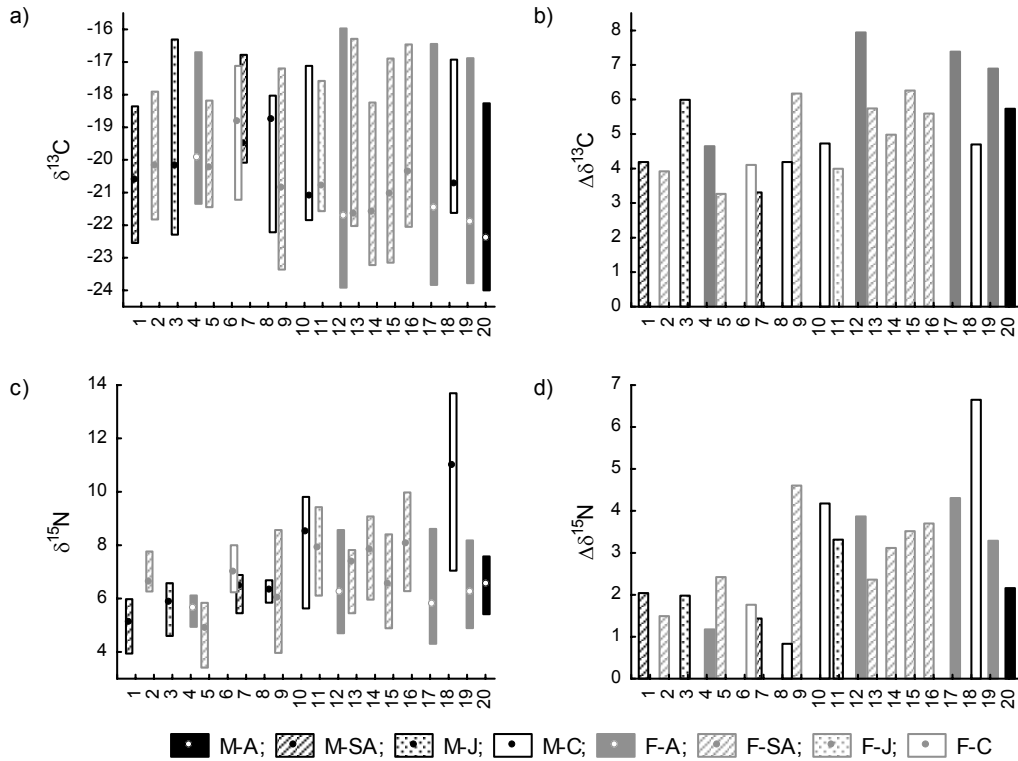


FIGURE 4.10. – Comparison of $\delta^{13}\text{C}$ (a, b) and $\delta^{15}\text{N}$ (c, d) ranges (minimum-maximum = $\Delta\delta$) along elephant hair profiles between individuals. Medians (symbols), minima and maxima (columns) are shown in a) and c); ranges are shown in b) and d). Individuals 1 to 8 are from northern Kruger Park, 9 to 20 from the southern regions. M = male; F = female; A = adult; SA = sub-adult; J = juvenile; C = calf.

Comparisons of hair isotope profiles between individuals, using both the resampling method and Kruskal-Wallis tests revealed very few differences between individuals (Fig. 4.10). From $\delta^{13}\text{C}$ resampling iterations, only 3.7% of all comparisons yielded a 95% probability of significant differences at the 0.5‰ level; doubtless this figure would decrease even further if the subject of these tests was set at 1.0‰. Medians for $\delta^{13}\text{C}$ of each individual were quite similar (Fig. 4.10), so that significant differences were only found for individual UCT 10854 from Sabie Sands reserve, which had higher $\delta^{13}\text{C}$ values compared with northern and some southern Kruger

Park hairs ($P < 0.05$), and one individual from the southern Kruger Park had higher $\delta^{13}\text{C}$ compared with four of the eight northern individuals ($P < 0.05$). Intra-individual differences in $\delta^{15}\text{N}$ were slightly more pronounced. The resampling iterations revealed that 16% of all comparisons had a 95% probability of significant differences at 0.5‰, and four of the northern Kruger Park individuals had significantly lower medians compared with southern animals (Kruskal-Wallis $P < 0.01$).

Based on findings from faeces, i.e. that isotopic and dietary changes between habitats are due mainly to differences in seasonality within habitats, the lack of multiple significant differences between elephant tail hairs from different individuals is not really surprising. More important to these data are the ranges (seasonal shifts) in values recorded within each hair. Thus, similarly to $\delta^{13}\text{C}$ trends in faeces, northern Kruger Park elephants showed smaller temporal variations in $\delta^{13}\text{C}$ within hair strands (by magnitudes of 4.2‰ on average) compared with southern individuals (5.7‰ on average) (Figs 4.10a & b). In terms of sex-based differences, female individuals varied more in $\delta^{13}\text{C}$ than did males (by magnitudes of 3.3 to 7.9‰ compared with 3.3 to 6.0‰, respectively), but males showed higher $\delta^{15}\text{N}$ variations (0.8 to 6.6‰) than did females (1.2 to 4.6‰) (Figs 4.10c & d). Ranges of variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were similar for calves, juveniles, sub-adults, and adults.

4.4. Discussion

4.4.1. Space/time Diet Shifts: A Complexity of Complexities

Carbon isotope data from faeces, supported by evidence from tail hair profiles, show that elephant diets can change significantly through the seasonal cycle, and across different habitats, even within a single savanna region such as Kruger Park. Though these effects agree with most predictions, quantifying and tracking these changes over the diversity of spatio-temporal scales included here is virtually impossible using traditional techniques. Typically, elephant diet studies would be limited to single habitats, and perhaps single herds if seasonality formed part of the

objectives, leading to disparate interpretations (see Owen-Smith 1988). For example, findings of different studies differ as to whether dry-to-rainy season shifts to increased grass intake occur at the start, middle, or end of the rainy season (Field 1971; Wyatt & Eltringham 1974; Laws et al. 1974; Williamson 1975; Guy 1976; Barnes 1982; van der Merwe et al. 1988; Skinner & Smithers 1990; Bowland & Yeaton 1997; Babaasa 2000; Stokke & du Toit 2000; Styles & Skinner 2000; Holdo & McDowell 2004). The current study covers the full seasonal cycle at monthly resolution, and results show that elephant diet shifts can occur during both the early and late parts of the wet season. Elephants were found to increase consumption of C₄ grasses at the onset of the rainy season (October/November), followed by a slight decrease in January and February, and then by a second increase at the end of the wet season (March). However, while gradual dry-to-rainy season diet shifts were consistent throughout, the dual-edged grazing peak described here only persisted in the four southern Kruger Park habitats included here. Thus, not only are seasonal switches evident in these data, but also the inconsistency here provides some indication of the effects of different habitat types on elephant diet.

Dietary differences between elephants from different habitats of Kruger Park have been documented in two previous carbon isotope studies, both using faeces, separated by >15 years (Vogel et al. 1990a; Codron et al. 2006; see also Codron 2004). Both studies found that faecal $\delta^{13}\text{C}$, and hence %C₄ grass consumption, was higher in northern compared with southern Kruger Park habitats. In the current study, the overall north-south difference in mean %C₄ grass intake (43 and 40%, respectively) was too small to represent a significant change. However, both these and data presented in Codron et al. (2006) for 2002 and 2003 show that regional dietary differences are related to differences in seasonality between these two regions. Switches in %C₄ grass intake were significantly greater through the seasonal cycle in the south, whereas there was a relative degree of stasis in the north. In fact, the monthly variation in southern elephant %C₄ intake extended to minimum and maximum values well below and above, respectively, the range of variation found in the north. Thus, during wet season months there were very few, if any,

differences in %C₄ grass consumption between habitats, but as resources presumably became more limiting through the dry season, the effects of habitat on diet became more pronounced, with elephants in southern habitats progressively eating less grass than those in northern habitats. Interestingly, one southern habitat, the south central basalts, seemed to have a similar effect on diet compared with most northern regions, with elephants here eating significantly more C₄ grass than those on other southern landscapes. Principal Components Analysis of these data confirmed that south central basalts elephants have different diets compared with other southern counterparts; yet seasonal diet variability here was still greater than in the far northern regions, so that this region is also distinct from most of the northern regions.

Therefore, elephant diets can be said to be a ‘complexity of complexities’. Habitat effects appear small and/or negligible, unless viewed in the context of seasonal (and perhaps other sources of intra-regional) variations. Indeed, seasonality in diet is widely held as an important factor regulating herbivore population dynamics (Demment & Van Soest 1985; Own-Smith 1994), as well as the evolution of species, with emphasis placed on the importance of fallback foods and critical feeding periods (Vrba 1995; du Toit 2003). My argument for “complexity” could appear non-parsimonious, but this viewpoint is well illustrated in contemporary theory on trophic differentiation at community levels. In many instances, authors have suggested that similarities between pairs or groups of species are so strong that these taxa should be considered ecologically redundant (Lawton & Brown 1993). Yet, long-term studies have shown that ‘redundant’ taxa will often display functional divergence in response to environmental changes (reviewed in Brown et al. 2001). I suggest the data presented here demonstrate that such heterogeneous response-linked trophic differentiations can also be found at the intra-species level, at least in generalist mixed-feeders like elephants. What remains is to determine whether such differentiation is a function of habitat, or of ecological idiosyncrasies at the population level. For example, if the former were the case, one might predict that northern Kruger Park elephants would adapt their dietary behaviour if faced with the same environmental conditions experienced

by their southern counterparts. On the other hand, elephant populations are known to develop distinctive dietary habits that persist even following translocation across habitats, such as has been found for elephants translocated from Kruger Park to the winter rainfall, coastal Afro-montane forests of Knysna in the southern Cape Province (Seydack et al.2000).

The spatial resolution of diet presented here for Kruger Park elephants offers some insight about regions in which impacts on woody vegetation are likely to be higher. For example, elephants in the southern regions likely place a more consistent browsing pressure on the woody vegetation than their northern counterparts. Whyte (2001) proposed that elephants in Kruger Park be managed on the basis of “high impact” and “low impact” zones. He suggested that four zones be demarcated, two in which elephant populations would be allowed to increase naturally, and two in which populations would be managed (culled) to limit impacts on woody plants. These zones, two in the north and two in the south, would be separated along a latitudinal gradient, but the boundaries are only loosely based on changes in vegetation composition and elephant movement patterns. The pattern of spatial heterogeneity in elephant diets revealed in the current study is somewhat different, and suggests that, although there are diet shifts from north to south, such a division is over-simplistic (see Fig. 4.4). I suggest that better-informed management decisions should be based on our ability to predict variations in feeding ecology (and impacts on plant populations). In the next section I discuss evidence for mechanistic links between diet selection and habitat condition.

4.4.2. Responses to Environment: Selecting Browse and Grass

From these analyses, it appears that elephant diets are primarily a function of the abundance and nutritional value of available grass. The relationship between C₄ grass consumption with rainfall implies that diet is primarily a function of productivity of the grass layer, since rainfall is an important driver of soil fertility, grass regeneration, and grass productivity (e.g. Tainton 1999). Indeed, herbivore population dynamics are thought to be

regulated by the limiting effects of rainfall on primary productivity (Coe et al. 1976). Although this hypothesis has been criticized because it considers only a single variable, and other factors such as soil nutrient status are more important at least to some feeding guilds (see Fritz et al. 2002), long-term rainfall variations have been shown to be the primary driver of herbivore population trends in Kruger Park (Owen-Smith & Ogutu 2003). In terms of diet, several studies have suggested that grass consumption varies independently of rainfall patterns, despite that seasonal rainfall trends are an important driver of soil fertility, grass regeneration, and grass productivity (McCullagh 1969a; Laws et al. 1974; Short 1981; Koch et al. 1991; Steyn & Stalmans 2001; Codron, D. et al. 2006). More recently, it has been shown that climate contributes significantly to the improvement of herbivore population growth models, based on the density-dependent effects climate imposes on food availability and hence fecundity (Hone & Clutton-Brock 2007). That rainfall was the best predictor of diet in the current study supports that elephants do respond to primary productivity of the grass layer, but clearly other factors are also playing a role.

The shape of the relationship between elephant diet with rainfall is intriguing, in that the best-fit of the models used here is the asymptotic function. Similar responses are well known for herbivores in terms of relationships between intake rate with food abundance, i.e. the Type II functional response (Spalinger & Hobbs 1992). While the functional response describes intake as units of food consumed per time interval, the implication here is that similar responses could be manifest over broader landscape scales when intake is described by the relative proportions in which certain food items (e.g. C₄ grass) are consumed. It is unclear, however, whether any asymptotic effect for elephants feeding on grass over such a wide range of rainfall regimes can be ascribed either to an environmental or a physiological constraint. A physiological limit to grass intake for elephants seems unlikely because i) there are several instances in which Kruger Park elephants consumed substantially more grass than the upper limit of ~50% predicted by the model used here (see Fig. 4.5a); and ii) elephant diets in other regions can comprise as much as 98%

grass (Wing & Buss 1970). Environmental constraints seem more plausible since i) diet is probably a function of several factors other than rainfall alone; and ii) the elephants studied by Wing & Buss (1970) were from tropical East African habitats where grass productivity and nutritional value is greater than is generally encountered in subtropical savannas.

Percent C₄ grass intake also increased with increases in grass nutritional (N) content, although here the relationship appeared to be exponential. But an upper limit to grazing as a function of grass nutritional value cannot be ruled out here, because available data for grass %N are incomplete, largely representing biannual rather than monthly trends. Further, changes in plant quality should be described in terms of both nutrient content and digestibility (e.g. Van Soest 1994); it is unclear what effects digestibility data would have had on the relationship between elephant grass intake with grass quality (but see below). Nonetheless, these results, combined with the effects of rainfall, support hypotheses that elephants are preferentially grazers, and will continue to graze provided a large quantity of grass is available (Guy 1976; Norton-Griffiths 1979; Tangley 1997). Indeed, elephant molar teeth appear to have retained a high-crowned form (hypsodont), which suggest adaptation to an abrasive grazing diet (Janis 1988; Owen-Smith 1988; Cerling et al. 1999). According to Guy (1976), elephants have not been forced by environmental changes to become grazers, but have always been grazers. Wing & Buss (1970) theorized that in grassland environments where browse production is below a certain threshold, elephants may even over-utilize available grasses.

Some authors have speculated that elephants are primarily browsers, and only graze in the absence of suitable browse (Jachmann & Bell 1985; Dublin 1995). These assertions are not supported here, because in Kruger Park, C₄ grass intake by elephants increased with increases in %N of available grass, and also (weakly) with the %N of available C₃ browse. Thus, when the nutritional quality of both resources was high, elephants favoured grass, and/or did not respond to browse availability at all. Further, the pattern of higher faecal %N associated with increased C₄ grass intake suggests that elephants obtain more nutritional value from a grass-based rather than a

browse-based diet. It is likely that, because of their bulk intake, elephants that browse consume substantial amounts of low quality foods such as bark and old leaves; they are simply unable to select the most nutritious plant parts, as do smaller browsers like kudu and steenbok *Raphicerus campestris* (Owen-Smith & Cooper 1989; du Toit 1993; Owen-Smith 1994). When nutritious grasses are available, such as during the wet season or around artificial waterholes, these are available in bulk, hence grazing elephants likely consume a higher proportion of high quality foods than when they browse.

The hypothetical browsing elephant is expected to eat (and destroy) a higher proportion of woody vegetation in more densely wooded areas (e.g. van der Merwe et al. 1990; Scholes et al. 2003). Results of the current and previous study (Codron 2004; Codron et al. 2006) do not support this prediction, and several other authors have made similar remarks (Wing & Buss 1970; Williamson 1975; Short 1981; Babaasa 2000; Seydack et al. 2000; Styles & Skinner 2000). The northern landscapes of Kruger Park have a higher tree leaf:grass ratio than do southern regions (Scholes et al. 2003; Venter et al. 2003), yet northern elephants did not switch to near-pure browse diets during the during season months, as did their southern counterparts. Similarly, there were no consistent differences in diet between granite- and basalt-based habitats, despite that granitic landscapes are more woody-plant dominated compared to basaltic landscapes, which are more productive in terms of grass layer and grazing herbivores (Naiman et al. 2003). Elephants from Punda Maria, the forested savanna of the far northern Kruger Park, consumed more C₄ grass than those in all other habitats, except on northern basalts, but the Punda Maria sample is too small for making conclusions based on meaningful statistical comparison.

A relationship between diet and availability of browse species is, by contrast, well-supported by these analyses. Relationships between diet with rainfall and grass %N both improved substantially with the inclusion of presence or absence of mopane (see Table 4.3); these results supported an increase in %C₄ grass intake when mopane was present. Mopane is a tree species often expected to be favoured by browsing herbivores including elephant (e.g. van Wyk

& Fairall 1969; Viljoen 1989; Skinner & Smithers 1990; De Villiers et al. 1991; Lewis 1991; Smallie & O'Connor 2000). However, some studies have suggested that mopane may deter browse consumption by elephants and other herbivores, because of its high indigestible cell wall (primarily lignin) and phenolic content (Styles & Skinner 2000; du Toit 2003; Codron 2004; Codron et al. 2006). In the northern Kruger Park, the woody vegetation is almost entirely dominated by mopane (Venter et al. 2003), hypothesized to be related to reductions in functional habitat heterogeneity that have characterized changes in these landscapes over recent decades (Kröger & Rogers 2006; see also Grant et al. 2002; Gaylard et al. 2003). Such homogenization of available browse could explain why elephants in northern Kruger Park habitats do not switch to browsing in the dry season. It is known that browsers must consume a wide variety of species to avoid ingesting toxic, or even lethal, doses of single-species secondary compounds (Freeland & Janzen 1974; Cooper & Owen-Smith 1985; Freeland et al. 1985). Similar browse-avoidance effects in homogeneous woody landscapes have been postulated for elephants feeding in *Brachystegia* woodlands, such as the Kasungu National Park, Malawi (Jachmann & Bell 1985; van der Merwe et al. 1988). Also, detergent fibre analysis of vegetation samples from Kruger Park does imply lower fibre digestibilities amongst browse from northern (mostly mopane) compared with southern habitats (Codron, D. et al. 2007c). To conclude, while variations in browse/grass consumption by elephants are driven primarily by changes in productivity of the grass layer, attention should also be given to patterns of diversity amongst available woody plant species.

4.4.3. Evolutionary Considerations

Despite the conclusion that elephants prefer grass as a resource above browse, they are largely C₃-browsers in most African savanna environments (Cerling et al. 1999). It is unlikely that most African savanna environments do not support sufficiently productive grasslands for elephants to maintain a grass-based diet. Some insights can be gleaned from elephants in the

fossil record. Stable carbon isotope evidence has revealed that elephants and their ancestors only switched from a presumed C₃ browsing diet to a C₄ grass-based diet after the radiation of C₄-grasslands in Africa between ca. 5 and 7Ma. (Owen-Smith 1988; Cerling et al. 1999, 2005). Yet, some time after 1 Ma., most proboscidean taxa reverted to a predominantly C₃-based browse diet, similar to the situation across Africa today (Cerling et al. 1999). The timing of this shift is uncertain but a Mid-Late Pleistocene elephant tusk specimen from Reunion Rocks on the east coast of South Africa shows a $\delta^{13}\text{C}$ value consistent with C₃-feeding (Lee-Thorp & Sponheimer 2003). A major mammal turnover event occurred around 1.1 Ma, as the global climate changed and entered into the high amplitude fluctuations of more than 20 glacial-interglacial cycles that characterized the second half of the Pleistocene (Vrba 1995). It is possible that these changes led to periodic reductions in grass productivity and/or availability for elephants, although no evidence exists for such a reduction. Conversely, the global shift after ca 1.0 Ma has been associated with a loss of woody vegetation and progressive opening of landscapes in many parts of southern Africa (Brink 1987). Elephants would have been unable to cope with the loss of trees, which they require at least for shade (Skinner & Smithers 1990) if not as a supplementary food base. They may then have been forced to utilize savanna woodlands where grass productivity had been lowered by climate-related stresses (such as reported here for the northern in Kruger Park) and focused more on browsing. Competition with sympatric grazers, especially the multitude of megagrazers (e.g. *Megalotragus* spp., *Equus capensis*, and *Homoioceras antiquus*) that dominated southern African landscapes until the terminal Pleistocene (e.g. Gentry 1978; Brink 1987; Vrba 1995), may also have played a role. It has already been demonstrated that competition with bulk-grazers can force elephants to switch from grazing to browsing, because they cannot access the short grasses that result from overgrazing by species such as buffalo (Van de Koppel & Prins 1998). Further evidence for elephant palaeoecological responses to Pleistocene environmental changes is needed.

4.4.4. Environmental Controls on $\delta^{15}\text{N}$

Faecal $\delta^{15}\text{N}$ decreased as a function of climate (especially increased temperature) and diet (%C₄ intake). The relationship with diet is likely the result of multicollinearity in these predictor variables (rainfall and temperature), given the strong relationship found between %C₄ intake with increasing rainfall, which in turn covaries, at least seasonally, with temperature in southern African savannas. High $\delta^{15}\text{N}$ in arid, cool conditions, and decreases with reductions in aridity and/or increased temperature, have been reported for numerous studies based on body tissues of large mammal herbivores, including African elephants (e.g. Heaton et al. 1986; Sealy et al. 1987; Ambrose 1991; Cormie & Schwarcz 1996). Climate controls on mammalian ^{15}N -abundances are ascribed primarily to water conservation mechanisms, and the urea mass-balance model of Ambrose & DeNiro (1986). This model is based on the fact that urea is ^{15}N -depleted relative to diet (whereas faeces are ^{15}N -enriched), and thus body tissue (and faecal) $\delta^{15}\text{N}$ should change depending on the proportion of N lost in urea to that lost in faeces (see also Ambrose 1991; Sponheimer et al. 2003a). Under water and/or heat-stressed conditions, herbivores increase kidney osmolality as they attempt to retain more water in the blood, thus the concentration of N (^{15}N -depleted) lost via urine increases, and the body ^{15}N pool increases relative to this exchange. Because faecal N is derived from the same nutrient pool as body tissue N, faecal $\delta^{15}\text{N}$ responses to climate should exhibit similar patterns of variation to that observed in body tissues (Codron, D. et al. 2005b). Although relationships between elephant faecal $\delta^{15}\text{N}$ with climate were weak ($R^2 = 0.06$ and 0.16 for effects of rainfall and temperature, respectively), they were significant at $P < 0.05$ after a handful of residual outliers were omitted from the analysis ($n = 6$). Thus, it can be concluded that climate does have a significant effect on faecal ^{15}N -abundance variations in elephants. The low coefficients of determination and relatively high residual scatter in these regression models indicate other sources of variation. One factor might be the N in faeces derived from non-dietary sources, i.e. gut microbes and epithelial tissue (Van Soest 1994; Sponheimer et al. 2003c), but these effects will prove difficult to account for.

There was no significant relationship between faecal $\delta^{15}\text{N}$ with changes in diet quality (faecal %N). This result is unexpected, since N intake is thought to be the main factor responsible for mammalian ^{15}N -abundance variations (Robbins et al. 2005), and forms a major component of the urea mass-balance model, as well as the urea-faeces mass-balance model (which accounts for N loss in faeces when dietary N levels are low) proposed by Sponheimer et al. (2003c). Typically, herbivores consuming protein rich diets, and/or diets in which the metabolizable value of the proteins is high, will also increase N loss via urea, and thus display higher body $\delta^{15}\text{N}$ values (Ambrose 1991; Roth & Hobson 2000; Sponheimer et al. 2003c; Robbins et al. 2005). Similarly, increases in faecal $\delta^{15}\text{N}$ associated with increased dietary protein content (faecal %N) have previously been described for mammal herbivores from southern African savannas at inter- and intra-species levels (Codron, D. et al. 2005c; Codron & Brink 2007). Perhaps elephants, because of bulk intake, their large body size, and their hindgut fermentation system, do not need to regulate kidney osmolality in response to dietary protein levels, because they perform equally well on low and high quality diets (Owen-Smith 1988; Gordon & Illius 1996).

The lack of relationship between elephant faecal $\delta^{15}\text{N}$ with faecal %N supports the argument above, and the AIC_c results shown in Table 4.3, that climate rather than diet underlies patterns of $\delta^{15}\text{N}$ variation. Had diet had a more important effect, one would have expected a stronger relationship of $\delta^{15}\text{N}$ with %N of faeces, given that %C₄ intake correlated well with both climate (rainfall) and faecal %N. Thus, whether urea mass-balance or some other mechanism is important here, it is clear that physiological processes that lead to ^{15}N fractionations within elephants are related to climate, so that climatic shifts lead to changes in $\delta^{15}\text{N}$. It is predicted, therefore, that $\delta^{15}\text{N}$ responses to climate (especially 20th century temperature changes) will also be evident in long-term records from elephant ivory.

4.5. Conclusion

In this chapter, I have presented a large, statistically robust dataset that provides important insights and advances into elephant ecological dynamics. Records of stable isotope analyses from faeces and tail hairs are congruent, thus a solid baseline has been laid for understanding changes in elephant diets over the long term. For example, shifts between C_3 or C_4 consumption cannot be interpreted simply as a response to changes in the availability of browse and grass, but rather to seasonal changes in productivity of the grass layer. In the following chapters, I explore isotope records from elephant ivory to reconstruct long-term historical records of diet, and draw from results of this chapter to elucidate possible mechanisms underlying perceived diet shifts in the past.

TABLE 4.1. – Stable carbon and nitrogen isotope composition of Kruger Park vegetation used as baseline data for this chapter (data from Chapter 3).

Region/ time	C₃ tree foliage/forbs					C₄ grass				
	<i>n</i>	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)		$\delta^{15}\text{N}_{\text{Air}}$ (‰)		<i>n</i>	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)		$\delta^{15}\text{N}_{\text{Air}}$ (‰)	
		Mean	S.E.	Mean	S.E.		Mean	S.E.	Mean	S.E.
NB										
Yr1 dry	6	-26.4	0.30	6.0	0.15	7	-12.7	0.32	4.7	0.28
Yr1 wet	9	-26.0	0.37	4.9	0.81	6	-12.3	0.21	5.5	0.37
Yr2 dry	8	-25.9	0.32	5.6	0.51	15	-12.9	0.11	3.8	0.44
Yr2 wet	11	-25.9	0.29	5.5	0.46	17	-12.3	0.22	4.6	0.59
Yr3 dry	40	-26.7	0.17	5.1	0.40	59	-13.4	0.12	3.6	0.33
Yr3 wet	37	-25.5	0.21	3.3	0.36	55	-13.2	0.13	2.7	0.30
NG										
Yr1 dry	13	-26.3	0.27	3.0	0.32	28	-12.2	0.34	1.6	0.17
Yr1 wet	12	-25.8	0.33	2.9	0.26	17	-12.0	0.17	2.7	0.38
Yr2 dry	11	-26.0	0.22	2.8	0.25	16	-12.4	0.23	1.4	0.27
Yr2 wet	20	-26.9	0.24	3.4	0.19	21	-12.2	0.17	3.4	0.34
Yr3 dry	24	-27.3	0.21	3.6	0.34	15	-12.9	0.15	1.5	0.35
Yr3 wet	15	-25.2	0.26	3.4	0.27	9	-14.0	0.30	2.8	0.58
PM										
Yr2 dry	16	-26.5	0.23	3.2	0.41	19	-12.3	0.09	1.9	0.31
Yr2 wet	27	-27.2	0.20	3.2	0.56	20	-12.0	0.21	2.5	0.35
SB										
Yr1 dry	68	-27.0	0.18	2.2	0.26	40	-11.2	0.25	1.1	0.12
Yr1 wet	40	-26.4	0.22	3.2	0.20	35	-12.9	0.14	2.6	0.19
Yr2 dry	62	-26.4	0.20	3.1	0.28	50	-11.3	0.15	1.5	0.25
Yr2 wet	65	-26.7	0.16	3.7	0.19	56	-12.5	0.08	2.7	0.19
Yr3 dry	50	-28.0	0.18	2.6	0.23	44	-13.2	0.08	2.0	0.18
Yr3 wet	61	-26.5	0.14	3.2	0.21	40	-13.9	0.08	2.4	0.14
SG										
Yr1 dry	49	-26.2	0.22	4.1	0.37	42	-12.1	0.17	3.3	0.20
Yr1 wet	46	-26.6	0.16	5.1	0.40	34	-12.4	0.09	5.5	0.45
Yr2 dry	53	-26.2	0.20	5.4	0.35	42	-11.6	0.14	4.2	0.32
Yr2 wet	47	-26.7	0.14	6.5	0.34	23	-12.6	0.14	7.1	0.46
Yr3 dry	49	-27.4	0.17	5.5	0.30	33	-13.3	0.16	3.2	0.46
Yr3 wet	55	-26.9	0.12	5.3	0.28	42	-14.1	0.14	4.7	0.24

n = number of samples; S.E. = standard error; NB = northern basalts; NG = northern granites; PM = Punda Maria; SB = southern basalts; SG = southern granites; Year 1 = June 2002 - May 2005; Year 2 = June 2003 - May 2004; Year 3 = June 2004 - May 2005; dry season = April to September; wet season = October to March

TABLE 4.2. – Stable carbon and nitrogen isotope composition, and %N, of elephant faeces collected over three years from Kruger National Park. Percent C₄ grass in the diet was estimated from faecal δ¹³C using a dual-mixing model.

Region	n	δ ¹³ C _{VPDB} (‰)		%C ₄ in diet			δ ¹⁵ N _{Air} (‰)		%N		Source
		X	SD	X	CV	Range (X _{monthly})	X	SD	X	SD	
Year 1											
NB	19	-20.8	2.7	45	41	30 to 58	4.7	0.9	1.5	0.4	1
NG	34	-22.0	3.0	36	59	31 to 40	4.8	0.8	1.2	0.3	1
SB	12	-25.6	1.4	15	62	13 to 41	3.5	1.4	1.2	0.4	1
SG	60	-24.1	2.6	22	89	8 to 44	5.1	1.4	1.5	0.6	1
<i>All north</i>	53	-21.5	2.9	39	52	36 to 41	4.8	0.8	1.3	0.4	
<i>All south</i>	72	-24.4	2.5	21	89	8 to 44	4.9	1.5	1.5	0.6	
Year 2											
NB	100	-20.7	2.0	46	33	34 to 53	3.6	1.5	1.3	0.4	1
NCB	11	-22.6	3.2	33	75	<i>na</i>	3.3	1.0	1.0	0.3	2
NG	11	-22.3	1.9	34	42	<i>na</i>	3.8	0.7	0.9	0.2	1
PM	17	-21.5	2.5	41	43	40 to 55	3.8	1.7	1.1	0.3	2
SB	3	-25.6	1.4	11	83	<i>na</i>	4.3	0.8	1.4	0.2	1
SCB	9	-23.5	3.3	25	88	<i>na</i>	3.9	1.0	1.0	0.2	2
SG	11	-25.4	2.6	12	143	<i>na</i>	3.4	0.7	1.2	0.2	1
<i>All north</i>	139	-21.1	2.3	44	39	33 to 75	3.6	1.4	1.2	0.4	
<i>All south</i>	23	-24.7	2.9	17	112	11 to 25	3.7	0.9	1.2	0.2	
Year 3											
NB	132	-21.3	2.1	44	33	29 to 61	4.5	1.8	1.6	0.5	2
NCB	110	-21.6	2.1	42	34	31 to 61	5.2	1.9	1.6	0.4	2
NCG	110	-21.6	1.7	44	27	34 to 51	5.3	1.2	1.6	0.4	2
NG	110	-21.9	1.7	40	31	27 to 54	4.9	1.1	1.6	0.4	2
SB	113	-22.9	3.1	38	54	19 to 71	4.9	1.4	1.8	0.3	2
SCB	103	-21.7	2.4	46	36	28 to 68	5.6	2.3	1.8	0.5	2
SCG	97	-22.6	2.5	41	44	24 to 64	5.2	2.5	1.7	0.5	2
SG	108	-23.4	2.5	34	52	15 to 62	5.6	1.9	1.8	0.4	2
<i>All north</i>	462	-21.6	1.9	43	32	27 to 61	4.9	1.6	1.6	0.4	
<i>All south</i>	421	-22.7	2.7	40	47	15 to 71	5.3	2.0	1.8	0.4	

n = number of samples; *X* = mean; *X*_{monthly} = max to min range in *X* between months; *SD* = standard deviation; *CV* = coefficient of variation; *na* = not applicable, only 1 month sampled; Source 1 = Codron *et al.* (2006), 2 = specimens collected for this study; Year 1 = June 2002, January 2003; Year 2 = June 2003 (February 2003 to January 2004 for NB); NB = northern basalts; NCB = north central basalts; NCG = north central granites; NG = northern granites; PM = Punda Maria; SB = southern basalts; SCB = south central basalts; SCG = south central granites; SG = southern granites; dry season = April to September; wet season = October to March.

TABLE 4.3. – Akaike’s second-order information criterion (AIC_c) for regression models of %C₄ in elephant diet as a function of rainfall, %N of available grass and browse foods, and diet quality (%N of faeces), and models of elephant faecal $\delta^{15}N$ as a function of maximum monthly temperature, rainfall, %N of faeces, and $\delta^{15}N$ of available vegetation.

%C ₄ in diet *					$\delta^{15}N_{faeces}$ **						
Model	K	R ²	AIC _c	ΔAIC_c	w_i	Model	K	R ²	AIC _c	ΔAIC_c	w_i
Rainfall + mopane (asy)	4	0.39	-374.08	0.00	0.90	T°C (exp)	2	0.16	-332.24	0.00	0.44
Rainfall (asy)	3	0.32	-367.41	6.67	0.03	T°C (lin)	2	0.16	-331.82	0.42	0.36
%Ngrass + mopane (lin)	3	0.31	-366.89	7.19	0.02	%C ₄ in diet (exp)	2	0.13	-329.20	3.04	0.10
%Ngrass (exp)	2	0.29	-366.88	7.20	0.02	%C ₄ in diet (lin)	2	0.12	-328.93	3.31	0.08
%Ngrass (lin)	2	0.27	-364.49	9.59	0.01	Rainfall (lin)	2	0.06	-323.58	8.66	0.01
%Nfaeces + mopane (lin)	3	0.29	-364.17	9.90	0.01	Rainfall (exp)	2	0.06	-323.58	8.66	0.01
Rainfall + mopane (lin)	3	0.24	-358.02	16.06	0.00	%N _{faeces} (lin)	2	0.01	-319.14	13.11	0.00
%Nfaeces (lin)	2	0.20	-356.66	17.42	0.00	%N _{faeces} (exp)	2	0.01	-319.12	13.12	0.00
Rainfall (lin)	2	0.20	-356.24	17.84	0.00	$\delta^{15}N_{plants}$ (lin)	2	0.00	-318.87	13.37	0.00
%Nfaeces (exp)	2	0.20	-356.06	18.02	0.00	$\delta^{15}N_{plants}$ (exp)	2	0.00	-318.87	13.38	0.00
Rainfall (exp)	2	0.17	-353.20	20.88	0.00						
%Nbrowse (lin)	2	0.11	-347.26	26.82	0.00						
%Nbrowse (exp)	2	0.11	-347.24	26.84	0.00						

lin (linear): $y = \alpha + Bx$; exp (exponential): $y = a \cdot e^{Bx}$; asy (asymptotic function): $y = (\alpha + Bx)/(1 + \alpha + Bx)$;
K = number of parameters in model; ΔAIC_c = strength of support (<2 = strongly supported model, < 10 = weakly supported model); w_i = Akaike weights (evidence ratio; likelihood of model being the best-fit among the candidate set); * = only models with realistic parameter estimates are shown (i.e. where parameter 95% confidence intervals exclude zero); ** = 6 observations below 0.4 (normalized value) had residuals above the 3- σ level, and were omitted from the analysis

- Chapter 5 -

Structure and Growth of Elephant Ivory

To use isotopic profiles in ivory to reconstruct past changes, an understanding of tusk morphology, and the sequence of dentine development, is required. This chapter describes the composition and accretion of dentine in mammal teeth, with emphasis on the incremental growth of dentine in African elephant ivory. The chapter includes a study of Kruger Park ivory, as well as observations on the morphology of tusks from Welgevonden Private Game Reserve, South Africa, and Etosha National Park, Namibia. The microscopic and radiocarbon dating methods used in this study for counting growth increments in elephant ivory and dating sequential microsamples are discussed.

5.1. Introduction

Mammal teeth are excellent archives of animal life history, because of their chemical and physical composition, and the incremental manner in which dentine and enamel are accreted (Schour & Hoffman 1939a; Takuma & Eda 1966; Klevezal' & Kleinenberg 1969; Schmidt & Keil 1971; Jones & Boyde 1984; Mjör 1984; Linde 1984; Koch 1989; Raubenheimer et al. 1990; Raubenheimer 1999; Fox & Fisher 2001). Teeth grow incrementally and continuously (throughout life in some species), providing an accurate record (“fingerprint”) of exposure to the environment at various stages of the animal’s life (Posner & Tannenbaum 1984; Koch 1989; Raubenheimer 1993). Moreover, the composition of tooth dentine remains stable and is not subject to turnover and remodeling after formation (Leicester 1949; Sognaes 1955; Boyde & Jones 1972; Butler 1984; Ericson 1985; Raubenheimer 1993; Sealy et al. 1995; Raubenheimer et

al. 1998a; but see Section 5.2.1). This is unlike bone, where processes of remodelling are ongoing (Leicester 1949; Sognaes et al. 1955; Boyde 1968; Butler 1984; Posner & Tannenbaum 1984).

Incremental growth layers in dentine and enamel of mammalian teeth have been studied since the early 1800s (Retzius 1837 in Schour & Hoffman 1939a; Owen 1840; Schour & Hoffman 1939a, 1939b; Laws 1952, 1962; Peabody 1961; Takuma & Eda 1966; Klevezal' & Kleinenberg 1969; Yilmaz et al. 1977; Mjör 1984; Ruch 1984). Early work on age determination using incremental growth in teeth (e.g. Scheffer 1950; Laws 1952) prompted a burgeoning interest in the structure and growth of the teeth of both marine (e.g. Hewer 1960, 1964; Laws 1962; Kenyon & Fiscus 1963; Ohsumi et al. 1963; Bow & Purday 1966; Klevezal' & Myrick 1984) and terrestrial mammals (e.g. Kingsmill 1962; Kraus & Jordan 1965; Klevezal' & Kleinenberg 1969; Newman & Poole 1974; Yilmaz et al. 1977; Molnar 1981; Jones & Boyde 1984; Linde 1984; Mjör 1984; Raubenheimer 1999; Raubenheimer et al. 1990, 1995). A significant portion of this research has focused on development, structure, chemical composition, and growth of the continuously growing upper incisor teeth (tusks) of modern (Perry 1954; Colyer & Miles 1957; Miles & White 1960; Miles & Boyde 1961; Elder 1970; Espinoza & Mann 1991; Raubenheimer 1993, 1999, 2000; Raubenheimer et al. 1990) and fossil proboscideans (Fisher 1987, 2001a, 2001b; Koch 1989; Koch et al. 1989; Espinoza & Mann 1991; Fox & Fisher 2001; Fisher & Beld 2002; Fisher & Fox 2003; Fisher et al. 2003; Fox et al. 2007; Rountrey et al. 2007).

The interest in proboscidean tusks is because ivory dentine is accreted in ordered layers consisting of annual and sub-annual (weeks to days) increments throughout the life of an animal that can live for more than half a century, and has been described in both fossil proboscidean (mammoth, mastodon, and gomphotheres) and extant Asian elephant tusks (Koch 1989; Fisher 2001a, 2001b; Fisher & Fox 2003; Fisher et al. 2003; Fox et al. 2007). Studies using ivory can therefore reveal changing environmental exposures at different life stages and at various time intervals, using methods based on elemental and stable isotope analyses (Raubenheimer 1993;

Prozesky et al. 1995; Fisher 2001a, 2001b; Fisher & Fox 2003; Fisher et al. 2003; Fox et al. 2007; Rountrey et al. 2007). This chapter describes the morphology and growth of dentine in proboscidean tusks, including a review on the nature and rate of dentinogenesis. Furthermore, the concept of a numerical hierarchy in African elephant ivory is more extensively investigated than has hitherto been reported for molar teeth (Koch et al. 1995) and tusks (Fisher 1996, 2001a) in this species, through examination of multiple growth records from the tusks of a total of 17 elephants from the Kruger National Park and the Welgevonden Private Game Reserve (WGR) in the Waterberg region of South Africa, and Etosha National Park, Namibia. Finally, approaches to study dentine development in these tusks (scanning electron microscopy, incident light microscopy, and accelerator mass spectrometry dating techniques) are described.

5.2. Morphology of the Elephant Tusk

The term “ivory” has conventionally been used to describe the dentine component in elephant (and other proboscidean) tusks. However, the chemical structure of all mammal teeth is the same regardless of species. The word “ivory” actually implies a mammalian tooth that has commercial value, and which is large enough to be carved (Espinoza & Mann 1991). Furthermore, all teeth have the same basic physical structure, i.e. a pulp cavity, dentine, cementum, and enamel, and comprise two parts: a crown protruding from the jaw, and a root embedded in the tooth alveolus (Klevezal' & Kleinenberg 1969; Sikes 1971).

The elephant tusk is an incisor that erupts at the age of approximately one year, following resorption of the tush (deciduous tooth) (Sikes 1971; Grzimek 1972; Raubenheimer et al. 1995; Raubenheimer 2000). The size of the tusk at any age is dependent on the sex of the individual (with males generally having much larger tusks in length and diameter than females), the chemical and physical properties of the tooth substance (Miles & Boyde 1961; Van Niekerk et al. 1991; Prozesky et al. 1995; Raubenheimer et al. 1998a, 1998b), and the rate of attrition and breakage of the tooth (related to chemical properties). It has also been suggested that genetic and environmental factors

may influence tusk size (Elder 1970; Hall-Martin 1982). Elephants are adept at using their tusks, e.g. for defense, digging for water, salt or roots, debarking trees, as a hoist or lever for manipulating heavy objects, for carrying new-born calves, or for assisting young elephants in danger (Eltringham 1982; Allen et al. 1984; Moss 1988; Forstenpointner et al. 2001; Weissengruber et al. 2005). Different tusk lengths in an individual distinguish between the “servant” (shorter) and the “master” (longer) tusks, thus elephants are perceived as being right or left “tusked”. A small percentage of elephants are ambidextrous in their tusk use, in which case the tusks are of similar length (Sikes 1971; Moss 1988).

The bulk of the tooth comprises dentine. In proboscidean tusks, an enamel ‘cap’ is initially present on the outer surface, but it quickly wears away, leaving the exterior surface coated only with a layer of “cementum” (Sikes 1971; Raubenheimer et al. 1995; see Fig. 5.1). Cementum is a mineralized, fibrous organic substance that, unlike dentine, has a similar composition and hardness to bone. This “hardness” is attributed to the presence of cementocytes (bone corpuscles) (Schour & Massler 1949). Cementum undergoes continuous appositional growth at the base of the tusk, but is abraded away in areas of the tusk (usually near the tip) that are exposed to mechanical, abrasive forces, e.g. during breaking off of branches, or digging for water or salt in soil (e.g. Raubenheimer et al. 1998b). In areas where cementum has been abraded, the tusk is weakened, and may fracture or break off (E.J. Raubenheimer 2007 pers. comm.). The “cementum-dentine junction” forms a topographical interface between the cementum and the underlying layers of dentine, or ivory (see Raubenheimer 1998a). The tip of the tusk is solid, while the root or base of the tusk (implanted in the skull) comprises a hollow, conical pulpal cavity that houses the nerve and vascular supply to the tooth (Raubenheimer 1998a).

“New” layers of dentine are accreted incrementally throughout the life of an elephant, along the interface between the pulp cavity and inner surface of the “old” dentine. This type of growth is referred to as “permanent” or “continuous” tooth growth, and is evident in the incisors of all proboscideans as well as in some smaller mammals (e.g. rodents and lagomorphs), in the

canines of animals such as walruses, warthogs, and hippopotamuses, and in all the teeth of odontocetes. In teeth with limited growth (e.g. human teeth), dentine accretion takes place only for a certain period of life and then ceases (Klevezal' & Kleinenberg 1969).

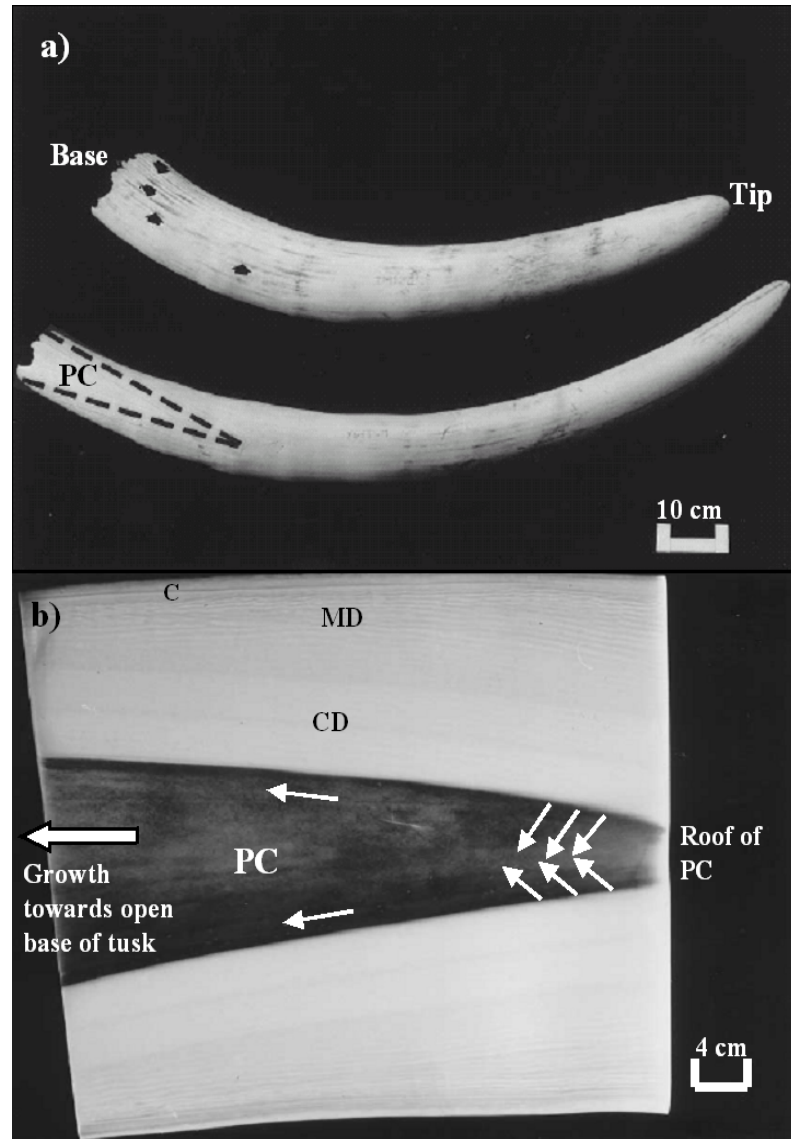


FIGURE 5.1. – Modern elephant tusks, showing a) the part comprising the hollow pulpal cavity (approximately one third of the tusk; black arrows and dotted line), and b) sagittal section through a tusk showing the conical shape of the pulpal cavity (PC), direction of dentine accretion (white arrows), and the relative positioning of the cementum (C), mantle dentine (MD), circumpulpal dentine (CD), and “roof” of the pulpal cavity. Schreger lines (dark and light wavy grooves) run parallel to the longitudinal axis of the tusk. Photographs adapted from Raubenheimer et al. (1998b).

Continuous growth in a tusk results in the tooth becoming elongated at its proximal end (the base), while the distal part (tip) is often worn down, broken, or damaged (see above; Klevezal' & Kleinenberg 1969; Hall-Martin 1982; Raubenheimer et al. 1998a). The conical pulp cavity retains its shape and length relative to the tusk (approximately one third the total length) through becoming enclosed from its distal end (i.e. from the roof of the cavity), while lengthening at the base of the tusk (Fig. 5.1).

5.1.1. Dentine and Dentinogenesis

Two types of dentine are present in the tusk: mantle dentine, which is located immediately adjacent to the outer cementum layer (separated from the cementum by the cementum-dentine junction), and circumpulpal dentine, which forms the bulk between the mantle dentine and the pulpal aspect of the tooth (Fig. 5.1b; Mjör 1984; Raubenheimer 1999). Dentine is a mineralized connective tissue, comprising an inorganic and organic phase. The inorganic phase (~70% of total dentine) is composed mostly of calcium phosphate minerals in the form of a biological apatite, which resembles the mineral hydroxyapatite [$\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$], but has a variable number of substitutions including CO_3 for PO_4 and OH (LeGeros 1991). The organic phase (~18% of total dentine) comprises mainly collagen, but also non-collagenous proteins, lipids, carbohydrate molecules, and citrate, collectively referred to as the organic matrix. The remaining ~12% of the dentine consists of water (Mjör 1984; Espinoza & Mann 1991).

As with all other mineralized tissues, dentine is initially deposited in the form of the organic matrix, formed by odontoblasts (the cells of the dentine), and subsequently mineralizes (Fig. 5.2; Mjör 1984). Each odontoblast consists of two parts: the cell body, and the odontoblastic process, which is a cytoplasmic projection of the odontoblast (Holland 1976; Frank 1979; Mjör 1979, 1984; Jones & Boyde 1984; Raubenheimer 1999). During initial dentinogenesis (formation of the mantle dentine), odontoblasts have several odontoblastic processes. These later die off, leaving only one odontoblast process extending from the cell body, which remains throughout the life of the

odontoblast (Fig. 5.2; Frank & Nalbandian 1963; Holland 1976; Thomas & Payne 1981; Jones & Boyde 1984; Mjör 1984). The odontoblast cell bodies are responsible for producing pre-dentine - the unmineralized matrix in which they are embedded (Furseth 1971; Mjör 1979, 1984; Thomas & Payne 1981; Jones & Boyde 1984). Pre-dentine lines the entire pulpal aspect (root) of the tooth, and is present during dentinogenesis and throughout life (Fig. 5.2; Mjör 1984). The odontoblastic processes reach from their cell bodies into the mineralized dentine layers of the tooth (Fig. 5.3; Holland 1976; Thomas & Payne 1981; Mjör 1984).

Morphologically, pre-dentine may be differentiated into two layers, old and new pre-dentine (Mjör & Shackelford 1966; Jones & Boyde 1984; Mjör 1984). The “new” pre-dentine zone remains throughout the life of the tooth, while the “old” pre-dentine zone (marking the dentine/pre-dentine interface) mineralizes once the new pre-dentine reaches a certain width. This mineralization is spherical, and is characterized by the presence of spherical hydroxyapatite crystals, or calcospherites (Jones & Boyde 1984; see also Höhling et al. 1971a, 1971b, 1974). Calcospherites (or mineralization foci) are small globular structures that fuse with neighbouring spheres during this mineralization phase of dentine, and mark the transformation of “old” pre-dentine into dentine (Takuma & Nagai 1971; Jones & Boyde 1984; Mjör 1984). If the fusion of calcospherites, which occurs in all directions, does not take place evenly during spherical mineralization, small, unmineralized islands (interglobular areas) remain in the organic matrix of circumpulpal dentine (Schour & Massler 1949; Klevezal' & Kleinenberg 1969; Furseth 1974; Scott & Symons 1977; Mjör & Fejerskov 1979; Hughes et al. 1982). The newly mineralized dentine accumulates on the pulpal surface of the tooth, and a new layer of pre-dentine will be formed over the mineralized dentine by the odontoblasts (Mjör 1984; Raubenheimer 1999). Thus the most recent growth is found on the inner surface (pulp) and at the proximal end (base) of the tusk, becoming increasingly older towards the outer cementum layer and the distal end/tip of the tusk (Raubenheimer 1999).

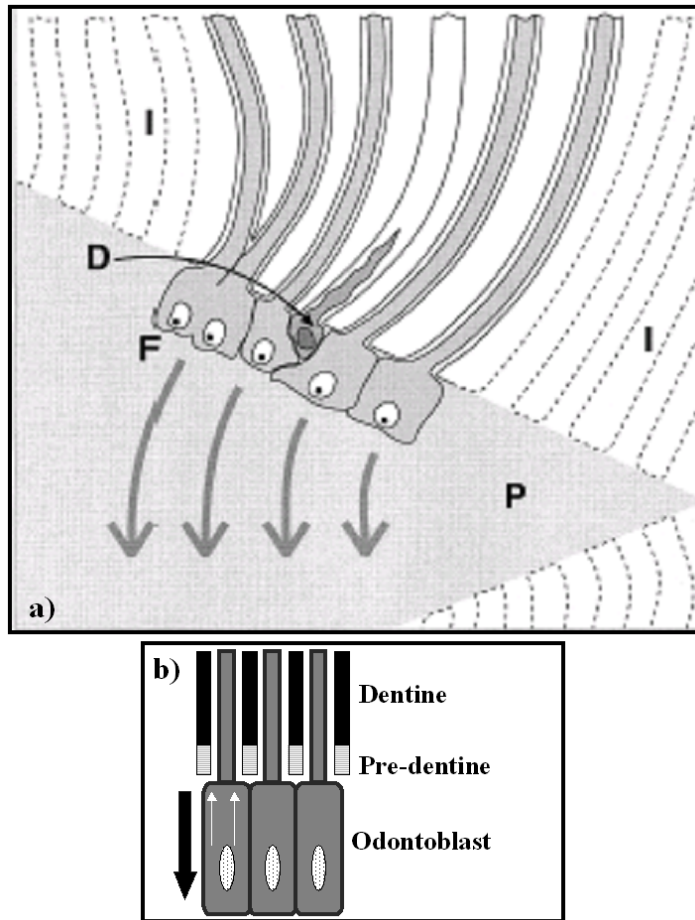


FIGURE 5.2. – Schematic representation of a) part of the sinusoidal pathway followed by the dentinal tubules during their centripetal growth in the ivory (I) (adapted from (Raubenheimer et al. 1998b), and b) dentinogenically active odontoblasts showing how, while the odontoblasts retract in a centripetal direction (black arrow), collagen is secreted at the proximal level (white arrows) (adapted from Linde et al. (1984). Note the odontoblast crowding, fusion (F), and degeneration (D) along the wall of the pulpal cavity (P) in a), and the pre-dentine and dentine zones relative to the odontoblast cell bodies and processes in b).

Secondary, Tertiary, and Reparative Dentine

In teeth with limited growth, dentine that forms after the teeth are fully developed is called regular secondary dentine (e.g. Mjör 1984). This is a very slow process resulting in a few microns of dentine being deposited along the entire pulpal aspect annually, which ultimately contributes to a reduction in the size of the pulpal cavity over time (Massler & Schour 1946; Mjör 1983, 1984; Karjalainen 1984). Secondary dentine that forms in the case of injury to the tooth (e.g. pathological circumstances) is called irregular secondary dentine (or reparative dentine/tertiary dentine). In teeth with continuous growth, such as proboscidean tusks, dentine deposition occurs at much the same rate before and after tooth eruption. This continuous deposition of dentine therefore differs from regular secondary dentine. Under pathological circumstances, however, reparative or tertiary dentine forms in the same way as in teeth with limited growth (E.J. Raubenheimer 2007 pers. comm.).

5.1.1. Incremental Growth of Dentine

Patterns of dentine mineralization may be described at several levels of magnification (Jones & Boyde 1984). Thus, apart from spherical (calcospherite) mineralization, dentine also exhibits a linear type of mineralization, which is characterized by rhythmical increments of paired light and dark bands (Fig. 5.3; Eda & Takuma 1965; Mjör 1984). Linear mineralization of dentine forms as a result of the accretion of “peritubular dentine” by the odontoblast cell bodies (Eda & Takuma 1965; Jones & Boyde 1984; Mjör 1984). Peritubular dentine lines the inner walls of microtubules/dentinal tubules, which are tubules enveloping individual odontoblast processes. Thus, it has been suggested that the light and dark incremental bands formed by linear mineralization of dentine reflect differences in the density of peritubular dentine (Eda & Takuma 1965; Takuma & Eda 1966; Mjör 1984). This is because the concentration of peritubular dentine varies in a rhythmic fashion along the length of any one tubule (Eda & Takuma 1965; see also the “Becke line effect” below). The amount of peritubular matrix that develops varies significantly between species

(Takuma & Eda 1960; Shimoyama 1967; Lester & Boyde 1968), and is, for example, particularly plentiful in elephant dentine (Boyde & Jones 1972).

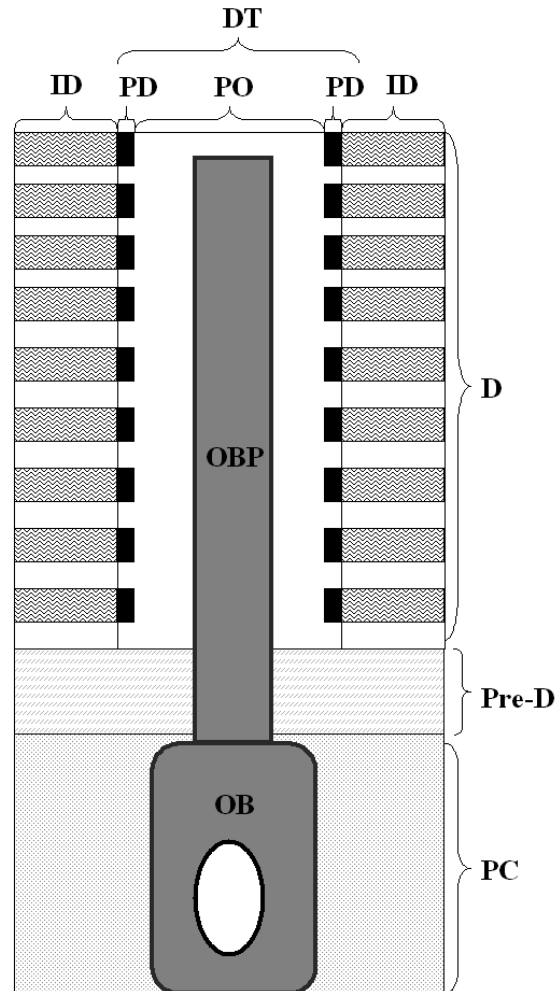


FIGURE 5.3. – Schematic representation of peritubular (PD) and intertubular (ID) dentine deposition zones, and the periodontoblastic space (PO). The dentinal tubule (DT) comprises the PD, the PO, and the odontoblast process (OBP), and is surrounded by ID. Odontoblast cell bodies (OB) line the pulp cavity (PC), and are separated from the mineralized dentine by the pre-dentine (Pre-D) zone. Note the collagen fibrils of the ID are continuous with those of the PD.

The mineralized dentine external to the dentinal tubules is referred to as the “intertubular matrix”; its mineral phase comprises calcospherite crystals (although in lower concentrations than in peritubular dentine), and its organic component comprises mostly collagen, the fibrils of which are continuous with those of the peritubular dentine (Jones & Boyde 1984). The collagen fibrils are considered to be orientated roughly parallel to the incremental pattern observed in teeth (see the “growth lines of von Ebner” and the “Becke line effect” below; Schmidt & Keil 1971; Mjör 1984). The odontoblastic space between the wall of the dentinal tubule and the odontoblast process contains fluid and a few collagen fibres, and is an important interface for the growth of peritubular dentine (see Fig. 5.3; Mjör 1984).

The Growth Lines of von Ebner

Narrow incremental lines (comprising pairs of light and dark bands) with a spacing of between 2 and 20 μm (species dependent) are well documented for enamel and dentine (Yilmaz et al. 1977). For example, von Ebner (1922) described the rhythmic banding in mammal tooth dentine as lamellae that were 18-20 μm apart. Schour and Hoffman (1939a) later provided a detailed description of the growth lines of von Ebner in the tooth dentine of 17 species (from fish to human), reporting paired light and dark incremental bands that were, on average, 16 μm wide. They also found no significant differences in the width of von Ebner growth lines between teeth of continuous or limited growth, between incisors, canines, or molars, or between teeth of the different species examined. The incremental growth lines of von Ebner appear to exhibit a diurnal periodicity, contributing significantly to the hypothesis that they are a visible manifestation of a daily rhythm of dentine deposition (Kraus & Jordan 1965; Yilmaz et al. 1977). McGuigan & Brough (1923) pointed out that such rhythmic, incremental banding is a common phenomenon in biology, e.g. lamellae of the Haversian canals in bone, annual growth rings in trees, and the shells of molluscs.

The Becke Line Effect

von Ebner growth lines in dentine consist of pairs of parallel dark and light portions, which appear to be interference effects caused by refraction (Schmidt & Keil 1971). The refractive index of each layer of dentine changes across its width with a resultant abrupt change in the boundary between two adjacent layers. This is known as the “Becke line effect” (Fig. 5.4a; Schmidt & Keil 1971). The Becke line effect seems to occur because odontoblast secretions vary throughout the day, resulting in variations in peritubular dentine density. Hence the composition and refractive index of each dentinal layer varies accordingly (Eda & Takuma 1965; Takuma & Eda 1966; Schmidt & Keil 1971; Yilmaz et al. 1977). Furthermore, the orientation of collagen fibrils and calcospherites in the intertubular dentine may both change from layer to layer in circumpulpal dentine, or calcospherites may fuse to a greater or lesser extent, contributing to the physical appearance of the growth lines of von Ebner (Mummery 1924; Schour & Hoffman 1939a; Schmidt & Keil 1971; Lavelle et al. 1977; Yilmaz et al. 1977; see also Miles & Boyde 1961; Kaye & Herold 1966; Jones & Boyde 1984).

The physiological and rhythmic deposition of the mineral is likely associated with other basic rhythms/alternate rhythms, cellular activity, and exhaustion, which would account for the alternately more-complete (light bands) and less-complete (dark bands) fusion of calcospherites (Schour & Hoffman 1939a). For example, the composition of saliva shows circadian variation in the amount of protein and carbohydrate, as well as in the concentration of important mineralization ions such as calcium and phosphate (Ferguson & Fort 1974). The composition of odontoblast secretions may vary in a similar way, so that changes in the levels of any of these components during the 24-hour cycle would effect corresponding changes in the organic matrix and mineral resulting from the secretions, and also in the refractive index of the relevant dentinal layer (Yilmaz et al. 1977). Incremental lamellae, such as the growth lines of von Ebner, are thus also of physiological significance because they represent daily archives of the nutritional and metabolic variations that occur during the growth and mineralization of dental tissues. Importantly, once tooth

dentine has undergone mineralization, such nutritional records are permanent (Schour & Hoffman 1939a).

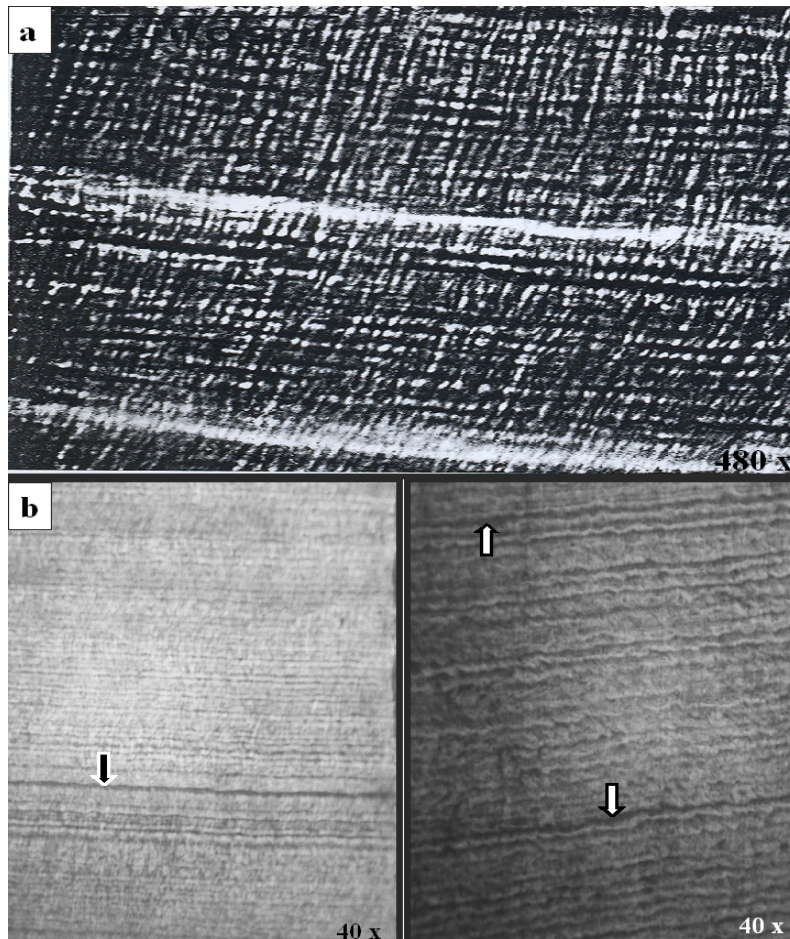


FIGURE 5.4. – Transverse sections showing a) “Becke line effect” in the molar root of a pig (photograph from Yilmaz et al. (1977)), and b) accentuated contour lines of Owen in elephant ivory (arrows). The Becke line effect is manifest as dark and light bands in the tooth. The two fluorescent lines in (a) are a result of the pig being injected with marker dyes at 2-weekly intervals, indicating that 14 layers of dentine had been deposited over this time period. Lines of Owen (b) involve several von Ebner lines, as they are visible at the second-order growth increment level.

Owen's Lines of Contour

von Ebner growth increments, which occur at daily intervals, reflect a basic physiological rhythm in calcification. Hence, the histological appearance of von Ebner growth lines provides an indication of the degree of calcification (mineralization) within a particular growth line (Schour & Hoffman 1939a; Schmidt & Keil 1971). As a result of systemic disturbances (e.g. physiological, pathological, or environmental factors) affecting calcium metabolism, the incremental line forming at any given time in the tooth dentine may become accentuated (e.g. the neonatal ring formed at birth; Schour 1936 in Schour & Hoffman 1939a; Mjör 1984). These accentuations were named after Owen (1840), who first described their presence in tooth dentine (Fig. 5.4b). Depending on the degree of disturbance in the calcification process, a given Owen's contour line may include only a part of the normal incremental ring (the light or dark component), an entire increment (both the light and dark portions), or even several incremental rings.

A Numerical Hierarchy

Geometrically, the dentine component of a proboscidean tusk is comparable to a stack of cone-shaped layers added sequentially from tip to base (e.g. Fox et al. 2007). The dentine comprises a hierarchy of structural increments that parallel the conical pulp cavity, i.e. forming on annual (first-order), weekly (second-order), and daily (third-order, or von Ebner lines) timescales (Fig. 5.5; Fisher 1987, 2001a; Koch 1989). The age of fossil proboscideans has been estimated using annual markings in tusks (e.g. Fisher 2001a; Fisher & Beld 2002), and the hypothesis that macroscopic, paired (light and dark) growth layers represent annual growth was tested by investigating animals with known age (Sergeant 1959; Hewer 1960, 1964; Mansfield & Fisher 1960; Rausch 1961; Laws 1962; Scheffer & Krauss 1964; van Nostrand & Stephenson 1964; Gilbert 1966; Ransom 1966) and also by examining animals caught in various seasons of the year (McLaren 1958; McEwan 1963; Mitchell 1963).

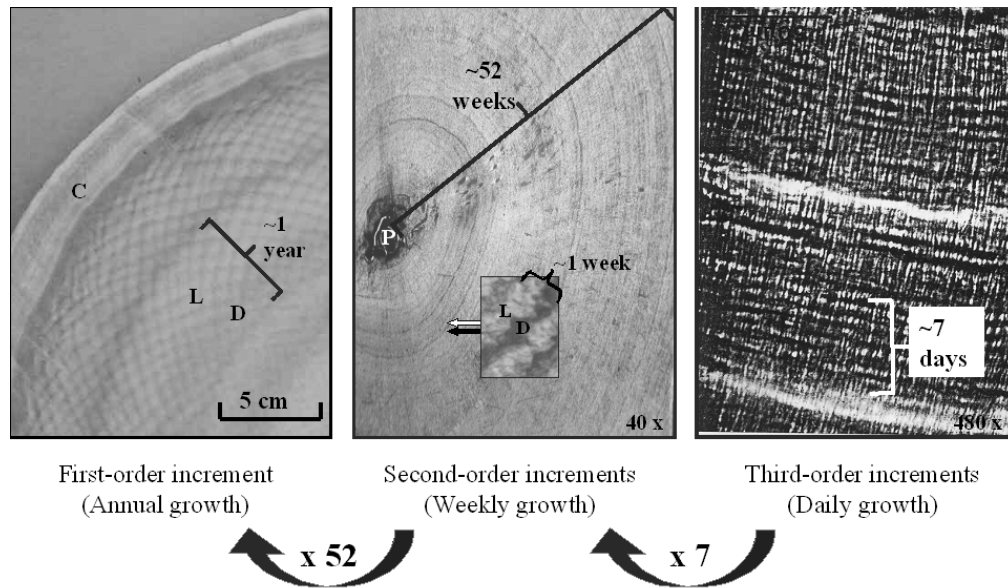


FIGURE 5.5. – a) First-order, b) second-order, and c) third-order growth increments in mammal teeth. First- and second-order bands are shown in transverse sections of elephant tusks, and third-order in pig dentine (adapted from Yilmaz et al. (1977)). Growth increments at all three timescales are defined by light (L) and dark (D) portions. Each first-order (annual) increment comprises ~52 second-order (weekly), and ~365 third-order (daily/von Ebner), while second-order increments are each composed of ~7 third-order increments. 1=first-order increment; 2=second-order increment; C=cementum; P=pulp.

The annual nature of first-order increments has also been demonstrated in previous studies of stable oxygen isotope ($\delta^{18}\text{O}$) profiles in tusk dentine (Koch 1989; Koch et al. 1998; Fisher & Fox 2003; Fisher et al. 2003; Fox et al. 2007). The periodicity of second-order increments has been examined in extinct proboscidean taxa, where they appear to reflect biweekly (~26 second-order increments per first-order increment) timescales in mastodons (Fisher 1987), and weekly (~52 second-order increments per first-order increment) timescales in mammoths (Fisher et al. 2001a; Fox et al. 2007). Extant elephants also exhibit weekly second-order increments, as is evident in mammoth tusks (Fisher et al. 2001a; D. Fisher 2005 pers. comm.). The occurrence of a weekly

periodicity in dentine accretion is likely related to the interaction between different physiological rhythms associated with tusk growth and mineralization (Fox et al. 2007). The daily periodicity of third-order increments (von Ebner growth lines) has been demonstrated for numerous extant species (e.g. Schour & Hoffman 1939a; Yilmaz et al. 1977; Molnar et al. 1981), as well as for extinct taxa (e.g. Fisher 1987; Koch 1989; Koch et al. 1989). Incremental lines are defined by paired dark/light bands at all three timescales (Figs 5.4b and 5.5). In the dark portion of an annual increment, the weekly increments are more closely packed than in the light portion of that increment, where they are often more difficult to distinguish. Similarly, the dark portions of weekly increments comprise daily increments that are more closely packed than in the light portions (Fisher 1987). Within daily increments, dentine is accreted and mineralized at different rates at different times of the day (Becke line effect), so that dark and light portions are created within every daily increment (Takuma & Eda 1966; Schmidt & Keil 1971; Yilmaz et al. 1977).

The dark-band portions of the annual layers in a tusk are likely derived from slower dentine apposition and mineralization rates, which may reflect a phase of nutritional and/or thermal stress (e.g. dry season), while the light-band portions (faster rates of dentine apposition and mineralization) likely reflect wet season growth (Koch et al. 1989). This would explain the relatively smaller distances between weekly increments in the dark bands, compared with those in the light bands, of annual increments (Koch et al. 1989). Indeed, studies on the ecology of modern African elephants have shown that there is seasonal variation in the growth rate of the whole animal, with slowest growth occurring during the stressful periods, such as during the dry season (McCullagh 1969a). Dry season periods are also related to other forms of stress, such as migration and limited resources, which create physiological conditions conducive to dark-band formation in the teeth (Laws 1953; see also Schour & Hoffman 1939b).

5.2.3. Non-incremental Lines in Ivory

Schreger Lines in Elephant (African and Asian) and Mammoth Tusks

Dentinogenesis takes place during the centripetal growth of odontoblast processes. The dentinal tubules that house the odontoblast processes follow a sinusoidal course during this growth, and relative tubule densities within different segments of the growth curve are variable (Fig. 5.6). That is, tubule density is higher in parts of the curve slanting towards the tusk apex (tip), and lower in parts slanting towards the pulpal cavity (Fig. 5.6a; Raubenheimer 1999). The differences in tubule density result in alternating light and dark lines, which appear macroscopically as “wavy”, tightly packed grooves running parallel to the incremental growth bands on the longitudinal axis of a tusk (Figs 5.1b and 5.6b; Espinoza & Mann 1991; Raubenheimer et al. 1998a). In cross-section, these grooves lie oblique to the incremental features of the tusk to form Schreger lines (first described by the German anatomist Bernhard Gottlob Schreger in 1800; see Obermayer 1881), otherwise known as the “chequer board” or “diamond” pattern characteristic of proboscidean ivory (Fig. 5.6c & d; Miles & Boyde 1961; Espinoza & Mann 1991; Raubenheimer 1999). The chequer board effect is visible only on the transverse plane (cross-section) of the tusk, where the dentinal tubules radiate from the axis of the tusk. The dentinal tubules radiate in the form of two systems (clockwise and anti-clockwise, respectively) of light and dark waves moving in smooth, intersecting curves towards the periphery (Fig. 5.6e; Miles & Boyde 1961; Raubenheimer 1999). Schreger lines situated closest to the cementum are easily visible and are referred to as “outer” Schreger lines, while “inner” Schreger lines describe those faintly discernable lines found around the tusk pulp cavity (Fig. 5.6f; Raubenheimer 1998a). The intersections between the two systems of Schreger lines form characteristic concave and convex angles (creating the chequer board/diamond pattern), which are obtuse ($>115^{\circ}$) in transverse sections of extant proboscidean tusks, and acute ($<90^{\circ}$) in those of mammoth tusks (Fig. 5.6e; Espinoza & Mann 1991; D. Fisher 2008 pers. comm.). The Schreger pattern should not be confused with the light and dark bands formed during incremental growth of ivory dentine.

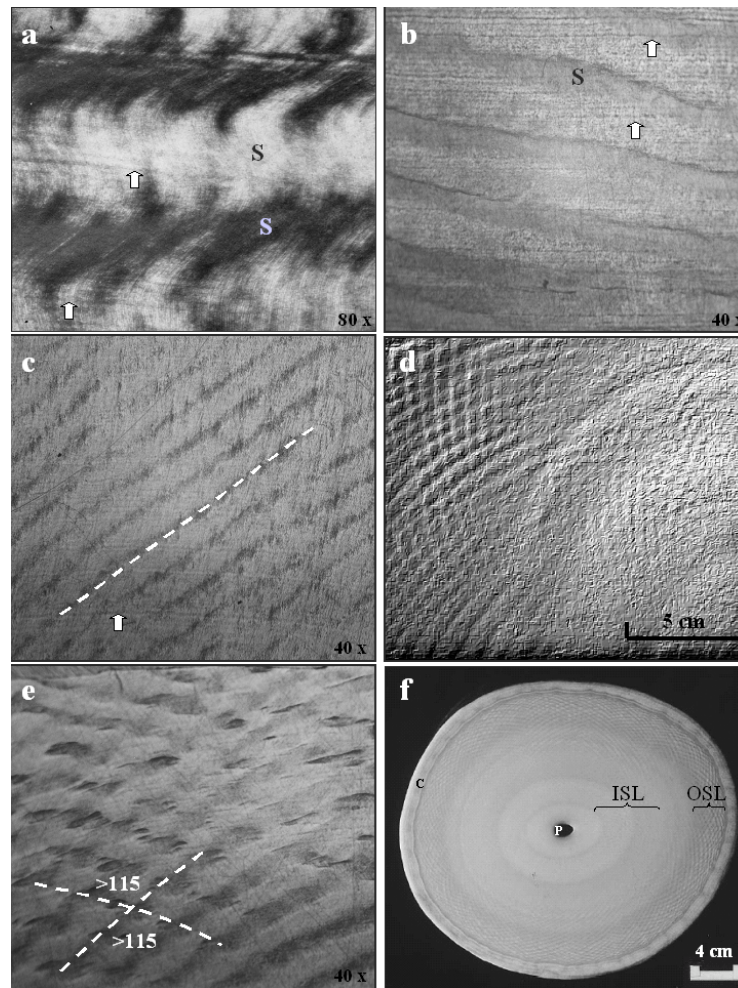


FIGURE 5.6. – Schreger lines in elephant ivory. a) Microscopic appearance of the regular sinusoidal course followed by the odontoblastic tubules when viewed on longitudinal plane. Note the alternating dark and light bands corresponding to apical and pulpal orientation of the tubules, respectively; b) These alternating bands (Schreger lines) are orientated parallel to incremental growth lines when viewed on longitudinal sections; c-e) The characteristic “chequer board” or “diamond” pattern created by Schreger lines in cross-section, where they lie at oblique angles to incremental lines. Note the obtuse angles formed by intersecting Schreger lines; f) Outer (OSL) and inner (ISL) Schreger lines on the transverse section of a tusk. (S= Schreger lines; White arrows = second-order incremental growth lines; dotted lines indicate orientation of Schreger lines). Photographs (a) and (f) adapted from Raubenheimer et al. (1998a).

The centripetal movement of odontoblasts during ivory formation leads to a decline in the pulpal circumference of the tusk, causing increased pressure on the odontoblast processes (Raubenheimer 1999). He noted that the increasing pressure on a decreasing perimeter (“odontoblastic crowding”) is accommodated by two processes. First is the movement of odontoblasts towards the pulpal opening, and second is the release of intercellular pressure through odontoblast cell death and fusion of several odontoblast tubules. The relief of intercellular pressure through these mechanisms initiates a change in direction and movement of odontoblast processes towards the tip of the tusk (apical direction) and an increase in odontoblast density in the pre-dentine. Subsequent odontoblast crowding initiates repetition of the movement of odontoblast processes towards the base of the tusk (pulpal direction) and odontoblast cell death; these processes are likely responsible for the regular sinusoidal course followed by odontoblasts (Raubenheimer 1999).

5.2. Examining Ivory Growth in African Elephant Tusks

Materials

Ivory specimens were obtained for examining incremental growth in African elephant tusks (see Table 5.1.). One tusk per elephant, from a total of 17 individuals, was sampled along the transverse plane, either by removing a ~10 mm thick disc of ivory, or by coring (10 mm diameter) different parts of the tusk (tip, middle and base, where possible). Prior to the sampling of ivory from Kruger Park, a cross-section from a tusk from the Etosha National Park, Namibia (archived material at the Archaeology Department, UCT) was examined for incremental growth lines.

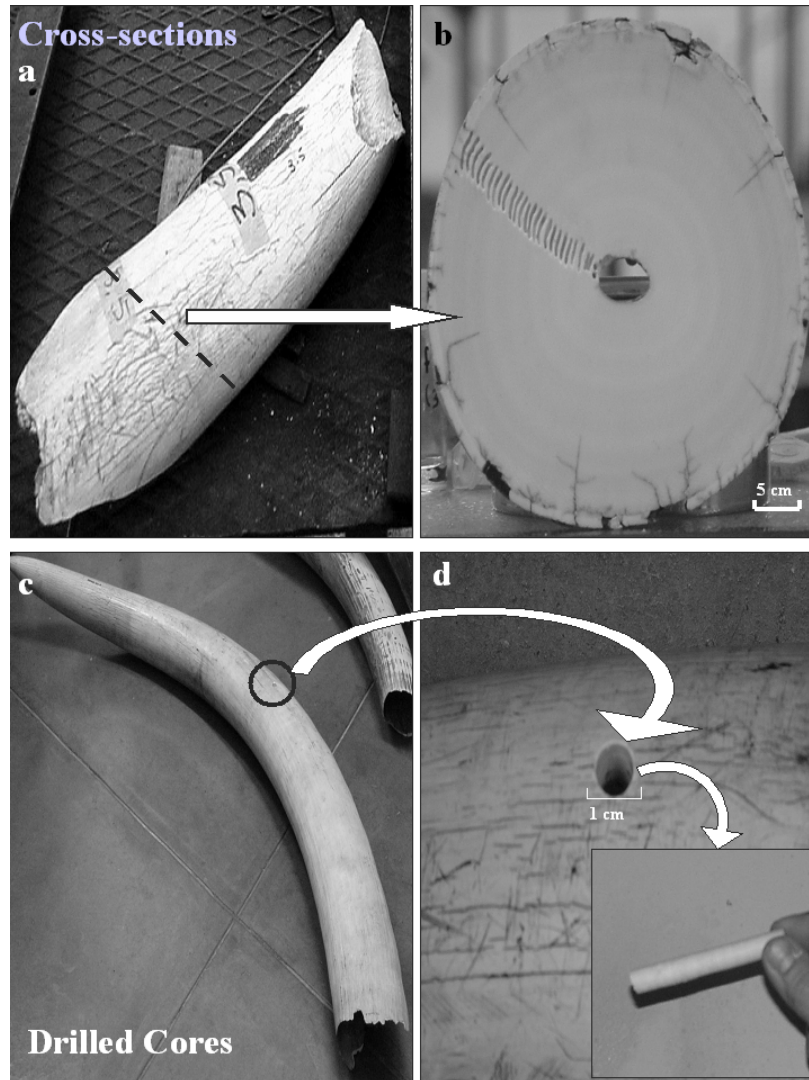


FIGURE 5.7. – Photographs showing an example of one of the ivory cross-sections sampled in Skukuza (a, b), and one of the three cores removed from the Transvaal Museum (TM) tusk (c, d). Note the cracked, brittle texture, and the woody appearance on the outer surface of the Skukuza disc, indicating that this specimen had been exposed to the elements for some time before being collected in the field. The TM tusk has scratches on the outer surface, yet it has not become brittle or cracked, indicating that the collector removed the tusks from the field soon after the death of the animal.

In January 2003, eight cross-sections were obtained from six different adult tusks from the ivory stockpiles at the Skukuza Game Processing Plant (SKU) in Kruger Park (Fig. 5.7a & b). Cross-sections were also obtained from two juvenile elephants that had been translocated from Kruger Park to the WGR in 1994, and had died in 1998 and 1999, respectively. One tusk of an elephant that died in 1949 in the southern Kruger Park area was sampled at the Transvaal Museum (TM), Pretoria, South Africa. However, rather than sectioning the TM tusk, cores (10 mm in diameter) were removed from the tip, middle, and base, respectively, using a hole-saw attached to a low-speed drill (Fig. 5.7c & d).

In January 2005, permission was granted by the South African National Parks Board (SANParks) to remove cross-section cores from six of the mounted tusks on display in the Letaba Elephant Hall (LEH) situated in Kruger Park's Letaba tourist camp. These are amongst the largest tusks collected (with recorded histories) since the inception of the Kruger Park more than 100 years ago, and as such, will offer the best long-term records of elephant diet in this environment. Drilling the wall-mounted ivory in the LEH (Fig. 5.8) required a different approach to that used for the TM tusk (which could be placed on the floor, as it was not set in a permanent display mounting on a wall). Only the left tusks of LEH individuals were sampled, as these were consistently longer than the right tusks. Since the tusks remain on display in the LEH, particular care was taken during the sampling process: an appropriate coring device was constructed for the purpose, using a steel hole-saw and piping, as well as a wooden "guide" specifically for the coring tool, complete with straps and rubber mats to prevent sliding along the ivory surface. Three ~10mm cores were removed per tusk: one near the tip (~ 10 cm away from tip), one near the base (just past the pulpal cavity, at the point where the tusk becomes solid), and one centrally between the tip and base samples, i.e. a total of 18 cores were removed. The cores were drilled perpendicularly to the longitudinal axis of the tusk without penetrating the entire width, i.e. they were broken off at their bases just past the central axis, by chiseling with a narrow rod and hammer between the core and rim of the hole. Wherever possible, the cores were drilled on the

side of the tusk closest to the wall (being unable to remove the tusks from their mountings complicated maneuverability of the drill into a suitable position every time), to avoid excessive tampering with the surfaces visible to visitors. In most cases, the display boxes alongside the tusks could be moved away from the wall to allow for maximum access behind the tusks. The holes left by the coring were filled with resin, and the cementum layer from each core was replaced on the surface to retain their natural appearance. The service of a professional artist, who had previously been involved with creating the original elephant display at LEH, was employed to undertake conservation of the tusks.

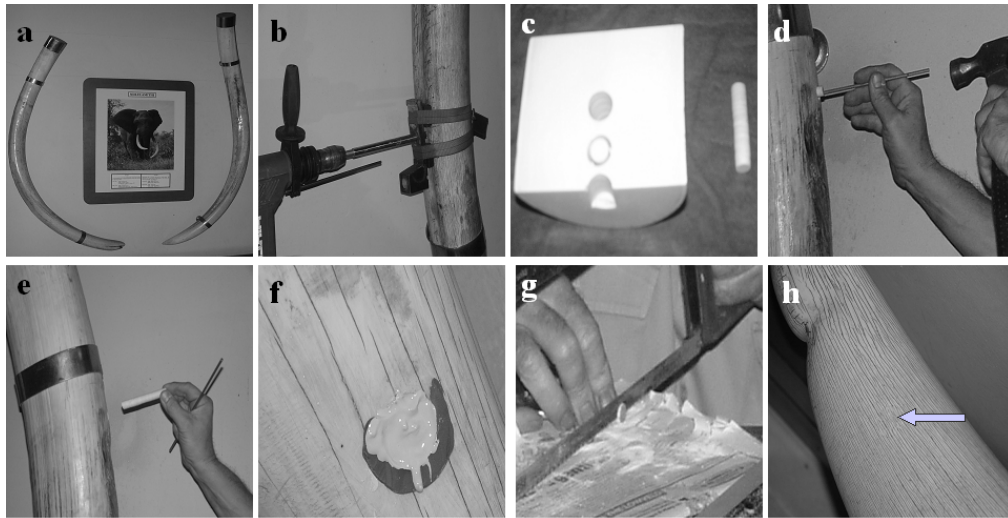


FIGURE 5.8. – Sampling of tusks on display in the Letaba Elephant Hall. a) Tusks mounted on the wall; b) Drill, coring device and wooden guide; c) Sample ivory on which the coring and chiseling process was tested. Note how the core did not penetrate the tusk completely; d) Chiseling with a narrow metal rod between the drilled core and the rim of the hole to break the core off; e) The core once removed measured ~10 mm in diameter; f) The holes in the tusks were filled with resin, and g) the cementum layer of each core was removed using a hand-held saw; h) The aesthetic value of the tusks was retained by replacing the cementum layer on the outer surface once the holes had been filled (arrow indicates the site where core was removed).

Preparation for Microscopic Examination

To become familiar with the physical appearance of growth increments, a cross-sectioned ivory disc was prepared for viewing growth increments under a Scanning Electron Microscope (SEM). At the time of the SEM work Kruger Park samples had not yet been collected, thus only the tusk from Etosha was used. The tusk was sectioned and one disc ~10 mm thick was removed. The disc was polished for two hours on 0.3 μ polishing paper, using a Micropolish Alumina Suspension (Fine, 0.3 μ) solution. After polishing and washing in distilled water, the disc was mounted on a SEM stub using a water-based glue mixed with carbon graphite (making the ivory sample conductive), cleaned ultrasonically in distilled water, and left to dry for 45 minutes, before being sputter-coated with rod-heated carbon dust. The sample did not require etching. The disc was examined using an Analytical Leo S440 SEM at 10 kV, and 200x instrument magnification using a Centaurus backscatter detector. Microphotographs were taken in reverse chronological order, starting at the pulpal cavity and working to the outer rim, and growth bands counted.

Growth lines on Kruger Park and WGR ivory specimens were examined by incident light microscopy (ILM), using a Reichert-Jung Polyvar Pol Dual Incident / Transmitted Light Microscope. Incident light microscopy allows for the image to be viewed using light from above, while transmitted light microscopy uses light from below (as with conventional light microscopy). Incident light was used to view the polished ivory sections (see Figs 5.4b & c, 5.5b, and 5.6b, c & e). ILM is particularly useful for viewing flat sections of hard materials, e.g. rocks, shells, bone, and teeth, because the objective lenses have a wide field of view but a very shallow depth of focus (D. Miller 2005 pers. comm.). The microscope was also fitted with a Nomarski interference contrast facility, which detects subtle differences in polishing hardness and sample composition, to examine whether incremental images would be enhanced.

Ivory cores were embedded in resin for ILM. Each core was halved longitudinally using an electrical saw, cleaned with acetone, then glued, flat sides down, in sets of 3 (tip, middle, base

of each tusk) onto the bases of six labeled plastic containers lined with a lubricant (petroleum jelly). The resin mixture used for the embedding was made by mixing Colbrite Polyester resin with a catalyst (1 drop of catalyst per 1 ml resin) in a sample bag. Care was taken to mix the resin and the catalyst thoroughly – the sample bag was sealed and the mixture hand-pressed until no catalyst “streaks” remained in the resin when the bag was held up to the light. The casting mixture for the cores of each tusk was made in a separate sample bag. The corner of each sample bag was cut once the mixture had been made, and the resin poured into the containers and over the cores. The containers were placed into a desiccator coupled to a vacuum chamber for a few minutes to remove air bubbles from the resin, and then left overnight in an evaporation chamber to allow the resin to set. The resin casts were removed from their plastic containers the following day and polished (see below) only on the surface exposing the flat sides of the ivory cores.

Ivory cross-sections (discs) required only polishing. There was no need to embed the cross-sections in resin, as these were flat and could be placed directly onto the microscope stage. To polish the ivory discs and core casts, a Buehler flat bed rotary Ecomet V grinder/polisher with varying grades of waterproof silicon carbide paper (220 – 1 200 mesh grit size) was used. This was followed by polishing with three grades (6 μ , 1 μ , and 0.25 μ) of diamond paste, lubricated with an alcohol-based product DP Blue, using a DP nap cloth on a Buehler Ecomet III rotary grinder/polisher, to produce a scratch-free polish. The polished ivory cores and discs were viewed at a low magnification (40x) under the microscope. A camera was mounted on top of the microscope, and loaded with 35 mm slow colour film (100 ASA) to ensure high-resolution (fine-grained) images. Serial photographs of each of the ivory cores/discs were taken (18x camera magnification), starting at the core and moving outwards (see Appendix III). Photographs were printed and overlaid in series, so that incremental growth lines could be manually counted, starting at the pulpal surface and working towards the outermost increment (marked by the dentine-cementum junction). The growth lines on every cross-section were counted at least three

times over, several days apart. The widths of first-order increments, and the number of second-order increments per first-order increment, are reported as means \pm standard error (SE).

Accelerator Mass Spectrometer (AMS) Radiocarbon (^{14}C) Dating

Counts of growth increments are used to determine the number of years represented by individual cross-sections (see also Koch 1989; Hoppe 2000; Fisher 2001a), as well as the date for each increment for specimens for which dates of birth and/or death are known (such as the LEH individuals). For individuals where death dates were unknown (i.e. individuals sampled from the SKU stockpiles), I used accelerator mass spectrometry (AMS) radiocarbon (^{14}C) dating to establish the time period represented by each animal. Sub-samples were removed from the innermost growth layer (time of death), and resultant AMS date was used as a starting point for further temporal calibration. For two individuals, AMS sub-samples representing most recent and oldest growth were used to further refine chronologies. Thus, radiocarbon dates could also be used as an independent method to cross-check temporal durations yielded by manual counts. The number of cross-sections to be dated in this manner was limited to two due to the cost of AMS radiocarbon dating.

The AMS dating technique produces radiocarbon dates using tandem accelerators in high-energy mass spectrometer systems (Stuiver & Polach 1977; Gillespie 1984; Manning & Melhuish 1994). The radioactive ^{14}C isotope is measured directly by ion counting rather than waiting for decay events as in conventional methods. Because of the input of ^{14}C into the atmosphere by nuclear testing between 1955 and 1966 (the so-called “Bomb Effect”, Gillespie 1984), dates from 1950 onwards can be calibrated to within about a year of the actual date of the sample (Stuiver & Polach 1977; F. Petchey 2006 pers. comm.). This technique is therefore particularly useful for this study (which examines historical records at timescales of year and/or season), at least for samples that post-date 1950. AMS is also the preferred method for dating well preserved modern samples that are too small to be dated by the standard radiometric dating

method (Gillespie 1984). In the case of ivory, 100 mg of dentine powder is sufficient for analysis, which meant that dates could be obtained for a single annual increment from each ivory cross-section.

As stated above, AMS radiocarbon dating could only apply to specimens post-dating 1950, but this did not present a constraint to the current study. Older individuals are represented by the LEH tusks, all with recorded birth and death dates, and by TM 10046, which has a recorded death date (1949). Of the LEH tusks, only Phelwana does not have a recorded date of birth, but based on elephants and tusks of comparable size, Phelwana's birth date can be assumed to be within the range of the other LEH individuals (see Table 5.1). To allow for loss of years represented in tusks due to tooth abrasion and wear at the tip, the time period represented in each of the "tip" cross-sections of the LEH tusks (see Results) was consistently assumed to start five years after the date of birth. The WGR tusks have recorded death dates and did not require independent age assessments. Thus only the SKU tusks were sampled for AMS dating (Table 5.2). Innermost (i.e. from the pulpal surface) and/or outermost (rim) ivory powder samples, representing the most recent and oldest growth on an ivory cross-section, respectively, were removed. The powdered samples were sent to the Radiocarbon Dating Laboratory at the University of Waikato, New Zealand for AMS dating.

Pretreatment of powder samples involved routine physical and chemical procedures carried out at the laboratory in Waikato. Physical pretreatment included sample cleaning, grinding (more finely), and removing of visible contaminants. For chemical pretreatment, samples were decalcified in 2% hydrochloric acid (HCl), rinsed and dried. They were then gelatinised at pH=3 with HCl at 90°C for 4 hours, rinsed and dried.

Radiocarbon dates may be quoted with the precision of one standard deviation (1σ), which implies a 68% probability that the true value lies between $+1\sigma$ and -1σ limits. Broadening the limits to $\pm 2\sigma$ means that the probability rises to 95%. It is not possible to achieve 100% probability (Gillespie 1984). Thus, results for AMS radiocarbon dates of ivory samples are

presented with 1σ and 2σ ranges (Appendix IV), but only the 2σ range was used when considering the most likely date for a sample (except in the case of ZA-0008-02; see Appendix IV). The AMS date(s) used for each individual is reported in Table 5.2.

5.1. Results and Discussion

Results from the SEM study showed that incremental growth bands are present on the ivory cross-section in the form of paired dark and light bands (Figure 5.9). The more recent growth lines (proximal to the pulpal cavity) are, however, less prominent compared with the more distinct previously deposited growth lines towards the outer surface of the disc. Schreger lines are not visible on the SEM photomicrographs. This is likely because this method was sensitive only to changes in dentine density across the section (growth increments) rather than to changes in the angles of microtubules (which are responsible for the formation of Schreger lines). From the counts it was determined that the observed increments represent weekly growth (Table 5.2). These findings are congruent with those previously reported for mammoths (Fisher 2001a; Mol et al. 2001; Fox et al. 2007). The characteristic “grey-scale” quality of the SEM images (see Fig. 5.9) made the counting of the less prominent growth increments difficult, prompting the decision to use ILM for counting growth bands on the Kruger Park and WGR ivory.

Growth increments on the ivory sections using ILM, viewed at low microscope magnification (40x), are clear and distinct (Figure 5.10). Growth lines were clearer when viewed without the use of the Nomarski interference contrast filter. Growth increments each comprise a set of dark and light band pairs; these were considered as starting at the beginning of a dark band, and ending at the beginning of the next dark band, with a light band separating them (see Figure 5.10), in order to be counted. Results for the total number of growth bands counted per core / disc indicated that these reflect weekly growth, or second-order banding (49.5 ± 0.42 , $n = 33$ bands per yearly band; Table 5.2). This finding is in accordance with previous findings for mammoths and Asian elephants (Fisher 2001a; Mol et al. 2001; D. Fisher 2005 pers. comm.; Fox et al. 2007).

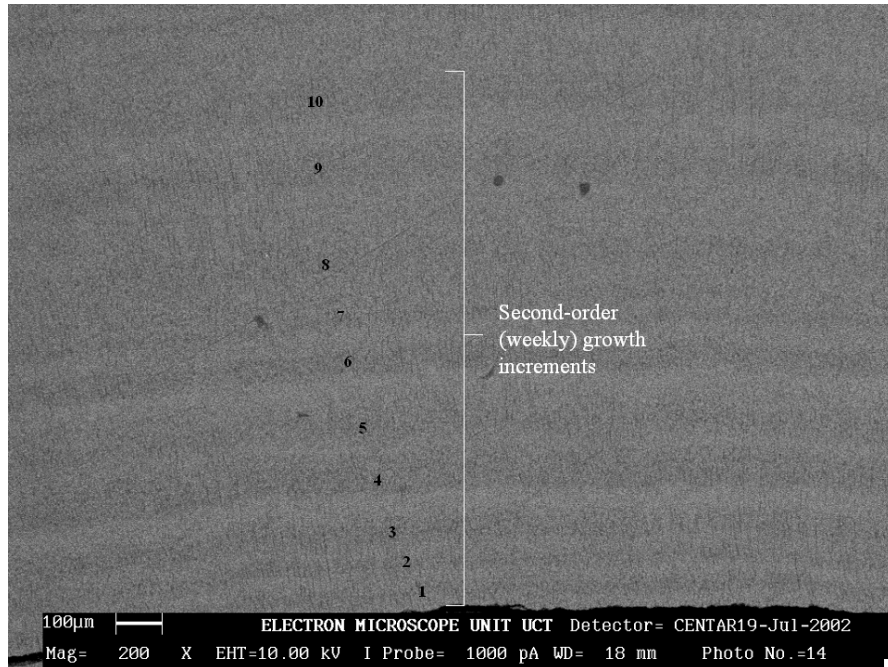


FIGURE 5.9. – Scanning electron micrograph of an ivory cross-section (tusk from Etosha) showing faint second-order (weekly) increments (the dark portion of increments are numbered). Note the increments are not uniform in width, which serves as a record of physiological and environmental affects on dentine accretion rates.

First-order, second-order, and third-order incremental features were previously recognized in mammoth and mastodon tusks through inspection of luminance transects, which display variations in light transmission through thin sections of ivory (Koch 1989; Koch et al. 1998). Mol et al. (2001) also found that thin sections of dentine from a mammoth tusk specimen, viewed at 40x magnification, displayed a clear record of hierarchically organized first-order, second-order, and third-order increments. Nearly four years are recorded in their sample ($n = 1$), with annual increments of about 4.5 mm each (see also Koch et al. 1989). In this study, the number of years recorded in the ivory discs and cores examined varied within and between specimens ($n = 33$), with tusk tip sections rendering fewer years (~2 to 10) than middle (~9 to 14) and base (~4 to 14) samples. Annual increment width ranged from 4.0 to 6.9 mm (excluding the tip section of

Phelwana, see below), with an average of $5.3 \text{ mm} \pm 0.11$ ($n = 31$, excluding Phelwana and UCT 3440) or $5.5 \text{ mm} \pm 0.18$ ($n = 32$, excluding UCT 3440 but including Phelwana) (see Table 5.2). The annual increments observed in the tip of Phelwana's tusk were much wider (10.0 mm) when compared with the rest of the tusk (5.6 and 5.7 mm, for middle and base sections, respectively), and to the other specimens, possibly because this particular individual experienced unusually fast growth of its tusks during the early years of its life. Apart from the Phelwana tip, annual increment width of different sections within tusks were highly regular, regardless of the life phase represented by each part, i.e. base (younger years), middle (mid-life), and tip (older/most recent years before death) sections averaged $5.4 \text{ mm} \pm 0.18$ ($n = 14$), $5.3 \text{ mm} \pm 0.15$ ($n = 10$), and $5.2 \text{ mm} \pm 0.27$ ($n = 7$, excluding Phelwana tip), respectively.



FIGURE 5.10 – Incident light microscopic photograph of a cross-section of ivory showing clear second-order growth increments (numbered). The dark (D) and light (L) portions of each increment are distinct, and are measured from the start of one dark increment to the start of the next dark increment.

The total number of weekly increments per core/section reflected the number of annual increments for all the tusks (Table 5.2). Manual counts showed that the number of weekly increments per annual increment varied between 41 and 53, with an average of 50 ($n = 33$; see Table 5.2). Thus, second-order increments in African elephant tusks represent weekly growth. Variation in the number of weekly increments within each annual increment is likely due to variation in second-order increment width, causing very narrow increments to be overlooked during counting, or very wide increments to be interpreted as two increments, especially if these are interspersed by accentuated lines of Owen.

Schour & Hoffman (1939a) measured daily increments (von Ebner growth lines) in the dentine of 17 animal species. In their study, a total of 5 466 measurements revealed a mean value of 15.92 μm per pair of light and dark layers (measured from the beginning of one dark band to start of the next one), with 80% of these between 15 and 17 μm and 66% between 15.5 and 16.5 μm . Daily increments were not examined in here. However, based on the average width observed for annual increments (5.5 mm) in this study, and the width of weekly increments observed in Figs. 5.9 and 5.10 (~100 μ), the average width of daily increments would be 15.068 μm , which is similar to findings of Schour & Hoffman (1939a) for other species. In a study of von Ebner growth lines, Yilmaz et al. (1977) injected young pigs (*Sus* sp.) at 2-weekly intervals with fluorescent marker dyes, and found that 13 von Ebner lines (third-order increments), and therefore 14 increments (or seven pairs of light and dark bands), existed between 2 successive fluorescing lines. They also concluded that von Ebner lines exhibit a diurnal periodicity.

The most probable AMS dates for SKU samples are reported in Table 5.2, based on the full AMS date ranges (1σ and 2σ) for each specimen (Appendix IV). They were compared with those obtained from manual counts of weekly growth increments within each cross-section. All but two of the AMS dates fell within the range of those estimated from the manual counts (see Table 5.2). In the case of individuals ZA-123-01 and ZA-0008-02, the AMS dates suggest that the tusks were

found in the field by Kruger Park patrol staff only decades after their respective deaths, thus the accession dates do not match the years of death.

5.5. Conclusion

To permit recovery of its life history, the tusk of each elephant in the sample set was sampled at the base, middle, and tip, unless this was not possible due to damage or breakage. It was hoped that the core/section spacing along tusks would allow for overlap of the diet record between cores/sections. Judging from the AMS dates, however, it would seem that some years are not accounted for in the sections sampled. Nevertheless, a continuous overall diet record is obtained for the Kruger elephants by combining and overlaying the individual sequence(s). The surfaces of polished ivory cross-sections, as well as those of the polished cores (diameter ~10mm), were sufficient to allow macroscopic and microscopic examination of annual and weekly growth increments, respectively, in the circumpulpal dentine. Therefore, the presence of a numerical hierarchy in proboscidean ivory dentine, as reported in previous studies (Fisher 1987; Koch 1989; Koch et al. 1989; Fisher 2001a, 2001b; Mol et al. 2001; Fisher & Beld 2002; Fisher et al. 2003; Fox et al. 2007; Rountrey et al. 2007) was shown for African elephant tusks. The different time frames represented by the various layers of dentinal growth were shown to be a reliable way of reconstructing chronologies for individual elephants. Therefore the combination of structural (growth increments) and compositional (stable isotope records; next chapter) data will allow for dietary histories to be reconstructed, and for environmental influences on diet to be inferred.

TABLE 5.1. – Tusk details for ivory samples collected for this study. Dates in regular font indicate recorded birth/death dates; * symbols indicate AMS-confirmed dates, and italics indicate the collection date only, because the death date is unknown. The death date for individual ZA-R is in bold text, because the mid-section of this tusk has an AMS-confirmed date (1983) that corresponds with the estimated year of death based on collection date.

Individual	Died /		Age	Sex	Mass (kg)	Length	Diameter of base (cm)	Circumference of base (cm)
	Born	collected						
Letaba Hall								
Kambaku	1930	1985	55	Male	63.2	259.0	-	51.0
Nhlangulene	1932	1987	55	Male	62.6	262.0	-	-
Phelwana	-	1988	-	Male	63.8	257.0	-	54.0
Dzombo	1935	1985	50	Male	56.8	237.0	-	50.0
Ndlulamithi	1927	1985	58	Male	64.6	287.0	-	48.5
Shingwedzi	1934	1981	47	Male	58.1	264.0	-	48.0
Transvaal Museum								
TM 10046	-	1949	-	Male	-	178.0	11.5	46.5
Skukuza Stock								
ZA-0023-02	-	1993*	-	-	19.5	152.5	12.5	-
ZA-123-01	-	1975*	-	-	-	123.0	10.5	-
ZA-502-92	-	1989*	-	-	-	-	11.0	-
ZA-0008-02	-	1958*	-	-	-	-	8.0	-
ZA-359-90	-	1989*	-	-	12.7	100.5	13.0	-
ZA-0131-89	-	1984*	-	-	-	-	8.5	-
ZA-R	-	2005	-	-	-	-	-	-
Welgevonden								
ZA-2238-01	-	1998	-	-	0.7	48.0	4.0	-
ZA-2239-01	-	1999	-	-	0.8	45.0	4.5	-
Etosha								
UCT 3440	-	1988	-	-	-	-	-	-

TABLE 5.2. – Number and date of years represented within ivory samples, based on counts of first- and second-order increments and AMS radiocarbon techniques.

Individual	Section	Increments in Section				Date Range		
		First-order	Mean width of first-order (mm)	Second-order	Second per first	Counted	AMS	Combined Estimate
Kambaku	Tip	10	4.9	507	51	1935-1944	-	1935-1944
	Middle	13	5.8	656	50	1952-1964	-	1952-1964
	Base	14	5.1	692	49	1972-1985	-	1972-1985
Nhlangulene	Tip	5	6.7	263	53	1937-1941	-	1937-1941
	Middle	12	5.9	597	50	1953-1964	-	1953-1964
	Base	13	5.3	655	50	1975-1987	-	1975-1987
Phelwana	Tip	3	10.0	123	41	1935-1937	-	1935-1937
	Middle	15	5.6	749	50	1951-1965	-	1951-1965
	Base	14	5.7	743	53	1975-1988	-	1975-1988
Dzombo	Tip	5	5.6	247	49	1940-1944	-	1940-1944
	Middle	14	5.1	718	51	1951-1964	-	1951-1964
	Base	14	6.0	692	49	1972-1985	-	1972-1985
Ndlulamithi	Tip	9	4.7	466	52	1931-1939	-	1931-1939
	Middle	13	4.8	666	51	1951-1963	-	1951-1963
	Base	13	5.0	642	49	1973-1985	-	1973-1985
Shingwedzi	Tip	6	4.7	274	46	1939-1944	-	1939-1944
	Middle	13	4.9	660	51	1952-1964	-	1952-1964
	Base	10	6.1	507	51	1972-1981	-	1972-1981
TM 10046	Tip	8	5.0	411	51	1903-1910	-	1903-1910
	Middle	10	5.6	494	49	1921-1930	-	1921-1930
	Base	9	5.6	433	48	1941-1949	-	1941-1949
ZA-0023-02	Middle	11	4.7	570	52	1955-1965	? - 1962	1952-1962
	Base	9	6.9	421	47	1987-1995	1986 - 1993	1985-1993
ZA-123-01	Tip	10	5.0	494	49	1935-1944		1935-1944
	Base	11	5.1	556	51	1990-2000	? - 1975	1965-1975
ZA-502-92	Base	12	5.0	587	49	1976-1987	? - 1989	1978-1989
ZA-0008-02	Base	9	5.0	423	47	1987-1995	? - 1958	1950-1958
ZA-359-90	Middle	11	5.5	560	51	1979-1989		1979-1989
ZA-0131-89	Base	8	5.7	388	49	1976-1983	? - 1984	1977-1984
ZA-R	Middle	12	4.7	611	51	1989-2000	? - 1993	1982-1993
ZA-2238-01	Base	4	4.0	198	50	1995-1998	-	1995-1998
ZA-2239-01	Base	4	5.4	181	45	1995-1998	-	1995-1998
UCT 3440	Base	6	-	289	48	1983-1988	-	1983-1988
All sections			5.5 ± 0.18 SE		50± 0.42 SE			

Mean width of first-order = radius (in mm) of cross-section / total number of first-order increments recorded for section;
 Second-order = total number of increments counted in cross section (manual counts repeated 3x, several days apart);
 Second per first = number of first- divided by number of second-order increments, i.e. number of weeks per yearly band;
 Counted = date range based on band counts, year of death, & birth year;
 AMS dates are calibrated using the 2-sigma range (See Appendix III)

- Chapter 6 -

Long-Term Ecological and Environmental Change in African Elephants from Stable Isotope Profiles in Ivory

This chapter uses sequential stable isotope records archived in elephant ivory to reconstruct patterns of dietary variability through the 20th century. The aim is to determine whether and how elephant browse and grass utilization changed during this period, and to identify the limiting factor(s) that may have led to these changes. The temporal resolution achieved using this approach is discussed, and the timing of diet shifts is matched with life history records (where available). Individual profiles are then combined to reconstruct a 20th-century record (dating from 1903 to 1993) for elephant diets in the region, which in turn is compared with stochastic and long-term changes in climate, the elephant population, population trends of sympatric herbivores, and changes in management regime.

6.1. Introduction

Elephant (and other herbivore) diets are thought to be regulated by a combination of factors, including changes to the physical environment (climate, food availability and abundance, and disturbance), and intra- and inter-specific competition for resources (e.g. Senft et al. 1987; Owen-Smith 1988). Any of these limiting factors can be influenced by natural or anthropogenic causes. Long-term diet records may offer our best hope of identifying and differentiating between the potential causes of diet shifts, as well as the role of populations in ecosystem functioning, and their responses to environmental change (Olson 1952; Carpenter 1988; Jones & Lawton 1995; Brown et al. 2001). However, such records are scarce, confined largely to selected species that

have been monitored over long time periods. This gap can potentially be addressed using sequential stable isotope analysis in continuously growing mammal teeth, such as proboscidean tusks (Koch 1989; Koch et al. 1998; Fisher 2001a, 2001b; Fisher & Beld 2002; Fisher & Fox 2003; Fisher et al. 2003; Fox & Fisher 2004; Fox et al. 2007; Rountrey et al. 2007). The theoretical basis for ^{13}C and ^{15}N abundances in mammals is described in Chapter 3; details for variations in ^{18}O abundances are described below. Environmental information archived in incremental tissues such as teeth preserve a chronological series, because no turnover occurs after deposition and hence each incremental layer preserves a temporally intact isotopic record of diet (e.g. Gage et al. 1989; Koch et al. 1989; Balasse et al. 2001). High-resolution records are available because ivory dentine is accreted concentrically to produce third-order/daily (von Ebner lines), second-order/weekly (biweekly in mastodons), and first-order/annual incremental layers. This numerical hierarchy, previously documented in Asian elephant, and fossil mammoth, mastodon, and gomphothere tusks, was described in modern African elephant ivory in Chapter 5 (see also Fisher 2001a; Trapani & Fisher 2003). Isotope “profiling” of ivory has not yet been applied to studies of modern African elephants, but previous work on other taxa (and results of Chapter 5) suggest that this approach should yield long-term (multidecadal) records of ecological change at annual or sub-annual resolution in this species as well.

The aim of this chapter is to reconstruct historical records of elephant diet in Kruger Park throughout the 20th century. I used stable carbon, nitrogen, and oxygen isotope profiles of African elephant ivory to document ecological changes since the early 20th century to recent. Results are presented for 14 individuals that lived in the Kruger National Park, and 2 individuals relocated from Kruger Park to the Welgevonden Private Game Reserve in the Waterberg in 1994. These records represent fluctuations at sub-annual (seasonal) resolution over one to several decades within individuals, and were predicted to show the timing and magnitude of diet shifts within and between individuals, which could be compared with the environmental history of Kruger Park. Three hypotheses were tested: i) isotope abundance variations in elephant ivory, and hence

elephant diets, reflect responses to climate trends through the 20th century; ii) elephant diets responded to changes in abundances of sympatric large mammal herbivores, including their own species, due to effects of exploitation competition; and iii) elephant diets changed during different management regimes (e.g. policy with respect to elephant population control, burning, and fencing).

Stable Oxygen Isotope Abundances in Mammals

Variation in the $^{18}\text{O}/^{16}\text{O}$ (reported as $\delta^{18}\text{O}$; see Chapter 1) composition of herbivores is determined mostly by oxygen isotopic variations in drinking water, in water bound within food sources (browse and grass), and in atmospheric oxygen (O_2) (e.g. Longinelli 1984; Luz & Kolodny 1985; Bryant & Froelich 1995; Quade et al. 1995; Bryant et al. 1996; Kohn 1996; Kohn et al. 1996; Koch et al. 1989, 1998; Sponheimer & Lee-Thorp 1999, 2001; Smith et al. 2002). Early studies of mammalian $\delta^{18}\text{O}$ showed that body water and bone phosphate values can be directly related to $\delta^{18}\text{O}$ values of meteoric water sources (Longinelli 1984; Luz et al. 1984). $\delta^{18}\text{O}$ in the carbonate (mineral) phase of bone/tooth material is measured routinely along with $\delta^{13}\text{C}$, and reflects water sources in the same way as do body water and bone phosphate values (Bryant et al. 1996; Iacumin et al. 1996). Thus, the primary source of $\delta^{18}\text{O}$ variation in plants and animals is meteoric water, the $\delta^{18}\text{O}$ value of which is derived chiefly from precipitation, but also varies with latitude, altitude, and temperature (Dansgaard 1964).

Based on the relationship to meteoric water, plant $\delta^{18}\text{O}$ is also affected by environmental conditions such as relative humidity, temperature, and precipitation (Yakir 1992). For example, higher plant $\delta^{18}\text{O}$ is associated with increased aridity (Koch et al. 1989; Yakir 1992). The leaves of terrestrial plants are ^{18}O -enriched relative to local meteoric water, because water evaporation from leaf surfaces involves a discrimination against the lighter isotope (^{16}O), resulting in an overall increase in leaf $\delta^{18}\text{O}$ (Epstein et al. 1977; Kohn 1996). As such, the $\delta^{18}\text{O}$ values of herbivore tissues

are influenced by their diet (e.g. Koch et al. 1989; Kohn 1996). For example, herbivores that obtain water mostly from the plants they eat (usually browser species) appear to be more enriched in ^{18}O relative to species that obtain water by drinking (usually grazers) (e.g. Kohn et al. 1996; Sponheimer & Lee-Thorp 1999, 2001; Carter 2001; Smith et al. 2002). Furthermore, plants that have a higher exposure to sunlight, such as C_4 grasses and the uppermost leaves of C_3 plants, have higher evapotranspiration rates than shaded plants, which also contributes to ^{18}O -enrichment (Yakir 1992). This potentially provides for differentiation of mammal feeding habits into open versus dense habitats (e.g. Quade et al. 1995). Plant roots, however, have lower $\delta^{18}\text{O}$ than leaves (Epstein et al. 1977; Yakir 1992), a factor that may complicate interpretation of patterns in animals if roots form a substantial component of the diet.

Mammalian ^{18}O -abundances also vary across species, populations, or individuals having different ecophysiological adaptations. Luz et al. (1984) proposed that, amongst small mammal species, smaller species with higher metabolic rates have different $\delta^{18}\text{O}$ values compared to larger species. In an effort to apply this observation to larger mammals, Bryant & Froelich (1995) suggested that mammalian $\delta^{18}\text{O}$ is negatively correlated with body size. However, these authors also found that dependence on the water bound in food decreased with increasing body size. Given the observation that drinking mammals display lower $\delta^{18}\text{O}$ values than those that obtain water from their food (Kohn et al. 1996; Sponheimer & Lee-Thorp 1999, 2001; Smith et al. 2002), the findings of Bryant & Froelich (1995) likely reflect differential reliance on drinking water rather than on water bound in food.

The mode in which water is lost in mammals may also be reflected in the $\delta^{18}\text{O}$ values of their tissues (Sponheimer & Lee-Thorp 2001). Respiratory carbon dioxide, urine, faeces, and sweat all comprise oxygen with a similar ^{18}O composition to that of body water, but excreted water vapour is relatively ^{18}O -depleted (Wong et al. 1988). Thus it has been suggested that

animals losing water through panting should have higher $\delta^{18}\text{O}$ values than animals that sweat, but empirical data for testing this hypothesis is needed (Sponheimer & Lee-Thorp 1999, 2001).

In all, mammalian $\delta^{18}\text{O}$ compositions have the potential to be valuable sources of climate information, especially if combined with $\delta^{13}\text{C}$. For example, Koch (1989) used $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis of fossil ivory growth increments, and changes in tusk growth rates, to determine seasonal mortality patterns for mammoths and mastodons. Nevertheless, in order to further exploit this tool, a better understanding of $\delta^{18}\text{O}$ compositions in modern ecosystems, populations, species, and individuals is needed (Sponheimer & Lee-Thorp 2001). In this study, I use $\delta^{18}\text{O}$ in the carbonate phase of ivory dentine not only as a supplement to ecological records based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, but also to test hypotheses about the relationship(s) of mammalian $\delta^{18}\text{O}$ with rainfall, seasonality, and other climate changes over time.

6.2. Methods

6.2.1. Sampling Procedures

Ivory cross-sections were obtained from 14 elephants that lived in the Kruger Park, including six of the so-called ‘Magnificent Seven’ on display in the Letaba Elephant Hall (LEH) at the Letaba restcamp. In cases where both tusks of an individual were available, the longer tusk (master tusk) of a pair was sampled to maximize the number of “earlier” years sampled (due to tooth abrasion at the distal end, one tusk is usually shorter than the other, see Chapter 5). Where possible, a cross-section was removed from the base (most recent growth prior to death), middle (mid-life), and tip (oldest growth, i.e. representing juvenile years) of the tusk, either by coring with a custom-made coring device and hand-held drill, or by removing 10 mm thick sections/discs from broken/damaged tusks with an electric saw (see Chapter 5). Thus 18 ivory cores (at tip, middle and base of tusk) were removed from the six LEH tusks, nine discs from seven individuals from the ivory stockpiles at the Skukuza Animal Processing Plant (SKU) just

outside Kruger Park's Skukuza tourist camp, and three cores from one Kruger Park tusk in storage at the Transvaal Museum (TM) in Pretoria. A further two discs were removed from tusks of two juvenile individuals that were translocated from the Shangoni region in northern Kruger Park to the Welgevonden Private Game Reserve (WGR) in the Waterberg (North-West Province) in 1994 (Table 6.1; see Chapter 5 for details).

Microsamples were removed in powder form at 1 mm increments from each cross-section, starting at the pulp (most recent growth in section) and working towards the outermost growth band adjacent to the cementum (oldest growth in section), using a Dremel Minidrill fitted with a 1 mm diamond-tipped drill bit. The time periods represented in each cross-section, and within each microsample, were estimated by counting second-order (weekly) growth bands at 40x magnification, using Incident Light Microscopy (ILM; Fig. 6.1), and first-order (annual) bands in macroscopic view (the series of ILM photographs for each individual is provided in Appendix III). The start and end date for base and tip cross-sections were determined from the date of birth and/or death (LEH, TM, and WGR specimens), or by ^{14}C dating techniques using Accelerator Mass Spectrometry (AMS; Stuiver & Polach 1977; Gillespie 1984; Manning & Melhuish 1994) for the SKU tusks (see Chapter 5 for details of AMS radiocarbon dating technique). This combination of macroscopic, microscopic, and radiocarbon dating methods allowed for each microsample to be placed within a well-defined time frame (year and season, where light band samples represent wet season growth) (Table 6.1).

The total number of annual and weekly growth increments, as well as the approximate number of weekly increments per annual increment counted in each section (tip, middle, or base), is presented in Table 6.1. Also, the total number of microsamples per tip, middle, or base for each cross-section is presented, together with a breakdown of the average number of weekly increments in each microsample, the number of microsamples per year, and the total number of weekly increments represented in isotope analyses (see also Chapter 5). In all, ivory cross-

sections comprise three (in sections from the tip of a tusk) to 15 (sections from the base or middle of a tusk) years of growth that can be divided sub-annually based on light/dark band pairing.

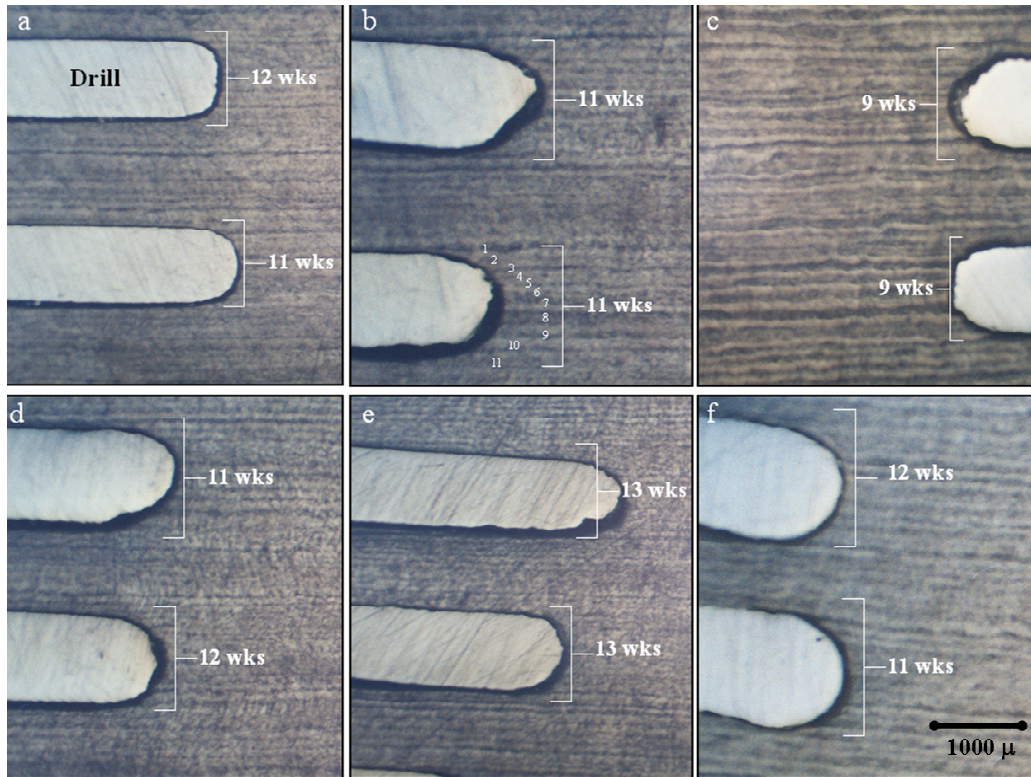


FIGURE 6.1. – Second-order (weekly) growth increments in cross-sections of elephant ivory dentine showing drill marks from where microsamples were removed. Each microsample covered between 11 and 13 second-order increments (weeks). One individual (Phelwana) experienced a faster dentine accretion rate in its tip, thus only 9 weeks are covered by the drill bit (c). All microsamples were removed at 1 mm increment spacing, thus for every ~52 second-order increments (equivalent to one year’s growth), ~26 would be included in the sample for isotope analyses (equivalent to 6 months in total, or two seasons, separated by one season not included).

Approximately 50 weekly bands are present within each annual band, and the diameter of the drill bit covered approximately 13 weeks in the ivory sections (Table 6.1; Chapter 5). Thus, each microsample represents ~ three months, i.e. one season in cases where the microsample lies

within the light or dark portion of the annual growth band, or a mix of two seasons in cases where the microsample traverses a light and a dark band. The 1 mm incremental spacing of microsamples ensured that (in most cases) each annual increment in a section was represented by at least 2 or 3 microsamples (seasons).

6.2.2. Analytical Techniques

A portion of each dentine powder sample was treated in a 0.2M HCl solution to isolate the organic (collagen) fraction. Samples were then centrifuged, rinsed, and freeze-dried at -40°C . The molar C/N ratio of all but 11 dentine collagen samples analyzed (total $n = 881$) was between 2.9 and 3.6, which is the normal range expected for collagen (e.g. DeNiro 1985). The 11 samples outside this range were included in the data set, because they deviated only slightly from the normal range (2.7 to 3.8; see Appendix I). Collagen samples were combusted in an automated Carlo-Erba device (Carlo Erba, Milan) and the resultant N_2 and CO_2 gases were introduced to a Finnigan MAT 252 Mass Spectrometer (Finnigan, Bremen) via a continuous flow inlet system, for measurement of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios, as well as elemental composition (%C, %N). Samples of ivory from SKU, TM, and WGR were also treated for analysis of the inorganic (carbonate) phase of dentine. Carbonate was isolated by treatment in a 1.5% sodium hypochlorite (bleach) solution (50% bleach, 50% water) to remove humics and other organic contaminants. Samples were then centrifuged, rinsed, and freeze-dried. Dentine carbonate $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ 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. Stable light isotope ratios are presented in conventional delta (δ) notation in parts per thousand (‰) relative to the VPDB standard ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) and the atmospheric N_2 standard ($\delta^{15}\text{N}$). Standard deviations of repeated measurements of international

and laboratory standards were less than 0.1‰ for $\delta^{13}\text{C}$ (collagen and carbonate), 0.3‰ for $\delta^{15}\text{N}$, and 0.2‰ for $\delta^{18}\text{O}$. All isotope data for ivory are provided in Appendix I.

Recent elevation of atmospheric CO_2 concentration ($[\text{CO}_2]_{\text{atm}}$), related primarily to fossil fuel combustion (especially during the latter half of the 20th century), has reduced the $\delta^{13}\text{C}$ of atmospheric CO_2 , and this change in isotopic baseline has, in turn, reduced plant and animal tissue $\delta^{13}\text{C}$ in terrestrial and aquatic organisms (e.g. Marino & McElroy 1991; Arens et al. 2000; Richards & Hedges 2003; Long et al. 2005). Thus, to account for the change in $[\text{CO}_2]_{\text{atm}}$ during the 20th century, dentine $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ values were adjusted by applying a correction factor for atmospheric CO_2 $\delta^{13}\text{C}$ (Long et al. 2005; based on data from Francey et al. 1999, and Keeling & Whorf 2005):

$$\Delta\delta^{13}\text{C} = -5.5656 - e^{(6.0932 \times 10^{-5})t/2}$$

where t = year index (starting at 1880 where $t = 1$). The relevant year-specific correction factor was then added to raw $\delta^{13}\text{C}$ values (Fig. 6.2).

To interpret changes in diet along ivory profiles, carbon isotope data were used to estimate values for % C_4 grass in the diet, calculated using the dual-mixing model described in Chapter 4. For the model, diet-tissue fractionations were assumed to be +5.0‰ for collagen samples (e.g. Ambrose & Norr 1993), and +14.1‰ for $\delta^{13}\text{C}$ in carbonate (Cerling & Harris 1999; Passey et al. 2005). Plant values used to define dietary inputs are from Chapter 3 (mean $\delta^{13}\text{C}$ for C_3 vegetation = $-26.6\text{‰} \pm 1.4$ SD, $n = 1375$; for C_4 vegetation = $-12.7\text{‰} \pm 1.2$ SD, $n = 1038$). Statistical analyses of Kruger Park vegetation data showed that variations were small across a wide range of climatic, geological, and habitat conditions (see Chapter 3), and therefore these mean values can be used with confidence in the mixing model for long term diet in Kruger Park. Nonetheless, % C_4 grass intake values remain estimates, and are used here only to support interpretations of diet shifts evaluated based on $[\text{CO}_2]_{\text{atm}}$ -corrected $\delta^{13}\text{C}$ values.

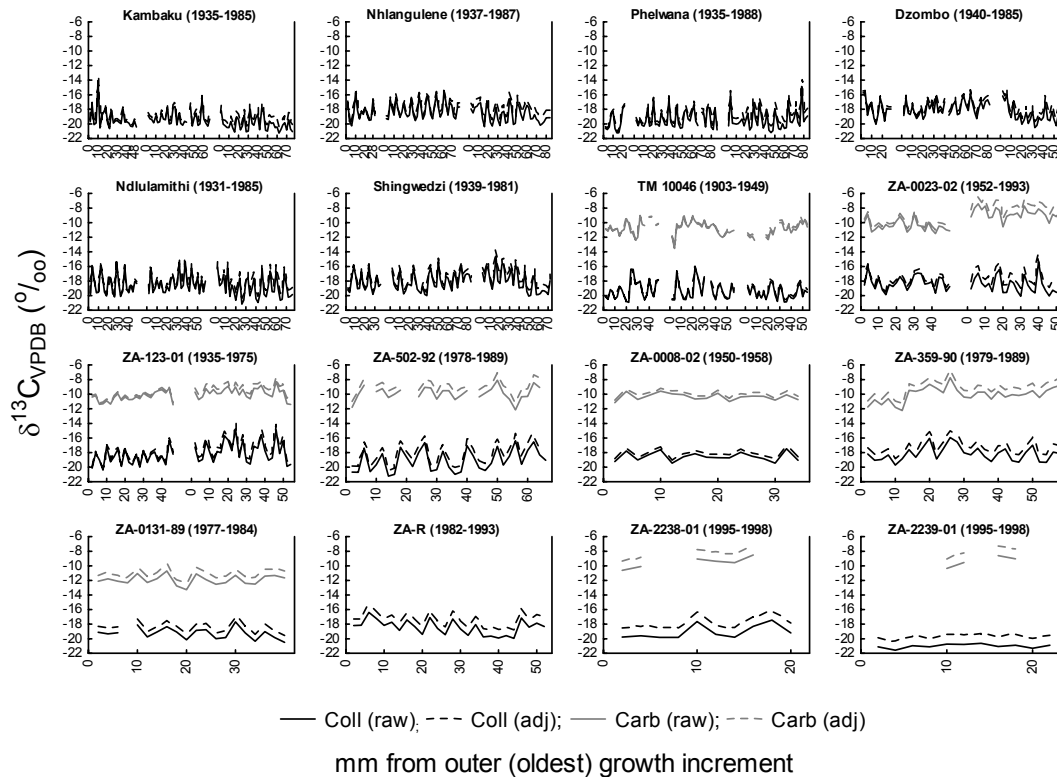


FIGURE 6.2. – Stable carbon isotope profiles in elephant ivory collagen and carbonate, showing the correction curve for 20th-century ¹³C-depletion of atmospheric CO₂ (based on the model of Long et al. 2005).

6.2.3. Statistical Treatment of Isotope Profiles

Diet histories for each individual were evaluated visually (graphically) by plotting the $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$, as well as $\delta^{15}\text{N}_{\text{collagen}}$ and $\delta^{18}\text{O}_{\text{carbonate}}$, profiles through time. The time period represented per microsample was estimated by microscopic counts of annual and seasonal (dry or rainy) growth bands, and chronologies based on the death of the animal and/or ¹⁴C AMS dates (Table 6.1; see also Chapter 5). These plots facilitated evaluation of the magnitude and timing of dietary changes within individuals, and I focus discussions on individuals whose life histories (age, ranging patterns, behaviour, etc.) are known (primarily the LEH individuals; Anon, anecdotal records).

To test hypotheses for environmental effects (e.g. diet, climate, and competition with sympatric herbivores) on isotope abundance variations in ivory, a cumulative approach was used to test for global effects based on significant correlations recorded at the level of individuals. Significance levels of correlation coefficients for each individual were obtained using the classical Student t-test. Overall significance of correlations between different variables was estimated with the Fisher global probability test (Fisher 1932; Loughin 2004). Fisher’s method is based on the observation that, if n independent tests are made of the same null hypothesis, resulting in the P probability values P_1, P_2, \dots, P_n , then the quantity is

$$\sum_{i=1}^n (-2 \ln P_i)$$

distributed as an χ^2 with $2n$ degrees of freedom. This provides a combined P value for all n tests (significance level $P = 0.05$).

To improve confidence in results, the possibility of serial correlation (autocorrelation) between sequences was also taken into account. If unaccounted for, serial correlation would make the statistical tests less stringent. That is, the null hypothesis could be incorrectly rejected with a probability greater than the nominal significance level. One way to deal with serial correlation is to estimate an effective sample size from the autocorrelation properties of the time series (Dawdy & Matalas 1964). Since the time series (composed here of yearly averages) for individuals are very short, only first-order serial correlations (dependence on lag-1 only) were considered. In other words, only the effect of year to year “memory”, or simple persistence, was taken into account. The effective sample size is defined as $N_{eff} = N(1 - r_x r_y) / (1 + r_x r_y)$, where r_x and r_y are the first-order autocorrelation coefficients of the time series x and y of length N (Dawdy & Matalas 1964). The significance level of the correlation is obtained by using the effective sample size (N_{eff}) instead of the sample (n) in the Student t-test.

This method was used to estimate the significance levels of the correlation coefficients between all the couples in the isotopic time series ($\delta^{13}\text{C}_{\text{collagen}}$ with $\delta^{13}\text{C}_{\text{carbonate}}$, $\delta^{13}\text{C}_{\text{collagen}}$ with

$\delta^{15}\text{N}_{\text{collagen}}$, and $\delta^{13}\text{C}_{\text{carbonate}}$ with $\delta^{18}\text{O}_{\text{carbonate}}$), as well as between each of the isotopic variables with long-term climate (annual rainfall in mm; temperature in mean maximum daily $^{\circ}\text{C}$, yearly; and $[\text{CO}_2]_{\text{atm}}$ in ppm) and herbivore population series (numbers of elephant, buffalo, blue wildebeest, giraffe, kudu, and roan antelope per year). Climate data for Kruger Park and Welgevonden are from the South African weather Bureau (rainfall 1921-1998; temperature 1975-1998); global $[\text{CO}_2]_{\text{atm}}$ data are from Francey et al. (1999) and Keeling & Whorf (2005) (semi-continuous from 1903, and continuous from 1958 onwards); elephant population data are from Whyte (2001) and Whyte et al. (2003) (1903 to 1993; semi-continuous before 1967); and data for other Kruger Park herbivore species were supplied by N. Owen-Smith (1969 to 1993). In the case of relationships to elephant, buffalo, and wildebeest numbers, $\delta^{13}\text{C}_{\text{collagen}}$ was treated (statistically and graphically, see below) as the response variable because of the prediction that trends are a response to exploitation competition at intra- and interspecies levels. For the browsers (giraffe and kudu) and the rare grazer (roan antelope), $\delta^{13}\text{C}_{\text{collagen}}$ was treated as the effect variable, given the prediction that elephants impact negatively on these species, especially browsers.

On average, the effective sample size (N_{eff}) was 20% lower than the real sample size (n). It was therefore concluded that there is relatively low autocorrelation in the data set and that the statistical values presented for comparisons of serial data can be accepted with confidence. The global significance level was then estimated with the Fisher's test. Global trends are presented for visual effect by cross-matching individual profiles in time, and then calculating the overall mean, as well as means for dry and rainy/wet seasons per year (microsamples from dark and light 1st-order growth bands, respectively). This procedure also allowed for annual rates of change in diet (λ_t) to be computed from the $\delta^{13}\text{C}_{\text{collagen}}$ series:

$$\lambda_t = \left[\sum_{i=1}^k (\delta_{i(t-1)} - \delta_{i(t)}) / \delta_{i(t)} \right] / k$$

where t is time (the year), i the individual elephant, and k the number of elephants per t . Absolute annual changes in diet ($\Delta\%C_4$) are presented as

$$\Delta\%C_4 \text{ in diet} = |\%C_4 \text{ intake}_t - \%C_4 \text{ intake}_{t-1}|$$

where $\%C_4$ intake is estimated from $\delta^{13}C_{\text{collagen}}$ (see mixing model described above). The shape of the relationships between isotopic and environmental time series are shown using the best-fit (maximum adjusted R^2) derived from linear, exponential, and polynomial regressions, although the significance of these relationships are inferred only from results of the global tests.

Last, to test for effects of changes in management regime, the $\delta^{13}C_{\text{collagen}}$ series was compared with changes in elephant management, burning, artificial water provision, fencing, and tourism (Kruger Park individuals only, i.e. dates are from 1903 to 1993). These effects were discrete variables: pre- and post-elephant management era (1903-1966, 1967-1993, respectively); occasional burning (1903-1947), no burning (1948-1956), prescribed burning (1957-1992), and lightning fires only (1993); no/little water provision (1933-1961) and extensive provision (1962-1993); limited fencing (1903-1958), partially complete fencing (1959-1980), and complete fencing (1981-1993); and tourism as visitors per year (<38 000 until 1961; 38 000 to 60 000 from 1962-1988; and >60 000 from 1989-1993) (see Chapter 2). Effects of management on elephant diet were tested using one-way ANOVA to compare mean $^{13}C_{\text{collagen}}$ between the categories, and Tukey's post hoc HSD where multiple comparisons were necessary (P -level = 0.05).

6.3. Results

6.3.1. Stable Isotope Chronologies in Elephant Ivory

Carbon isotope profiles varied substantially both within and between individuals (Table 6.2; Figs. 6.3 to 6.5). $\delta^{13}\text{C}_{\text{collagen}}$ varied by up to 7.2‰ within an individual, and $\delta^{13}\text{C}_{\text{carbonate}}$ by up to 4.6‰. Overall, $\delta^{13}\text{C}_{\text{collagen}}$ values ranged from -21.6‰ to -14.1‰ (mean = -18.8‰, $n = 881$), while the $\delta^{13}\text{C}_{\text{carbonate}}$ ranged between -13.4‰ and -6.4‰ (mean = -9.6‰, $n = 282$). These data correspond roughly to diet shifts of anywhere between ~20 to 45%, in terms of relative proportions of C_3 versus C_4 food consumption, within individuals. Most of this variation can be ascribed to seasonality in diet, i.e. higher $\delta^{13}\text{C}$ (and hence higher C_4 grass consumption) is associated with microsamples representing wet season growth. Indeed, mean $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ for microsamples representing wet season growth (light portions of annual ivory bands) were 1.0 to 2.0‰ higher than the means representing dry season growth (dark bands) in each individual ($P < 0.0001$), implying dry-to-wet season increases in C_4 consumption. Moreover, in more than 90% of cases the $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ values corresponding to light bands were higher than the value associated with the preceding dark band. Overall, the regularity of sinusoidal patterning within each of the profiles strongly supports that these diet reconstructions are seasonal. The seasonal regularity recorded was likely because each microsample represents approximately 13 weeks' growth (~ three months, or one season).

The $\delta^{13}\text{C}_{\text{carbonate}}$ profiles of individuals showed annual and seasonal dietary changes similar to those observed in $\delta^{13}\text{C}_{\text{collagen}}$, demonstrating that both records track diet changes over the long term. However, in the carbonate series, $\delta^{13}\text{C}$ fluctuations occurred at lower amplitudes and frequencies than they did in the collagen series, and as a result there were differences between $\delta^{13}\text{C}_{\text{carbonate}}$ and $\delta^{13}\text{C}_{\text{collagen}}$ values that cannot be ascribed to differences in ^{13}C -discrimination alone (~14.1 versus 5.0‰, respectively). In 61% of microsamples (total $n = 282$), $\delta^{13}\text{C}_{\text{carbonate}}$ values were >9‰ higher (i.e. the expected spacing between collagen and carbonate;

see Lee-Thorp et al. 1989; Ambrose & Norr 1993) than $\delta^{13}\text{C}_{\text{collagen}}$ values (by up to 12.5‰), such that $\delta^{13}\text{C}_{\text{carbonate}}$ data reflected up to 32% more C_4 grass intake relative to $\delta^{13}\text{C}_{\text{collagen}}$ values for the same microsample. In 35% of cases, $\Delta_{\text{diet-carbonate}}$ was <9‰ (as low as 4.2‰), thus in these instances $\delta^{13}\text{C}_{\text{carbonate}}$ data reflect substantially less C_4 grass consumption than $\delta^{13}\text{C}_{\text{carbonate}}$ data. Only in 4% of cases was the estimated % C_4 grass intake the same in both phases of dentine. Despite these differences, the $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ series were significantly correlated in most individuals (Student t-test, $r^2 = 0.18$ to $r^2 = 0.61$; $P < 0.02$ to $P < 0.0001$) and the global relationship was significant (Fisher's Test $P < 0.0001$; Table 6.3; Fig. 6.6a).

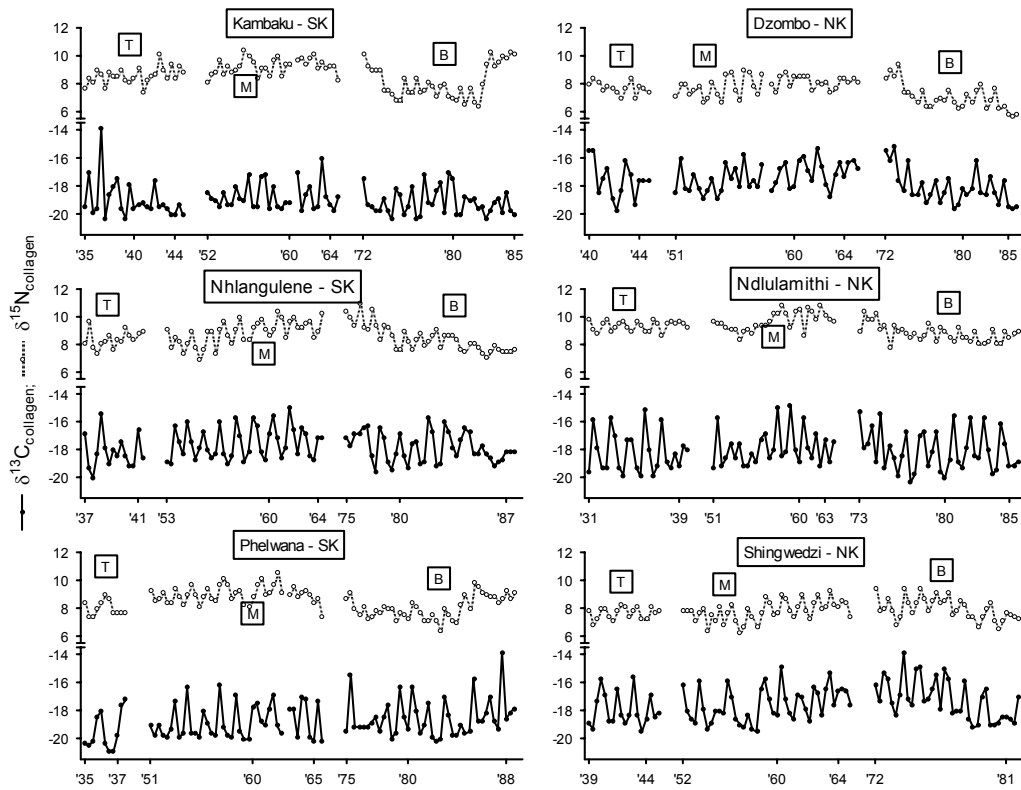


FIGURE 6.3. – Chronological $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}_{\text{collagen}}$ records from ivory of six elephant tusks in the Letaba Elephant Hall, Kruger Park. $\delta^{13}\text{C}$ values are adjusted for 20th-century ^{13}C -depletion of atmospheric CO_2 based on the model of Long et al. (2005). SK = animals that lived in the southern regions of Kruger Park, NK = animals from northern regions. T, M, and B indicate position of the sample along the longitudinal axis of each tusk, i.e. tip (oldest growth), middle, and base (recent growth).

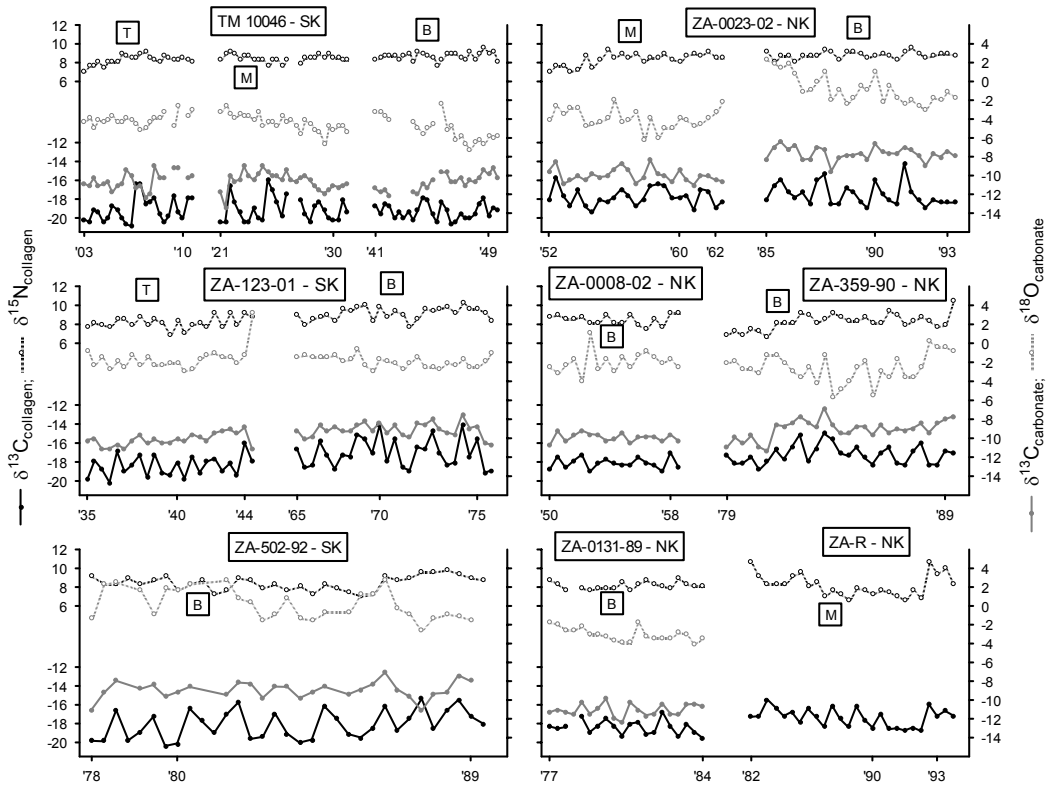


FIGURE 6.4. – Chronological $\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{15}\text{N}_{\text{collagen}}$, $\delta^{13}\text{C}_{\text{carbonate}}$, and $\delta^{18}\text{O}_{\text{carbonate}}$ records from ivory of eight elephants from Kruger Park (one tusk from the Transvaal Museum, TM, and seven from the Skukuza stockpiles). $\delta^{13}\text{C}$ values are adjusted for 20th-century ^{13}C -depletion of atmospheric CO_2 based on the model of Long et al. (2005). SK = animals that lived in the southern regions of Kruger Park, NK = animals from northern regions. T, M, and B indicate position of the sample along the longitudinal axis of each tusk, i.e. tip (oldest growth), middle, and base (recent growth).

In both dentine phases, $\delta^{13}\text{C}$ profiles showed an increase in overall $\delta^{13}\text{C}$ through the sampled portion of their lives, some individuals showed a decrease, and some remained more-or-less static apart from their seasonal shifts (Figs. 6.3 to 6.5). Often, however, multiple individuals showed $\delta^{13}\text{C}$ increases (C_4 grass “peaks”) or decreases around similar times. For example, there was a common increase in $\delta^{13}\text{C}$ for multiple individuals during the late 1930s (e.g. Kambaku,

Nhlangulene, Phelwana), and a similarly common decrease in $\delta^{13}\text{C}$ was recorded for the early-mid 1970s (e.g. Kambaku, Dzombo, Ndulamithi) and again in the early 1990s (ZA-0023-02, ZA-R).

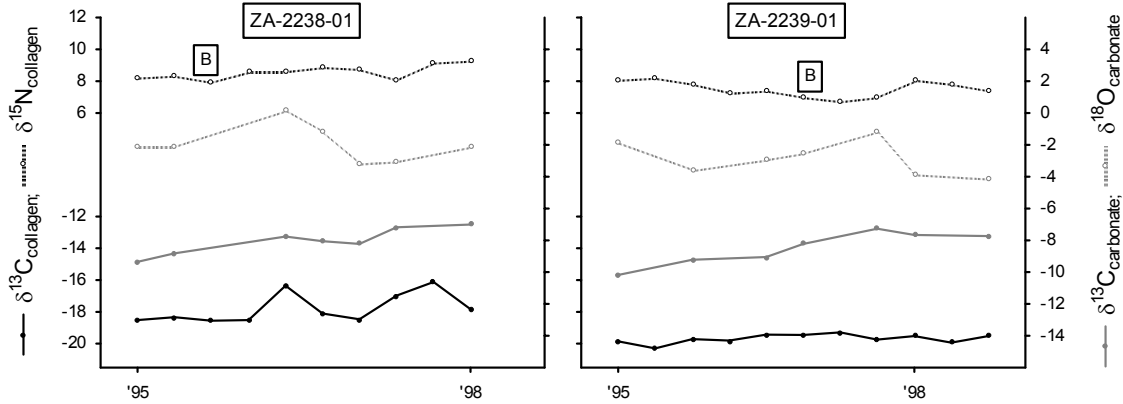


FIGURE 6.5. – Chronological $\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{15}\text{N}_{\text{collagen}}$, $\delta^{13}\text{C}_{\text{carbonate}}$, and $\delta^{18}\text{O}_{\text{carbonate}}$ records from ivory of two elephant tusks from Welgevonden Private Game Reserve. $\delta^{13}\text{C}$ values are adjusted for 20th-century ^{13}C -depletion of atmospheric CO_2 based on the model of Long et al. (2005). B indicates position of the section sampled along the longitudinal axis of each tusk, i.e. base (recent growth).

When individuals were cross-matched in time, the general trend revealed by both the collagen and carbonate $\delta^{13}\text{C}$ series was a slight, but significant (ANOVA, $P < 0.0001$), gradual shift towards increased C_4 grass intake through the 20th century (Fig. 6.6a). However, even though the $\delta^{13}\text{C}_{\text{carbonate}}$ series did show a greater overall shift compared with the $\delta^{13}\text{C}_{\text{collagen}}$ series, and the long-term record was sufficiently robust to persist for both dry and rainy seasons (Fig. 6.6b; $r^2 = 0.37$, $P < 0.0001$), the overall change was slight (~15% increase in % C_4 in diet since 1903). This is portrayed by relative stasis in the annual rate of $\delta^{13}\text{C}$ change within the collagen series (λ_t), which was maintained at or below 0.1 (diet shifts of less than 10% C_4 intake from year-to-year) almost all through the sequence (Fig. 6.6c).

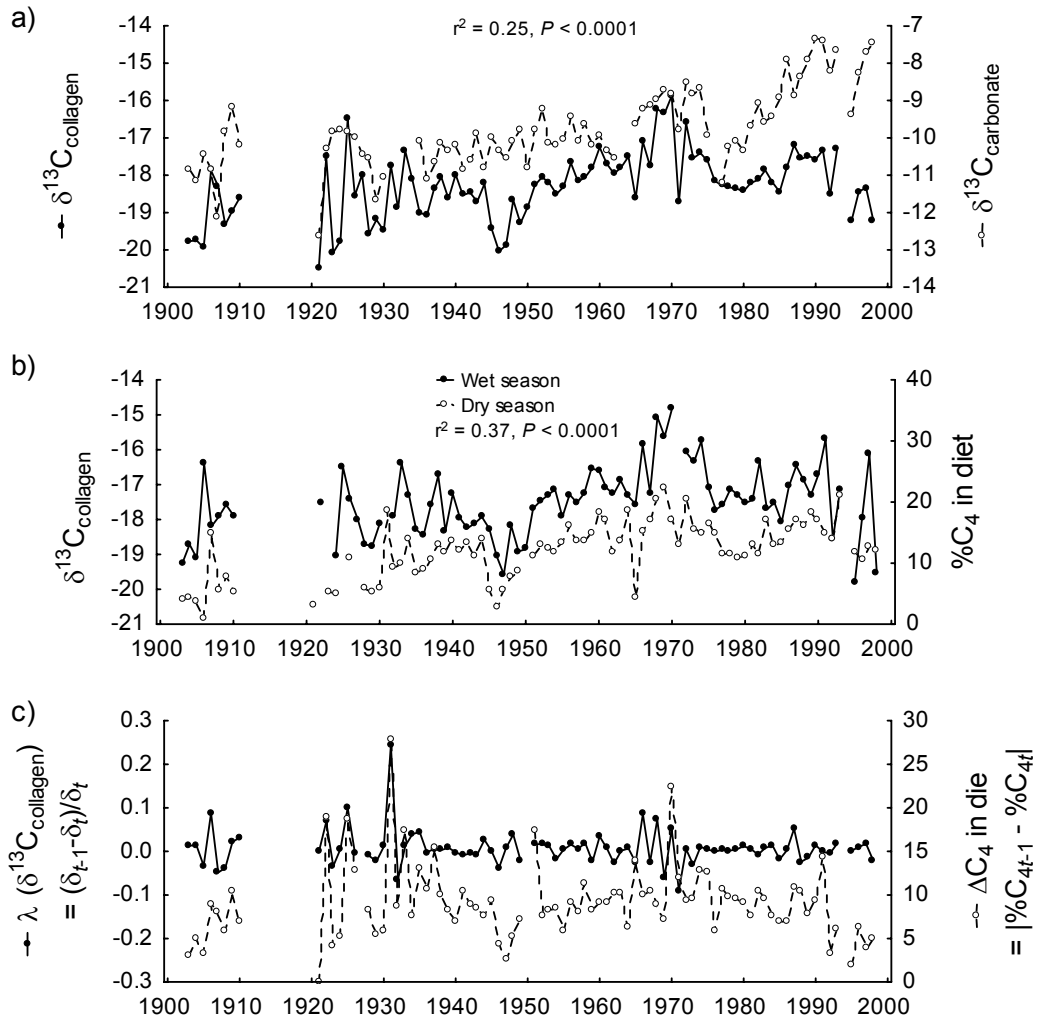


FIGURE 6.6. – Graphical representation of the overall 20th century diet history of elephants, showing a) a comparative record of mean annual changes in $\delta^{13}\text{C}$ between ivory collagen and carbonate; b) a seasonal record based on wet and dry season annual mean $\delta^{13}\text{C}_{\text{collagen}}$ (wet season = microsamples taken from ‘light’ portions/bands of 1st-order (annual) growth increments; dry season = microsamples from ‘dark’ bands); and c) proportional changes in mean $\delta^{13}\text{C}_{\text{collagen}}$ with corresponding absolute changes in mean estimated $\%C_4$ grass intake from year-to-year ($t = \text{year}$). All symbols represent means for all individuals per year. Relationships in a) and b) are presented as r^2 from simple linear correlations, but significance is based on cumulative P -values for each individual elephant (Fisher’s global test).

However, pronounced annual fluctuations were evident for at least two separate time periods. First, annual changes in $\delta^{13}\text{C}$ in the period before 1935 were larger than for most of the sequence, and appeared to represent cyclical diet shifts of $>10\%$ C_4 grass intake from year-to-year. This result could be due to the fact that the pre-1935 period is represented by only two individuals (Ndlulamithi and TM 10046), so that reducing annual trends across all individuals per year did not dampen the effects of intra-individual variability (as could be the case further on in the time series because averages were drawn from multiple individuals each year). Nonetheless, the perturbations leading up to 1935 are followed by a steady yearly increase in $\delta^{13}\text{C}$ until the late 1960s when the annual rate of change again fluctuated cyclically. After 1971, overall mean $\delta^{13}\text{C}$ (and hence C_4 grass intake) in fact decreased at a stable rate until the early 1980s, after which annual trends again became relatively stable.

Intra-individual differences in $\delta^{15}\text{N}_{\text{collagen}}$ ranged between ~ 1.0 and 4.0% (Table 6.2; Figs. 6.3 to 6.5). Mean $\delta^{15}\text{N}_{\text{collagen}}$ for individuals ranged between 7.5 and 9.3% , similar to values reported previously for elephants in Kruger Park and elsewhere (see Tieszen et al. 1989; Vogel et al. 1990a). Fluctuations in $\delta^{15}\text{N}_{\text{collagen}}$ were not significantly different between microsamples representing dry versus wet season growth (ANOVA $P = 0.17$), but $\delta^{15}\text{N}_{\text{collagen}}$ values did correlate (positively) with $\delta^{13}\text{C}_{\text{collagen}}$ in most individuals (Table 6.3), and thus a significant global relationship was found (Fisher's Test, $P < 0.0001$).

Intra-individual $\delta^{18}\text{O}_{\text{carbonate}}$ values varied by magnitudes of between 2.3 to 8.6% , although differences between the means for each individual were somewhat smaller (mean ranged from -4.5% in TM 10046 to 0.2% in ZA-502-92; Table 6.2; Figs 6.4 and 6.5). The $\delta^{18}\text{O}$ of sympatric herbivores in Kruger Park were not recorded, but all the elephants in this study had lower $\delta^{18}\text{O}_{\text{carbonate}}$ than herbivore species from a study area immediately to the west of Kruger Park (see Sponheimer & Lee-Thorp 2001). As was the case for $\delta^{15}\text{N}$, no significant seasonal change was recorded for ivory $\delta^{18}\text{O}_{\text{carbonate}}$ values (ANOVA $P = 0.81$). $\delta^{18}\text{O}_{\text{carbonate}}$ records of

individuals were not significantly correlated with their $\delta^{13}\text{C}_{\text{carbonate}}$ profiles, except in the cases of ZA-502-92 ($r = 0.60$, $P < 0.05$) and ZA-0023-02 ($r = 0.60$, $P < 0.001$). There was an overall significant relationship between the $\delta^{18}\text{O}_{\text{carbonate}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ series (Fisher's $P < 0.05$; Table 6.3), but this result is treated with caution as it originates from the very high significance level observed in the ZA-0023-02 series.

6.3.2. Relationships to Environmental Change

Climate

Ivory $\delta^{13}\text{C}$ series showed few significant correlations with annual rainfall records (with the exception of $\delta^{13}\text{C}_{\text{collagen}}$ in ZA-0008-02 where $r = 0.77$, $P < 0.001$), and hence there was also no global relationship with rainfall (Fisher's Test $P = 0.37$ and 0.59 for $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$, respectively; Table 6.4; Fig. 6.7a). There was also no significant effect of rainfall on $\delta^{15}\text{N}$, nor on $\delta^{18}\text{O}$ ($P = 0.98$ and 0.25 , respectively; Figs 6.7b & c). Similarly, changes in temperature had no significant effect on either of the isotopic series (Figs 6.7d-f). However, 20th century changes in atmospheric $[\text{CO}_2]$ correlated significantly with all isotopic series (Fisher's global test $P < 0.001$ in all cases; Table 6.4; Figs 6.7g-i). This relationship is shown to be positive with $\delta^{13}\text{C}_{\text{collagen}}$, but appears to be curvilinear based on 2rd-order (quadratic) polynomial regression ($R^2 = 0.62$); however, visual inspection of Fig. 6.7g suggests this relationship may in fact be asymptotic. The effect of $[\text{CO}_2]_{\text{atm}}$ on $\delta^{15}\text{N}$ appears to be polytonic (3rd-order polynomial $R^2 = 0.15$; Fig. 6.7h), while with $\delta^{18}\text{O}$ the shape is similar to that found for $\delta^{13}\text{C}$ (quadratic $R^2 = 0.37$).

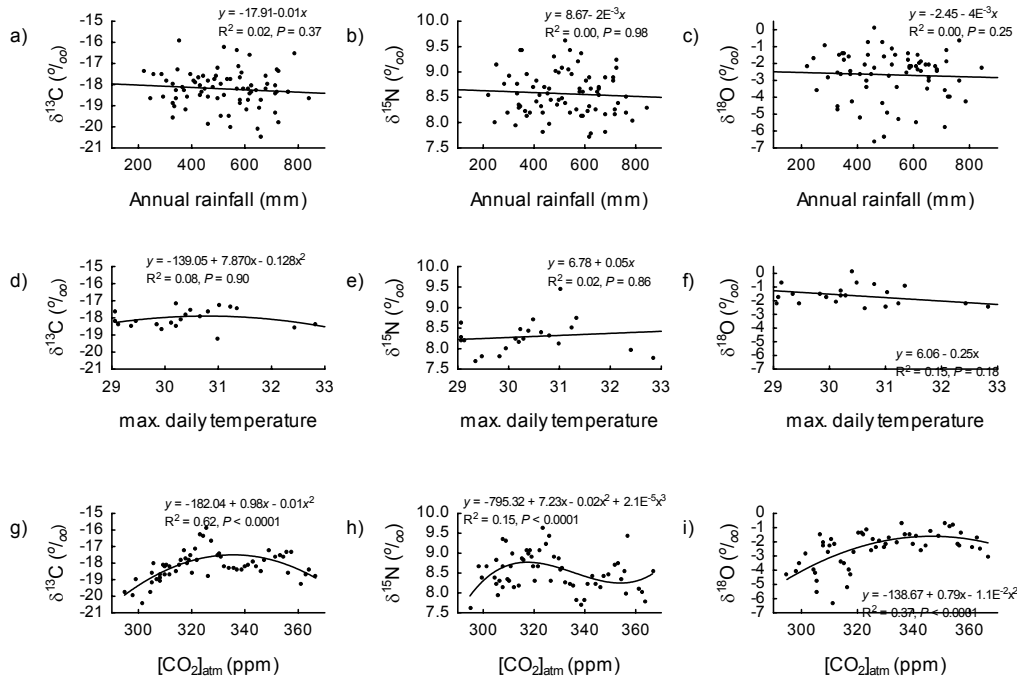


FIGURE 6.7. – Graphical representation of global relationships between isotope series ($\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{15}\text{N}_{\text{collagen}}$, and $\delta^{18}\text{O}_{\text{carbonate}}$) in elephant ivory with climate series for the 20th century: a, b & c) show relationships with annual rainfall; d, e & f) show relationships to annual temperature changes; and g, h, & i) show relationships to 20th century changes in $[\text{CO}_2]_{\text{atm}}$. Relationships are shown with best-fit (i.e. highest adjusted R^2) amongst linear, exponential, and polynomial regression models, where symbols represent annual means for all individuals, but overall significance of the relationships are based on cumulative P values for each individual elephant (Fisher’s global test).

Herbivore Abundances

The $\delta^{13}\text{C}_{\text{collagen}}$ series of very few individuals showed significant relationships to changes in herbivore (including elephant) population trends (Table 6.5). It is possible that this lack of significance is due to relatively short time series (small n), since herbivore numbers were, for the most part, available only from 1967 onwards. This is likely confirmed by the fact that global tests

revealed significant correlations between elephant diet with herbivore numbers in most instances (Fisher's P ranged from 0.03 to 0.10). Visually, the shape of these relationships appear to be non-linear, and coefficients of determination were weak in several instances ($R^2 = 0.09, 0.13,$ and 0.09 for the effects of elephant, buffalo, and wildebeest numbers on elephant diet; Figs 6.8a to c). The general pattern was that %C₄ grass intake increased with increased elephant and wildebeest numbers, but decreased with an increase in buffalo numbers. When the annual means of the $\delta^{13}\text{C}_{\text{collagen}}$ series were plotted as the predictor variable to test for effects of elephant diet on browser and roan antelope numbers, nonlinear, polytonic (cubic) relationships were apparent in all instances (Figs 6.8d to f). For the two browsers, giraffe and kudu, browser numbers were negatively correlated with elephant $\delta^{13}\text{C}$ for most of the series (i.e. positively related to elephant C₃ browsing), but when C₃ browse intake by elephants was high (low $\delta^{13}\text{C}$ to the left of the X-axis scale in Figs 6.8d & e), numbers of both browser species declined ($R^2 = 0.53$ and 0.38 , respectively). For roan antelope, a decline in numbers was observed in response to increases in ivory $\delta^{13}\text{C}$ (and hence elephant C₄ grass consumption), but the regression model predicts an increase in roan numbers at the highest levels of elephant grazing ($R^2 = 0.08$).

Management

There was a significant effect of all 5 management regime variables included in this study on $\delta^{13}\text{C}_{\text{collagen}}$ (elephant management $F_{1, 858} = 14.260$; burn policy $F_{3, 856} = 18.349$; water provision strategy $F_{1, 858} = 22.248$; fencing $F_{2, 857} = 20.838$; and tourism $F_{2, 857} = 11.881$; $P < 0.001$ in all cases). However, in most instances differences in mean %C₄ grass intake between management levels were negligible (less than 10%; Fig. 6.9). Viewed in this light, the only significant change in $\delta^{13}\text{C}_{\text{collagen}}$ that represents a true diet shift occurred between levels pre- and post-dating the 1960s, respectively (<10 % C₄ grass intake before 1960; 10 to 30% C₄ grass intake thereafter). Thus, these analyses confirm the overall trend of a significant increase in C₄ grass intake by

Kruger Park elephants through the 20th century, but it is not possible, based on these analyses, to determine which, if any, of the management variables impacted on diet.

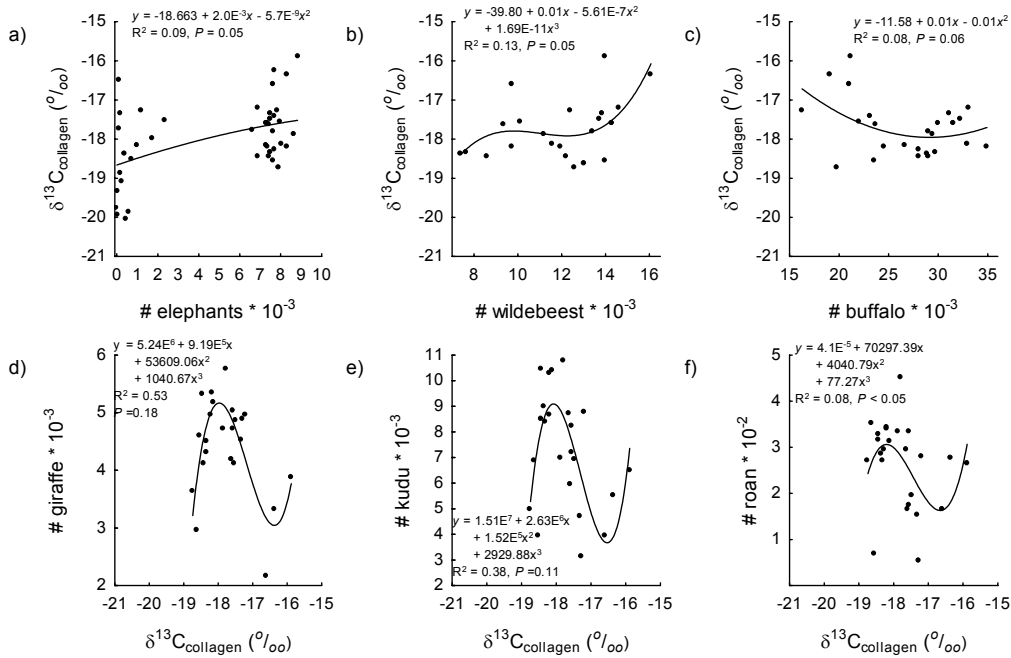


FIGURE 6.8. – Graphical representation of global relationships between elephant diet (ivory $\delta^{13}\text{C}_{\text{collagen}}$ series) with herbivore population trends in Kruger Park: a, b & c) show relationships with potential competitors at intra- and interspecific levels (wildebeest and bulk-grazing buffalo); d, e & f) show potential effects of elephant feeding ecology on abundances of sympatric browsers (giraffe, kudu) and rare grazers (roan antelope). Relationships are shown with best-fit (i.e. highest adjusted R^2) amongst linear, exponential, and polynomial regression models, where symbols represent annual means for all individuals, but overall significance of the relationships are based on cumulative P values for each individual elephant (Fisher’s global test).

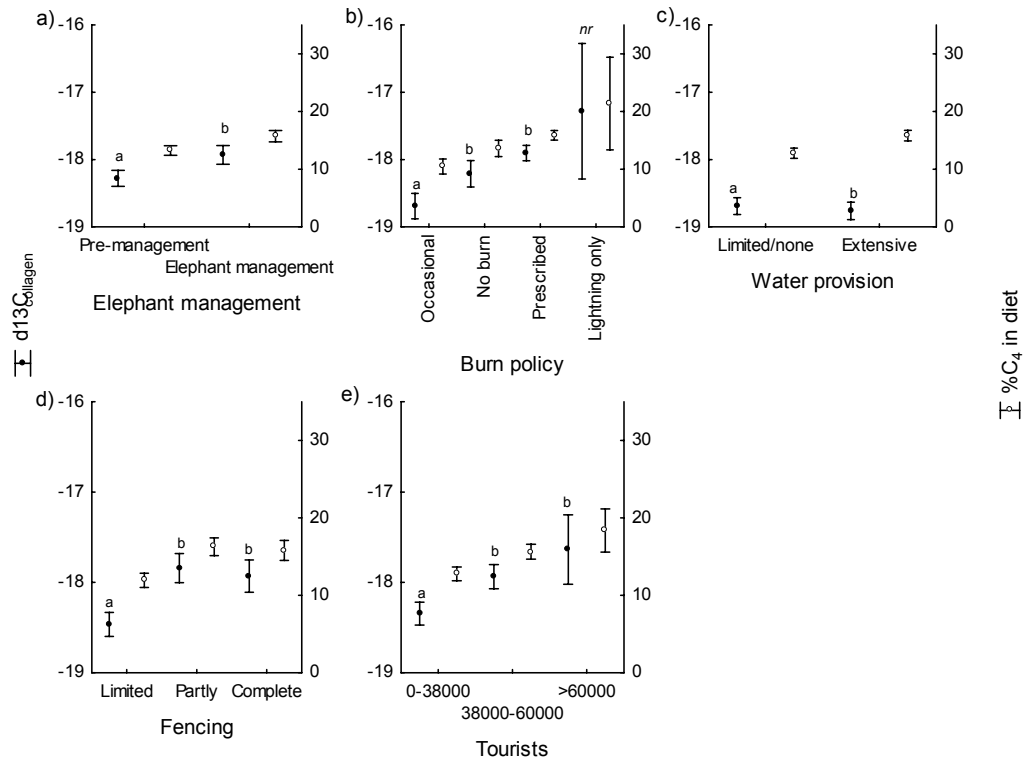


FIGURE 6.9 – Changes in $\delta^{13}\text{C}_{\text{collagen}}$ of ivory, and estimated $\%C_4$ intake, through time, in relation to different Kruger Park management regimes through the 20th century: a) pre- and post-population control regimes; b) four burning policies; c) artificial water provision policy; d) progress of fencing through the 20th century; and e) increase in annual tourists visiting Kruger Park over time. Alternate lettering (a, b) indicate significantly different sub-groups (ANOVA and Tukey’s post hoc for multiple comparisons, $P < 0.05$). *nr* = no result for post hoc test because sample size is too small ($n = 6$).

6.4. Discussion

6.4.1. Individual Life Histories

Stable isotope profiles, particularly $\delta^{13}\text{C}$ series, in elephant ivory recorded ecological and environmental shifts over multiple decades, at sub-annual (seasonal) resolution. The degree of variability in ^{13}C within individuals, demonstrates that elephant diets are extremely variable in terms of the proportions in which C_3 versus C_4 foods are consumed. Regular sinusoidal

fluctuations in $\delta^{13}\text{C}$ profiles along individual tusks indicate that the approach used here is sensitive to seasonality. Even after these seasonal effects are accounted for, annual and decadal scale changes amounted to diet shifts exceeding 30% in terms of $\text{C}_3:\text{C}_4$ intake within most individuals. Each of the individuals included in this study had different lifetime ranging patterns and other life history nuances, and accordingly each has a unique isotopic record. The implication is that broader notions about elephant feeding ecology, such as that grass consumption decreases with age (see Chapter 4 for results from hair; e.g. Sukumar et al. 1987; Sukumar & Ramesh 1992 for the Asian elephant; Koch et al. 1995), and increases with rainfall (e.g. Owen-Smith 1988; van der Merwe et al. 1988; Skinner & Smithers 1990; Codron 2004; Cerling et al. 2006; Codron et al. 2006), are not upheld at the intra-individual level over extended time periods. Thus, extrinsic environmental factors appear more important determinants of diet than biological life history traits such as age (except perhaps in very old individuals with worn teeth; see also Koch et al. 1995). Indeed, several individuals included in the current study, though showing non-uniformity in diets through time, all showed a decrease in $\delta^{13}\text{C}$ (and hence C_4 grass intake) towards the end (last 2/3 years) of life.

It is thus possible to link observed isotopic changes through time with individual life histories. I discuss the isotopic records of each individual below, starting with the six animals from the LEH, for which life histories are known from anecdotal evidence, followed by the individuals from the SKU and TM, and ending with the two juveniles from WGR.

Kambaku (1930 – 1985)

Kambaku's home range stretched from Satara/Orpen (south-central region) to the southern Kruger Park border at Crocodile Bridge (Fig. 6.10). The very high $\delta^{13}\text{C}$ recorded during the late 1930s could have been a response to the implementation of artificial water provision promoting the growth of nutritious grasses in surrounding areas (see Grant et al. 2002), which

started in the early 1930s. An abrupt increase in $\delta^{15}\text{N}$, coinciding with an equally abrupt decrease in $\delta^{13}\text{C}$, was recorded for Kambaku in 1982. Kambaku was known to spend much time alongside and around the Crocodile River, even crossing it from time to time and roaming into neighbouring sugar cane fields. The “new” isotopic values for this animal shortly before his death may reflect his apparent preference for the Crocodile River and similar habitats, notably in the form of a diet shift to include more C_3 reeds and sedges which are known to have higher $\delta^{15}\text{N}$ values higher than other plant types in Kruger Park (Codron et al. 2005). This behavioural change was likely a response to the prolonged drought of the early 1980s, but unfortunately, it was to be his downfall. Kambaku was eventually shot, but not killed, in the cane fields, suffering until being mercifully killed in late 1985 by Park officials.

Nhlangulene (1932 – 1987)

Nhlangulene for the most part frequented the western boundary of the Tshokwane/Satara sections in south-central Kruger Park (open savanna), where his home range was traversed only by a few visitors and a firebreak (Fig. 6.10). He also spent much time at the Nhlangulene “spruit” (stream), after which he was named. Nhlangulene’s home range, including the time spent by the spruit, explains the relatively high $\delta^{13}\text{C}$ (and hence high $\% \text{C}_4$ grass intake) during the wet seasons of his life, especially in the late 1930s (as noted for Kambaku as well). However, a diet change is recorded for the last two years of life (1985-1987), when Nhlangulene decreased overall C_4 grass intake to around only $\sim 15\%$ or less, regardless of season. Nhlangulene died of natural causes in 1987, at the age of 55 years. Death by natural causes is usually a result of the last set of molar teeth being worn down, which might explain the lack of grass in this animal’s diet shortly before death. Nhlangulene’s right tusk was shorter and lighter than the left, since he had broken it at some point earlier in life (the highest $\delta^{15}\text{N}$ value is noted for 1976, which could be a reflection of the stress associated with breaking the tooth).

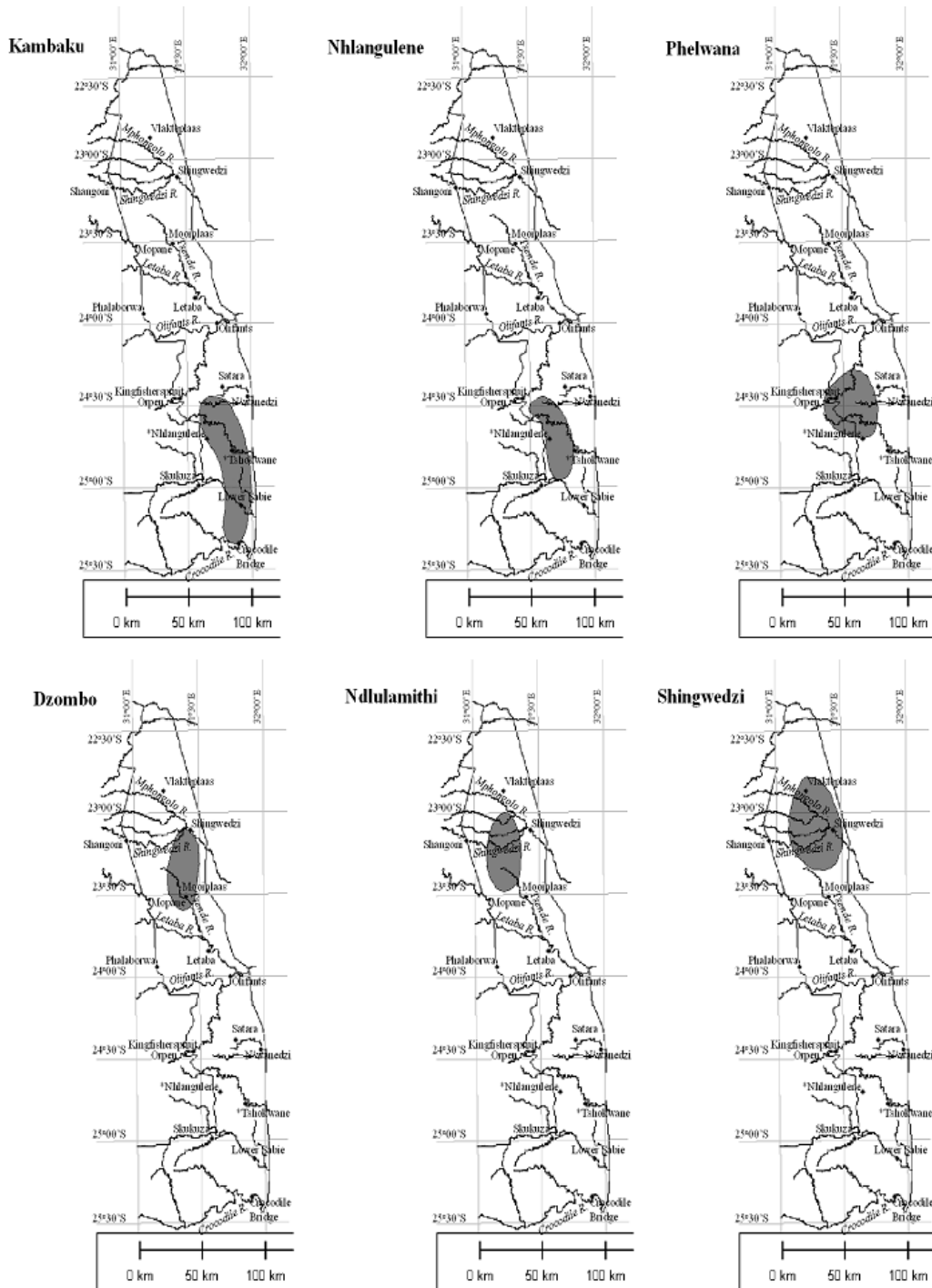


FIGURE 6.10 – Home ranges for six of the “Magnificent Seven” elephants that were analysed for stable light isotope ratios (Range information obtained from maps in the LEH, as recorded by section rangers and other field staff of the Kruger Park). Ranges are indicated by shaded areas; Place names are indicated by regular font; Tourist picnic areas are indicated by an * symbol; River names are italicized.

Phelwana (ca. 1930 – 1988)

Phelwana frequented the Kingfisherspruit region west of Satara (Fig. 6.10), and was named after a spruit that crosses the Satara/Orpen road. During the latter part of the 1980s Phelwana adopted a habit of breaking through the western boundary fence of the Kruger Park, and was often seen in the neighbouring Manyeleti Game Reserve, as well as other nature reserves in the vicinity. A change in Phelwana's diet is observed in 1985/6, when both the dry and wet season $\delta^{13}\text{C}$ values became higher than previously recorded. Similarly, an abrupt increase in Phelwana's $\delta^{15}\text{N}$ coincided with the overall increase in $\delta^{13}\text{C}$. These changes may imply an increase in C_4 grass consumption when visiting adjacent reserves, but it can also be an indication of crop raiding on neighbouring agricultural lands, especially because higher $\delta^{15}\text{N}$ values are often associated with artificially fertilized sources (Yoo et al. 1995). An alternative is that the vegetation in surrounding reserves has different isotopic compositions to that of the Kruger Park, although this is unlikely, given that the carbon isotopic variability within C_3 and C_4 plant groups throughout the Park are relatively small (see Chapter 3; Codron et al. 2005). In January 1988, Phelwana was found in a poor physical condition caused by a bullet wound to the neck (possibly from a farmer, if he was crop raiding, or from poachers). The shot had also shattered the lower jawbone, and accordingly Phelwana has very low $\delta^{13}\text{C}$ values for the year 1988, likely because the animal was forced to opt for less abrasive C_3 foliage rather than C_4 grasses.

Dzombo: 1935-1985

Dzombo's home range included the area bounded by the Tsende, Letaba, and Shingwedzi Rivers in northern Kruger Park (Fig. 6.10), and was most frequently seen along the grassy "vlei" (meadow) system of the Shawu valley. The $\delta^{13}\text{C}$ profile of this individual, which shows some of the highest values year-round, bears witness to high levels of C_4 grass consumption in these vleis. Since the early 1970s, however, Dzombo probably spent more time in the wooded parts of

his home range, as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values both decreased, indicating lower C_4 grass intake. This change in behaviour may have been a response to increased anthropogenic activities, e.g. the start of population control, increased tourism, and/or poaching. In fact, Dzombo was the only one of the “Magnificent Seven” to be killed by poachers.

Ndlulamithi (1927-1985)

Ndlulamithi’s home range included a large area between the main road from Mooiplaas to the western boundary of the Kruger Park, and stretched from Byashishi drainage system across to the Mphongolo River (Fig. 6.10). The $\delta^{13}\text{C}$ time-series for this individual shows a steady increase in C_4 grass consumption throughout life, but a decrease from about 1975 to the early 1980s, followed by a subsequent increase. Ndlulamithi was known as an aggressive, secretive elephant, and was seldom seen, thus the drop in $\delta^{13}\text{C}$ in late life is possibly because Ndlulamithi spent more time foraging in closed/wooded areas where grass production may have been lower than in the drainage lines. On the other hand, he may have been responding to extrinsic factors that resulted in most individuals lowering C_4 grass consumption during the 1970s.

Shingwedzi (1934-1981)

Shingwedzi frequented the northeastern Northern Basalt Plains (NBP) of Kruger Park, moving as far east as the Lebombo Mountain range bordering Mozambique, although he sometimes moved as far west as Nkokodzi and Chugamila hills (Fig. 6.10). At the time of death, the last molar tooth was well worn, corresponding to a steady decrease in $\delta^{13}\text{C}$ (and hence C_4 grass consumption) from the late-1970s and especially during the last two years of life (1980/1). The implication of this is that elephants can sense the diminishing occlusal function of their molars towards the end of their life and adjust their diets accordingly (D. Fisher 2008 pers. comm.) Prior to that, this individual shows a significant increase in $\delta^{13}\text{C}$ for about 15 years

(~1960 to ~1975), having some of the highest dry season $\delta^{13}\text{C}$ values of all the LEH individuals during this time. He is assumed to have died of natural causes, consistent with the very worn molar. Shingwedzi's right tusk had been broken off at some point in life. There is, however, no evidence of a stress period in $\delta^{15}\text{N}$ profile. This is surprising, given that the right tusk was the servant (working) tusk, and its breakage may be expected to have caused the elephant some distress.

Individuals from the Skukuza Stockpile and the Transvaal Museum: 1903-1993

The $\delta^{13}\text{C}$ records from single cross-sections, i.e. ZA-0131-89, ZA-0008-02, ZA-502-92, ZA-359-90, and ZA-R, show similar patterns of seasonal change in C_4 -grass consumption, and response to certain environmental conditions, as do all the other individuals (Fig. 6.4). For example, individuals ZA-131-89 (1977-1984) and ZA-R (1982-1993) showed a consistent decrease in $\delta^{13}\text{C}$, both records coinciding with an extended dry period (below-average rainfall) in Kruger Park from ca. 1980 to 1995. In 1993, however, a substantial increase in $\delta^{13}\text{C}$ is noted for individual ZA-R, despite the fact that this year was even drier than the preceding one (mean annual rainfall in 1993 was ~350 mm compared to ~460 mm in 1992). The record for individual ZA-0008-02 (1950-1958) corresponds with a dry period, which is reflected in its overall low $\delta^{13}\text{C}_{\text{collagen}}$, showing few seasonal shifts in the amount of C_4 grass eaten. Having only a single cross-section from each of these elephants provides a "snapshot" into the long-term diet, but does not allow for ascertaining whether other factors, such as age, may have played a role in the observed diet shifts of these individuals. Conversely, the two individuals for whom two cross-sections were obtained (ZA-123-01 and ZA-0023-02) showed an overall increase in $\delta^{13}\text{C}$ through time. Thus, the impression is created that the diets of some individuals (mainly the ones with single cross-section records) were not as variable as those of animals with longer-term records, e.g. the LEH individuals. However, individual TM 10046 (the only individual representing the

period before 1930) has an isotopic record as long as those of the LEH elephants, and shows no directional change in $\delta^{13}\text{C}$ composition through time. TM 10046 does, however, show more irregular year to year variations in $\delta^{13}\text{C}$ (as do LEH individuals for the period 1930 to 1935) than do other individuals representing the latter time periods of the 20th century. These changes between pre- and post-1935 coincide with the onset of more rigorous management regimes, and might therefore have substantial implications for elephant management protocol. This will be discussed in detail below.

Both the $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ results from SKU and TM individuals reveal elephants from northern Kruger to have slightly higher overall mean $\delta^{13}\text{C}$ than those from the south (mean $\delta^{13}\text{C}_{\text{collagen}} = -17.7\text{‰}$ and -18.4‰ , and mean $\delta^{13}\text{C}_{\text{carbonate}} = -9.6\text{‰}$ and -9.7‰ for north and south, respectively). These differences in the body tissues, although small, mirror those geographical differences in elephant faecal $\delta^{13}\text{C}$ between samples collected from northern and southern Kruger Park regions from 2002 to 2005 (see Chapter 4).

Juveniles from the Welgevonden Private Game Reserve: 1995-1998

The WGR individuals did not show much variability in their diets ($<1.0\text{‰}$ variations in $\delta^{13}\text{C}$ after the effects of season are taken into account). The Waterberg is a nutrient-poor, recovering, sourveld savanna environment, hence many grazers in this region such as buffalo and wildebeest supplement their diets with significant proportions of C_3 based browse foods (Codron, D. et al. 2005b). Similarly, results from elephant faeces suggest that in WGR they eat less C_4 grass (between ~ 10 and 20% of bulk) than they do in Kruger Park ($\sim 50\%$ in the wet season) (see Chapter 4; Codron 2004; Codron, D. et al. 2005b; Codron et al. 2006). Similarly, ivory $\delta^{13}\text{C}_{\text{collagen}}$ values for these two individuals, especially ZA-2239-01, suggest lower C_4 consumption than in Kruger Park individuals. Unfortunately, the time-series represented in their ivory samples does not extend as far back to the period prior to their translocation from Kruger Park (it was originally

hoped that these data would facilitate a test of the hypothesis that elephant diets remain the same even if they are relocated to new regions; Seydack et al. 2000).

6.4.2. Global Trends in Responses to Environment

Relationships between isotope chronologies in ivory with records of environmental change were inconsistent across the different individuals, confirming that intra-individual diet variations are significant in this species. Nonetheless, several statistically significant global trends are highlighted when cumulative probabilities of the various individuals were taken into account (Fisher's Global Test). These results highlight the significance levels of relationships between isotopic and environmental variability, and offer explanations for anomalies in the data. For example, the $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ series both recorded shifts in proportions of C_3 browse to C_4 grass consumption at annual and seasonal time scales, and the two series were strongly correlated. Despite this relationship, there were differences in $\delta^{13}\text{C}$ between the two series that often exceeded expected spacings based on different fractionation effects. The isotopic difference between $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ is expected to be about 9‰ (Lee-Thorp et al. 1989), since collagen is $\sim 5.0\%$ ^{13}C -enriched relative to diet (e.g. Ambrose & Norr 1993), while carbonate is $\sim 14\%$ ^{13}C -enriched relative to diet (Cerling & Harris 1999; Passey et al. 2005), although others have suggested that $\Delta_{\text{diet-carbonate}}$ may be slightly higher, depending on the species (Passey et al. 2005). Results of this study suggest that although both sources of information can be used to reconstruct diet histories, they do so in different ways. These differences can be attributed to differences in ^{13}C -compositions of body nutrient pools from which the materials are synthesized. Collagen represents the protein component of the diet most strongly, whereas carbonate provides a more integrated signal of whole diet (Ambrose & Norr 1993; Howland et al. 2003). The larger overall shift in the $\delta^{13}\text{C}_{\text{carbonate}}$ series could thus indicate under-representation of C_4 grass in body proteins, for example, if seasonal diet shifts to increased grass consumption were very short-lived,

and/or if elephants obtained less of their protein from C₄ grass foods than they did from C₃ browse, regardless of absolute intake of either food base. Alternatively, carbon in the mineral (carbonate) phase of ivory may undergo relatively slow turnover so that temporal cyclic fluctuations were dampened (see Ambrose & Norr 1993), but substantial differences in tissue turnover rates at time scales included here (six-monthly) are unlikely.

The lack of significant relationships between C₃:C₄ diet variations (in both the $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{carbonate}}$ series) with rainfall were unexpected, since rainfall is an important driver of soil fertility, grass regeneration, and grass productivity (Tainton 1999). These effects of rainfall are predicted to have important consequences for diet and, ultimately, regulation of herbivore populations (Coe et al. 1976; Owen-Smith & Ogotu 2003). Nonetheless, several previous studies have suggested that grass consumption by elephant and other herbivores varies independently of rainfall patterns (McCullagh 1969a; Laws et al. 1974; Short 1981; Koch et al. 1991; Steyn & Stalmans 2001; Codron, D. et al. 2006). But these findings are contrary to isotopic results from elephant faeces from Kruger Park, which revealed a strong positive (but asymptotic) relationship between C₄ grass intake with rainfall (Chapter 4). The implication is that while rainfall might have important outcomes for elephant diet over the short-term, e.g. through the seasonal cycle, effects are limited over longer time scales, including the near-decadal cyclical rainfall flux expected for the Kruger Park region (Tyson & Dyer 1975). Over the long-term, rainfall only appeared to influence elephant diets during climatic extremes, $\delta^{13}\text{C}$ series revealing C₄ grazing “troughs” during prolonged droughts (e.g. the 1980s) and “peaks” in flood years (e.g. 1925) for individual TM 10046.

The finding that rainfall cycles had minimal effects on elephant diet is exemplified by the fact that the global trend reveals a gradual, non-cyclical, increase in C₄ grass intake through the 20th century. This trend immediately implies a relationship to current and future global change trajectories. For example, rising ambient temperatures could be expected to improve the

nutritional value of C₄ grasses, because at higher temperatures grasses undergo slower growth and thus contain lower levels of fibre, especially indigestible lignin (Minson 1990; Ellery et al. 1995). Yet ivory data revealed no significant global relationship between elephant diet with temperature. Isotope series did, however, show strong significant relationships to changes in [CO₂]_{atm}, in that C₄ grass intake increased curvilinearly with increasing [CO₂]_{atm}. While this study is correlational in nature, there is good reason to suspect a functional mechanism to explain these relationships. At higher [CO₂]_{atm}, levels of carbon-based anti-herbivore defense compounds in C₃ plants increase (e.g. tannins; Lindroth & Dearing 2005); elephants may be compensating by switching their diets to include more C₄ grass. In addition, rising [CO₂]_{atm} levels should be favouring growth of C₃ above C₄ vegetation (Bond et al. 2003). In homogeneous woody landscapes, such as occurs in the *Colophospermum mopane*-dominated regions of the northern Kruger Park (Venter et al. 2003), a positive feedback mechanism between woody plant dominance and elephant C₄ grass intake could occur as elephants turn to grasses as an alternative food source to maintain dietary diversity and avoid ingesting toxic doses of homogeneous plant metabolites (Freeland et al. 1985). Indeed, models describing relationships between short term elephant diet variations with grass availability (based on rainfall trends) and grass nutritional value (based on %N content) both improved significantly, in terms of capacity to predict increases in C₄ grass intake, when the presence of mopane was included as an explicit parameter (see Chapter 4). This hypothesis is supported by the finding that ivory from individuals that lived in northern Kruger Park habitats had higher overall δ¹³C, revealing higher levels of C₄ grass consumption, than did those from the southern regions.

Isotope chronologies from elephant ivory also provide some evidence for the role of exploitation competition as a mechanism for diet variations. Significant global relationships were found for the δ¹³C_{collagen} series with changes in both elephant numbers, as well as numbers of sympatric grazers (wildebeest and buffalo). It has been proposed previously that large-bodied

grazers, particularly buffalo, have a competitive exclusion effect forcing elephants to switch to increased levels of browsing (Prins & Douglas-Hamilton 1990; Prins 1996; Van de Koppel & Prins 1998). De Boer & Prins (1990) reported elephants eating grass at grazing patches only when buffalo were absent in the preceding days. Even though their results were based on observational data over several days only, the negative relationship found between elephant C₄ grazing with buffalo abundances in the current study suggest that these competitive effects may be manifest over longer time-scales. Evidence also exists for competition for grazing resources between elephants and wildebeest (a true grazer species) (Beekman & Prins 1989; Dublin 1995, 1996; see also Van de Koppel & Prins 1998). However, the long-term sequence from ivory shows that elephants in fact had elevated dietary C₄ levels during periods of high densities of wildebeest. It is possible that these data represent a facilitative interaction, because grazing of short grasses by wildebeest stimulates growth of new, high quality grasses (*cf.* Van de Koppel & Prins 1998; Arsenault & Owen-Smith 2002). It is equally likely, however, that conditions favouring grazing by elephants also favoured wildebeest.

The relationships found for long-term elephant diet shifts with sympatric browsers (giraffe and kudu) are interesting, because the shape of the trend implies a common shift towards increased C₃ browsing by elephants occurring alongside increases in browser abundances. This contradicts proposals that elephants competitively exclude browsers (e.g. van Wyk & Fairall 1969; Laws 1970; Cumming et al. 1997; Fritz et al. 2002), but supports suggestions that they are facilitative, in fact improving browse availability (e.g. Skarpe et al. 2000; Rutina et al. 2005; Makhabu et al. 2006). Yet at high levels of C₃ browse consumption by elephants (i.e. for $\delta^{13}\text{C}_{\text{collagen}}$ values below $\sim -18.5\text{‰}$), there appeared to be a decline in browser densities. Again, while it remains that this study is a correlational approach to these ecological questions, these results do suggest that understanding elephant impacts on woody vegetation, and other species dependent on these resources, is highly dependent on the degree to which elephants are utilizing, and hence impacting on, woody plants. Disparity between proponents of elephant-induced

biodiversity loss versus arguments for elephant-induced biodiversity gain can now easily be ascribed to variations in elephant diet between the different regions and/or time frames over which studies are conducted. Unequivocal results can only be achieved through further investigation of long-term trends.

There was also a negative relationship between elephant C₄ grass consumption with densities of the grazing rare antelope species included here (roan antelope). Hypotheses for their decline include degradation of the grass layer, competition for grazing, loss of habitat and sufficient heterogeneity of habitat, and predation (Harrington et al. 1999; Grant et al. 2002; Kröger & Rogers 2006). The negative correlation between elephant $\delta^{13}\text{C}$ and roan antelope numbers might simply be a reflection of environmental forces that drove sympatric grazing ungulates to become more abundant, thus negatively affecting the more selective rare antelope species. Or, it might indicate that elephants themselves contributed to competition pressures on the rare species. This possibility, coupled with the suggestion put forward in Chapter 4 that elephants are primarily grazers if given the opportunity, suggests that elephant-grass interactions may have at least as many consequences to biodiversity as expected for their effects on woody vegetation.

Changes in management policy in Kruger Park during the 20th century may also have influenced elephant diets, but the analyses used here revealed only minor (if any) changes, and could not differentiate the importance of the different effects tested. Results do confirm a dietary difference before (<10% C₄ grass intake) to after (~15 to 30% C₄ intake) 1960. This finding may in itself represent a response to human activity, because management in Kruger Park intensified during the 1960s (see Chapter 2). Before this time, policy was less rigorous in terms of ecological understanding and final implementation, and before the proclamation of the Park in 1898 (see Chapter 2) human impacts on wildlife ecology would have been imposed by unregulated hunting, farming, etc.

Potential influences of management become more apparent by visual inspection of the long-term $\delta^{13}\text{C}$ record (Fig. 6.6). Despite the overall increase in C_4 grass consumption through the 20th century, the change is small (<20% at best), and year-to-year shifts are generally smaller. Figure 6.6c shows that for much of the century, $\delta^{13}\text{C}$ values usually changed by less than 0.1‰ of initial values from year-to-year, corresponding to annual diet shifts of less than 10% in C_4 consumption. However, there were two events in which this trajectory was substantially disrupted, i.e. the relative stasis of diet at annual scales changed to become a series of cyclical fluctuations to the order of 20-30% in terms of diet switching annually over several years. The first disruption occurs around 1935, when inter-year dietary variations decreased and annual diet shifts stabilized at a more-or-less constant rate of increase in C_4 consumption. This disruption suggests a shift from foraging in a more variable environment to one of reduced heterogeneity. Such an environmental effect has been suggested for Kruger Park since this period, owing largely to the initiation of artificial water supply programs, and less so controlled-burning regimes, since the mid 1930s (Pienaar 1983; Eckhardt et al. 2000; Gaylard et al. 2003). Construction of artificial watering points since that time is expected to have had two main outcomes. One, these promote the growth of palatable grasses in the vicinity, which attracts elephants and other grazer species, especially if natural surface water is scarce during dry periods (Grant et al. 2002; Gaylard et al. 2003; Chamaille-Jammes et al. 2007). Two, waterhole abundance reduced the functional heterogeneity of Kruger Park habitats, due to a much reduced proportion of areas more than 5 km away from water, and replacement of ephemeral streams with grazing lawns (Gaylard et al. 2003; Kroger & Rogers 2006). These changes could easily account for the fact that elephants appear to have been spending more time in open habitats since 1935, as well as for reductions in levels of dietary variability.

The second major disruption to the 20th century diet trajectory of elephants occurs in the late 1960s. This disruption entailed an initial shift to greater inter-annual oscillations in $\delta^{13}\text{C}$,

settling into a constantly declining C₄ grass intake level from 1971 for a further 10 years. By far the most substantial change to the Kruger Park elephant population around this time was the onset of population control programs (primarily through annual culling operations) in 1967 (see Chapter 2; Whyte 2001; Whyte et al. 2003). Little is known of the effects culling may have had on elephant ecology, especially feeding ecology, but the most parsimonious view to take here is that the culling programs directly influenced their diets. If so, culling may first have disrupted any stability in the dynamics of elephant-plant interactions, and secondly may have initiated an increase in the use of woody vegetation. This conclusion for the effects of culling would be in direct contrast to the primary incentive for population control, i.e. to alleviate elephant-induced pressure on woody vegetation. It is not unreasonable to propose that elephants would have targeted more sheltered, woody habitats during culling operations. This interpretation is supported by the fact that the 1970s were, for the most part, a period of above average rainfall (Tyson & Dyer 1975; Gertenbach 1983), which (even given the absence of a global relationship of diet with rainfall) is unlikely to have driven elephants to decrease their C₄ grass intake.

These arguments imply that management regime, rather than climate and biotic interactions, may have had the biggest influence on the ecological dynamics of Kruger Park's elephant population through the 20th century. It is possible, though, that the disruptions observed in the mid 1930s and late 1960s represent ~30-year cyclicality in elephant diet. However, available data for the first three decades of the 20th century (i.e. TM 10046, Ndlulamithi, Kambaku, Phelwana, Nhlangulele, Shingwedzi, and ZA-123-01 long-term profiles) imply that a highly variable diet was previously a persistent state (although data for multiple individuals are available only from 1930 onwards). Also, towards the end of the sequence (early 1990s), more pronounced oscillations again become evident (only 20 years after the previous disruption). At present, ivory data for the post-culling era (1994 onwards) are few (represented here only for the WGR individuals), but results from faeces suggest that C₄ grass intake has increased even further since the early 1990s (see Chapter 4; Codron 2004; Codron et al. 2006). In other words, it seems that

since the cessation of population control, these elephants have re-established an earlier trajectory of annually increasing C₄ grass consumption at a more-or-less stable rate.

6.4.3. A Source of Palaeoenvironmental Information?

Many studies use $\delta^{13}\text{C}$, and more so $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$, as climate proxies, especially for reconstructions of palaeoclimate records. Stable light isotope ratios are considered to reflect climatic and other environmental changes, as have been extracted from materials such as tree rings, ice cores, speleothems, and in animals including mammals (Talma & Vogel 1992; Dansgaard et al. 1993; Livingstone & Spittlehouse 1993; Lauritzen 1995; Thompson et al. 1995, 2002; Baker et al. 1997; Gröcke et al. 1997; Blünier et al. 1998; Dorale et al. 1998; Holmgren et al. 1999, 2003; Trudinger et al. 1999; Ammann et al. 2000; Masson et al. 2000; Steig et al. 2000; Levin et al. 2006). The lack of meaningful relationships of isotope profiles from elephant ivory with long-term climate records observed in this study implies that palaeoenvironmental reconstructions based on elephant isotope data, and likely other mammals as well, should be treated with caution. Indeed, there was even no significant effect of season (dry versus wet) on ivory $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ means.

Recent studies have shown that aridity and water stress seldom elicit predicted changes in ecophysiological fractionation of ^{15}N in mammals (Codron, D. et al. 2005b; Murphy & Bowman 2006; Codron, D. & Codron in press). A more important source of ^{15}N -abundance variations in mammals appears to be the variations that occur in the plant food base. Nonetheless, physiological fractionation of stable nitrogen isotopes does occur, but differential fractionation effects are founded primarily on the level of dietary proteins; in general, higher protein intake results in elevated body tissue $\delta^{15}\text{N}$ (Roth & Hobson 2000; Sponheimer et al. 2003a; Robbins et al. 2005). More precisely, elevated $\delta^{15}\text{N}$ occurs with consumption of proteins having greater metabolic value, i.e. a relatively larger proportion of proteins available to the animal for

metabolism (Robbins et al. 2005). This model could well explain why $\delta^{15}\text{N}$ in ivory profiles, while not fluctuating in response to climate, is related to changes in $\delta^{13}\text{C}$: where elephants increase C_4 grass consumption, the relative quality of their diets increases, as seen in correlations with faecal %N as a proxy for diet quality (Chapter 4). The relationship between $\delta^{15}\text{N}$ with $\delta^{13}\text{C}$ in ivory suggests a similar trend – the primary source of variation in ^{15}N -fractionation is the changes in the proportions of C_3 versus C_4 foods consumed, in turn representing shifts to diets on which elephants obtain maximum nutritive value (i.e. elevated C_4 intake).

In this study the long-term record of elephant $\delta^{18}\text{O}$ showed no relationship with rainfall trends, but a general increase in $\delta^{18}\text{O}$ seemed to track ambient temperature increases during the latter parts of the 20th century. The basis for models of relationships between mammalian $\delta^{18}\text{O}$ with climate is that herbivore tissues record the $\delta^{18}\text{O}$ values of meteoric water, which in turn reflects local climate conditions, the most influential factors being aridity and evaporation rates (Longinelli 1984; Luz & Kolodny 1985; Koch 1989; Koch et al. 1989, 1998; Bryant & Froelich 1995). The lack of fit between elephant $\delta^{18}\text{O}$ with rainfall at intra- and inter-individual levels suggests that ambient temperatures and resultant variations in evaporation rates have a more important effect. Levin et al. (2006) proposed that elephant ^{18}O -abundance variations are largely unaffected by changes in evaporation rate, based on results that suggested minimal regional shifts in elephant $\delta^{18}\text{O}$ after the isotopic composition of meteoric water is accounted for. If their model holds, then the high degree of $\delta^{18}\text{O}$ variations recorded in the current study must surely be due largely to environmental effects on the ^{18}O -composition of meteoric and standing water.

Environmental shifts may also influence plant ^{18}O -composition, and it is possible that the ivory records track (in part) these changes. For example, plants, especially C_4 plants, tend to show higher $\delta^{18}\text{O}$ under the influence of elevated ambient temperatures and humidity, because more ^{18}O -depleted water is lost via an increase in evapotranspiration rates (Gonfiantini et al. 1965; Yakir 1992). The net effect of higher plant $\delta^{18}\text{O}$ in hotter conditions can explain the trend of

increasing $\delta^{18}\text{O}$ with higher temperatures in elephant ivory. Similarly, because C_4 plants are shallow-rooted, they experience more water stress (hence more variable evapotranspiration rates) than do C_3 plants (Goldstein & Sarmiento 1987), and this might account for the effect of increasing $\delta^{18}\text{O}$ with temperature in ivory being consistent with the overall increase in $\delta^{13}\text{C}$ (i.e. C_4 consumption) through time.

6.5. Conclusion

This study confirms that isotope trajectories in ivory can reconstruct long-term diet shifts. Within one individual, records of up to 50 years were obtained, including annual and sub-annual/seasonal changes. Such long-term records for diet of any species are scarce, but here provided insights into the dynamics of elephant ecology, including the influence(s) of “natural” versus anthropogenic factors that are otherwise difficult to distinguish. Much of the interpretation presented in this chapter is nevertheless speculative because i) the data set includes a relatively small number of individuals (although this problem was partially alleviated by statistically removing autocorrelation effects and incorporating inter- and intra-individual variability in the models of diet change); and ii) the hypotheses put forward (with particular relevance to the effects of management regimes in Kruger Park) are unique, since no similar long-term, continuous records exist for this species. Mainly, while global trends are apparent in these data, it is difficult to differentiate environmental from biotic effects, as is often the case in the ecological literature. The approaches presented here suggest that, at least for some animal species, these scenarios can now be subject to further testing based on empirical evidence for long-term ecological change.

TABLE 6.1. – Individual elephants from which ivory samples were removed for this study, with the number of annual (first-order) and weekly (second-order) growth increments counted in each, and the number of growth increments represented in microsamples.

Individual	Section	Incremental growth bands			Microsamples			Years	
		Annual	Weekly	Weeks per year	Weeks per sample	Weeks per year sampled	Weeks		
Letaba Hall									
Kambaku (SK)	Tip	10	507	51	25	11	3	286	1935-1944
	Middle	13	656	50	33	11	3	354	<i>1952-1964</i>
	Base	14	692	49	38	13	3	488	1972-1985
Nhlangulene (SK)	Tip	5	263	53	15	10	3	157	1937-1941
	Middle	12	597	50	39	10	3	379	<i>1953-1964</i>
	Base	13	655	50	42	10	3	430	1975-1987
Phelwana (SK)	Tip	3	123	41	11	8	4	83	1935-1937
	Middle	15	749	50	43	12	3	513	<i>1951-1965</i>
	Base	14	743	53	42	11	3	460	1975-1988
Dzombo (NK)	Tip	5	247	49	14	11	3	159	1940-1944
	Middle	14	718	51	41	12	3	473	<i>1951-1964</i>
	Base	14	692	49	30	14	2	405	1972-1985
Ndlulamithi (NK)	Tip	9	466	52	24	14	3	335	1931-1939
	Middle	13	666	51	29	12	2	349	<i>1951-1963</i>
	Base	13	642	49	38	13	3	484	1973-1985
Shingwedzi (NK)	Tip	6	274	46	18	16	3	288	1939-1944
	Middle	13	660	51	42	9	3	363	<i>1952-1964</i>
	Base	10	507	51	36	11	4	391	1972-1981
TVL Museum									
TM 10046 (SK)	Tip	8	411	51	24	16	3	382	<i>1903-1910</i>
	Middle	10	494	49	28	13	3	377	<i>1921-1930</i>
	Base	9	433	48	27	16	3	432	1941-1949
Skukuza									
ZA-0023-02 (NK)	Middle	11	570	52	25	18	2	446	1952-1962*
	Base	9	421	47	27	13	3	344	1985*-1993*
ZA-123-01 (SK)	Tip	10	494	49	23	19	2	427	<i>1935-1944</i>
	Base	11	556	51	27	16	2	429	1965-1975*
ZA-502-92 (SK)	Base	12	587	49	33	13	3	430	1978-1989*
ZA-0008-02 (NK)	Base	9	423	47	17	21	2	361	1950-1958*
ZA-359-90 (NK)	Base	11	560	51	29	17	3	479	1979-1989*
ZA-0131-89 (NK)	Base	8	388	49	20	13	3	267	1977-1984*
ZA-R (NK)	Middle	12	611	51	26	27	2	694	1982-1993*
Welgevonden									
ZA-2238-01	Base	4	198	50	10	12	3	119	1995-1998
ZA-2239-01	Base	4	181	45	11	12	3	130	1995-1998

SK = southern Kruger Park; NK = northern Kruger Park; Dates: Regular font = birth/death date known; * = AMS confirmed date; Italicized font = time period estimated from date of birth and/or death and number of years in relevant section.

TABLE 6.2. – Mean and minimum-maximum range for $\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{15}\text{N}_{\text{collagen}}$, $\delta^{13}\text{C}_{\text{carbonate}}$, and $\delta^{18}\text{O}_{\text{carbonate}}$ extracted from serial microsampling of individual tusks. Estimated %C₄ grass in diet is calculated from $\delta^{13}\text{C}$ using a dual-mixing model.

COLLAGEN		$\delta^{13}\text{C}$ (corrected for CO ₂ change)				%C ₄ in diet				$\delta^{15}\text{N}$ (‰)			
Individual	<i>n</i>	Mean	Min	Max	Range	Mean	Min	Max	Range	Mean	Min	Max	Range
Kambaku (SK)	95	-19.0	-20.4	-13.8	6.6	8	0	45	45	8.6	6.4	10.5	4.0
Nhlangulene (SK)	96	-17.8	-20.0	-15.0	5.1	17	1	37	36	8.6	6.9	11.0	4.0
Phelwana (SK)	95	-18.8	-21.0	-13.8	7.2	10	0	45	45	8.5	6.5	10.6	4.2
Dzombo (NK)	84	-17.7	-19.8	-15.3	4.5	18	2	35	32	7.6	5.7	9.5	3.8
Ndlulamithi (NK)	91	-18.1	-20.4	-14.9	5.5	15	0	38	38	9.3	7.9	10.9	3.1
Shingwedzi (NK)	96	-17.5	-19.5	-13.8	5.7	19	4	45	41	7.9	6.2	9.5	3.2
TM 10046 (SK)	77	-19.2	-20.8	-16.0	4.9	7	0	30	30	8.5	7.0	9.6	2.6
ZA-123-01 (SK)	50	-17.7	-20.2	-14.1	6.0	18	0	43	43	8.8	7.0	10.4	3.4
ZA-502-92 (SK)	33	-18.1	-20.4	-15.4	5.0	14	0	34	34	8.5	7.1	9.9	2.8
ZA-0023-02 (NK)	52	-17.6	-19.5	-14.2	5.2	18	5	42	38	8.7	7.0	9.6	2.6
ZA-0131-89 (NK)	19	-18.4	-19.5	-16.8	2.8	12	4	24	20	8.2	7.8	9.0	1.2
ZA-0008-02 (NK)	17	-18.1	-19.0	-17.0	2.1	14	8	22	15	8.5	7.6	9.2	1.6
ZA-359-90 (NK)	29	-17.2	-18.8	-15.0	3.8	21	9	37	28	8.3	6.7	10.6	3.9
ZA-R (NK)	26	-17.3	-18.8	-15.5	3.3	21	11	33	22	8.3	6.7	10.8	4.1
ZA-2238-01 (WGR)	10	-17.8	-18.6	-16.1	2.4	17	11	29	18	8.6	7.9	9.3	1.4
ZA-2239-01 (WGR)	11	-19.7	-20.3	-19.3	1.0	3	0	6	6	7.5	6.7	8.2	1.5
<i>Combined</i>	<i>881</i>	<i>-18.1</i>	<i>-21.0</i>	<i>-13.8</i>	<i>7.2</i>	<i>14</i>	<i>0</i>	<i>45</i>	<i>45</i>	<i>8.4</i>	<i>5.7</i>	<i>11.0</i>	<i>5.3</i>

CARBONATE		$\delta^{13}\text{C}$ (corrected for CO ₂ change)				%C ₄ in diet				$\delta^{18}\text{O}$ (‰)			
Individual	<i>n</i>	Mean	Min	Max	Range	Mean	Min	Max	Range	Mean	Min	Max	Range
TM 10046 (SK)	72	-10.6	-13.4	-9.0	4.4	11	0	22	22	-4.5	-7.3	-2.4	4.9
ZA-123-01 (SK)	50	-9.6	-11.1	-7.5	3.6	18	7	33	26	-1.7	-2.9	3.3	6.2
ZA-502-92 (SK)	28	-8.9	-11.1	-7.1	4.0	23	7	36	29	0.2	-2.5	2.9	5.4
ZA-0023-02 (NK)	52	-8.8	-11.0	-6.4	4.6	24	8	41	33	-2.3	-6.1	2.4	8.6
ZA-0131-89 (NK)	20	-11.1	-12.4	-9.9	2.6	8	0	16	16	-3.0	-3.9	-1.6	2.3
ZA-0008-02 (NK)	17	-9.9	-10.8	-9.2	1.6	16	9	21	12	-1.9	-3.8	1.1	4.9
ZA-359-90 (NK)	29	-9.1	-11.4	-6.8	4.6	22	5	38	33	-2.5	-5.7	0.4	6.1
ZA-2238-01 (WGR)	7	-8.1	-9.4	-7.0	2.3	29	20	37	17	-1.9	-3.2	0.3	3.5
ZA-2239-01 (WGR)	7	-8.5	-10.2	-7.3	2.9	26	14	35	21	-2.9	-4.2	-1.1	3.0
<i>Combined</i>	<i>282</i>	<i>-9.6</i>	<i>-13.4</i>	<i>-6.4</i>	<i>7.0</i>	<i>18</i>	<i>0</i>	<i>41</i>	<i>41</i>	<i>-2.5</i>	<i>-7.3</i>	<i>3.3</i>	<i>10.6</i>

NK = northern Kruger Park; SK = southern Kruger Park; WGR = Welgevonden Private Game Reserve

TABLE 6.3. – Correlation co-efficients for relationships between stable isotopes in ivory profiles, based on the Students t-test. Global relationships are tested using Fisher’s global test. Significant correlations are indicated as bold text.

Variables:	$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{15}\text{N}_{\text{collagen}}$		$\delta^{18}\text{O}_{\text{carbonate}}$	
	$\delta^{13}\text{C}_{\text{carbonate}}$		$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{carbonate}}$	
Individual	r	P	r	P	r	P
Kambaku (SK)	-	-	0.00	1.00	-	-
Nhlangulene (SK)	-	-	0.04	0.05	-	-
Phelwana (SK)	-	-	0.08	0.01	-	-
Dzombo (NK)	-	-	0.47	0.00	-	-
Ndlulamithi (NK)	-	-	0.04	0.05	-	-
Shingwedzi (NK)	-	-	0.52	0.00	-	-
TM 10046 (SK)	0.01	0.37	0.01	0.54	0.00	0.93
ZA-123-01 (SK)	0.61	0.00	0.16	0.02	0.04	0.19
ZA-502-92 (SK)	0.14	0.05	0.28	0.01	0.16	0.03
ZA-0023-02 (NK)	0.18	0.00	0.03	0.21	0.60	0.00
ZA-0131-89 (NK)	0.35	0.01	0.19	0.06	0.00	0.95
ZA-0008-02 (NK)	0.32	0.02	0.11	0.19	0.01	0.66
ZA-359-90 (NK)	0.40	0.00	0.20	0.02	0.02	0.43
ZA-R (NK)	-	-	0.56	0.00	-	-
ZA-2238-01 (WGR)	0.38	0.14	0.08	0.43	0.00	0.94
ZA-2239-01 (WGR)	0.15	0.38	0.43	0.03	0.01	0.83
Fisher global test		0.00		0.00		0.02

SK = southern Kruger Park; NK = northern Kruger Park; WGR = Welgevonden Private Game Reserve

TABLE 6.4. – Correlation co-efficients for relationships between stable isotopes in ivory profiles with 20th century climate and [CO₂]_{atm} change, based on the Students t-test. Global relationships are tested using Fisher’s global test. Significant correlations are indicated as bold text.

Effect: Response variable: Individual	Rainfall (annual mm)				Temperature (Max °C)				[CO ₂] _{atm} (ppm)			
	$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{15}\text{N}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{15}\text{N}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{15}\text{N}_{\text{collagen}}$	
	r	P	r	P	r	P	r	P	r	P	r	P
Kambaku (SK)	0.01	0.63	0.00	0.93	-0.19	0.57	0.10	0.78	-0.31	0.10	-0.22	0.25
Nhlangulene (SK)	0.00	0.91	0.00	0.81	-0.40	0.18	-0.07	0.82	-0.38	0.07	-0.42	0.04
Phelwana (SK)	0.04	0.27	0.00	0.81	0.13	0.65	0.01	0.96	0.43	0.03	-0.33	0.10
Dzombo (NK)	0.00	0.79	-0.02	0.45	-0.05	0.94	0.25	0.68	-0.44	0.03	-0.61	0.00
Ndlulamithi (NK)	-0.03	0.32	-0.02	0.44	0.09	0.89	-0.01	0.98	0.07	0.72	-0.60	0.00
Shingwedzi (NK)	0.00	0.73	-0.02	0.52	-	-	-	-	0.25	0.25	0.14	0.54
TM 10046 (SK)	-0.06	0.31	-0.02	0.61	-	-	-	-	0.50	0.12	0.61	0.05
ZA-123-01 (SK)	-0.07	0.22	-0.04	0.41	-	-	-	-	0.65	0.00	0.77	0.00
ZA-502-92 (SK)	0.00	0.85	0.00	0.88	0.29	0.37	0.32	0.31	0.72	0.01	0.41	0.19
ZA-0023-02 (NK)	-0.06	0.52	0.00	0.91	-0.33	0.38	-0.24	0.54	0.17	0.54	0.63	0.01
ZA-0131-89 (NK)	-0.10	0.18	-0.07	0.26	0.19	0.81	-	-	-0.59	0.12	0.43	0.28
ZA-0008-02 (NK)	0.77	0.00	-0.10	0.44	-	-	-0.18	0.82	0.99	0.08	0.98	0.14
ZA-359-90 (NK)	-0.20	0.17	-0.13	0.28	0.25	0.51	0.69	0.04	0.04	0.92	0.65	0.03
ZA-R (NK)	0.00	0.94	0.00	0.89	-0.33	0.29	-0.34	0.28	-0.55	0.06	-0.56	0.06
ZA-2238-01 (WGR)	0.14	0.62	0.36	0.40	0.34	0.66	0.61	0.39	0.44	0.56	0.98	0.02
ZA-2239-01 (WGR)	0.15	0.61	-0.03	0.82	0.36	0.64	-0.14	0.86	0.55	0.45	-0.17	0.83
Fisher global test		0.37		0.98		0.90		0.86		0.00		0.00

Response variable: Individual	$\delta^{13}\text{C}_{\text{carbonate}}$		$\delta^{18}\text{O}_{\text{carbonate}}$		$\delta^{13}\text{C}_{\text{carbonate}}$		$\delta^{18}\text{O}_{\text{carbonate}}$		$\delta^{13}\text{C}_{\text{carbonate}}$		$\delta^{18}\text{O}_{\text{carbonate}}$	
	r	P	r	P	r	P	r	P	r	P	r	P
	TM 10046 (SK)	0.00	0.95	0.00	0.88	-	-	-	-	-0.12	0.74	-0.63
ZA-123-01 (SK)	-0.07	0.26	-0.20	0.04	-	-	-	-	0.68	0.00	-0.34	0.18
ZA-502-92 (SK)	0.04	0.53	0.42	0.03	0.58	0.06	-0.13	0.70	0.36	0.27	-0.73	0.01
ZA-0023-02 (NK)	-0.10	0.17	0.00	0.91	-0.20	0.60	-0.43	0.25	0.93	0.00	0.73	0.00
ZA-0131-89 (NK)	0.00	0.94	0.05	0.58	-0.01	0.99	-0.26	0.74	0.50	0.20	-0.60	0.11
ZA-0008-02 (NK)	0.09	0.44	0.21	0.22	-	-	-	-	-0.72	0.49	-0.88	0.32
ZA-359-90 (NK)	-0.11	0.32	-0.01	0.78	0.40	0.29	-0.04	0.93	0.58	0.06	0.45	0.16
ZA-2238-01 (WGR)	0.35	0.40	-0.63	0.21	0.61	0.39	-0.78	0.22	0.95	0.05	-0.21	0.79
ZA-2239-01 (WGR)	0.74	0.14	-0.01	0.91	0.85	0.15	-0.13	0.87	0.89	0.11	-0.53	0.47
Fisher global test		0.50		0.25		0.26		0.18		0.00		0.00

SK = southern Kruger Park; NK = northern Kruger Park; WGR = Welgevonden Private Game Reserve

TABLE 6.5. – Correlation co-efficients for relationships between stable carbon isotope profiles of elephant ivory with changes in Kruger Park elephant and other herbivore abundances, based on the Students t-test. Global relationships are tested using Fisher’s global test. Significant correlations are indicated as bold text.

Response variable:	Effect: #Elephants			#Buffalo			#Wildebeest			$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		
	$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		$\delta^{13}\text{C}_{\text{collagen}}$		#Giraffe		#Kudu		#Roan	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Individual																
Kambaku (SK)	-0.49	0.03	-0.13	0.67	-0.71	0.01	-0.58	0.06	-0.41	0.21	-0.59	0.04				
Nhlangulene (SK)	-0.15	0.55	-0.34	0.26	0.08	0.82	-0.15	0.66	-0.41	0.21	-0.24	0.45				
Phelwana (SK)	0.08	0.75	0.12	0.67	0.13	0.66	0.07	0.83	-0.04	0.90	-0.18	0.53				
Dzombo (NK)	-0.28	0.25	-0.41	0.15	-0.06	0.86	-0.69	0.02	-0.72	0.01	-0.44	0.15				
Ndlulamithi (NK)	0.15	0.53	-0.56	0.05	-0.01	0.98	-0.47	0.17	-0.64	0.05	0.05	0.88				
Shingwedzi (NK)	0.36	0.20	-0.62	0.05	0.36	0.42	-0.69	0.09	-0.67	0.10	-0.61	0.11				
TM 10046 (SK)	-0.26	0.61	-	-	-	-	-	-	-	-	-	-				
ZA-123-01 (SK)	0.69	0.02	-0.02	0.97	0.27	0.56	-0.15	0.74	-0.14	0.77	-0.28	0.55				
ZA-502-92 (SK)	-0.23	0.50	0.46	0.13	0.74	0.01	0.29	0.36	-0.08	0.80	-0.44	0.15				
ZA-0023-02 (NK)	0.50	0.08	0.59	0.10	0.44	0.24	0.16	0.67	0.33	0.39	0.45	0.22				
ZA-0131-89 (NK)	-0.35	0.43	0.61	0.11	-0.49	0.26	-0.35	0.44	0.36	0.43	-0.69	0.06				
ZA-359-90 (NK)	0.47	0.17	0.25	0.47	0.21	0.54	0.12	0.72	-0.22	0.51	0.14	0.67				
ZA-R (NK)	0.45	0.14	-0.13	0.69	-0.60	0.04	0.46	0.13	0.35	0.26	0.54	0.07				
Fisher global test		0.03		0.06		0.05		0.10		0.08		0.04				

SK = southern Kruger Park; NK = northern Kruger Park

- Chapter 7 -

Conclusion

This study is, to my knowledge, the first successful reconstruction of multidecadal diet records for individuals from a single population of extant African elephants. In addition, the approach used has provided detail about diet switching in this same population at ecological time scales (i.e. across space and through the seasonal cycle). Stable isotope compositions of elephant ivory, tail hair, and faeces were used to resolve questions raised in an earlier study (Codron 2004; Codron et al. 2006) regarding short-term (seasonal and spatial) variations in elephant diet within Kruger Park, and then to address the hypothesis that elephants adapt their diets to environmental change (natural and human-induced) over the long term. In this chapter I synthesize what has been learned in relation to the research objectives. Following that, I elaborate on some of the implications and applications of this thesis for predicting responses of elephants to environmental change, and for management and conservation policy development of elephants in the 21st century.

The use of stable isotope records to reconstruct elephant diets over ecological and long-term scales was strengthened by the extensive survey of variations in plant isotope composition. Contrary to many expectations, results showed that, in Kruger Park, environmental changes in baseline isotopic signatures were smaller than expected given the range of climate regimes and habitats in the Park (Chapter 3; see also Codron et al. 2005). These results also concur with a recently published synthesis for plants from across southern Africa (Swap et al. 2004), which found that rainfall variations have little effect on plant isotope composition. Thus, the plant study shows that animal isotopic data in Kruger Park are unlikely to be affected by environmentally-

induced variations in plants, and in turn, isotope-based reconstructions of diet could be made with high levels of confidence.

Before attempting to reconstruct and assess long-term diet shifts, this project studied feeding responses of elephants to landscape differences (i.e. geology and vegetation composition) and climate over the short term (seasonal), based on faecal and tail hair isotope data. An earlier, less rigorous study of elephant diet composition found dietary differences between northern and southern populations in Kruger Park (Codron 2004; Codron et al. 2006). This is because while elephants in the southern regions of Kruger Park show massive diet switches from the dry (~10% C₄ grass in diet) to the wet season (~50% grass), northern elephants maintain a relatively high grass intake year-round (~40-50%). The current study confirmed this pattern, but the latitudinal cline was not as continuous as predicted. At monthly scale, the timing of diet shifts can be seen, the increase from C₃ (browse)-dominated to more C₄ grass-rich diets in southern elephants generally occurring in the late dry/early wet season. These data also show more subtle variations in diet at higher spatial resolution than was previously available (central regions of Kruger Park included), which allows estimation of distinctness in elephant feeding ecology amongst different “sub”-populations. The updated faecal database shows that, besides a latitudinal gradient (i.e. a trend towards increased total grass intake, and decreasing seasonal heterogeneity, in diet from southern to northern Kruger Park), there was an influence of vegetational differences across longitudinal zones of differing geological substrate. For example, elephants in the regions underlain by southern granites (SG) and southern basalts (SB) showed similar ecological variations, but those on south-central granites (SCG) were very different from the south-central basalts (SCB), which in turn bore more similarities with the north-central granites (NCG). Multivariate analysis (treating monthly means as different variables) of the faeces data revealed at least four distinct elephant “diet-ecozones” within Kruger Park (Chapter 4), which should have useful implications for management policies in the Park (see below).

Along the chronological series of $\delta^{13}\text{C}$ in each elephant hair, wet season grazing “peak(s)” are observed, and are also evident in the monthly chronological sequences of faecal $\delta^{13}\text{C}$. Variations in $\delta^{13}\text{C}$ along individual hair strands show significant correlations with changes in faecal $\delta^{13}\text{C}$ at monthly scale. Hair $\delta^{13}\text{C}$ also followed the geographical patterns observed from faeces, in that hairs from northern Kruger Park individuals showed less variation in $\delta^{13}\text{C}$ (suggesting lower seasonal variability in their diets), higher grass intake in the dry season, and a higher overall $\delta^{13}\text{C}$ (i.e. higher overall grass intake), than did hairs from southern individuals. Apart from the gross north-south difference in grass intake, no differences were observed in the percentage grass content in the diets of male and female elephants of different ages within different regions of Kruger Park. Males and females did, however, differ overall, with females in Kruger Park having a marginally higher $\delta^{13}\text{C}$ ($\sim 0.5\%$), and therefore a slightly higher grass component in their diet than do males. Thus, geographical separation of populations (and less so age or sex) appears to be the most important predictor of diet composition in Kruger Park.

The second objective in this study was to test the factors that likely influence the observed north-south diet dichotomy in the Kruger Park elephants. It was predicted that elephant diet changes reflect changes in the relative nutritional value of available grasses, and the dominance of browse-deterring mopane in the north. This hypothesis was tested by comparing faecal and hair data at multiple landscape and seasonal scales. Trends within each landscape were contrasted against each other, as well as against climatic, nutritional (e.g. faecal %N), and other available information about differences in habitat composition. The emerging picture is that elephants appear to prefer grass above browse under most circumstances. Thus the effects of mopane acting as a browse-deterrent for elephants are probably less pronounced than the effects of factors such as the number of artificial waterholes, which promotes the growth and abundance of palatable grass species, thus favouring increased grass consumption.

Despite the above, the role of browse-deterrents as a limiting factor could not be ruled out (see Chapter 4). This finding is one of many results that clearly exemplify that elephant diets, and the processes that govern diet switching, can change substantially. The proportions in which browse and grass are consumed can change almost entirely across the browsers-grazer spectrum, depending on various factors, e.g. season, habitat, and nutrient availability. This switching likely changes the extent to which elephants alter habitat composition, since resultant effects will generally be greater when more woody plants are consumed (Styles & Skinner 2000; Scholes et al. 2003). In predicting the extent of impact to guide management policies, most models have *perforce* assumed a constant value for browse:grass intake, since few managers “on-the-ground”, and indeed researchers, have had access to sufficient data to predict dietary variation. One major implication of the current thesis is that isotopic techniques can fill the gaps faced by many previous studies, and if used correctly, can lead to improved models of impact and more ecologically-sound elephant management policies. For example, the spatial diversity in diet of the contemporary Kruger Park elephant population, as revealed by stable carbon and nitrogen isotope data from faeces, intuitively identifies and/or differentiates high versus low-impact zones. In Chapter 4, Fig. 4.5 shows higher browse consumption by elephants in areas like SG and SCG than on, for example, the NB and PM (even though PM is densely-wooded, even forested in places), thus one can predict higher impact on woody vegetation in the former regions. This offers a novel perspective in light of most recent policies for Kruger Park that aim to sub-divide the elephant population into zones of high- and low-impact on woody vegetation (see Chapters 2 and 4; Whyte et al. 1999; Whyte 2001). At present, this proposal rests on the assumption that higher elephant densities results in higher impact on woody vegetation (e.g. Scholes et al. 2003; Whyte et al. 2003), and therefore the management of these zones is intended to control elephant numbers in some areas (low impact) but not in others (high impact). Further, the spatial scales along which these zones are proposed are based mainly on the latitudinal gradient of the Park, and then loosely on elephant herd movement patterns and changes in vegetation composition, in

each region. While this approach may suffice for some purposes, the new data generated in this thesis certainly offers a viable alternative to develop improved management policies.

Serial microsampling of growth bands in ivory showed that lifetime isotopic histories can be reconstructed for individuals, and in turn these records can be matched with life history and/or environmental data (see Chapter 6). Despite the few individuals represented in this study, some commonality exists across individuals in terms of their response to environmental change events (and, in some cases, environmental trends). Hence, overlaying all individuals into one sequence could also be used as a preliminary assessment of changes at population level.

The main reason for extracting these long-term diet records was to test the hypothesis that diet switching follows climate (mainly rainfall) cycles, i.e. during wet periods elephants were expected to have consumed more grass, and during dry periods more browse. This hypothesis, prominent in the mammal herbivore literature, cannot be substantiated by ivory data for most individuals included here. There is a distinct lack of any significant relationship between elephant diet and rainfall at both intra- and inter-individual levels, across space (faeces and hair data) and through time (faeces, hair, and most importantly, the ivory profiles). If rainfall has had any effect on diet, it was a) seasonal, and b) by far not the most limiting factor, and its effects are only evinced during extreme events (such as eating more grass after floods, and less after droughts). The tendency for individuals to respond in similar ways during these climatic extremes, rather than responding uniformly to rainfall cycles over the long term, supports contemporary ideas that the most dramatic population-level responses to global change are likely to be event-based, as opposed to trend-based (Jentsch et al. 2007).

Hypotheses for competition from more stenotopic grazers like buffalo, that when present in high densities have been predicted to force elephants into a more browse-dominated feeding niche (e.g. de Boer & Prins 1990; Prins & Douglas-Hamilton 1990; Dublin 1996; Van de Koppel & Prins 1998), are also not supported in these data. In all, the hypothesis that cyclical changes in the Kruger Park environment have density-dependent limiting effects for elephant diet

must be rejected. Another hypothesis, i.e. that anthropogenic modifications to the environment, both locally (management) and globally, have had more far-reaching effects is considered here in detail.

The overall trend implied by the ivory data is a gradual, continuous increase in grass intake through the 20th century. It is possible that this increase was (and is) functionally related to effects such as increasing atmospheric CO₂ levels (and its associated effects on woody vegetation; e.g. Lindroth & Dearing 2005), increasing global temperatures (which may improve the nutritive quality of grasses; e.g. Minson 1990; Ellery et al. 1995), the number of waterholes constructed in the Kruger Park throughout most of the last century (and the associated increase in grazing lawns created around these waterholes; e.g. Grant et al. 2002; Gaylard et al. 2003; Chamaille-Jammes 2007; Codron, D. et al. 2007c), or even the different fire regimes through the 20th century (which are predicted to have had a deleterious effect on the woody vegetation, but improved the condition of the grass layer; e.g. Eckhardt et al. 2000).

Conversely, the trend of increasing grass intake may be part of a longer cycle, for example a 200-year stable limit cycle of grassland/woodland utilization by elephants, as proposed by Caughley (1976). There are, nevertheless, dynamics within this 100-year period that, based on the date of their occurrence, are of no small consequence. While there was relative instability in annual diet changes in the earliest decades of the 20th century, the steady rate of increase in grass consumption only becomes apparent after 1935, coinciding with the first major management developments in the Kruger Park, such as the “Water for Game Program”, controlled burning, and even the introduction of tourists into the reserve (Pienaar 1983; Joubert 1986; Foxcroft & Freitag-Ronaldson 2003). A second disruption in the long-term sequence occurs in the late 1960s in the form of a disturbance to the post-1935 diet trajectory, resulting in erratic annual diet shifts until 1971. After 1971, elephants settled on a more stable diet trajectory once more, but in this case decreasing grass intake for approximately ten years. Moreover, when one considers that the period ~1971-1981 was one of above-average rainfall, it becomes extremely difficult to conceive

that the disruption of the late 1960s and the proceeding decrease in grass intake were not somehow related to the onset of culling programs in 1967.

If the above patterns persist for more individuals, then a more robust data set for population level changes can be generated. Based on current evidence, some hypotheses can be put forward that will be testable as more individuals are added to the ivory database. With regards culling, two possibilities present themselves. First, this form of management appears to disrupt equilibria in elephant-plant interactions. Second, culling operations result in increased levels of woody plant consumption per capita, which is entirely contradictory to the desired effect of alleviating pressure on the woody vegetation. Prior to the onset of culling, elephants were on a trend of decreasing the amount of browse eaten, at least per individual. Indeed, such attempts to solve one ecological problem, but cascading in a series of other unpredictable events having even more detrimental consequences than the initial “problem” itself, are well-known from wildlife reserves across the globe (Sinclair et al. 2006).

To conclude, this study has justified the analytical investment in, and the use of, elephant ivory for experimental research (see also Van der Merwe et al. 1990; Vogel et al. 1990a, 1990b; Koch et al. 1995). It is proposed here that the scientific value of elephant ivory, clearly demonstrated in this thesis, far exceeds the notional monetary and aesthetic value so often associated with ivory (e.g. Barnes 1996; Burton 1999). Proposals of southern African countries to CITES to temporarily raise the ban on ivory trade and allow a once-off sale of ivory stockpiles, in some cases followed by annual harvest yields, remain heavily debated in the media and within conservation circles (e.g. Bulte & van Kooten 1999; Gillson & Lindsay 2003). While the debate swings back and forth between the potential financial gain that would be ploughed back into sustainable conservation efforts versus the effect that lifting the trade ban (even temporarily) might have on reviving illegal poaching activities and trade (see Bulte & van Kooten 1999), very little attention has been given to the scientific value ivory can offer to conservation (see also Koch et al. 1995; Cerling et al. 2007). Indeed, contrary to the opinions of officials and delegates

supporting the sale of stockpiles, such practices are likely to represent an unsustainable use of natural resources: the monetary gain from episodic ivory sales, even though it may be destined to finance local conservation activities, will be inevitably short-lived due to the nature of economics (Gillson & Lindsay 2003; see also Bond 1994; Child et al. 1997). Knowledge, on the other hand, lasts forever.

References

- Acocks, J.P.H. 1988. *Veld Types of South Africa*. Memoirs of the Botanical Survey of South Africa No. 57. 3rd Edition. Pretoria: Botanical Research Institute.
- Allen, J.L., Welsch, B., Jacobson, E.R., Turner, T.A., & Tabeling, H. 1984. Medical and surgical management of a fractured tusk in an African elephant. *Journal of the American Veterinary and Medical Association*. 185: 1447–1449.
- Ambrose, S.H. 1991. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. *Journal of Archaeological Science*. 18: 293-317.
- Ambrose, S.H., & DeNiro, M.J. 1986. The isotopic ecology of East African mammals. *Oecologia*. 69: 395-406.
- Ambrose, S.H., & Norr, L. 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J.B., & Grupe, G. (Eds.). *Prehistoric human bone: Archaeology at the molecular level*. Springer-Verlag, Berlin, Germany. pp. 1-37.
- Ammann, B., Birks, H.J.B., Brooks, S.J., Eicher, U., von Grafenstein, U., Hofmann, W., Lemdahl, G., Schwander, J., Tobolski, K., & Wick, L. 2000. Quantification of biotic responses to rapid climate changes around the Younger Dryas – a synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 159: 313-347.
- Arens, N.C., Jahren, A.H., & Amundson, R. 2000. Can C3 plants faithfully record the carbon isotopic composition of atmospheric carbon dioxide? *Paleobiology*. 26(1): 137-164.
- Arman, P., Hopcraft, D., & McDonald, I. 1975. Nutritional studies on East African herbivores. 2. Losses of nitrogen in the faeces. *British Journal of Nutrition*. 33: 265-276.
- Arsenault, R., & Owen-Smith, N. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos*. 97: 313-318.

- Astle, W.L. 1971. Management in the Luangwa Valley. *Oryx*. 11: 135-139.
- Ayliffe, L.K., Cerling, T.E., Robinson, T., West, A.G., Sponheimer, M., Passey, B.H., Hammer, J., Roeder, B., Dearing, M.D., & Ehleringer, J.R. 2004. Turnover of carbon isotopes in tail hair and breath CO₂ of horses fed an isotopically varied diet. *Oecologia* 139: 11-21.
- Babaasa, D. 2000. Habitat selection by elephants in Bwindi Impenetrable National Park, southwestern Uganda. *African Journal of Ecology*. 38(2): 116-122.
- Bacastow, R.B., Keeling, C.D., & Whorf, T.P. 1985. Seasonal amplitude increase in atmospheric CO₂ concentration at Mauna Loa, Hawaii, 1959-1982. *Journal of Geophysical Research*. 90(D6): 10529-10540.
- Baker, A., Ito, E., Smart, P.L., & McEvan, R.F. 1997. Elevated and variable values of ¹³C in speleothems in a British cave system. *Chemical Geology*. 136: 263-270.
- Balasse, M., Bocherens, H., Mariotti, A., & Ambrose, S.H. 2001. Detection of dietary changes by intra-tooth carbon and nitrogen isotopic analysis: An experimental study of dentine collagen of cattle (*Bos taurus*). *Journal of Archaeological Science*. 28: 235-245.
- Barnes, J.I. 1996. Changes in the economic use value of elephant in Botswana: the effect of international trade prohibition. *Ecological Economics*. 18(3): 215-230.
- Barnes, R.F.W. 1980. The decline of the baobab tree in Ruaha National Park, Tanzania. *African Journal of Ecology*. 18: 243-252.
- Barnes, R.F.W. 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology*. 20: 123-136.
- Barnes, R.F.W. 1983. Effects of browsing on woodlands in a Tanzanian National Park: measurements, models, and management. *Journal of Applied Ecology*. 20: 521-539.
- Bax, P.N., & Sheldrick, D.L.W. 1963. Some preliminary observations on the food of elephants in the Tsavo National Park (East) of Kenya. *East African Wildlife Journal*. 1: 40-53.

- Beekman, J.H., & Prins, H.H.T. 1989. Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, *Syncerus caffer*. *African Journal of Ecology*. 27: 129-147.
- Bell, R.H.V. 1983. Decision-making in wildlife management with reference to problems of overpopulation. In: Owen-Smith, R.N. (Ed.). *Management of large mammals in African conservation areas*. Haum Educational Publishers, Pretoria. pp. 145-172.
- Bell, R.H.V., & Jachmann, H. 1984. Influence of fire on the use of *Brachystegia* woodland by elephants. *African Journal of Ecology*. 22: 157-163.
- Bengis, R.G., Grant, R., & de Vos, V. 2003. Wildlife diseases and veterinary controls: a savanna ecosystem perspective. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger Experience*. Island Press, Washington DC. pp. 349-369.
- Bengis, R.G., Kriek, N.P.J., Keet, D.F., Raath, J.P., de Vos, V., & Huchzermeyer, H.F.A.K. 1996. An outbreak of bovine tuberculosis in a free-living buffalo (*Syncerus caffer* – Sparrman) population in the Kruger National Park, a preliminary report. *Onderstepoort Journal of Veterinary Research*. 63: 15-18.
- Ben-Shahar, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation*. 65: 249-256.
- Ben-Shahar, R. 1998. Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology*. 136(2): 189-194.
- Berner, R.A. 1994. GEOCARB II: a revised model of atmospheric CO₂ over Phanerozoic time. *American Journal of Science*. 294: 56–91.
- Bishop, C. 1995. *Neural Networks for Pattern Recognition*. Oxford: University Press.
- Blünier, T., Chappellaz, J., Schwander, J., Dällenbach, A., Stauffer, B., Stocker, T.F., Raynaud, D., Jouzel, J., Clausen, H.B., Hammer, C.U., & Johnsen, S.J. 1998. Asynchrony of Antarctic and Greenland climate change during the last glacial period. *Nature*. 394: 739–743.

- Boisserie, J.-R., Zazzo, A., Merceron, G., Blondel, C., Vignaud, P., Likius, A., Taisso Mackaye, H., & Brunet, M. 2005. Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 221: 153-174.
- Bond, I. 1994. The importance of sport-hunted elephants to campfire in Zimbabwe. *TRAFFIC Bulletin*. 14: 117–119.
- Bossen, B. 1998. Research on African elephants *Loxodonta africana* (Blumenbach 1797): A bibliography. *African Journal of Ecology*. 36(4): 371-376.
- Boutton, T.W., Tieszen, L.L., & Imbamba, S.K. 1988. Seasonal changes in the nutrient content of East African grassland vegetation. *African Journal of Ecology*. 26: 103-115.
- Bow, J.M., & Purday, C. 1966. A method for sperm whale teeth for age determination. *Nature*. 210: 437-438.
- Bowen, G.J., Chesson, L., Nielson, K., Cerling, T.E., & Ehleringer, J.R. 2005. Treatment methods for the determination of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of hair keratin by continuous-flow isotope-ratio mass spectrometry. *Rapid Communications in Mass Spectrometry*. 19: 2371-2378.
- Bowland, J.M., & Yeaton, R.I. 1997. Impact of domesticated African elephants *Loxodonta africana* on Natal bushveld. *South African Journal of Wildlife Research*. 27(2): 31-36.
- Boyde, A. 1968. Studies on the mineralizing fronts in calcified connective tissues using the scanning electron microscope. In: Borianelli, D.S. (Ed.). *Electron Microscopy, Volume 2*. Tipografia Poliglotta Vaticana, Rome. pp. 427
- Boyde, A., & Jones, S.J. 1972. Scanning electron microscope studies of the formation of mineralised tissues. In: Slavkin, H.C., & Bavetta, L.A. (Eds.). *Developmental Aspects of Oral Biology*. Academic Press, New York. Chapter 11.
- Braack, L.E.O., & Marais, C. 1997. Contribution towards a policy on tourism in the KNP. In: *Policy proposals regarding issues relating to biodiversity maintenance, maintenance of*

- wilderness qualities, and provision of human benefits. *A revision of parts of the management plan for the Kruger National Park, Vol. 8*. Online: <http://www.parks-sa.co.za>.
- Brink, J.S. 1987. The archaeozoology of Florisbad, Orange Free State. *Memoirs van die Nasionale Museum Bloemfontein*. 24: 1-151.
- Brink, J.S., & Lee-Thorp, J.A. 1992. The feeding niche of an extinct springbok, *Antidorcas bondi* (Antelopini, Bovidae) and its palaeoenvironmental meaning. *South African Journal of Science*. 88: 227-229.
- Brown, J.H., Whitham, T.G., Ernest, S.K.M., & Gehring, C.A. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science*. 293: 643-650.
- Bryant, J.D., & Froelich, P.N. 1995. A model of oxygen isotope fractionation in body water of large mammals. *Geochimica et Cosmochimica Acta*. 59: 4523-4537.
- Bryant, J.D., Koch, P.L., Froelich, P.N., Showers, W.J., & Genna, B.J. 1996. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. *Geochimica et Cosmochimica Acta*. 60: 5145-5148.
- Bryden, H.A. 1903. The decline and fall of the South African elephant. *Fortnightly Review* 79: 100-108.
- Buechner, H.K. & Dawkins, H.C. 1961. Vegetation change induced by elephants and fire in Murchinson Falls National Park, Uganda. *Ecology*. 42: 752-766.
- Bulte, E.H. & van Kooten, G.C. 1999. Economic efficiency, resource conservation and the ivory trade ban. *Ecological Economics*. 28(2): 171-181.
- Burnham, K.P. & Anderson, D.R. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*. 28: 111-119.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.

- Burton, M. 1999. An assessment of alternative methods of estimating the effect of the ivory trade ban on poaching effort. *Ecological Economics*. 30(1): 93-106.
- Butler, W.T. 1984. Dentin collagen: Chemical structure and role in mineralization. In: Linde, A. (Ed.). *Dentin and Dentinogenesis, Volume 2*. CRC Press, Inc., Boca Raton, Florida.
- Carpenter, S.R. 1988. *Complex Interactions in Lake Communities*. Springer-Verlag, New York.
- Carruthers, J. 1995. The Kruger National Park: A social and political history. Pietermaritzburg: University of Natal Press.
- Carter, M.L. 2001. Sensitivity of stable isotopes (^{13}C , ^{15}N , and ^{18}O) in bone to dietary specialization and niche separation among sympatric primates in Kibale National Park, Uganda. Ph.D. Thesis, University of Chicago.
- Caughley, G. 1976. The elephant problem – an alternative hypothesis. *East African Wildlife Journal*. 14: 265-283.
- Census report for elephant and buffalo in the Kruger National Park. 2005. Unpublished internal memorandum. Skukuza, SANParks (provided by I. Whyte).
- Cerling, T.E., & Harris, J.M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia*. 120: 347-363.
- Cerling, T.E., & Viehl, K. 2004. Seasonal diet changes of the forest hog (*Hylochoerus meinertzhageni* Thomas) based on the carbon isotopic composition of hair. *African Journal of Ecology*. 42: 88-92.
- Cerling, T.E., Harris, J.M., Ambrose, S.H., Leakey, M.G., & Solounias, N. 1997a. Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. *Journal of Human Evolution*. 33: 635-650.
- Cerling, T.E., Harris, J.M., & Leakey, M.G. 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia*. 120: 364-374.

- Cerling, T.E., Harris, J.M., & Leakey, M.G. 2005. Environmentally driven dietary adaptations in African mammals. In: Ehleringer, J.R., Cerling, T.E., & Dearing, M.D. (Eds). *A History of Atmospheric CO₂ and its Effects on Plants, Animals, and Ecosystems*. Springer, USA. pp. 258-272.
- Cerling, T.E., Harris, J.M., Macfadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., & Ehleringer, J.R. 1997b. Global vegetation change through the Miocene/Pliocene boundary. *Nature*. 389: 153-158.
- Cerling, T.E., Harris, J.M., & Passey, H. 2003. Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy*. 84: 456-470.
- Cerling, T.E., Hart, J.A., & Hart, T.B. 2004b. Stable isotope ecology in the Ituri Forest. *Oecologia* 138: 5-12.
- Cerling, T.E., Omondi, P., & Macharia, A.N. 2007. Diets of Kenyan elephants from stable isotopes and the origin of confiscated ivory in Kenya. *African Journal of Ecology*. DOI: 10.1111/j.1365-2028.2007.00784.x
- Cerling, T.E., Passey, B.H., Ayliffe, L.K., Cook, C.S., Ehleringer, J.R., Harris, J.M., Dhidha, M.B., & Kasiki, S.M. 2004a. Orphan's tales: seasonal dietary changes in elephants from Tsavo National Park, Kenya. *Palaeogeography Palaeoclimatology, Palaeoecology*. 206: 367-376.
- Cerling, T.E., Wang, Y., & Quade, J. 1993. Expansion of C₄ ecosystems as an indicator of global ecological change in the late Miocene. *Nature*. 361: 344-345.
- Cerling, T.E., Wittemyer, G., Rasmussen, H.B., Vollrath, F., Cerling, C.E., Robinson, T., & Douglas-Hamilton, I. 2006. Stable isotopes in elephant hair document migration patterns and diet changes. *Proceedings of the National Academy of Sciences of the USA*. 103: 371-373.
- Chamaillé-Jammes, S., Valeix, M., & Fritz, H. 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*. 44: 625-633

- Chapman, L.J., Chapman, C.A., & Wrangham, R.W. 1992. *Balanites wilsoniana*: elephant dependant dispersal? *Journal of Tropical Ecology*. 8: 275-283.
- Child, B., Ward, S., & Tavengwa, T. 1997. Zimbabwe's CAMPFIRE Programme: Natural Resource Management by the People. IUCNROSA Environmental Issues Series No. 2, IUCN-ROSA, Harare.
- Chiyo, P.I., Cochrane, E.P., Naughton, L., & Basuta, G. I. 2005. Temporal patterns of crop raiding by elephants: a response to change in forage quality or crop availability? *African Journal of Ecology*. 43: 48–55.
- Coates, D.B., van der Weide, A.P.A., and Kerr, J.D. 1991. Changes in faecal ^{13}C in response to changing proportions of legume (C_3) and grass (C_4) in the diet of sheep and cattle. *Journal of Agricultural Science*. 116: 287–295.
- Codron, J. 2004. An isotopic comparison of elephant (*Loxodonta africana*) diets in the Kruger National Park and Welgevonden Game Reserve. M.Sc. dissertation. University of Cape Town.
- Codron, D., & Brink, J.S. 2007. Trophic ecology of two savanna grazers, blue *Connochaetes taurinus* and black wildebeest *C. gnou*. *European Journal of Wildlife Research*. 53: 90-99.
- Codron, D., & Codron, J. Reliability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in faeces for reconstructing savanna herbivore diet. *Mammalian Biology*. In press.
- Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., & de Ruiter, D. 2005b. Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research*. 35: 43-52.
- Codron, D., Codron, J., Sponheimer, M., Lee-Thorp, J.A., Robinson, T., Grant, C.C., & de Ruiter, D. 2005a. Assessing diet in savanna herbivores using stable carbon isotope ratios of faeces. *Koedoe*. 48: 115-124.

- Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., & Brink, J.S. 2006. Dietary variation in impala *Aepyceros melampus* recorded by carbon isotope composition of feces. *Acta Zoologica Sinica*. 52(6): 1015-1025.
- Codron, D., Lee-Thorp, J.A., Sponheimer, M., & Codron, J. 2007c. Nutritional content of savanna plant foods: implications for browser/grazer models of ungulate diversification. *European Journal of Wildlife Research*. 53: 100-111.
- Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., Sealy, J., Grant, R., & Fourie, N. 2007a. Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*. 273: 21-29.
- Codron, D., Lee-Thorp, J.A., Sponheimer, M., & Codron, J. 2007b. Stable carbon isotope reconstruction of ungulate diet changes through the seasonal cycle. *South African Journal of Wildlife Research*. 37(2): 117-125.
- Codron, J., Codron, D., Lee-Thorp, J.A., Sponheimer, M., Bond, W.J., de Ruiter, D., & Grant, R. 2005. Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. *Journal of Archaeological Science*. 32: 1757-1772.
- Codron, J., Lee-Thorp, J.A., Sponheimer, M., Grant, C.C., Codron, D., & de Ruiter, D. 2006. Elephant (*Loxodonta africana*) diets in the Kruger National Park, South Africa: Spatial and Landscape Differences. *Journal of Mammalogy*. 87: 27-34.
- Coe, M.J., Cumming, D.H., & Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*. 22: 341-354.
- Colyer, F., & Miles, A.E.W. 1957. Injury to and rate of growth of an elephant tusk. *Journal of Mammalogy*. 38: 243-247.
- Cooke, C.K. 1969. *Rock art of southern Africa*. Books of Africa, Cape Town.
- Cooper, S.M., & Owen-Smith, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African Savanna. *Oecologia*. 67: 142-146.

- Coppens, Y., Maglio, V.J., Madden, C.T., Beden, M. 1978. Proboscidea. In: Maglio, V. J., & Cooke, H.B.S. (Eds.). *Evolution of African Mammals*. Cambridge Mass, Harvard University Press. pp. 336-367.
- Cormie, A.B., & Schwarcz, H.B. 1996. Effects of climate on deer bone $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$: lack of precipitation effects on $\delta^{15}\text{N}$ for animals consuming low amounts of C_4 plants. *Geochimica et Cosmochimica Acta*. 60: 4161-4166.
- Cowling, R.M., Esler, K.J., & Rundel, P.W. 1999. Namaqualand, South Africa: an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology*. 142: 3–21.
- Croze, H. 1974. The Seronera bull problem. II: The trees. *East African Wildlife Journal*. 12: 29-47.
- Cumming D.H.M.; Fenton M.B.; Rautenbach I.L.; Taylor R.D.; Cumming G.S.; Cumming M.S.; Dunlop J.M.; Ford A.G.; Hovorka M.D.; Johnston D.S.; Kalcounis M.; Mahlangu Z.; Portfors C.V.R. 1997. Elephants, woodlands and biodiversity in Southern Africa. *South African Journal of Science*. 93(5): 231-236.
- Cumming, D.H.M., du Toit, R.F., & Stuart, S.N. 1990. *African elephants and rhinos: Status survey and conservation action plan*. IUCN, Gland, Switzerland.
- Dalerum, F., & Angerbjorn, A. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia*. 144: 647-658.
- Dansgaard, W. 1964. Stable isotopes in precipitation. *Tellus*. 16: 436-468.
- Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjörnsdottir, A.E., Jouzel, J., & Bond, G. 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature*. 364: 218–220.
- Darling, F.F. 1960. *Wildlife in an African Territory*. Oxford University Press, London.

- Dawdy, D.R., & Matalas, N.C. 1964. Statistical and probability analysis of hydrologic data, Part 3. Analysis of variance, covariance, and time series, Section 8.3. In: (Ed.: Ven Te Chow) *Handbook of applied hydrology*. McGraw-Hill, New York.
- De Boer, W.F., & Prins, H.H.T. 1990. Large herbivores that strive mightily but eat and drink like friends. *Oecologia*. 82: 264-274.
- De Boer, W.F., Ntumi, C.P., Correia, A.U., & Mafuca, J.M. 2000. Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology*. 38: 188-201.
- De Villiers, P.A., Pietersen, E.W., Meissner, H.H., Hugo, T.A., & Kok, O.B. 1991. Method of sampling food consumption by free-ranging elephant. *South African Journal of Wildlife Research*. 21: 23.
- Deacon, H.J., & Deacon, J. 1999. *Human beginnings in South Africa: uncovering the secrets of the Stone Age*. Cape Town: David Philip Publishers.
- Delwiche, C.C., & Steyn, P.L. 1970. Nitrogen isotope fractionation in soils and microbial reactions. *Environmental Science and Technology*. 4: 929-935.
- Demment, M.W., & van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*. 125: 641-672.
- DeNiro, M.J. 1985. Postmortem preservation and alterations of *in vitro* bone collagen isotope ratios in relation to paleodietary reconstruction. *Nature*. 317: 806-809.
- DeNiro, M.J., & Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*. 42: 495-506.
- DeNiro, M.J., & Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*. 45: 341-351.
- Dorale, J.A., Edwards, R.L., Ito, E., & Gonzalez, L.A. 1998. Climate and vegetation history of the midcontinent from 75 to 25 ka: a speleothem record from Crevice Cave, Missouri, USA. *Science*. 282: 1871-1874.

- Dougall, H.W., & Sheldrick, D.L.W. 1964. The chemical composition of a day's diet of an elephant. *East African Wildlife Journal*. 2: 51-59.
- Douglas-Hamilton, I. & Michelmore, F. 1996. *Loxodonta africana*: range and distribution, past and present. In: Shohani, J. & Tassy, P. (Eds.). *The proboscidea: Evolution and palaeoecology of elephants and their relatives*. Oxford University Press, Oxford. pp. 321-326.
- Dowson, T.A., & Holliday, A. 1989. Zig-zags and eland: An interpretation of an idiosyncratic combination. *South African Archaeological Bulletin*. 44(149): 46-48.
- du Toit, J.T. 1993. The feeding ecology of a very small ruminant, the steenbok (*Raphicerus campestris*). *African Journal of Ecology*. 31: 35-48.
- du Toit, J.T. 2003. Large herbivores and savanna heterogeneity. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger experience*. Island Press, Washington DC. pp. 292-309.
- Dublin, H. 1996. Elephants of the Masai Mara, Kenya: seasonal habitat selection and group size patterns. *Pachyderm*. 22: 25-35.
- Dublin, H.T. 1995. Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire, and other factors. In: Sinclair, A.R.E., & Arcese, P. (Eds.). *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, pp. 71-90.
- Dublin, H.T., & Niskanen, L.S. 2003. *IUCN/SSC AfESG Guidelines for the in situ translocation of the African elephant for conservation purposes: prepared by the IUCN/SSC African Elephant Specialist Group in collaboration with the Re-introduction and Veterinary Specialist Groups* IUCN.
- Dublin, H., Sinclair, A.R.E., & McGlade, J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology*. 59: 1147-1164.

- Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G., & Lloyd, M. 1990. Comparative nutrient extraction from forages by grazing bovids and equids: A test of the nutritional model of equid/bovid competition and co-existence. *Oecologia*. 84: 411-418.
- Eckhardt, H.C., van Wilgen, B.W., & Biggs, H.C. 2000. Trends in woody vegetation cover in the Kruger National Park between 1940 and 1998. *African Journal of Ecology*. 38: 108-115.
- Eda, S., & Takuma, S. 1965. Microstructure of the peritubular matrix in horse dentine. *Bulletin of the Tokyo Dental College*. 6: 1
- Ehleringer, J.R. 1993. Carbon and water relations in desert plants: an isotopic perspective. In: Ehleringer, J.R., Hall, A.E., & Farquhar, G.D. (Eds.). *Stable Isotopes and Plant Carbon-Water Relations*. Academic Press, San Diego. pp. 155-172.
- Ehleringer, J.R., & Cerling, T.E. 2001. Photosynthetic pathways and climate. In: Schulze, E.-D., Heimann, M., Harrison, S.P., Holland, E.A., Lloyd, J., Prentice, I.C., & Schimel, D. (Eds.). *Global Biogeochemical Cycles in the Climate System*. San Diego: Academic Press. pp. 267-77.
- Ehleringer, J.R. & Cooper, T.A. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia*. 76: 562-566.
- Ehleringer, J.R., & Rundel, P. W. 1989. Stable isotopes: history, units, and instrumentation. In: Rundel, P.W., Ehleringer, J.R., & Nagy, K.A. (Eds.). *Stable Isotopes in Ecological Research*. Springer-Verlag, New York. pp. 1-15.
- Ehleringer, J.R., Cerling, T.E., & Helliker, B.R. 1997. C₄ photosynthesis, atmospheric CO₂ and climate. *Oecologia*. 112: 285-299.
- Elder, W.H. 1970. Morphometry of elephant tusks. *Zoologica Africana*. 5(1): 143-159.
- Ellery, W.N., Scholes, R.J., & Scholes, M.C. 1995. The distribution of sweetveld and sourveld in South Africa's grassland biome in relation to environmental factors. *African Journal of Range and Forage Science*. 12: 38-45.
- Eltringham, S.K. 1982. *Elephants*. Blandford Books, Poole, Dorset, UK.

- Epstein, S., Thompson, P., & Yapp, C.J. 1977. Oxygen and hydrogen isotope ratios in plant cellulose. *Science*. 198: 1209-1215.
- Erasmus, T., Penzhorn, B.L., & Fairall, N. 1978. Chemical composition of faeces as an index of veld quality. *South African Journal of Wildlife Research*. 8: 19-24.
- Ericson, J.E. 1985. Strontium isotope characterization in the study of prehistoric human ecology. *Journal of Human Evolution*. 14: 503-514.
- Espinoza, E.O., & Mann, M-J. 1991. Identification guide for ivory and ivory substitutes. *World Wildlife Fund & The Conservation Foundation*. WWF Publications.
- Etheridge, D.M., Steele, L.P., Langenfelds, R.L., Francey, R.J., Barnola, J.-M., & Morgan, V.I. 1996. Natural and anthropogenic changes in atmospheric CO₂ over the last 1000 years from air in Antarctic ice and firn. *Journal of Geophysical Research*. 101: 4115-4128.
- Farquhar, G.D., Ehleringer, J.R., & Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*. 40: 503-537.
- Farquhar, G.D., Hubrick, K.T., Condon, A.G., & Richards, R.A. 1988. Carbon isotope fractionation and plant water-use efficiency. In: Rundel, P.W., Ehleringer, J.R., & Nagy, K.A. (Eds.). *Stable isotopes in ecological research*. Springer-Verlag. pp. 21-40.
- Farquhar, G.D., O'Leary, M.H., & Berry, J.A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*. 9: 121-137.
- Fayrer-Hosken, R.A., Grobler, D., van Altena, J.J., Bertschinger, H.J., & Kirkpatrick, J.F. 2000. Immunocontraception of African elephants. *Nature* 407: 149.
- Fayrer-Hosken, R.A., Grobler, D., van Altena, J.J., Bertschinger, H.J., & Kirkpatrick, J.F. 2001. African elephants and contraception (brief communication - reply). *Nature* 411: 766.

- Feng, X., & Epstein, E. 1995. Carbon isotopes of trees from arid environments and implications for reconstructing atmospheric CO₂ concentrations, *Geochimica Cosmochimica Acta*. 59: 2599-2608.
- Ferguson, D.B., & Fort, A. 1974. Circadian variations in human resting submandibular saliva flow rate and composition. *Archives of Oral Biology*. 19: 47-55.
- Ferreira, S.L.A., & Harmse, A.C. 1999. The social carrying capacity of the Kruger National Park, South Africa: policy and practice. *Tourism Geographies*. 1: 325-342.
- Field, C. R., & Ross, I. C. 1976. The savanna ecology of Kidepo Vley National Park, II. Feeding ecology of elephant and giraffe. *East African Wildlife Journal*. 14: 1-15.
- Field, C.R. 1971. Elephant ecology in the Queen Elizabeth National Park, Uganda. *East African Wildlife Journal*. 9: 99-123.
- Finaughty, W. 1916. *Recollections of William Finaughty - Elephant Hunter*. Bulawayo, Books of Rhodesia.
- Fisher, D.C. 1987. Mastodon procurement by Paleoindians of the Great Lakes Region: hunting or scavenging? In: Nitecki, M.H., & Nitecki, D.V. (Eds.). *The Evolution of Human Hunting*. Plenum Press, New York. pp. 309-421.
- Fisher, D.C. 2001a. Season of death, growth rates, and life history of North American mammoths. In: West, D. (Ed.). *Proceedings of the International Conference on Mammoth Site Studies. Publications in Anthropology* 22. University of Kansas, Lawrence, KS. pp. 121-135.
- Fisher, D.C. 2001b. Entrained vs. free-running physiological rhythms and incremental features in the tusks of woolly mammoths. *Journal of Vertebrate Paleontology*. 21 (Suppl. 3): 49A-50A (Abstract).
- Fisher, D.C., & Beld, S.G. 2002. Whole-tusk growth records of late Pleistocene woolly mammoth from the Taimir Peninsula, Siberia. *Journal of Vertebrate Paleontology*. 22 (Suppl. 3): 53A (Abstract).

- Fisher, D.C., & Fox, D.L. 1998. Oxygen isotopes in mammoth teeth: Sample design, mineralization patterns, and enamel-dentin comparisons. *Journal of Vertebrate Paleontology*. 18: 41-42A.
- Fisher, D.C., & Fox, D.L. 2003. Season of death and terminal growth histories of Hiscock mastodons. In: Laub, R.S. (Ed.): *The Hiscock Site: Late Pleistocene and Holocene Paleoecology and Archaeology in Western New York State. Bulletin of the Buffalo Society of Natural Sciences*. 37: 83–100.
- Fisher, D.C., Fox, D.L., & Agenbroad, L.D. 2003. Tusk growth rate and season of death of *Mammuthus columbi* from Hot Springs, South Dakota, USA. *Deinsea*. 9: 117-133.
- Fisher, R.A. 1932. *Statistical methods for research workers*. 4th Edition. Oliver and Boyd, London.
- Fisk, A.T., Tittlemier, S.A., Pranschke, J.L., & Norstrom, R.J. 2002. Using anthropogenic contaminants and stable isotopes to address the feeding ecology of Greenland sharks. *Ecology*. 83: 2162-2172.
- Fogel, M.L., Tuross, N., & Owsley, D.W. 1989. Nitrogen isotope tracers of human lactation in human and archaeological populations. *Annual Report of the Director, Geophysical Laboratory, Carnegie Institution of Washington*. Washington. pp. 111-117.
- Foreman, R.T.T., & Alexander, L.E. 1998. Roads and their major ecological effects. *Annual Review of Ecological Systems*. 29: 207-231.
- Forstenpointner, G., Weissengruber, G.E., Kuebber-Heiss, A., Burger, H., & Voracek, T. 2001. Healing and repair in tusk, incisivum and maxilla of an African elephant. In: *Proceedings of the Joint Conference of the AAZV, AAWV, ARAV, NAZWV, Orlando, FL*. American Association of Zoo Veterinarians. pp. 393.
- Fox, D.L. 2000. Growth increments in *Gomphotherium* tusks and implications for late Miocene climate change in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 156: 327-348.

- Fox, D.L., & Fisher, D.C. 2001. Stable isotope ecology of a late Miocene population of *Gomphotherium productus* (Mammalia, Proboscidea) from Port of Entry Pit, Oklahoma, USA. *Palaios*. 16: 279-293.
- Fox, D.L., & Fisher, D.C. 2004. Dietary reconstruction of Miocene *Gomphotherium* (Mammalia, Proboscidea) from the Great Plains region, USA, based on the carbon isotope composition of tusk and molar enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 206: 311-335.
- Fox, D.L., Fisher, D.C., Vartanyan, S., Tikhonov, A.N., Mol, D., & Buigues, B. 2007. Paleoclimatic implications of oxygen isotopic variation in Late Pleistocene and Holocene tusks of *Mammuthus primigenius* from northern Eurasia. *Quaternary International*. 169-170: 154-165.
- Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., & Steele, L.P. 1999. A 1000-year high precision record of $\delta^{13}\text{C}$ in atmospheric CO_2 . *Tellus*. 51B: 170-193.
- Frank, R.M., & Nalbandian, J. 1963. Comparative aspects of development of dental hard structures. *Journal of Dental Research*. 42: 422.
- Frank, R.M. 1979. Electron microscopy autoradiography of calcified tissues. *International Rev. Cytology*. 56: 183.
- Freeland, W.J., & Janzen, D.H. 1974. Strategies in herbivory in mammals: the role of plant secondary compounds. *American Naturalist*. 108: 269-289.
- Freeland, W.J., Calcott, P.H., & Anderson, L.R. 1985. Tannins and saponin: interaction in herbivore diets. *Biochemical Systematics and Ecology*. 13: 189-193.
- Freitag-Ronaldson, S., & Foxcroft, L.C. 2003. Anthropogenic influences at the ecosystem level. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger experience*. Island Press, Washington DC. pp. 391-421
- Friedli, H., Lotscher, H., Oeschger, H., & Siegenthaler, U. 1986. Ice core record of the $^{13}\text{C}/^{12}\text{C}$ ratio of atmospheric CO_2 in the past two centuries. *Nature*. 324: 237-238.

- Fritz, H., Duncan, P., Gordon, I.J., & Illius, A.W. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*. 131: 620-625.
- Furseth, R. 1971. The fine structure of the odontoblast predentin area in the root. *Scandinavian Journal of Dental Research*. 79: 141.
- Furseth, R. 1974. The structure of peripheral root dentine in young human premolars. *Scandinavian Journal of Dental Research*. 82: 557.
- Gage, J.P., Francis, M.J.O., & Triffitt, J.T. 1989. *Collagen and Dental Matrices*. London: Wright.
- Garten, C.T., & Taylor, G.E. 1992. Foliar $\delta^{13}\text{C}$ within a temperate deciduous forest: spatial, temporal and species sources of variation. *Oecologia*. 90: 1-7.
- Gaylard, A., Owen-Smith, N., and Redfern, J. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger experience*. Island Press, Washington DC. pp. 171-188.
- Gentry, A.W. 1978. Bovidae. In: Maglio, V.J., & Cooke, H.B.S. (Eds). *Evolution of African Mammals*. Cambridge Mass, Harvard University Press, Cambridge, Massachusetts, USA. pp. 540-572.
- Gertenbach, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe*. 23: 35-43.
- Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe*. 26: 9-122.
- Gilbert, F.F. 1966. Aging white-tailed deer by annuli in the cementum of the first incisor. *Journal of Wildlife Management*. 30(1): 200-202.
- Gillespie, R. 1984. *Radiocarbon user's handbook*. Oxford University Committee for Archaeology Monograph Number 3. Oxonian Rewley Press, Oxford, UK.
- Gillson, L., & Lindsay, K. 2002. Ecological reality questions the need to cull. *CITES Briefing Document*. 7 pp.
- Gillson, L., & Lindsay, K. 2003. Ivory and ecology - changing perspectives on elephant management and the international trade in ivory. *Environmental Science & Policy*. 6: 411-419.

- Gonfiantini, R., Gratziu, S., & Tongiorgi, E. 1965. Oxygen isotope composition of water in leaves. In: *Isotope and Radiation in Soil-Plant-Nutrition Studies*. International Atomic Energy Commission, Vienna. pp. 405–411.
- Goldstein, G., & Sarmiento, G. 1987. Water relations of trees and grasses and their consequences for the structure of savanna vegetation. In: Walker, B.H. (Ed.). *Determinants of Tropical Savannas*. Oxford, IRL Press (Ltd). pp. 13-38.
- Grant, C.C., Davidson, T., Funston, P.J., & Pienaar, D.J. 2002. Challenges faced in the conservation of rare antelope: a case study on the northern basalt plains of the Kruger National Park. *Koedoe*. 45: 45-66.
- Grant, C.C., Meissner, H.H., & Schultheiss, W.A. 1995. The nutritive value of veld as indicated by faecal phosphorous and nitrogen and its relation to the condition and movement of prominent ruminants during the 1992-1993 drought in the Kruger National Park. *Koedoe*. 38: 17-31.
- Grant, C.C., Peel, M.J.S., Zambatis, N., & van Ryssen, J.B.J. 2000. Nitrogen and phosphorus concentration in faeces: an indicator of range quality as a practical adjunct to existing range evaluation methods. *African Journal of Range and Forage Science*. 17: 81-92.
- Gröcke, D.R., Bocherens, H., & Mariotti, A. 1997. Annual rainfall and nitrogen-isotope correlation in macropod collagen: application as a palaeoprecipitation indicator *Earth and Planetary Science Letters*. 153: 279-285.
- Grzimek, B. 1972. *Grzimek's Animal Life Encyclopedia, Vol. 12*. Van Nostrand Reinhold, New York. pp. 479.
- Guy, P.R. 1976. The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area, Rhodesia. *South African Journal of Wildlife Research*. 6: 55-63.
- Hall-Martin, A. 1982. Kruger's tuskiers. *African Wildlife*. 35(1): 65-88.

- Hall-Martin, A.J. 1991. Elephant conservation in the Kruger National Park, South Africa – from protection to management. In: *Proceedings of the Kalahari Conservation Society Elephant Workshop. Gaborone: KCS.*
- Hall-Martin, A.J. 1992. Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652-1992. *Koedoe*. 35(1): 65-88.
- Handley, L.L., & Raven, J.A. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. *Plant, Cell and Environment*. 15: 965-985.
- Handley, L.L., Odee, D., & Scrimgeour, C.M. 1994. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ patterns in savanna vegetation: Dependence on water availability and disturbance. *Functional Ecology*. 8: 306-314.
- Hare, P.E., Fogel, M.L., Stafford, T.W., Mitchell, A.D., & Hoering, T.C. 1991. The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins. *Journal of Archaeological Science*. 18: 277-292.
- Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R., & Funston, P. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*. 90: 69-78.
- Hattersley, P.W. 1982. $\delta^{13}\text{C}$ Values of C_4 types in grasses. *Australian Journal of Plant Physiology*. 9: 139-154.
- Havemann, B. 2006. Major conservation NGOs feel action is needed in managing elephant numbers. *African Wildlife*. 60: 37–38.
- Heaton, T.H.E. 1987. The $^{15}\text{N}/^{14}\text{N}$ ratios of plants in South Africa and Namibia: relationship to climate and coastal/saline environments. *Oecologia Berlin*. 74: 236-246.
- Heaton, T.H.E. 1999. Spatial, species, and temporal variations in the $^{13}\text{C}/^{12}\text{C}$ ratios of C_3 plants: Implications for palaeodiet studies. *Journal of Archaeological Science*. 26: 637-649.

- Heaton, T.H.E., Vogel, J.C., von la Chevallerie, G., & Collett, G. 1986. Climatic influence on the isotopic composition of bone nitrogen. *Nature*. 322: 823-824.
- Hewer, H.R. 1960. Age determination of seals. *Nature*. 187: 959.
- Hewer, H.R. 1964. The determination of age, sexual maturity, longevity, and a life-table in the grey seal (*Halichoerus grypus*). *Proceedings of the Zoological Society of London*. 142(4): 593-624.
- Hibberd, J.M., & Quick, W.P. 2002. Characteristics of C₄ photosynthesis in stems and petioles of C₃ flowering plants. *Nature*. 415: 451-454.
- Hiscocks, K. 1999. The impact of an increasing elephant population on the woody vegetation in the southern Sabi Sand Wildtuin, South Africa. *Koedoe*. 42(2): 47-55.
- Hoare, R.E., & du Toit, J.T. 1999. Coexistence between people and elephants in African savannas. *Conservation Biology*. 13(3): 633-639.
- Höhling, H.J., Ashton, B.A., & Köster, H.D. 1974. Quantitative electron microscopic investigations of mineral nucleation in collagen. *Cell Tissue Research*. 148: 11.
- Höhling, H.J., Kreilos, R., Neubauer, G., & Boyde, A. 1971a. Electron microscopy and electron microscopical measurements of collagen mineralization in hard tissues. *Z. Zellforsch*. 122: 36.
- Höhling, H.J., Scholz, F., Boyde, A., Heine, H.G., & Reimer, L. 1971b. Electron microscopical and laser diffraction studies of the nucleation and growth of crystals in the organic matrix of dentine. *Z. Zellforsch*. 117: 381.
- Holdo, R. M., & McDowell, L.R. 2004. Termite mounds as nutrient-rich food patches for elephants. *Biotropica*. 36(2): 231-239.
- Holds, R.M., Dudley, J.P., & McDowell, L.R. 2002. Geophagy in the African elephant in relation to availability of dietary sodium. *Journal of Mammalogy*. 83(3): 652-664

- Holecheck, J.L., Vavre, M., & Pieper, R.D. 1982. Methods for determining the nutritive quality of range ruminant diets: a review. *Journal of Animal Science*. 54: 363-376.
- Holland, G.R. 1976. The extent of the odontoblast process in the cat. *Journal of Anatomy*. 121: 133.
- Holmgren, K., Lee-Thorp, J.A., Cooper, G.R.J., Lundblad, K., Partridge, T.C., Scott, L., Sithaldeen, R., Talma, A.S., & Tyson, P.D. 2003. Persistent millennial-scale climatic variability over the past 25, 000 years in southern Africa. *Quaternary Science Reviews*. 22: 2311-2326.
- Holmgren, K., Karlén, W., Lauritzen, S.E., Lee-Thorp, J.A., Partridge, T.C., Piketh, S., Repinski, P., Stevenson, C., Svanered, O., & Tyson, P.D. 1999. A 3000-year high-resolution record of palaeoclimate for north-eastern South Africa. *The Holocene*. 9(3): 295–309.
- Hopkins, D.W., Wheatley, R.E., & Robinson, D. 1998. Stable isotope studies of soil nitrogen. In: Griffiths, H. (Ed.). *Stable isotopes – integration of biological, ecological and geochemical processes*. Bios Scientific Publishers. pp. 75-88.
- Hoppe, K.A. 2000. The biogeochemistry and paleoecology of Late Pleistocene proboscideans from the southern United States. Unpublished Ph.D. Thesis, Princeton University.
- Howland, M.R., Corr, L.T., Young, S.M.M., Jones, V., Jim, S., van der Merwe, N.J., Mitchell, A.D. & Evershed, R.P. 2003. Expression of the dietary isotope signal in the compound-specific $\delta^{13}\text{C}$ values of pig bone lipids and amino acids. *International Journal of Osteoarchaeology*. 13: 54-65.
- Hughes, K., Mead, R., & Adams, D. 1982. A scanning electron microscope study of root development in human unerupted wisdom teeth. *Journal of Dental Research*. 61: 557.
- Hummel, J., Südekum, K.H., Streich, W.J., & Clauss, M. 2006. Forage fermentation patterns and their implications for herbivore ingesta retention times. *Functional Ecology*. 20: 989-1002.

- Iacumin, P., Bocherens, H., Mariotti, A., & Longinelli, A. 1996. Oxygen isotope analyses of co-existing carbonate and phosphate in biogenic apatite: a way to monitor diagenic alteration of bone phosphate? *Earth and Planetary Science Letters*. 142: 1-6.
- Inamdar, A. 1996. The ecological consequences of elephant depletion. Ph.D. Thesis, University of Cambridge, Cambridge.
- Irwin, L.L, Cook, J.G., McWhirter, D.E., Smith, S.G., & Arnett, E.B. 1993. Assessing winter dietary quality in bighorn sheep via faecal nitrogen. *Journal of Wildlife Management*. 57: 413-421.
- IUCN/SSC/AfESG Guidelines for the management of local overabundance of elephants. July 2006.
- Jachmann, H. & Bell, R.H.V. 1985. Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology*. 23: 245-258.
- Janis, C.M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. In: Russell, D.E., Santoro, J.P., Sigogneau-Russel, D. (Eds). Proceedings of the VIIth International Symposium on Dental Morphology 1986. *Memoirs of the Museum of Natural History, Paris, France*. pp. 367-387.
- Jentsch, A., Kreyling, J., & Beierkuhnlein, C. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*. 5(7): 365-374.
- Johnson, C.F., Cowling, R.M., & Phillipson, P.B. 1999. The flora of the Addo Elephant National Park, South Africa: Are threatened species vulnerable to elephant damage? *Biodiversity and Conservation*. 8(11): 1447-1456.
- Jones, S.J. & Boyde, A. 1984. Ultrastructure of dentin and Dentinogenesis. In: Linde, A. (Ed.). *Dentin and Dentinogenesis*, Vol. II. CRC Press, Inc., Boca Raton, Florida. pp. 81-134.
- Jones, C.D., & Lawton, J.H. 1995. *Linking Species and Ecosystems*. Chapman & Hall, New York.

- Jones, R.J., Ludlow, M.M., Troughton, J.H., & Blunt, C.G. 1981. Changes in the natural carbon isotope ratios of the hair from steers fed diets of C₄, C₃ and C₄ species in sequence. *Search*. 12: 85-87.
- Joubert, S.C.J. 1986. *Masterplan for the management of the Kruger National Park, Vols. 1-6*. Unpublished documents. Skukuza archives, Kruger National Park, South Africa. Online: <http://www.parks-sa.co.za>.
- Karjalainen, S. 1984. Secondary and reparative dentin formation. In: Linde, A. 1984. *Dentin and Dentinogenesis*. CRC Press, Inc., Boca Raton, Florida. pp. 107-120.
- Kaye, H., & Herold, R.C. 1966. Structure of human dentine. *Archives of Oral Biology*. 11: 355.
- Keeley, J.E. 1998. CAM photosynthesis in submerged aquatic plants. *Botanical Review*. 64: 121–175.
- Keeley, J.E., & Keeley, S.C. 1989. CAM in high elevation tropical alpine cacti. *Plant Cell and Environment*. 12: 331–336.
- Keeley, J.E., & Rundel, P.W. 2003. Evolution of CAM and C₄ carbon-concentrating mechanisms. *International Journal of Plant Science*. 164 (3 Suppl.): S55-S77.
- Keeling, C.D. 1960. The concentration and isotopic abundance of carbon dioxide in the atmosphere. *Tellus*. 12: 200-203.
- Keeling, C.D. 1984. Atmospheric and oceanographic measurements needed for establishment of a data base for carbon dioxide from fossil fuels. In: *The Potential Effects of Carbon Dioxide-Induced Climatic Changes in Alaska. (Miscellaneous, etc.)*. The Proceedings of a Conference. Fairbanks, Alaska, April 7-8, 1982. School of Agriculture and Land Resources Management, University of Alaska, Fairbanks.
- Keeling, C.D., & Whorf, T.P. 2005. Atmospheric CO₂ records from sites in the SIO air sampling network. In: *Trends: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee, U.S.A.

- Keeling, C.D., Bacastow, R.B., Bainbridge, A.E., Ekdahl, Jr., C.A., Guenther, P.R., Waterman, L.S., & Chin, J.F.S. 1976. Atmospheric carbon dioxide variations at Mauna Loa Observatory, Hawaii. *Tellus*. 28(6): 538-551.
- Keeling, C.D., Bacastow, R.B., & Whorf, T.P. 1982. Measurements of the concentration of carbon dioxide at Mauna Loa Observatory, Hawaii. In: Clark, W.C. (Ed.). *Carbon Dioxide Review: 1982*. Oxford University Press, New York.
- Keeling, C.D., Chin, J.F.S., & Whorf, T.P. 1996. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature*. 382: 146-149.
- Keeling, C.D., Whorf, T.P., Wahlen, M., & van der Plicht, J. 1995. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature*. 375: 666-670.
- Kellogg, E.A 1999. Phylogenetic aspects of the evolution of C₄ photosynthesis. In: Sage, R.F., & Monson, R.K. (Eds.). *C₄ Plant Biology*. Academic Press, San Diego, Calif. pp. 411-444.
- Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*. 78: 1-27.
- Kennedy, A.D. 2000. Wildfire reduces elephant herbivory on *Colophospermum mopane* (Fabaceae). *African Journal of Ecology*. 38: 175-177.
- Kenyon, K., & Fiscus, C.H. 1963. Age determination in the Hawaiian monk seal. *Journal of Mammalogy*. 44(2): 280-281.
- King, L.C. 1967. *South African Scenery, 3rd Edition*. Edinburgh: Oliver & Boyd.
- Kingsmill, E. 1962. An investigation of criteria for estimating age in the marsupials *Trichosurus vulpecula* Kerr and *Perameles nasuta* Geoffroy. *Australian Journal of Zoology*. 10(4): 597-616.
- Klevezal, G.A., & Myrick, Jr., A.C. 1984. Marks in tooth dentine of female dolphins (genus *Stenella*) as indicators of parturition. *Journal of Mammalogy*. 65(1): 103-110.

- Klevezal', G.A., & Kleinenberg, S.E. 1969. Age determination in mammals from annual layers in teeth and bones. *Jerusalem, Israel program for Scientific Translations*. Translated from Russian. 128 pp.
- Koch, P.L., 1989. Paleobiology of Late Pleistocene mastodons and mammoths from southern Michigan and western New York. Ph.D. Thesis, University of Michigan.
- Koch, P.L., & Hoppe, K.A. 1996. Isotopes and elephants. *American Palaeontologist*. 4: 1-3.
- Koch, P.L., Behrensmeyer, A.K., Fogel, M.L. 1991. The isotopic ecology of plants and animals in Amboseli National Park, Kenya. *Geophysical Laboratory*. 2250: 163-171.
- Koch, P.L., Fisher, D.C., & Dettman, D. 1989. Oxygen isotope variation in the tusks of extinct proboscideans: A measure of season of death and seasonality. *Geology*. 17: 515-519.
- Koch, P.L., Heisinger, J., Moss, C., Carlson, R.W., Fogel, M.L., & Behrensmeyer, A.K. 1995. Isotopic tracking of change in diet and habitat use in African elephants. *Science*. 267: 1340-1343.
- Koch, P.L., Hoppe, K.A., & Webb, S.D. 1998. The isotopic ecology of late Pleistocene mammals in North America, Part 1: Florida. *Chemical Geology*. 152: 119-138.
- Kohn, M.J. 1996. Predicting animal oxygen-18: accounting for diet and physiological adaptation. *Geochimica et Cosmochimica Acta*. 60: 4811-4829.
- Kohn, M.J., Schoeninger, M.J., & Valley, J.W. 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochimica et Cosmochimica Acta*. 60: 3889-3896.
- Kraus, B.S. & Jordan, E.S. 1965. *The Human Dentition before Birth*. Henry Kimpton, London.
- Kröger, R., & Rogers, K.H. 2006. Roan *Hippotragus equinus* population decline in Kruger National Park, South Africa: an alternative complimentary hypothesis. *Acta Zoologica Sinica*. 52: 406-409.
- Laetsch, W.M. 1974. The C₄ syndrome: A structural analysis. *Annual Review of Plant Physiology*. 25: 27-52.

- Lamprey, H.F., Glover, P.E., Turner, M.I.M., & Bell, R.H.V. 1967. Invasion of the Serengeti National Park by elephants. *East African Wildlife Journal*. 5: 151-166.
- Lauritzen, S.E. 1995. A high-resolution palaeotemperature proxy record during the last interglaciation in Norway from speleothems. *Quaternary Research*. 43: 133-146.
- Lavelle, C.L.B., Shellis, R.P., & Poole, D.F.G. 1977. *Evolutionary Changes to the Primate Skull and Dentition*. Charles C. Thomas, Springfield, Illinois.
- Laws, R.M. 1952. A new method of age determination for mammals. *Nature*. 169: 972
- Laws, R.M. 1953. A new method of age determination in mammals with special reference to the elephant seal (*Mirounga leonina*). *Falklands Island, Dependent Survey and Scientific Report*. Vol. 2.
- Laws, R.M. 1962. Age determination of Pinnipedia with special reference to growth layers in the teeth. *Zeitschrift das Säugetierkunde*. 27(3): 129-146.
- Laws, R.M. 1966. Age criteria for the African elephant, *Loxodonta africana africana*. *East African Wildlife Journal*. 4: 1-37.
- Laws, R.M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos*. 21: 1-15.
- Laws, R.M., & Parker, I.S.C. 1968. Recent studies on elephant populations in East Africa. *Symposium of the Zoological Society of London*. 21: 319-359.
- Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. 1974. *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda*. Oxford, Clarendon. 376 pp.
- Lawton, R.M. 1971. Destruction or utilization of wildlife habitat? *Symposium of the British Ecological Society*. 11: 333-336.
- Lawton, R.M., & Gough, M. 1970. Elephants or fire – which is to blame? *Oryx*. 10: 244-248.
- Lee, P.C., & Graham, M.D. 2006. African elephants *Loxodonta africana* and human–elephant interactions: implications for conservation. *International Zoology Yearbook*. 40: 9-19.

- Lee-Thorp, J., & Sponheimer, M. 2003. Three case studies used to reassess the reliability of fossil bone and enamel isotope signals for paleodietary studies. *Journal of Anthropological Archaeology*. 22: 208-216.
- Lee-Thorp, J.A. 2000. Preservation of biogenic carbon isotope signals in Plio-Pleistocene bone and tooth mineral. In: Ambrose, S.H., & Katzenberg, M.A. (Eds.). *Biogeochemical approaches to paleodietary analysis*. Kluwer Academic/Plenum Publishers, New York. pp. 89-115.
- Lee-Thorp, J.A., & van der Merwe, N.J. 1987. Carbon isotope analysis of fossil bone apatite. *South African Journal of Science*. 83: 712-715.
- Lee-Thorp, J.A., Manning, L., & Sponheimer, M. 1997. Problems and prospects for carbon isotope analysis of very small samples of fossil tooth enamel. *Bull Soc Geol France*. 168: 767-773.
- Lee-Thorp, J.A., Sealy, J.C., & van der Merwe, N.J. 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science*. 16: 585-599.
- LeGeros, R.Z. 1991. Calcium phosphate in oral biology and medicine. In: Myers, H. (Ed.). *Monographs in Oral Science, Volume 15*. Karger, Basel.
- Leicester, H.M. 1949. *Biochemistry of the teeth*. St. Louis.
- Leslie, D.M.Jr., & Starkey, E.E. 1985. Faecal indices to dietary quality of cervids in old-growth forests. *Journal of Wildlife Management*. 49: 142-146.
- Lester, K.S. & Boyde, A. 1968. The surface morphology of some crystalline components of dentine. In: Symons, N.B.B. (Ed.). *Dentine and Pulp*. University of Dundee Press, Dundee, Scotland. pp. 197
- Levin, N., Cerling, T.E., Passey, B.H., Harris, J.M., & Ehleringer, J.R. 2006. A stable isotope aridity index for terrestrial environments. *Proceedings of the National Academy of Sciences of the USA*. 103: 11201-11205.

- Lewis, D.M. 1991. Observations of tree growth, woodland structure and elephant damage of *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology*. 29: 207-221.
- Lewis-Williams, J.D., & Dowson, T.A. 1989. *Images of Power*. University of Witwatersrand Press, Johannesburg.
- Linde, A. 1984. *Dentin and Dentinogenesis*. CRC Press, Inc., Boca Raton, Florida.
- Lindeque, M. 1988. Population dynamics of elephants in the Etosha National Park. Ph.D. Thesis, University of Stellenbosch, Stellenbosch.
- Lindroth, R.L., & Dearing, M.D. 2005. Herbivory in a World of Elevated CO₂. In: Ehleringer, J.R., Cerling, T.E., & Dearing, M.D. (Eds). *A History of Atmospheric CO₂ and its Effects on Plants, Animals, and Ecosystems*. Springer, USA. pp. 468-486.
- Livingstone, N.J., & Spittlehouse, D.L. 1993. Carbon isotope fractionation in tree rings in relation to the growing season water balance. In: Ehleringer, J.R., Hall, A.E., & Farquhar, G. (Eds.). *Stable isotopes and plant carbon-water relations*. Academic Press. pp. 141-153.
- Long, E.S., Sweitzer, R.A., Diefenbach, D.R., & Ben-David, M. 2005. Controlling for anthropogenically induced atmospheric variation in stable carbon isotope studies. *Oecologia*. 146: 148-156.
- Longinelli, A. 1984. Oxygen isotopes in mammal bone phosphate: A new tool for paleohydrological and paleoclimatological research? *Geochimica et Cosmochimica Acta*. 48: 385-390.
- Loughin, T.M. 2004. A systematic comparison of methods for combining p-values for independent test. *Computational Statistics & Data Analysis*. 47: 467-485.
- Lüttge, U. 2002. CO₂-concentrating: consequences in crassulacean acid metabolism. *Journal of Experimental Botany*. 53: 2131-2142.
- Luz, B., & Kolodny, Y. 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. *Earth and Planetary Science Letters*. 75: 29-36.

- Luz, B., Kolodny, Y., & Horowitz, M. 1984. Fractionation of oxygen isotopes between mammalian bone phosphate and environmental drinking water. *Geochimica et Cosmochimica Acta*. 48: 1689-1693.
- Mabunda, D., Pienaar, D.J., & Verhoef, J. 2003. The Kruger National Park: a century of management and research. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger Experience*. Island Press, Washington DC. pp. 3-21.
- Makhabu, S.W., Skarpe, C., & Hytteborn, H. 2006. Elephant impact on shoot distribution on trees and rebrowsing by smaller browsers. *Acta Oecologica*. 30: 136-146.
- Manning, M.R., & Melhuish, W.H. 1994. Delta ¹⁴CO₂ record from Wellington. In: Boden, T.A., Kaiser, D.P., Sepanski, R.J., & Stoss, F.W. (Eds.). *Trends: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee, U.S.A. pp. 173-202.
- Mansfield, A.W., & Fisher, H. 1960. Age determination in the harbor seal, *Phoca vitulina*. *Nature*. 186: 92-93.
- Marino, B.D., & McElroy, M.B. 1991. Isotopic composition of atmospheric CO₂ inferred from carbon in C₄ plant cellulose. *Nature*. 349: 127-131.
- Massler, M., & Schour, I. 1946. The appositional lifespan of the enamel and dentin-forming cells. I. Human deciduous teeth and first permanent molars. *Journal of Dental Research*. 25: 145.
- Masson, V., Vimeux, F., Jouzel, J., Morgan, V., Delmotte, M., Ciais, P., Hammer, C., Johnsen, S., Lipenkov, V.Y., Mosley-Thompson, E., Petit, J.R., Steig, E.J., Stievenard, M., & Vaikmae, R. 2000. Holocene climate variability in Antarctica based on 11 ice-core isotopic records. *Quaternary Research*. 54: 348-358.
- McCullagh, K. 1969a. The growth and nutrition of the African elephant I. Seasonal variations in the rate of growth and the urinary excretion of hydroxyproline. *East African Wildlife Journal*. 7: 85-90.

- McCullagh, K. 1969b. The growth and nutrition of the African elephant II. The chemical nature of the diet. *East African Wildlife Journal*. 7: 91-97.
- McEwan, E.H. 1963. Seasonal annuli in the cementum of the teeth of Barren Ground caribou. *Canadian Journal of Zoology*. 41(1): 111-113.
- McGuigan, H. & Brough, G.A. 1923. *Journal of Biological Chemistry*. 58: 415.
- McLaren, I.A. 1958. The biology of the Ringed seal (*Phoca hispida* Schreber) in the Eastern Canadian Arctic. *Bulletin of the Fisheries Research Board, Canada, Volume 118*.
- Meissner, H.H., Zacharias, P.J.K., And O'reagain, P. J. 1999. Forage quality (feed value). In: Tainton, N.M. (Ed.). Veld management in South Africa. University of Natal Press: Pietermaritzburg, South Africa. pp. 139-168.
- Midgley, J.J., Balfour, D., Kerley, G.I. 2005. Why do elephants damage savanna trees? *South African Journal of Science*. 101: 213-215.
- Miles, A.E.W., & Boyde, A. 1961. Observations on the structure of elephant ivory. *Journal of Anatomy (London)*. 95: 450.
- Miles, A.E.W., & White, J.W. 1960. Ivory. *Proceedings of the Royal Society of Medicine*. 53: 775-780.
- Mills, M.G.L., Whyte, I.J., Viljoen, A.J., Zambatis, N., & Potgieter, A.L.F. 1996. *Background Information for the National Parks Board's Review of the Kruger National Park's Elephant Management Policy*. Scientific Report no. 1/96, National Parks Board, Pretoria.
- Minagawa, M., & Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta*. 48: 1135-1140.
- Minson, D.J. 1990. *Forage in Ruminant Nutrition*. Academic Press, San Diego, California.
- Mitchell, V. 1963. Determination of age in Scottish red deer from growth layers in dental cement. *Nature*. 198: 350-351

- Mjör, I.A. 1979. Dentin and pulp. In: Mjör, I.A. & Fejerskov, O. (Eds.). *Histology of the human tooth*. Munksgaard, Copenhagen. pp. 43
- Mjör, I.A. 1984. The morphology of dentin and dentinogenesis. In: Linde, A. (Ed.). *Dentin and Dentinogenesis, Vol. I*. CRC Press, Inc., Boca Raton, Florida. pp. 1-18
- Mjör, I.A. & Fejerskov, O. 1979. *Histology of the Human Tooth, 2nd Edition*. Munksgaard, Copenhagen.
- Mjör, I.A. & Shackelford, J.M. 1966. Microradiography of human pulp tissue and decalcified coronal dentine. *Archives of Oral Biology*. 11: 1307-
- Mjör, I.A. 1983. Dentin and pulp. In: Mjör, I.A. (Ed.). *Reaction Patterns in Human Teeth*. CRC Press, Inc., Boca Raton, Florida.
- Mol, D., Coppens, Y., Tikhonov, A.N., Agenbroad, L.D., MacPhee, R.D.E., Flemming, C., Greenwood, A., Buigues, B., de Marliave, C., van Geel, B., van Reenen, G.B.A., Pals, J.P., Fisher, D.C., & Fox, D. 2001. The Jarkov Mammoth: 20,000-year-old carcass of a Siberian woolly mammoth *Mammuthus primigenius* (Blumenbach, 1799). In: Cavarretta, G., Gioia, P., Mussi, M., & Palombo, M.R. (Eds). *La Terra Degli Elefanti – The World of Elephants*. Atti del 1^o Congresso Internazionale – Proceedings of the 1st International Congress. pp. 305-309.
- Mole, S., Joern, A., O’Leary, M.H., & Madhavan, S. 1994. Spatial and temporal variation in carbon isotope discrimination in prairie graminoids. *Oecologia*. 97: 316-321.
- Molnar, S., Przybeck, T.R., Gantt, D.G., Elizondo, R.S. & Wilkerson, J.E. 1981. Dentin apposition rates as markers of primate growth. *American Journal of Physical Anthropology*. 55: 443-453.
- Moodley, S. 2002. The rare and the enigmatic: the rock art of Kilham 1 Rock Shelter, Bergville district, northern uKhahlamba Drakensberg. Unpublished Honours Thesis, University of Witwatersrand, Johannesburg.
- Moon, B.P., & Dardis, G.F. 1988. *The Geomorphology of Southern Africa*. Johannesburg, Southern Book Publishers.

- Mooney, H., Troughton, J.H., & Berry, J.A. 1974. Arid climates and photosynthetic systems. *Carnegie Institution Washington Year Book*. 73: 793–805.
- Morgan, M.E., Kingston, J.D., & Marino, B.D. 1994. Carbon isotopic evidence for the emergence of C₄ plants in the Neogene from Pakistan and Kenya. *Nature*. 367: 162–165.
- Moss, C.J. 1988. *Elephant Memories. Thirteen Years in the Life of an Elephant Family*. Elm Tree Books, London.
- Motulsky, H.J. & Christopoulos, A. 2003. Fitting models to biological data using linear and nonlinear regression. A practical guide to curve fitting. GraphPad Software Inc., San Diego, CA. www.graphpad.com.
- Mtui, M., & Owen-Smith, N. 2006. Impact of elephants (*Loxodonta africana*) on woody plants in Malolotja Nature Reserve, Swaziland. *African Journal of Ecology*. 44: 407-409.
- Murphy, B.P., & Bowman, D.M.J.S. 2006. Kangaroo metabolism does not cause the relationship between bone collagen $\delta^{15}\text{N}$ and water availability. *Functional Ecology*. 20: 1062-1069.
- Muzuka, A. 1999. Isotopic compositions of tropical East African flora and their potential as source indicators of organic matter in coastal marine sediments. *Journal of African Earth Sciences*. 28: 757-766.
- Mummery, J.H. 1924. *The Microscopic and General Anatomy of the Teeth, Human and Comparative*. Oxford University Press, London. Second Edition. 240 pp.
- Mwangi, P.N., Milewski, A., & Wahungu, G.M. 2004. Chemical composition of mineral licks used by elephants in Aberdares National Park, Kenya. *Pachyderm*. 37: 59-67.
- Naiman, R.J., Braack, L., Grant, R., Kemp, A.C., du Toit, J.T., & Venter, F.J. 2003. Interactions between species and ecosystem characteristics. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger Experience*. Island Press, Washington DC. pp. 221-241.

- Newman, H.N., & Poole, D.F.G. 1974. Observations with scanning and transmission electron microscopy on the structure of human surface enamel. *Archives of Oral Biology*. 19: 1135-1143.
- Nobel, P.S. 1981. Influence of freezing temperatures on a cactus *Coryphantha vivipara*. *Oecologia*. 48: 194-198.
- Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. In: Serengeti: dynamics of an ecosystem. Sinclair, A.R.E., & Norton-Griffiths, M. (Eds.). University of Chicago Press, Chicago. pp. 310-352.
- O'Connell-Rodwell, C.E., Rodwell, T., Rice, M., & Hart, L.A. 2000. Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biological Conservation*. 93: 381-391.
- O'Keeffe, J. & Rogers, K.H. 2003. Heterogeneity and management of the Lowveld rivers. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger Experience*. Island Press, Washington DC. pp. 447-468.
- O'Leary, M.H. 1981. Carbon isotope fractionation in plants. *Phytochemistry*. 20: 553-567.
- O'Leary, M.H. 1988. Carbon isotopes in photosynthesis. *Bioscience*. 38: 328-336.
- O'Leary, M.H. 1993. Biochemical basis of carbon isotope fractionation. In: Ehleringer, J.R., Hall, A.E., & Farquhar, G. (Eds.). *Stable Isotopes and Plant Carbon-Water Relations*. Academic Press. pp. 19-28.
- O'Leary, M.H. 1995. Environmental effects on carbon isotope fractionation in terrestrial plants. In: Wada, E., Yoneyama, T., Minagawa, M., Ando, T., & Fry, B.D. (Eds.). *Stable Isotopes in the Biosphere*. Kyoto University Press, Kyoto, Japan. pp. 78-91.

- Obermayer, F. 1881. Beitrag zur kenntnis des zahnbeines von elefanten, nilpferd, walross und narwal. *Verlag des Vereines der Wiener Handels-Akademie*: 102-113.
- Ohsumi, S., Kasuya, T., & Nishiwaki, M. 1963. Accumulation rate of dentinal growth layers in the maxillary tooth of the sperm whale. *Scientific Report of the Whales Research Institution, Vol. 17*.
- Olson, E.C. 1952. The evolution of a Permian vertebrate chronofauna. *Evolution*. 6: 181–196.
- Osborn, H.F. 1934. Evolution and geographic distribution of the Proboscidea: moeritheres, deinotheres and mastodonts. *Journal of Mammalogy*. 15: 177-184.
- Osmond, C.B. 1984. CAM: regulated photosynthetic metabolism for all seasons. In: Sybesma, C. (Ed.). *Advances in Photosynthesis Research*. Junk, The Hague. pp. 557-563.
- Ouzman, S. 1995. The fish, the shaman and the peregrination: San rock art paintings of Mormyrid fish as religious and social metaphors. *South African Field Archaeology*. 4: 3-17.
- Owen, R. 1840. *Odontography or a Treatise of the Comparative Anatomy of the Teeth, Their Physiological Relations, Mode of Development, and Microscopic Structure in the Vertebrate Animals*. London.
- Owen-Smith, R. N. 1988. Megaherbivores - The influence of very large body size on ecology. Cambridge University Press, Cambridge.
- Owen-Smith, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*. 13(3): 351-362.
- Owen-Smith, N. 1994. Foraging responses of kudu to seasonal changes in food resources: Elasticity in constraints. *Ecology*. 75: 1050-1062.
- Owen-Smith, N., & Cooper, S.M. 1989. Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle. *Journal of Zoology (London)*. 219: 29-43.

- Owen-Smith, N., & Ogutu, J. 2003. Rainfall influences on ungulate population dynamics. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger experience*. Island Press, Washington DC. pp. 310-331.
- Owen-Smith, N., Kerley, G.I.H., Page, B., Slotow, R., & van Aarde, R.J. 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science*. 102: 389-394.
- Pales, J.C., & Keeling, C.D. 1965. The concentration of atmospheric carbon dioxide in Hawaii. *Journal of Geophysical Research*. 24: 6053-6076.
- Paley, R.G.T., & Kerley, G.I.H. 1998. The winter diet of elephant in Eastern Cape Subtropical Thicket, Addo Elephant National Park. *Koedoe*. 41(1): 37-45.
- Palombo, M.R., & Ferretti, M.P. 2005. Elephant fossil record from Italy: knowledge, problems, and perspectives. *Quaternary International*. 126-128: 107-136.
- Passey, B.H., & Cerling, T.E. 2002. Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series. *Geochimica et Cosmochimica Acta*. 66: 3225-3234.
- Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., & Ehleringer, J.R. 2005. Carbon isotope fractionation between diet, breath CO₂, and bioapatite in different animals. *Journal of Archaeological Science*. 32: 1459-1470.
- Patterson, H.D. 1956. A simple method for fitting an asymptotic regression curve. *Biometrics*. 12: 323-329.
- Peabody, F.B. 1961. Annual growth zones in living and fossil vertebrates. *Journal of Morphology*. 108(1): 11-62.
- Perry, J.S. 1954. Some observations on growth and tusk weight in male and female African elephants. *Proceedings of the Zoological Society of London*. 124: 97-104.
- Peterson, B.J., & Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*. 18: 293-320.

- Pickett, S.T.A., Cadenasso, M.L., & Benning, T.L. 2003. Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger experience*. Island Press, Washington DC. pp. 22-40.
- Pienaar, U. de V. 1970. Water resources of the Kruger Park. *African Wildlife*. 24: 180-191.
- Pienaar, U. de V. 1983. Management by intervention: the pragmatic/economic option. In: Owen-Smith, R.N. (Ed.). *Management of Large Mammals in African Conservation Areas*. Pretoria: Haum Boekhandel. pp. 23-26.
- Pienaar, U. de V., Joubert, S.C.J., Hall-Martin, A., De Graaff, G., & Rautenbach, I.L. 1987. *Field Guide to the Mammals of the Kruger National Park*. Cape Town, Struik Publishers.
- Pienaar, U. de V., Van Wyk, P., & Fairall, N. 1966. An aerial census of elephant and buffalo in the Kruger National Park, and the implications thereof on intended management schemes. *Koedoe*. 9: 40–107.
- Pitman, C.R.S. 1934. *A Report of a Faunal Survey of Northern Rhodesia*. Govt. Printer, Livingstone.
- Plug, I. 1982. Man and animals in the prehistory of the Kruger National Park. *Transvaal Museum Bulletin*. 18: 9-10.
- Plug, I. 1989. Aspects of life in the Kruger National Park during the early iron age. *South African Archaeological Society Goodwin Series*. 6: 62-68.
- Plug, I., & Badenhorst, S. 2001. The distribution of macromammals in Southern Africa over the past 30,000 years as reflected in animal remains from archaeological sites. *Monographs of the Transvaal Museum*. Transvaal Museum, Pretoria
- Pollard, S., Shackleton, C., & Carruthers, J. 2003. Beyond the fence: people and the lowveld landscape. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger experience*. Island Press, Washington DC. pp. 422-446.

- Posner, A.S., & Tannenbaum, P.J. 1984. The mineral phase of dentine. In: A. Linde (Ed.). *Dentine and Dentinogenesis, Vol. II*. CRC Press, Boca Raton, Florida. pp. 17-36.
- Posner, A.S., Betts, F., & Blumenthal, N.C. 1980. Maturation and structure of bone mineral. *Progress in Crystal Growth Characterization*. 3: 49
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*. 83: 703-718.
- Preller, G.S. 1917. *Dagboek van Louis Trichardt (1836-1838)*. Het Volksblad-drukkerij, Bloemfontein.
- Prins, H.H.T. 1996. *Ecology and Behaviour of the African Buffalo: Social Inequality and Decision Making*. Chapman & Hall, London. 293 pp.
- Prins, H.H.T., & Douglas-Hamilton, I. 1990. Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia*. 83: 392-400.
- Prozesky, V.M., Raubenheimer, E.J., Van Heerden, W.F.P., Grotepass, W.P., Przybylowicz, W.J., Pineda, C.A., & Swart, R. 1995. Trace element concentration and distribution in ivory. *Nuclear Instruments and Methods in Physics Research*. 104B: 638-644.
- Punt, W.H.J. 1990. Die eerste blankes besoek die Laeveld. In: Pienaar, U. de V. (Ed.). *Neem uit die verlede*. National Parks Board, Pretoria.
- Quade, J., Cerling, T.E., Andrews, P., & Alpagut, B. 1995. Paleodietary reconstruction of Miocene faunas from Pasalar, Turkey using stable carbon and oxygen isotopes of fossil tooth enamel. *Journal of Human Evolution*. 28: 373-384.
- Quade, J., Cerling, T.E., & Bowman, J.R. 1989. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature*. 342: 163-166.
- Raubenheimer, E.J. 1993. Ivory...Fingerprints of the past. *Medunsa Trust News*. 2(1): 3.
- Raubenheimer, E.J. 1999. Morphological aspects and composition of African elephant (*Loxodonta africana*) ivory. *Koedoe*. 42(2): 57-64.

- Raubenheimer, E.J. 2000. Development of the tush and tusk and tusklessness in African elephant (*Loxodonta africana*). *Koedoe*. 43(2): 57-64.
- Raubenheimer, E.J., Bosman, M.C., Vorster, R., & Noffke, C.E. 1998a. Histogenesis of the chequered pattern of ivory of the African elephant (*Loxodonta africana*). *Archives of Oral Biology*. 43: 969-977.
- Raubenheimer, E.J., Brown, J.M.M., Rama, D.B.K., Dreyer, M.J., Smith, P.D., & Dauth, J. 1998b. Geographic variations in the composition of ivory of the African elephant (*Loxodonta africana*). *Archives of Oral Biology*. 43: 641-647.
- Raubenheimer, E.J., Dauth, J., Dreyer, M.J., Smith, P.D., & Turner, M.L. 1990. Structure and composition of ivory of the African elephant (*Loxodonta africana*). *South African Journal of Science*. 86: 192-193.
- Raubenheimer, E.J., van Heerden, W.F.P., Van Niekerk, P.J., de Vos, V., & Turner, M.J. 1995. Morphology of the deciduous tusk (tush) of the African elephant (*Loxodonta africana*). *Archives of Oral Biology*. 40(6): 571-576.
- Rausch, R.L. 1961. Notes on the black bear, *Ursus americanus* Pallas, in Alaska, with particular reference to dentition and growth. *Zeitschrift für Säugetierkunde*. 26(2): 77-107.
- Ransom, A.B. 1966. Determining age of white-tailed deer from layers in cementum of molars. *Journal of Wildlife Management*. 30(1): 197-199.
- Reed, K.E. 1997. Early hominid evolution and ecological change through the African Pliocene. *Journal of Human Evolution*. 32: 289-322.
- Richards, M.P., & Hedges, R.E.M. 2003. Variations in bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fauna from Northwest Europe over the last 40,000 years. *Palaeogeography, Palaeoclimate, Palaeoecology*. 193: 261-267.
- Robbins, C.T. 1993. *Wildlife Feeding and Nutrition*. Academic, New York.
- Robbins, C.T., Felicetti, L.A., & Sponheimer, M. 2005. The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia*. 144: 534-540.

- Robbins, C.T., Hanley, T.A., Hagerman, A.E., Hjejord, O., Baker, D.L., Schwartz, C.C., & Mautz, W.W. 1987. Role of tannins in defending plants against ruminants: Reduction in protein availability. *Ecology*. 68: 98-107.
- Rode, K.D., Chiyo, P.I., Chapman, C.A., & McDowell, L.R. 2006. Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of Tropical Ecology*. 22: 441-449.
- Rogers, K.H. & O'Keeffe, J. 2003. River heterogeneity: ecosystem structure, function, and management. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger experience*. Island Press, Washington DC. pp. 189-218.
- Roth, J.D., & Hobson, K.A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. *Canadian Journal of Zoology*. 78: 848-852.
- Rountrey, A.N., Fisher, D.C., Vartanyan, S., & Fox, D.L. 2007. Carbon and nitrogen isotope analyses of a juvenile woolly mammoth tusk: Evidence of weaning. *Quaternary International*. 169-170: 166-173.
- Ruch, J-V. 1984. Tooth morphogenesis and differentiation. In: Linde, A. (Ed.). *Dentin and Dentinogenesis, Vol. I*. CRC Press, Inc., Boca Raton, Florida. pp. 47-79.
- Rundel, P.W., Ehleringer, J.R., & Nagy, K.A. (Eds.). 1989. *Stable Isotopes in Ecological Research*. New York: Springer-Verlag.
- Rundel, P.W., Esler, K.J., & Cowling, R.M. 1999. Ecological and phylogenetic patterns of carbon isotope discrimination in the winter-rainfall flora of the Richtersveld, South Africa. *Plant Ecology*. 142: 133-148.
- Rutina, L.P., Moe, S.R., Swenson, J.E. 2005. Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. *Wildlife Biology*. 11(3): 207-213.

- Sage, R.F. 2005. Atmospheric CO₂, environmental stress, and the evolution of C₄ photosynthesis. In: Ehleringer, J.R., Cerling, T.E., & Dearing, M.D. (Eds). *A History of Atmospheric CO₂ and its Effects on Plants, Animals, and Ecosystems*. Springer, USA. pp. 185-213.
- Sage, R.F., Li, M., & Monson, R.K. 1999. The taxonomic distribution of C₄ photosynthesis. In: Sage, R.F., & Monson, R.K. (Eds.). *C₄ plant biology*. Academic press, San Diego. pp. 551-584.
- Salisbury, F.B., & Ross, C.W. 1992. *Plant Physiology, 4th Edition*. Wadsworth Publishing Company, Belmont, California. 682 pp.
- Scheffer, V.B. 1950. Growth layers on the teeth of Pinnipedia as an indication of age. *Science*. 112(2907): 309-311.
- Scheffer, V.B., & Kraus, B. 1964. Dentition of the northern fur seal. *Fisheries Bulletin of California*. 63(2): 293-342.
- Schmidt, W.J. & Keil, A. 1971. *Polarizing Microscopy of Dental Tissues*. Pergamon Press, New York.
- Schmidt, S., & Stewart, G.R. 2003. $\delta^{15}\text{N}$ values of tropical savanna and monsoon forest species reflect root specialisations and soil nitrogen status. *Oecologia*. 134: 569-577.
- Schoeninger, M.J., & DeNiro, M.J. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta*. 48: 625-639.
- Schoeninger, M.J., Moore, J., & Sept, J.M. 1999. Subsistence strategies of two "savanna" chimpanzee populations: The stable isotope evidence. *American Journal of Primatology*. 49: 297-314.
- Scholes, R.J., Bond, W.J., & Eckhardt, H.C. 2003. Vegetation dynamics in the Kruger ecosystem. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger Experience*. Island Press, Washington DC. pp. 242-262.

- Schour, I., & Massler, M. 1949. The teeth. In: Farris, E., & Griffith, J. (Eds.). *The Rat in Laboratory Investigation*. London.
- Schour, I. & Hoffman, M.M. 1939a. Studies in tooth development, I. The 16 microns calcification rhythm in the enamel and dentin from fish to man. *Journal of Dental Research*. 18: 91-102.
- Schour, I. & Hoffman, M.M. 1939b. Studies in tooth development, II. The rate of apposition of enamel and in dentin man and other mammals. *Journal of Dental Research*. 18: 161-175.
- Schweizer, M.K., Wooller, M.J., Toporski, J., Fogel, M.L., & Steele, A. 2006. Examination of an Oligocene lacustrine ecosystem using C and N stable isotopes. *Palaeogeography Palaeoclimatology, Palaeoecology*. 230: 335-351.
- Scott, J.H. & Symons, N.B.B. 1977. *Introduction to Dental Anatomy, 8th Edition*. E. & S. Livingstone, Edinburgh.
- Sealy, J.C., Armstrong, R., & Schrire, C. 1995. Beyond lifetime averages: tracing life histories through isotopic analysis of different calcified tissues from archaeological human skeletons. *Antiquity*. 69: 290-300.
- Sealy, J.C., van der Merwe, N.J., Lee-Thorp, J.A., & Lanham, J.L. 1987. Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. *Geochimica et Cosmochimica Acta*. 51: 2707-2717.
- Segalen, L., Renard, M., Lee-Thorp, J.A., Emmanuel, L., Le Callonnec, L., de Rafelis, M., Senut, B., Pickford, M., & Melice, J-L. 2006. Neogene climate change and emergence of C₄ grasses in the Namib, southwestern Africa, as reflected in ratite ¹³C and ¹⁸O. *Earth and Planetary Science Letters*. 244: 725-734.
- Selous, F.C. 1881. *A Hunter's Wanderings in Africa*. London, Richard Bentley & Sons.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., & Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience*. 37: 789-799.

- Sergeant, D.E. 1959. Age determination in odontocete whales from dentinal growth layers. *Norsk Hvalfangsttid.* 6: 273-288.
- Seydack, A.H.W., Vermeulen, C., & Huisamen, J. 2000. Habitat quality and the decline of an African elephant population: implications for conservation. *South African Journal of Wildlife Research.* 30(1): 34-42.
- Shimane, W.M., & Skarpe, C. 2006. Rebrowsing by elephants three years after stimulated browsing on five woody plant species in northern Botswana. *South African Journal of Wildlife Research.* 36: 99-102.
- Shimoyama, T. 1967. Peritubular hypercalcified zone of mammalian dentin. *Archives of Histology of Japan.* 28: 113
- Short, J. 1981. Diet and feeding behaviour of the forest elephant. *Mammalia.* 45(2): 177-185.
- Shoshani, J. 1997. It's a nose! It's a hand! It's an elephant's trunk! *Natural History.* 97(6): 36-44.
- Shoshani, J. 1998. Understanding proboscidean evolution: a formidable task. *Trends in Ecology and Evolution.* 13(12): 480-487.
- Sikes, S.K. 1971. *The Natural History of the African Elephant.* Weidenfeld & Nicolson, London.
- Sinclair, A.R.E., Fryxell, J.M., & Caughley, G. 2006. *Wildlife ecology, conservation, and management, 2nd edition.* Blackwell Publishing, Malden, USA.
- Sitati, N.W., Walpole, M.J., Smith, R.J., & Leader-Williams, N. 2003. Predicting spatial aspects of human–elephant conflict. *Journal of Applied Ecology.* 40: 667-677.
- Skarpe, C., Bergstrom, R., Braten, A.L., & Danell, K. 2000. Browsing in a heterogeneous savanna. *Ecography.* 23: 632-640.
- Skinner, J.D., & Smithers, R.H.N. 1990. *The Mammals of the Southern African Subregion, Second Edition.* University of Pretoria, Pretoria, South Africa.
- Smallie, J.J., & O'Connor, T.G. 2000. Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *African Journal of Ecology.* 38: 352-359.

- Smith, B.N., & Epstein, S. 1971. Two categories of $^{13}\text{C}/^{12}\text{C}$ ratios for higher plants. *Plant Physiology*. 47: 380-384.
- Smith, K.F., Sharp, Z.D., & Brown, J.H. 2002. Isotopic composition of carbon and oxygen in desert fauna: investigations into the effect of diet, physiology, and seasonality. *Journal of Arid Environments*. 52: 419-430.
- Smuts, G.L. 1974. Game movements in the Kruger National Park and their relationship to the segregation of sub-populations and the allocation of culling compartments. *Journal of the Southern African Wildlife Management Association* 4: 51-58.
- Sognaes, R.F. 1955. Microstructure and histochemical characteristics of mineralized tissues. *Annals of the New York Academy of Science*. 60: 545-574.
- Spinage, C.A. 1973. A review of ivory exploitation and elephant population trends in Africa. *East African Wildlife Journal*. 11: 281-289.
- Spinage, C.A. 1994. *Elephants*. T&A DPoyser, London.
- Sponheimer, M., & Lee-Thorp, J.A. 1999. Oxygen isotopes in enamel carbonate and their ecological significance. *Journal of Archaeological Science*. 26: 723-728.
- Sponheimer, M., & Lee-Thorp, J.A. 2001. The oxygen isotope composition of mammalian enamel carbonate from Morea Estate, South Africa. *Oecologia*. 126: 153-157.
- Sponheimer, M., Cerling, T.E., Robinson, T.F., Tegland, L., Roeder, B.L., Ayliffe, L., Dearing, M.D., & Ehleringer, J.R. 2006b. Turnover of stable carbon isotopes in the muscle, liver and breath CO_2 of alpacas (*Lama pacos*). *Rapid Communications in Mass Spectrometry*. 20: 1-5.
- Sponheimer, M., Lee-Thorp, J.A., de Ruiter, D.J., Smith, J.M., van der Merwe, N.J., Reed, K., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberg, C., & Marcus, W. 2003d. Diets of southern African Bovidae: Stable isotope evidence. *Journal of Mammalogy*. 84: 471-479.

- Sponheimer, M., Passey, B.H., de Ruiter, D.J., Guatelli-Steinberg, D., Cerling, T.E., & Lee-Thorp, J.A. 2006a. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science*. 314: 980-982.
- Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L., Lopez, E., Cerling, T., Dearing, D., & Ehleringer, J. 2003b. An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. *Canadian Journal of Zoology* 81: 871-876.
- Sponheimer, M., Robinson, T., Ayliffe, L., Roeder, B., Hammer, J., Passey, B., West, A., Cerling, T., Dearing, D., & Ehleringer, J. 2003a. Nitrogen isotopes in mammalian herbivores: Hair $\delta^{15}\text{N}$ values from a controlled-feeding study. *International Journal of Osteoarchaeology*. 13: 80-87.
- Sponheimer, M., Robinson, T.F., Roeder, B.L., Passey, B.H., Ayliffe, L.K., Cerling, T.E., Dearing, M.D., & Ehleringer, J.R. 2003c. An experimental study of nitrogen flux in llamas: is ^{14}N preferentially excreted? *Journal of Archaeological Science*. 30: 1649-1655.
- Steele, K.W., & Daniel, R.M.J. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. *Journal of Agricultural Science*. 90: 7-9.
- Stevens, R.E., Lister, A.M., & Hedges, R.E.M. 2006. Predicting diet, trophic level, and palaeoecology from bone stable isotope analysis: a comparative study of five red deer populations. *Oecologia*. 149: 12-21.
- Stevenson-Hamilton, J. 1905. *Annual report on the government game reserves*. Unpublished internal memorandum. South African National Parks, Skukuza, South Africa.
- Stewart, G.R., & Schmidt, S. 1999. The evolution and ecology of plant mineral nutrition. In: Press, M.C., Scholes, J.D., & Barker, M.G. (Eds.). *Physiological Plant Ecology*. Blackwell, Oxford. pp 91-114.

- Stewart, G.R., Turnbull, M.H., Schmidt, S., & Erskine, P.D. 1995. ^{13}C Natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. *Australian Journal of Plant Physiology*. 22: 51-55.
- Steyn, A., & Stalmans, M. 2001. Selective habitat utilization and impact on vegetation by African elephant within a heterogeneous landscape. *Koedoe*. 44(1): 95-103.
- Stock, W.D., Chuba, D.K., & Verboom, G.A. 2004. Distribution of South African C_3 and C_4 species of Cyperaceae in relation to climate and phylogeny. *Austral Ecology*. 29: 313-319.
- Stokke, S., & du Toit, J.T. 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*. 23(1): 70-80.
- Stuiver, M., & Polach, H.A. 1977. Discussion: Reporting of ^{14}C Data. *Radiocarbon* 19(3): 355–363.
- Styles, C.V., & Skinner, J.D. 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colophospermum mopane*, in Botswana's Northern Tuli Game Reserve. *African Journal of Ecology*. 38: 95-101.
- Sukumar, R., & Ramesh, R. 1992. Stable carbon isotope ratios in Asian elephant collagen: implications for dietary studies. *Oecologia*. 91: 536-539.
- Sukumar, R., Bhattacharya, S.K., & Krishnamurthy, R.V. 1987. Carbon isotopic evidence for different feeding patterns in an Asian elephant population. *Current Science*. 56: 11-14.
- Swanepoel, C.M., & Swanepoel, S.M. 1986. Baobab damage by elephant in the middle Zambezi Valley, Zimbabwe. *African Journal of Ecology* 24: 129-132.
- Swanepoel, C.M. 1993. Baobab damage in Mana Pools National Park, Zimbabwe. *African Journal of Ecology* 31: 220-225.
- Swap, R.J., Aranibar, J.N., Dowty, P.R., Gilhooly Iii, W.P., & Macko, A. 2004. Natural Abundance Of ^{13}c And ^{15}n In C_3 And C_4 Vegetation Of Southern Africa: Patterns And Implications. *Global Change Biology*. 10: 350–358.

- Steig, E.J., Morse, D.L., Waddington, E.D., Stuiver, M., Grootes, P.M., Mayewski, P.A., Twickler, M.S., & Whitlow, S.I. 2000. Wisconsin and Holocene climate history from an ice core at Taylor Dome, Western Ross Embayment, Antarctica. *Geografiska Annaler*. 82A(2-3): 213-235.
- Tainton, N.M. 1999. The ecology of the main grazing lands of South Africa: the Savanna biome. In: Tainton, N.M. (Ed.). *Veld management in South Africa*. University of Natal Press: Pietermaritzburg, South Africa. pp. 23-53.
- Takuma, S. & Eda, S. 1960. Peritubular matrix in mammalian dentin. *Bulletin of the Tokyo Dental College*. 1: 20
- Takuma, S. & Eda, S. 1966. Structure and development of the peritubular matrix in dentine. *Journal of Dental Research*. 45: 683
- Takuma, S., & Nagai, N. 1971. Ultrastructure of rat odontoblasts in various stages of their development and maturation. *Archives of Oral Biology*. 16: 993.
- Talma, A.S., & Vogel, J.C. 1992. Late Quaternary paleotemperatures derived from a speleothem from Cango Caves, Cape Province, South Africa. *Quaternary Research*. 37: 203-213.
- Tangley, L. 1997. In search of Africa's forgotten forest elephant. *Science*. 275(5305): 1417-1419.
- Tchamba, M.N. 1996. History and present status of the human/elephant conflict in the Waza-Logone region, Cameroon, West Africa. *Biological Conservation*. 75: 35-41.
- Theuerkauf, J., Waitkuwait, W.E., Guiro, Y., Ellenberg, H., & Porembski, S. 2000. Diet of forest elephants and their role in seed dispersal in the Bossematié forest reserve, Ivory coast. *Mammalia*. 64(4): 447-460.
- Thomas, H.F. & Payne, R.C. 1981. The ultrastructure of dentinal tubules from erupted human premolar teeth. *Journal of Dental Research*. 60: 351 (Abstract 161).
- Thompson, D.R., Bury, S.J., Hobson, K.A., Wassenaar, L.I., & Shannon, J.P. 2005. Stable isotopes in ecological studies. *Oecologia*. 144: 517-519.

- Thompson, L.G., Mosely-Thompson, E., Davis, M.E., Henderson, K.A., Brecher, H.H., Zagorodnov, V.S., Mashiotto, T.A., Lin, P.-N., Mikhaleiko, V.N., Hardy, D.R., & Beer, J. 2002. Kilimanjaro ice core records: evidence of Holocene climate change from tropical Africa. *Science*. 298: 589-593.
- Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Lin, P.-N., Henderson, K.A., Cole-Dai, J., Bolzan, J.F., & Liu, K.-b. 1995. Late glacial stage and Holocene tropical ice core records from Huascarán, Peru. *Science*. 269: 46-50.
- Tieszen, L.L. 1991. Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. *Journal of Archaeological Science*. 18: 227-248.
- Tieszen, L.L., & Fagre, T. 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO₂, bone collagen, bioapatite, and soft tissues. In: Lambert, J.B., & Grupe, G. (Eds.). *Prehistoric human bone: Archaeology at the molecular level*. Springer-Verlag. pp. 121-155.
- Tieszen, L.L., Boutton, T.W., Ottichilo, W.K., Nelson, D.E., & Brandt, D.H. 1989. An assessment of long-term food habits of Tsavo elephants based on stable carbon and nitrogen isotope ratios of bone collagen. *African Journal of Ecology*. 27: 219-226.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., & Slade, N.A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for ¹³C analysis of diet. *Oecologia Berlin*. 57:32-37.
- Tieszen, L., Hein, D., Qvortrup, S., Troughton, J., & Imbamba, S. 1979. Use of $\delta^{13}\text{C}$ values to determine vegetation selectivity in east African herbivores. *Oecologia*. 37: 351-359.
- Tolken, H.R. 1977. *A revision of the genus Crassula in southern Africa*. Bolus Herbarium, Rondebosch, South Africa. 595 pp.
- Trapani, J. & Fisher, D.C. 2003. Discriminating Proboscidean Taxa Using Features of the Schreger Pattern in Tusk Dentin. *Journal of Archaeological Science*. 30 (4): 429-438.

- Trollope, W.S.W., Trollope, L.A., Biggs, H.C., Pienaar, D., & Potgieter, A.L.F. 1998. Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. *Koedoe*. 41 (2): 103-112.
- Trudinger, C.M., Enting, I.G., Francey, R.J., & Ehteridge, D.M. 1999. Long-term variability in the global carbon cycle inferred from a high-precision CO₂ and δ¹³C ice-core record. *Tellus*. 51B: 233-248.
- Tshiguvho, T.E. 2000. *The Effects of Roads on Invertebrate Communities in the Pafuri-Punda Maria Area, Kruger National Park: Ants As Indicators*. Unpublished M.Sc. dissertation, University of Venda, South Africa.
- Tyson, P.D., & Dyer, T.D.G. 1975. Mean annual fluctuations of precipitation in the summer rainfall region of South Africa. *The South African Geographic Journal*. 57: 104-110.
- Tyson, P.D. 1985. *Climatic Change and Variability in Southern Africa*. Cape Town: Oxford University Press.
- Urton, E.J.M., & Hobson, K.A. 2005. Intrapopulation variation in gray wolf isotope (δ¹³C and δ¹⁵N) profiles: implications for the ecology of individuals. *Oecologia*. 145: 317-326.
- van Aarde, R., Ferreira, S., Jackson, T., & Shrader, A. 2004. Managing Kruger's elephants: the metapopulation metaphor. *Road Map to Comprehensive Elephant Management Framework, Berg-en-dal, Kruger National Parks, RSA, Septemeber 2004*.
- van Aarde, R., Whyte, I., & Pimm, S. 1999. Culling and the dynamics of the Kruger National Park African elephant population. *Animal Conservation*. 2: 287-294.
- van Aarde, R.J., Jackson, T.P., & Ferreira, S.M. 2006. Conservation science and elephant management in southern Africa. *South African Journal of Science*. 102: 385-388.

- van de Koppel J., & Prins, H.H.T. 1998. The importance of herbivore interactions for the dynamics of African savanna woodlands: A hypothesis. *Journal of Tropical Ecology*. 14: 565-576.
- van der Merwe, N.J., & Medina, E. 1989. Photosynthesis and $^{13}\text{C}/^{12}\text{C}$ ratios in Amazonian rainforests. *Geochimica et Cosmochimica Acta*. 53: 1091-1094.
- van der Merwe, N.J., & Medina, E. 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *Journal of Archaeological Science*. 18: 249-259.
- van der Merwe, N.J., Lee Thorp, J.A., & Bell, R.H.V. 1988. Carbon isotopes as indicators of elephant diets in African environments. *African Journal of Ecology*. 26: 163-172.
- van der Merwe, N.J., Lee-Thorp, J.A., Thackeray, J.F., Hall-Martin, A., Kruger, F.J., Coetzee, H., Bell, R.H.V., & Lindeque, M. 1990. Source-area determination of elephant ivory by isotopic analysis. *Nature*. 346: 744-746.
- van Niekerk, P.J., Raubenheimer, E.J., van Heerden, W.F.P., Dauth, J., Smith P.D., Turner, M.L., & Dreyer, M.J. 1991. The tush of the African elephant (*Loxodonta africana*). *Journal of Dental Research*. 70(4): 853.
- van Nostrand, F.C. & Stephenson, A.V. 1964. Age determination for beavers by teeth development. *Journal of Wildlife Management*. 28(3): 430-434.
- van Soest, P.J. 1994. *Nutritional Ecology Of The Ruminant, Second Edition*. Comstock, Ithaca, New York.
- van Wilgen, B.W., Biggs, H.C., O'Regan, S.P., & Mare, N. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Science*. 96: 167-178.
- van Wilgen, B.W., Biggs, H.C., & Potgieter, A.L.F. 1998. Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. *Koedoe*. 41: 69-87.

- van Wilgen, B.W., Trollope, W.S.W., Biggs, H.C., Potgieter, A.L.F., & Brockett, B.H. 2003. Fire as a driver of ecosystem variability. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger Experience*. Island Press, Washington DC. pp. 149-170.
- van Wyk, P., & Fairall, N. 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe*. 12: 57-89.
- Vaughn Kirby, F. 1896. *In haunts of wild game*. Edinburgh, Blackwood and Sons.
- Venter, F.J. 1990. A classification of land for management planning in the Kruger National Park. Ph.D. Thesis, University of South Africa.
- Venter, F.J., & Bristow, J.W. 1986. An account of the geomorphology and drainage of the Kruger National Park. *Koedoe*. 29: 117-124.
- Venter, F.J., & Gertenbach, W.P.D. 1986. A cursory review of the climate and vegetation of the Kruger National Park. *Koedoe*. 29: 139-148.
- Venter, F.J., Scholes, R.J., & Eckhardt, H.C. 2003. The abiotic template and its associated vegetation pattern. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds). *The Kruger Experience*. Island Press, Washington DC. pp. 83-129.
- Viljoen, P.J. 1989. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib Desert, South West Africa/Namibia. *African Journal of Ecology*. 27: 227-240.
- Virginia, R.A., & Delwiche, C.C. 1982. Natural ^{15}N abundance of presumed N_2 -fixing and non N_2 -fixing plants from selected ecosystems. *Oecologia*. 54: 317-325.
- Vogel, J.C. 1978. Isotopic assessment of the dietary habits of ungulates. *South African Journal of Science*. 74: 298-301.
- Vogel, J.C. 1980. Fractionation of the carbon isotopes during photosynthesis. IN: Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematisch – Naturwissenschaftliche Klasse Jahrgang. 1980. 3. Abhandlung. Springer-Verlag, Berlin/Heidelberg/New York. pp. 111-135.

- Vogel, J.C., Eglinton, B., & Auret, J.M. 1990b. Isotope fingerprints in elephant bone and ivory. *Nature*. 346: 747-749.
- Vogel, J.C., Fuls, A., & Ellis, R.P. 1978. The geographical distribution of Kranz grasses in South Africa. *South African Journal of Science*. 74: 209-215.
- Vogel, J.C., Talma, A.S., Hall-Martin, A.J., & Viljoen, P.J. 1990a. Carbon and nitrogen isotopes in elephants. *South African Journal of Science*. 86: 147-150.
- Voigt, E.A. 1983. Mapungubwe. An archaeozoological interpretation of an Iron Age community. *Transvaal Museum Monographs*. 1: 1-204.
- von Ebner, V. 1922. *Handbuch der Zahnheilkunde*. Wien, Holder-Pichler-Tempsky. Fourth Edition. 325 pp.
- Vrba, E.S. 1988. Late Pliocene climatic events and Hominid evolution. In: Grine, F.E. (Ed.). *Evolutionary History of the "Robust Australopithecines"*. Aldine de Gruyter, New York. pp. 405-426.
- Vrba, E.S. 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S. (Ed.). *Paleoclimate and evolution, with emphasis on human origins*. New Haven, Yale University Press. pp. 385-424.
- Walker, B.H., Emslie, R.H., Owen-Smith, N., & Scholes, R.J. 1987. To cull or not to cull: Lessons from a southern African drought. *Journal of Applied Ecology*. 24: 381-401.
- Watson, R.M., & Bell, R.H.V. 1969. The distribution, abundance and status of elephant in the Serengeti region of northern Tanzania. *Journal of Applied Ecology*. 6: 115-132.
- Weissengruber, G.E., Egerbacher, M., & Forstenpointner, G. 2005. Structure and innervation of the tusk pulp in the African elephant (*Loxodonta africana*). *Journal of anatomy*. 206(4): 387-393.
- WESSA Lowveld. 2004. Wildlife and Environment Society of South Africa Report on Great Elephant Debate Bundu Lodge, 6th August 2004.

- Western, D. & Lindsay, W.K. 1984. Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*. 22: 229-244.
- Whorf, T.P., & Keeling, C.D. 1998. Rising carbon. *New Scientist*. 157(2124): 54.
- Whyte, I.J. 1985. The present ecological status of the blue wildebeest (*Connochaetes taurinus* Burchell, 1823) in the Central District of the Kruger National Park. Unpublished M.Sc. Thesis, University of Natal, Pietermaritzburg.
- Whyte, I.J. 1996. Studying elephant movements. In: Kangwana, K. (Ed.). *AWF Technical Handbook Series: Studying Elephants*. African Wildlife Foundation, Nairobi.
- Whyte, I.J. 2001a. Conservation management of the Kruger National Park elephant population. Ph.D. Thesis, University of Pretoria, Pretoria.
- Whyte, I.J. 2001b. Headaches and heartaches: the elephant management dilemma. In: Schmidt, D., & Willot, E. (Eds.). *Environmental Ethics: What Really Matters, What Really Works*. New York, Oxford University Press. pp. 293-305.
- Whyte, I.J. 2004. Ecological tests of the new elephant management policy for Kruger National Park and expected outcomes. *Pachyderm*. 36: 99-109.
- Whyte, I.J., & Grobler, D. 1998. *The current status of contraception research in the Kruger National Park*. Scientific report 13/97. Skukuza, South African National Parks.
- Whyte, I.J., & Joubert, S.C.J. 1988. Blue wildebeest population trends in the Kruger National Park and the effects of fencing. *South African Journal of Wildlife Research*. 18(3): 78-87.
- Whyte, I.J., Biggs, H.C., Gaylard, A., & Braack, L.E.O. 1999. A new policy for the management of the Kruger National Park's elephant population. *Koedoe*. 42 (1): 111-133.
- Whyte, I.J., van Aarde, R.J., & Pimm, S.L. 1998. Managing the elephants of Kruger National Park. *Animal Conservation*. 1: 77-83.
- Whyte, I.J., van Aarde, R.J., & Pimm, S.L. 2003. Kruger's elephant population: its size and consequences for ecosystem heterogeneity. In: du Toit, J.T., Rogers, K.H., & Biggs, H.C. (Eds.). *The Kruger Experience*. Island Press, Washington DC. pp. 332-348.

- Williamson, B.R. 1975. The condition and nutrition of elephant in Wankie National Park. *Arnoldia Rhodesia*. 7 (12): 1-20.
- Wilson, E.O. 1993. *The Diversity of Life*. Harvard University Press.
- Wing, L.D., & Buss, I.O. 1970. Elephants and forest. *Wildlife Monographs*. 19: 1-92.
- Winter, K., & Holtum, J.A.M. 2002. How closely do the $\delta^{13}\text{C}$ values of Crassulacean acid metabolism plants reflect the proportion of CO_2 fixed during day and night? *Plant Physiology*. 129: 1843-1851.
- Wong, W.W., Cochran, W.J., Klish, W.J., Smith, E.O., Lee, L.S., & Klein, P.D. 1988. In vivo isotope fractionation factors and the measurement of deuterium and ^{18}O dilution spaces from plasma, urine, saliva, respiratory water vapour, and carbon dioxide. *American Journal of Clinical Nutrition*. 47: 1-6.
- Wrench, J.M., Meissner, H.H., & Grant, C.C. 1997. Assessing diet quality of African ungulates from faecal analyses: the effect of forage quality, intake and herbivore species. *Koedoe*. 40: 125-136.
- Wrench, J.M., Meissner, H.H., Grant, C.C., & Casey, N.H. 1996. Environmental factors that affect the concentration of P and N in faecal samples collected for the determination of nutritional status. *Koedoe*. 39: 1-6.
- Wyatt, J.R., & Eltringham, S.K. 1974. The daily activity of the elephant in the Rwenzori National Park, Uganda. *East African Wildlife Journal*. 12: 273-289.
- Yakir, D. 1992. Variations in the natural abundances of ^{18}O and deuterium in plant carbohydrates. *Plant, Cell and Environment*. 15: 1005-1020.
- Yilmaz, S., Newman, H.N., & Poole, D.F.G. 1977. Diurnal periodicity of Von Ebner growth lines in pig dentine. *Archives of Oral Biology*. 22: 511-513.
- Yoo, S.-H., Choi, W.-J., Han, G.H., Park, J.-G., Lee, S.-M., & Jin, S. 1999. Temporal variations in isotope ratios and concentrations of nitrate-nitrogen in groundwater as affected by chemical fertilizer and livestock manure. *Agricultural Chemical Biotechnology*. 42: 186-190.

Zambatis, N. & Biggs, H.C. 1995. Rainfall and temperatures during the 1991/92 drought in the Kruger National Park. *Koedoe*. 38: 1–16.

Zhang, L., & Wang, N. 2003. An initial study on habitat conservation of Asian elephant (*Elephas maximus*), with a focus on human-elephant conflict in Simao, China. *Biological Conservation*. 112: 453-459.