What drives the seasonal movements of African elephants (*Loxodonta africana*) in Ithala Game Reserve?

by

Kayleigh Muller

Submitted in fulfilment of the academic requirements for the degree of

Master of Science

In the Discipline of Ecology

School of Life Sciences

College of Agriculture, Engineering, and Science

University of KwaZulu-Natal

Pietermaritzburg

Supervisors:

Prof. David M. Ward and Dr. Adrian M. Shrader

November 2013
I, Kayleigh Muller, declare that

(i) The research reported in this dissertation/thesis, except where otherwise indicated, is my original research
(ii) This dissertation/thesis has not been submitted for any degree or examination at any other university
(iii) This dissertation/thesis does not contain other persons’ data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
(iv) This dissertation/thesis does not contain other peoples’ writing, unless specifically acknowledged as being sourced from other researchers.

Where other written sources have been quoted, then:

a) Their words have been re-written but the general information attributed to them has been referenced;
b) Where their exact words have been used, their writing has been placed inside quotation marks and referenced.

v) Where I have reproduced a publication of which I am author, co-author or editor, I have indicated in detail which part of the publication was actually written by myself alone and have fully referenced such publications.

Kayleigh Muller
November 2013
Preface

The work described in this thesis was carried out at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from January 2012 to November 2013, under the supervision of Professor David Mercer Ward and Dr. Adrian M. Shrader.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the authors and has not been submitted in any form to another university. Where use of other work was made, it has been acknowledged in the document.

K. Muller

Kayleigh Muller

Professor David Mercer Ward
Supervisor

Dr. Adrian M. Shrader
Co-supervisor
November 2013
Acknowledgements

SUCCESS is not final, FAILURE is not fatal; it is the COURAGE to continue that counts. – Winston Churchill

This study would not have been possible without the committed help of many people, to whom my sincere thanks are due. Firstly, I would like to thank my supervisor Professor David M. Ward for the continued support and advice throughout this project. Your knowledge of all things never ceases to surprise me. Dr. Adrian M. Shrader, my co-supervisor, for his assistance and constructive criticisms. Thank you to the staff and managers at Evemvelo KZN Wildlife who made this study possible, Pete and Celia Ruinard, Chris Barichiev, Jeffery Maivha and Gary Bawden. I really appreciated the help from my field assistants Erik Hanson and Matthew Becker.

I am very thankful to many people from the University of KwaZulu-Natal who assisted me in many capacities Simo Welcome Ngcobo, George Carlese, Professor Richard Beckett, Rogan Roth, Renny Noble, Alison Young and Martin Hampton. To Stephne Stuart for laboratory assistance and offering plenty of advice about many of my protocols, your patience is highly appreciated. To my lab mates; Tamanna Patel, Desale Okubamichael, Tiffany Pillay, Jennifer Russell, Keenan Stears and Melissa H. Schmitt; I thank you for the various help you provided throughout the project. I am also very grateful to Danielle Levesque for reading through drafts and offering comments on this manuscript. Tobz, you are awesome! I am very appreciative to my sources of funding provided by the College of Agriculture, Engineering and Science, University of KwaZulu-Natal; Gay Langmuir and National Research Foundation. Lastly, I would like to thank my parents, without your love and support this would not have been possible. S.S.
Summary

The changes in plant quality and availability in space and time present a substantial problem to mammalian herbivores. As a result, these herbivores need to alter their foraging behaviour to maximize their energy gain at both small (plant level) and large (landscape level) scales. A megaherbivore, the African elephant (*Loxodonta africana*), has been shown to be selective in its foraging choices at both of these scales. Furthermore, the ratio of palatability:defences (e.g. fibre and total polyphenols) has been highlighted as an important determinant of habitat selection in elephants. The elephants in Ithala Game Reserve (IGR) frequently leave IGR during the wet season and forage outside the reserve. However, they predominantly feed on the low-nutrient granite soils of the reserve and return to a high-nutrient area with dolerite soils during the dry season. In an attempt to understand these seasonal movements, I focused on how the small-scale foraging decisions of the elephants lead to large-scale seasonal movements in IGR, KwaZulu-Natal. Plant availability was determined seasonally for seven target species across four areas in the reserve. Crude protein, fibre, energy and total polyphenols as well as the ratios of palatability:digestion-reducing substances were analysed in the wet and dry seasons. All factors and their interactions were significant in a MANOVA. Consequently, I employed a dimension-reducing Principal Components Analysis (PCA) to better understand the factors of greatest importance. The PCA highlighted four of the six most important factors to be the ratios of palatability:digestion-reducing substances. The other two important variables were total polyphenols (negative effect) and crude protein (positive effect). At small spatial scales, I found that the elephants were selective in their decisions, especially during the dry season. For example, the increased inclusion of the principal tree species *Acacia nilotica* from 2.9% in the wet season to 39.3% during the dry season appears to be a result of a decline in total polyphenols and fibre during the dry season. At large spatial scales, the elephants moved back into IGR from the low-nutrient granite soils
in the east in response to an increase in forage quality in the west as the quality declined in
the east at the same time. However, it is unclear as to why the elephants are leaving the
reserve during the wet season. Some possible explanations for this are discussed.

Key-words: acid detergent fibre, crude protein, *Loxodonta africana*, neutral detergent fibre,
total polyphenols, plant part quality.
Table of Contents

Declaration: Plagiarism .......................................................................................................... 2
Preface .................................................................................................................................... 3
Acknowledgements ................................................................................................................ 4
Summary ................................................................................................................................ 5
Key-words: ............................................................................................................................. 6
List of Tables ...................................................................................................................... 8
List of Figures..................................................................................................................... 9
List of Appendices ............................................................................................................ 12
Thesis outline ........................................................................................................................... 13
Chapter 1: Literature review .................................................................................................... 15
FORAGING ................................................................................................................................. 15
PHYSIOLOGICAL FORAGING CONSTRAINTS ............................................................ 20
ELEPHANTS ....................................................................................................................... 22
RATIONALE FOR THIS STUDY: ELEPHANTS OF THE ITHALA GAME RESERVE .......... 25
Chapter 2: Materials and methods ........................................................................................... 29
STUDY AREA ....................................................................................................................... 29
DATA COLLECTION ..................................................................................................... 30
DATA ANALYSIS .......................................................................................................... 33
Chapter 3: Results .................................................................................................................... 34
AVAILABILITY OF PLANTS .................................................................................. 35
QUALITY OF PLANTS ............................................................................................... 36
PLANT PARTS ................................................................................................................ 49
Chapter 4: Discussion .............................................................................................................. 51
MANAGEMENT AND FUTURE STUDIES ..................................................................... 56
References ............................................................................................................................ 60
Appendix 1. ...................................................................................................................... 70
Appendix 2. ...................................................................................................................... 73
Table 1. Percentage of principal species making up the wet and dry season diets. Data taken from Shrader et al. (2012).

Table 2. MANOVA statistics of the effects of season, area, species and their interactions on the seven target species to determine forage quality. Forage quality was measured for: crude protein, acid detergent fibre (ADF), neutral detergent fibre (NDF) and total polyphenols (TP). Additionally, ratios of some of these parameters were also considered.

Table 3. Component weightings for the principal components analysis for log_{10} crude protein (CP), log_{10} total polyphenols (TP), acid detergent fibre (ADF), neutral detergent fibre (NDF), the log_{10} ratio of crude protein:total polyphenols (CP:TP), log_{10} crude protein:ADF ratio (CP:ADF), log_{10} crude protein:NDF ratio (CP:NDF), log_{10} reciprocal of acid detergent fibre: total polyphenol concentrations (ADF:TP) and log_{10} reciprocal of neutral detergent fibre:total polyphenol concentrations (NDF:TP). Note that it is the absolute value that determines importance.

Table 4: Contingency table analyses of total polyphenols (TP), the ratio of crude protein to total polyphenols (CP:TP), reciprocal of Acid Detergent Fibre:total polyphenol ratio (ADF:TP), crude protein:ADF ratio (CP:ADF), crude protein (CP), crude protein:Neutral Detergent Fibre ratio (CP:NDF) and elephant numbers between the four sections in the wet and dry seasons. Predictions are based on elephant numbers found in each quadrant in each season. Elephant numbers were based on satellite observations in 2011.
Table 5. MANOVA statistics from the ranked comparisons of leaf and branch for the different plant quality parameters. CP = crude protein; TP = total polyphenol concentrations; ADF = acid detergent fibre; NDF = neutral detergent fibre.
List of Figures

Fig. 1. Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2011 in Ithala Game Reserve between wet (grey triangles) and dry seasons (black stars). Most elephants were found in the eastern side of IGR in the wet season, while the west was most heavily used in the dry season. There was virtually no overlap in section use between wet and dry seasons in the elephant observations. The four sections sampled were: northwest (NW), northeast (NE), southwest (SW), and southeast (SE). The northern border is the Pongola River.

Fig. 2. Topography ranging from 320 m a.s.l to 1446 m a.s.l (light grey lines) and rivers (darker grey lines) of Ithala Game Reserve. The Pongola River forms the northern border of the reserve. The thick black northern line is the Pongola River.

Fig. 3. Percentage abundance of each of the seven target species. Bars represent 1±S.E. A. karroo= Acacia karroo, A. nilotica= Acacia nilotica and D. cinerea= Dichrostachys cinerea (the three principal species). S. pentheri= Searsia pentheri (formerly known as Rhus pentheri), E. natalensis= Euclea natalensis, P. africanum= Peltophorum africanum and G. buxifolia= Gymnosporia buxifolia (the four avoided species).

Fig. 4. The seasonal values of log_{10} total polyphenol concentrations for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.

Fig. 5. The seasonal values of the log_{10} crude protein:total polyphenol (CP:TP) ratios for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.

Fig. 6. The seasonal values of the log_{10} CP:ADF ratios for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.
**Fig. 7.** The seasonal values of the $\log_{10}$ crude protein values for a) principal and b) avoided species. Bars represent $1\pm$S.E. Dashed line is the overall mean. Full names as for Fig. 3.

**Fig. 8.** The seasonal values of the $\log_{10}$ reciprocal of ADF:TP ratios for a) principal and b) avoided species. TP= total polyphenol concentrations. High values indicate high quality vegetation. Bars represent $1\pm$S.E. Dashed line is the overall mean. Full names as for Fig. 3.

**Fig. 9.** The seasonal values of the $\log_{10}$ CP:NDF ratios for a) principal and b) avoided species. Bars represent $1\pm$S.E. Dashed line is the overall mean. Full names as for Fig. 3.
List of Appendices

Appendix 1

Appendix 1a: Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2008 in Ithala Game Reserve between seasons wet (black triangles) and dry seasons (grey stars).

Appendix 1b: Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2009 in Ithala Game Reserve between seasons wet (black triangles) and dry seasons (grey stars).

Appendix 1c: Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2010 in Ithala Game Reserve between seasons wet (black triangles) and dry seasons (grey stars).

Appendix 2: MANOVA statistics between the nutritional factors (season, area, species and second- and third-order interactions) and plant quality data. Error degrees of freedom = 1005.
Thesis outline

Herbivores forage in an environment that exhibits variation in food quality and availability (Senft et al. 1987; Shipley 2007). This is particularly evident in the seasonal fluctuations between wet and dry periods (van Aarde et al. 2008). In addition, spatial heterogeneity in quality differs from individual plants up to the landscape scale (Pickett & Cadenasso 1995; Skarpe et al. 2000; Shipley 2007). Consequently, as a result of changes in plant availability and quality herbivores need to alter their foraging behaviours in a way to maximize their energy gain, especially during forage-limited periods (Stephens & Krebs 1986; Owen-Smith 2002). At small scales, herbivores can alter diet breadths, intake rates and foraging durations while at larger scales, herbivores can increase their range use and the habitats they utilise (Senft et al. 1987; Ward & Saltz 1994; Searle et al. 2005).

The African elephant (*Loxodonta africana*, (Blumenbach, 1797)) is the largest terrestrial megaherbivore (>1000 kg). They have been shown to be selective in their feeding habits at both small (Pretorius et al. 2011; Pretorius et al. 2012) and large scales (Loarie, van Aarde & Pimm 2009b; Young, Ferreira & van Aarde 2009; Shrader et al. 2012).

Elephants in Ithala Game Reserve in northern KwaZulu-Natal

The elephants in Ithala Game Reserve alter their habitat use seasonally (Shrader et al. 2012). They forage in a relatively low-nutrient area with granite soils and occasionally venture outside the reserve during the wet season and move back to a higher nutrient area with dolerite soils during the dry season. This movement back into the reserve is also away from their largest source of water in the dry season (Shrader et al. 2012). As water is not limiting
within the reserve (van Rooyen & van Rooyen 2008), it is likely that food quality and/or availability influence these seasonal movement patterns.

To explore this possibility, I recorded the seasonal changes in food quality and availability across the IGR. I did this by dividing the reserve area into four sections, based on previously recorded feeding areas of preferences and avoidances (Shrader et al. 2012). Ultimately, I wanted to determine how changes in plant quality and availability influenced the elephants’ seasonal habitat use and movement patterns. I did this by determining the nutritive quality of three principal tree species and four avoided tree species in the elephants’ diet across the reserve, as determined by Shrader et al. (2012). I also wanted to see how the nutritive quality changed seasonally, so I recorded data in both the wet and dry seasons.

The thesis is formatted so that Chapter 1 comprises an introduction and literature review where I discuss factors that influence foraging and habitat selection in more detail and set up what is already known about elephant movement and forage quality. The subsequent chapters comprise the Materials and Methods, Results and Discussion, respectively. Formatting for this thesis follows the Journal of Animal Ecology.
Chapter 1: Literature review

FORAGING

Foraging forms a central part of a herbivore’s daily activities. Food items are not uniformly distributed across the environment, but instead both food quality and availability exhibit spatial and temporal variation (Senft et al. 1987; Pickett & Cadenasso 1995; Shipley 2007). Optimal foraging theory is one of the most commonly used theories to explain the decisions that animals employ (Stephens & Krebs 1986). Factors influencing foraging decisions include time spent travelling to a patch, the type and quality of food in a patch and the density of food found in the patch (Charnov 1976; Stephens & Krebs 1986; Brown 1999).

At a most fundamental level, plant quality is influenced by soil quality (Bardgett & Wardle 2010). Low concentrations of nutrients in the soil generally result in low concentrations of nutrients in plant organs (Coley, Bryant & Chapin 1985; Owen-Smith & Cooper 1987; Holdo 2003). Furthermore, plant species growing in nutrient-poor areas have been shown to have higher levels of secondary metabolites, which are compounds not involved in primary cell functions. Plants typically use these secondary metabolites to defend the parts that they have (Coley et al. 1985; Owen-Smith & Cooper 1987). As a result of heterogeneous plant quality and availability, a herbivore’s diet varies both spatially and temporally across the environment. Spatially, differences occur between plant species as well as between the parts of the plant eaten, and on larger scales, between feeding patches and habitats (Senft et al. 1987; Bailey et al. 1996). Food resources fluctuate naturally as vegetation grows and decays (Owen-Smith 2002). Furthermore, not all available food is accessible to herbivores. Accessibility may be temporary, such as results from the loss of leaves of deciduous plants (Shorrocks 2007). Additionally, leaves at the tops of trees are not
available to shorter herbivores, while woody matter is not edible for many smaller herbivores as their digestive systems are not equipped to handle high fibre diets (Lundberg & Astrom 1990; Owen-Smith 2002). Within feeding patches and habitats, the key determinant of food intake is how long it takes the herbivore to handle the food type (Emlen 1966). Food intake is limited by bite size and bite rate. Intake rate ultimately determines whether the herbivore will need to include other sources of less preferred species in their diets (Owen-Smith 2002).

Temporally, a herbivore’s diet is heterogeneous across seasons. This is particularly evident in systems where there are seasonal fluctuations between wet and dry periods (Shorrocks 2007; van Aarde et al. 2008). In southern African savannas, there are two distinct seasons, wet and dry (Scholes & Walker 1993; du Toit, Rogers & Biggs 2003). The wet season is associated with increased resource availability with a higher nutritive quality (Owen-Smith 1988). Conversely, the dry season is known to have limited water availability with a reduction in plant quality and availability (Chamaille-Jammes, Valeix & Fritz 2007). These seasonal changes result in range shifts in herbivores (Owen-Smith 1988; Holdo, Holt & Fryxell 2009). For example, the African buffaloes (Syncerus caffer) in Kruger National Park changed their grass species selection and habitat utilisations between seasons in responses to changes in quality and quantity of grass (Macandza, Owen-Smith & Cross 2004). Similarly, wildebeest (Connochaetes gnou) is the Serengeti National Park are known to shift their foraging in relation to plant quality (Holdo et al. 2009).

Another factor that influences food quality and thus potentially movement patterns, are digestion-reducing substances. Physical defences and plant secondary metabolites increase the difficulty of digestion and intake rates respectively (Freeland & Janzen 1974). These physical defences include spines, thorns and cell structure, e.g. cell wall thickness (Shipley 1999). Physical defences can be effective for smaller-bodied mammalian herbivores, the so-called “mesoherbivores” (35-180 kg) (Cooper & Owen-Smith 1986), but less effective
against the larger mouths of large-bodied herbivores, the so-called “megaherbivores” such as elephants, giraffes and rhinoceroses (Owen-Smith 1988; Sukumar 1992; Rafferty, Byron & Hanley 2005). Physical defences also interact with leaf size so that smaller leaves are hidden among long thorns (e.g. Cooper & Owen-Smith 1986; Rohner & Ward 1997).

A second, and more prevalent, form of plant defence is plant secondary metabolites. Secondary metabolites are chemicals found in plant cells that are not important for primary cell functions (Iason 2005). Phenolics are an abundant group of structurally diverse chemicals commonly used by plants. The most well-known phenolic compounds are tannins (Waterman & Mole 1994). There are two main types of tannins: hydrolysable tannins and condensed tannins (Cooper & Owen-Smith 1985; Bryant et al. 1991; Bryant, Reichardt & Clausen 1992). Hydrolysable tannins inhibit digestive enzymes by hindering the digestion of plant material (Waterman & Mole 1994). Condensed tannins bind to protein and reduce the digestibility of the plant (Robbins et al. 1987; Freeland 1991). Tannins have an dose-dependent effect, such that the more the herbivore ingests the less protein they are able to digest (Cooper & Owen-Smith 1985; Waterman & Mole 1994). As a result, herbivores have had to develop ways to maximise their forage intake while limiting the intake of secondary metabolites (Provenza et al. 2003).

To counteract these dietary limitations, herbivores have been found to avoid plants containing high concentrations of secondary compounds (e.g. Owen-Smith 1994; Frye et al. 2013). For example, kudus (Tragelaphus strepsiceros) avoided plants containing high concentrations of tannins (Cooper & Owen-Smith 1985). Similarly, giraffes avoided hydrocyanic acid (Zinn, Ward & Kirkman 2007). Interestingly, the ratio of digestion-enhancing:digestion-reducing ratio was the most important factor influencing elephant foraging decisions (Shrader et al. 2012). Elephants utilised tree species with lower tannins and higher crude proteins rather than trees based on crude protein alone. This highlights the
fact that the ratio of digestion-enhancing substances (such as crude protein) relative to the
digestion-reducing substances (such as structural fibre and defensive compounds) of the plant
are important for determining herbivore foraging decisions (Wallis et al. 2012). Similar
results have been obtained for vertebrates dispersing fruits (e.g. Cipollini & Levey 1997).
Furthermore, Wallis et al. (2012) highlights the importance of the use of available nitrogen,
dry matter digestibility and tannins as better indicators of the nutritional quality of leaves for
mammalian herbivores.

A key way that herbivores cope with plant defences is to have varied diets (Westoby
1978). A varied diet allows an animal to limit the intake of potentially lethal chemicals while
complementary chemicals partially neutralise the effects of other lethal chemicals if eaten
together (Westoby 1974; Westoby 1978; Provenza et al. 2003). This varied diet allows a
limitation on the chemical intake of unpalatable substances while still maintaining their
nutritional requirements (Freeland & Janzen 1974; Lundberg & Astrom 1990; Belovsky &
Schmitz 1994). For example, lambs that had the choice between diets containing three plant
secondary metabolites (i.e. tannins, terpenes or oxalates) ate more than lambs encountering
only one secondary metabolite (Villalba, Provenza & Han 2004). The lambs were able to eat
more when three plant secondary metabolites were presented to them because mixing
complementary chemicals reduces the toxicity of the chemical on its own. It is clear that
experience and availability of toxins alters perception of food quality for herbivores
(Provenza et al. 2003). Additionally, diet switching allows an individual to maintain high
quality diets (Freeland & Janzen 1974; Wiggins et al. 2006). For example, the common
brushtail possum (Trichosurus vulpecula) was found to have an increased intake when they
were given the opportunity to switch between food types rather than the no-choice diet. This
highlights the importance of diet switching when plants are heterogeneously distributed in
space and time (Wiggins, McArthur & Davies 2006). An increase in diet breadth also helps to
maximize nutritional gain when resources are limited, e.g. introduction of more plant species during resource-limiting periods (Emlen 1966).

Diet breadth is another way in which herbivores can compensate for changes in plant quality. An increased diet breadth, during forage-limited periods, allows an individual to maintain its metabolic requirements (Owen-Smith 1994; Macandza et al. 2004). In a study that assessed the seasonal foraging decisions and diet breadth of kudus (*Tragelaphus strepsiceros*) in response to changes in quality, these animals were found to increase their diet breadth substantially from 19 woody species in the wet season to 31 species during the dry season (Owen-Smith 1994). A similar pattern of increased diet breadth was seen in another experiment on kudus by Owen-Smith and Cooper (1989). These authors also found that there was inclusion of small amounts of unpalatable species, i.e. high in secondary plant metabolites, in late August (the end of the dry season).

Small-scale changes in diet quality have the ability to lead to large-scale patterns (Shipley 2007). Herbivores tend to select high-quality vegetation. Therefore, if an individual experiences numerous consecutive poor-quality foraging bouts they will be forced to search further for better quality food (Senft et al. 1987; Shipley 2007). These poor quality feeding bouts results in herbivores moving to adjacent patches and eventually adjacent habitats (Senft et al. 1987). Consequently, these movement changes may result in the seasonal movements of animals. As a result, small-scale decisions regarding bite quality have the ability to influence large-scale foraging patterns (Owen-Smith 2002; Shipley 2007).

The study of animal movement patterns allows ecologists to understand the factors influencing animal distributions in space and time. Changes in abiotic factors, including rainfall and temperature, have been found to be some of the determinants of herbivore migratory patterns (e.g. Saino et al. 2007). Changes in rainfall and temperature patterns alter the quality and availability of food resources. This change in forage quality is the trigger that
initiates the movement of herbivores (Holdo et al. 2009) because herbivores try to balance their metabolic requirements by means of seasonal changes in forage quality and abundance. A classic example is the migration of wildebeest (Connochaetes gnou) in the Serengeti National Park. The onset of seasonal movement patterns in this species was based on the quality of available forage (Holdo et al. 2009). The intake rate of green grass coupled with high nitrogen content were the best predictors of both the short- and long-distance movements of the wildebeest (Holdo et al. 2009). As grass declined in quality and availability the wildebeest moved on to adjacent habitats where availability and quality of grass remained higher. The migration of the wildebeest shows that small-scale foraging decisions and plant quality can lead to large-scale foraging patterns, and possibly migration (Holdo et al. 2009). Similarly, elk (Cervus canadensis) foraging could be explained by fine-scale foraging choices they made based on how much effort they invested in digging to find grass and forbs in the snow (Fortin, Morales & Boyce 2005). Elk foraging decisions were linked to habitat structure whereby they adjusted their foraging based on the spatial distribution of forage and snow.

PHYSIOLOGICAL FORAGING CONSTRAINTS
Several physiological factors influence herbivore forage selectivity, including metabolic rate (Owen-Smith 1988), body size (Bell 1971; Jarman 1974), gut size (Demment & van Soest 1985) and digestive morphology (Janis 1976; Owen-Smith 1988). The metabolic requirements of an animal are the maintenance energy requirements to fulfil all the basic needs of the animal (Owen-Smith 1988). These requirements vary in relation to body mass (White, Blackburn & Seymour 2009).
Body size is a key factor affecting foraging decisions (Jarman 1974). Larger animals have higher absolute food demands and require more total energy than their smaller counterparts (Demment & van Soest 1985). However, large animals have a lower energy cost per gram than smaller animals (Demment & van Soest 1985; White et al. 2009). Furthermore, gastro-intestinal tract (GIT) size increases in length with an increase in body size because there is increased gut volume space (Uden & van Soest 1982; Demment & van Soest 1985; Robbins 1993). Therefore, small-bodied herbivores need to be more selective than large-bodied herbivores because of their higher mass-specific metabolic requirements and smaller GIT (Jarman 1974). However, the influence of secondary compounds is not taken into account in these body-size:energetic-demand calculations, which will change with the relative nutritional quality of food (Cipollini & Levey 1997). Gut physiology will also influence energetic demands of an animal, such as those affecting ruminants and non-ruminants (Demment & van Soest 1985; Robbins 1993).

Non-ruminants, or hind-gut fermenters such as horses, rhinos and elephants, are able to have higher passage rates than ruminants because they do not need a separate fermentation chamber to digest fibre (Demment & van Soest 1985; Robbins 1993; Clauss et al. 2003). Hind-gut fermenters make use of an enlarged section of the colon. The increased passage rate in the hind-gut fermenter (Robbins 1993) allows an individual to process more food per unit time than a ruminant (Clauss et al. 2003). This also allows hind-gut fermenters to consume lower quality plant material (Demment & van Soest 1985; Robbins 1993). Furthermore, this faster passage rate and ability to process lower quality plant material becomes more beneficial during the dry season when hind-gut fermenters are able to survive on poorer quality forage than ruminants, while still maintaining their body condition (Demment & van Soest 1985; Robbins 1993).
ELEPHANTS

The African elephant (*Loxodonta africana*) is the largest terrestrial non-ruminant herbivore. Male elephants are 5500 - 6000 kg in mass while the average female is 2500 - 2800 kg (Owen-Smith 1988). This large size, however, results in high absolute food demands with high absolute energy requirements (Demment & van Soest 1985). Elephants also have shorter GITs in relation to their body sizes, but the widths of their GIT are larger than expected (Clauss *et al.* 2003; Clauss *et al.* 2005). This means that elephants have lower absorbance-surfaces:ingesta ratios, resulting in faster passage rates with lower nutritional gains (Clauss *et al.* 2003; Clauss *et al.* 2005).

Elephants typically have a mixed diet (Cerling, Harris & Leakey 1999). However, elephants have been shown to eat a large portion of woody plants throughout the year, especially during the dry season (Codron *et al.* 2006). Elephant selectivity at different spatial scales in Chobe National Park was studied by Owen-Smith and Chafota (2012). These authors found that 40-70% of the elephant’s diets were comprised of 1 or 2 prominent woody species in each season. Similarly, Shrader *et al.* (2012) found elephants, in Ithala Game Reserve (IGR), to select three principal (tree) species in both wet and dry seasons.

A number of studies have examined varying aspects of elephant movement patterns including daily movement (Dai *et al.* 2007; Fernando *et al.* 2010), seasonal movement (Wittemyer *et al.* 2007; Loarie, van Aarde & Pimm 2009a), and seasonal home ranges (Leggett 2005; Shannon *et al.* 2006; Thomas, Holland & Minot 2011). These studies highlight different uses of space during the wet and dry seasons. De Villiers and Kok (1997) found that elephants increased their range use during the wet season in the Mpumalanga lowveld. Similarly, Thomas *et al.* (2011) also found that elephants in the Kruger National Park and adjacent private Sabi Sand Reserve (Mpumalanga) increased their home ranges in wet seasons and concentrated their activities in certain habitats close to water in dry seasons.
Conversely, elephants increased their range use during the dry season in Pongola Private Game Reserve (Shannon et al. 2006). The authors attributed this increase in range use in the dry season to either the reduced availability of food and therefore the greater need to increase their ranges to maintain their metabolic requirements or because the higher quality habitats were more sparsely distributed throughout the area (Shannon et al. 2006). Leggett (2005), studying elephants in the arid regions of Namibia, demonstrated variability in home ranges of elephants between seasons, but attributed these differences to rainfall and water availability as water stress is more prominent in arid areas. As Shannon et al. (2006) pointed out, space use is usually a determinant of another more essential limiting resource, for example, surface-water availability.

Elephants are known to be a water-dependent species (Western 1975), requiring water every 2-4 days and daily when calves are present. Thus, surface-water availability tends to limit dry season distributions (Owen-Smith 1988; Chamaille-Jammes et al. 2007; van Aarde et al. 2008). In the wet season, there is a higher availability of surface water in temporary shallow water bodies, streams and rivers than in the corresponding dry season (Shorrocks 2007; van Aarde et al. 2008). In contrast, as the dry season progresses the availability of surface-water declines. In response to this reduction in water availability, elephants move to areas with permanent surface water (Chamaille-Jammes et al. 2007). For example, Loarie et al. (2009a) found that water availability drives elephant seasonal movements, concentrating their activities around larger water sources in the dry season. As a result, habitat selection and utilization of vegetation is influenced by water availability, especially during the dry season. Conversely, Shannon et al. (2006) found no movement away from water in the wet season or towards water in the dry season at Pongola Private Game Reserve. They suggest that the small size of the reserve, about 73 km², and the high availability of permanent water across the reserve allowed easy year-round access to water.
Despite their reliance on surface-water, diet selection is another important factor in determining elephant movement decisions. Although elephants have the ability to digest lower quality forage, they may still be selective in their foraging habits (e.g. Owen-Smith & Chafota 2012; Shrader et al. 2012). Furthermore, elephants do not utilise vegetation homogeneously (Boundja & Midgley 2009), but rather show selectivity and clear preferences (Boundja & Midgley 2009; Chira & Kinyamario 2009; Shrader et al. 2012). For example, elephants damaged tree species with higher nutritional composition than tree species that were less nutritious (Holdo 2003).

Within habitats, elephants show preferences for specific tree species (Shrader et al. 2012). For example, Boundja and Midgley (2009) found that elephants completely avoided *Acacia karroo* and *Dichrostachys cinerea* tree species in Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa. This was contrary to what Shrader et al. (2012) found where the elephants heavily utilised both these species. Chira and Kinyamario (2009) found elephants selected five woody species; *Acacia ataxacantha*, *A. brevispica*, *Grewia bicolor*, *G. tembensis* and *G. virosa*, as a result of their high coppice rates after utilization in Mwea National Reserve, Kenya. Elephants may show preferences for previously utilised trees because heavy browsing may promote shoot production and improve foliage quality (du Toit, Bryant & Frisby 1990; Chira & Kinyamario 2009).

At broader scales, elephants selecting areas of higher nutrition (Osborn 2004; Loarie et al. 2009b) could be a driver of seasonal movements. In Senwa Wildlife Research Area, Zimbabwe, elephants have been found to make large-scale movements in response to plant quality. When the quality of wild grasses declined below the quality of the adjacent crop species, elephants switched their diets from wild grasses to the crops (Osborn 2004). At a large scale, Loarie et al. (2009b) found that elephants selected habitats that were “greener” than expected in the dry season. Greenness may be a good indicator of plant nitrogen
concentrations and therefore crude protein (Loarie et al. 2009b). These elephants were found to follow the flush of green across the seven countries studied despite the constraint of surface-water availability, indicating that elephants change their habitat use seasonally (Loarie et al. 2009b).

The main conclusions of these studies are that despite their large body size, and thus ability to tolerate lower quality food, elephants are selective individuals when they forage (Boundja & Midgley 2009; Chira & Kinyamario 2009). They alter their home ranges between wet and dry seasons and thus utilise different habitats seasonally (Osborn 2004; Loarie et al. 2009b). Furthermore, they may show preferences for either the crude protein in their diets (see e.g. Loarie et al. 2009b) or the ratio of crude protein:digestibility inhibitors such as tannins (Shrader et al. 2012). This suggests that small-scale foraging changes in food quality may influence the large-scale movements of this large-bodied mixed-feeder.

RATIONALE FOR THIS STUDY: ELEPHANTS OF THE ITHALA GAME RESERVE

Ithala Game Reserve was proclaimed in 1972. Prior to that the area was used for crop lands and communal livestock farming (Gordijn, Rice & Ward 2012). Translocation of large mammalian herbivores predominantly occurred from 1973-1987 (Gordijn et al. 2012). From 1990-1994, about 50 elephants were released into the Ngubhu basin in the southwestern corner of IGR (Wiseman, Page & O'Connor 2004). In 2000, there were about 56 elephants (Wiseman et al. 2004). However, by 2007 there were about 130 elephants in the reserve (van Rooyen & van Rooyen 2008), indicating a very high population growth rate.

A 2009 study by Shrader et al. (2012) was done on the spatial scale of IGR elephant diets and distributions. Shrader et al. (2012) found that the elephants move away from their largest source of water, the Pongola River, during the dry season. Furthermore, they found
that during the wet season, the elephants in IGR utilised the northeastern (NE) portion of the reserve. The eastern section has granitic nutrient-poor soils while the west has doleritic nutrient-rich soils (van Rooyen & van Rooyen 2008). The elephants congregated in this relatively small area in the NE around the Pongola River that forms the northern border of the reserve (Shrader et al. 2012). Often during this time, the elephants also wandered out of the reserve and foraged in the areas surrounding IGR, despite the fact that nutrient availability was considered to be non-limiting during this wet season (Shrader et al. 2012).

More recently, there has been an increase in utilisation of areas outside of the reserve during the wet season (Fig. 1) and measures have had to be implemented by Ezemvelo KwaZulu-Natal Wildlife to chase the elephants back into the reserve with the use of helicopters (pers. comm. C. Barichievy). However, during the dry season, when nutrients are limited, the elephants of IGR move back into the reserve, dispersing into a larger area in the southwest (SW) (see supplementary material in Appendix 1). In 2011, the elephants utilised the East in the wet season and West in the dry season (Fig. 1). This is contrary to predictions that IGR has insufficient forage, because if IGR was not able to sustain the forage requirements of the elephants then we might expect the elephants to search for extra sources of forage during forage-limited periods in the dry season and not during the wet season as they currently do (e.g. Osborn 2004). Furthermore, Gordijn et al. (2012) recorded an increase in woody plant density from $2783.3 \pm 251.35$ indiv ha$^{-1}$ in 2000 to $9939.6 \pm 1522.52$ indiv ha$^{-1}$ in 2009. Reserve managers have expressed concern about the elephants foraging outside the reserve, where soil type and vegetation type are the same as the reserve, and approached me to find out why they were doing so.

Therefore, the aim of this study was to determine how the plant availability and/or plant quality of the seven target species influences elephant seasonal distributions in IGR. More specifically, I wanted to determine the quality of three principal tree species and four avoided
species in the elephants’ diet across the reserve. Principal species are determined as a function of preference and the abundance of those species (Shrader et al. 2012). I also wanted to determine how the quality changed seasonally. Ultimately, I did this because I expected the elephants to utilize areas with a higher nutritional quality and lower defence seasonally, which presumably influenced their movement patterns.

More specifically, I wanted to determine:

1) the seasonal quality of the seven target tree species (crude protein, neutral detergent fibre (NDF), acid detergent fibre (ADF) and the most common defensive compounds, total polyphenols),

2) how the ratio of digestion-reducing substances and digestion-enhancing substances explains elephant seasonal movement, and

3) how branch and leaf quality of the different tree species differ because it is often assumed that branches only add fibre to the diet and are less chemically defended.
Fig. 1. Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2011 in Ithala Game Reserve between wet (grey triangles) and dry seasons (black stars). Most elephants were found in the eastern side of IGR in the wet season while the west was most heavily used in the dry season. There was virtually no overlap in section use between wet and dry seasons in the elephant observations. The four sections sampled were: northwest (NW), northeast (NE), southwest (SW), and southeast (SE). The northern border is the Pongola River.
Chapter 2: Materials and methods

STUDY AREA

Ithala Game Reserve (IGR) is situated in northern KwaZulu-Natal near Louwsburg, South Africa (27°30’S, 31°25’E). The 29,653 ha reserve is highly variable with regard to elevation, vegetation, geology and soils. The Pongola River is the northern border of the reserve, flowing from west to east, with the confluence of the Bivane and Pongola Rivers lying in the northwestern corner of the reserve (van Rooyen & van Rooyen 2008). In addition, surface water is readily available year-round in smaller rivers, streams and dams spread across IGR (Fig. 2).

The landscape of the area is variable with cliffs, scarps, plateaux and valleys. Elevation ranges from 320 m a.s.l. at the Pongola River to 1446 m a.s.l. on the escarpment plateau (van Rooyen & van Rooyen 2008). The underlying geology is often directly related to soil types, especially as a result of in situ formation of soils in IGR (van Rooyen & van Rooyen 2008). The most common soil types occurring at Ithala are granites, dolerites and diabases. Granite soils are coarser-grained and are often associated with nutrient-poor soils (see e.g. Laffan, Grant & Hill 1998). Conversely, dolerites and diabases have more fertile soils, but usually have poorer drainage (Hillel 1998). The eastern section of IGR is dominated by granite soils whereas the western section is dominated by dolerites (van Rooyen & van Rooyen 2008). There are a number of vegetation types present in IGR: these are the northern Zululand mistbelt grassland, Ithala quartzite sourveld, KaNgwane montane grassland, Swaziland sour bushveld and northern Zululand sourveld (Mucina et al. 2006). The IGR essentially has two seasons, viz. a wet (November-February) and a dry (May-August) season with brief transitional periods in-between. The mean annual rainfall for the area is 791 mm.
van Rooyen & van Rooyen 2008). The mean rainfall for Kwasambane during 2012 was 1137 mm.

Fig. 2. Topography ranging from 320 m a.s.l to 1446 m a.s.l (light grey lines) and rivers (darker grey lines) of Ithala Game Reserve. The Pongola River forms the northern border of the reserve. Thick black northern line is the Pongola River.

DATA COLLECTION
To determine the seasonal changes in food quality and availability, two sampling trips were undertaken, each 14 days long, one in the peak of the dry season (10-24 July 2012) and one in the peak of the wet season (30 November – 14 December 2012). Sampling intensity increased from that described by Shrader et al. (2012) into four sections of IGR, viz. northeast (NE), southwest (SW), northwest (NW) and southeast (NE) (Fig. 1) to obtain a more complete
representation of elephant diets. Division of IGR into four sections occurred prior to any sampling. In each of these sections, two 4 km strip transects were set up. The strip transects were 8 m wide, which is approximately the width of an elephant’s foraging area (Owen-Smith 1988). In each of these strip transects, I counted the total number of trees available to elephants and the total number of target tree species available. The target species consisted of three principal species (i.e. plant species that make up most of the diet, which is a function of availability and preference) as determined by Shrader et al. (2012), viz. *Dichrostachys cinerea*, *Acacia karroo*, and *A. nilotica* (Table 1). In addition, I also focused on four species avoided by elephants in Ithala in both seasons, viz. *Seersia pentheri* (formerly known as *Rhus pentheri*), *Euclea natalensis*, *Gymnosporia buxfolia*, and *Peltophorum africanum* (Shrader et al. 2012). I note that physical defences appear not to be related to the choices that elephants make because the three principal species (*A. karroo*, *A. nilotica* and *D. cinerea*) are thorny while three of the four avoided species (*E. natalensis*, *P. africanum* and *S. pentheri*) have no physical defences. For each of the 7 target species (3 principal and 4 avoided), availability was determined in each of the four sections of IGR. Finally, to determine nutritive and secondary compound concentrations I collected approximately 10 g of leaves and branches from 10 individual trees of the seven target species in each of the 4 regions in the wet and dry seasons (N= 1120). Leaf and branch samples were taken from adult trees, during the sampling period mentioned above. Each sample was placed in its own brown paper bag with the species, area and season clearly marked. They were dried in an oven at 60 °C for 48 h and milled using a standard 1 mm sieve.
Table 1. Percentage of principal species making up the wet and dry season diets. Data taken from Shrader et al. (2012).

<table>
<thead>
<tr>
<th>Species</th>
<th>Wet</th>
<th>Dry</th>
<th>Deciduous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dichrostachys cinerea</td>
<td>48.4</td>
<td>40.9</td>
<td>Yes</td>
</tr>
<tr>
<td>Acacia nilotica</td>
<td>2.9</td>
<td>39.3</td>
<td>Semi</td>
</tr>
<tr>
<td>Acacia karroo</td>
<td>3.2</td>
<td>7.8</td>
<td>Yes</td>
</tr>
</tbody>
</table>

To determine the protein concentrations, secondary metabolites, and percentage fibre of both the preferred and avoided species, I used the protocol from the Association of Official Analytical Chemists (AOAC) (1970). Protein was determined by Kjeldahl nitrogen analysis and multiplied by 6.25 to obtain values in %. Fibre determination were done by neutral detergent fibre (NDF) and acid detergent fibre (ADF) analysis (van Soest 1994). NDF represents the fibre and cell wall content of forage (van Soest 1994) and includes cellulose, hemicellulose, and lignin. ADF measures the least digestible portion of the forage and includes lignin, cellulose, ash and silica but does not include hemicellulose. In addition, I ran a modified Prussian blue test for total polyphenol analysis (TP) (Hagerman 2011). Total polyphenols are represented as gallic acid equivalents (GAE) because there is no unique value for total polyphenols (Waterman & Mole 1994).

Elephant movement data were collected from a satellite-based Global Positioning System (GPS). Currently three cow elephants and two bull elephants are collared. Generally, they remain in herds. However, the bulls tend to wander between herds and on their own. The GPS positions are recorded on a computer where they are downloaded and utilized. These point data I then utilized to determine which areas of the reserve the elephants utilized during the different seasons by mapping the points (Appendix 1).
DATA ANALYSIS

To determine seasonal differences in plant abundance in each area between the seven target species, I ran an Analysis of Variance (ANOVA). Note that I use the term SE to indicate the southeast while I use S.E. to indicate standard error.

To determine the differences between each of the plant nutrient contents (crude protein, ADF, NDF, total polyphenol concentrations, and the ratios of crude protein:digestion-reducing substances), I ran a Multiple Analysis of Variance (MANOVA) to control for type I statistical error. I created the ratio of crude protein:total polyphenols, the ratio of crude protein:ADF and the ratio of crude protein:NDF as well as the ratio of the reciprocal of ADF and NDF relative to total polyphenols, with large values indicating high quality. I generated the reciprocal because a higher ratio will mean that there is less fibre, indicating a better quality. Calculating the reciprocal ratio is similar to (but not the same as) estimations of digestible dry matter (DDM) or dry matter digestibility (DMD) (van Soest 1994). Furthermore, the reciprocal of ADF and NDF may represent DDM, but this is only probably true for species with low concentrations of phenolic compounds, which reduce digestibility. I limited these analyses to leaf data. Prior to analysis, I log$_{10}$ transformed the data to meet assumptions of normality and homogeneity of variance. Significance was found among all parameters in the MANOVA. Therefore, I ran a principal components analysis (PCA) as a dimension-reduction technique. All tests were run using SPSS version 21.

To determine differences in quality and elephant habitat-selection, I used contingency tables in Excel 2010. I counted the number of elephants based on the proportion of satellite-determined observations in the wet and dry seasons in each of the four quadrants of the reserve in 2011. These served as the expected values of preference for the contingency tables. That is, I sought to determine whether the elephant preferences matched the dietary values for
the four sections of the reserve, based on the observations that elephants were most common in the west during the dry season and most common in the east during the wet season.

To determine the difference between plant parts (leaves and branches) I ran a ranked MANOVA between season, area and species (Seaman et al. 1994). A ranked MANOVA was used as a result of the data violating the assumptions of normality and equality of variances. Conventional transformations were tried, including log_{10}, square root and power transformations. I then employed a Box-Cox transformation and assumptions were still violated. Ranked transformations are widely accepted and are robust when testing main effects. However, they are less effective with interactions (Seaman et al. 1994; Conover 2012).
Chapter 3: Results

AVAILABILITY OF PLANTS

The seven target species’ abundances did not differ significantly between areas (p=0.61) or seasons (p=0.259). However, abundance differed between species (p=0.0001). A Bonferroni post hoc test revealed that *D. cinerea* had the highest abundance (22.98 ± 5.1% abundance across the reserve) of all seven target species. *A. karroo* (2.64 ± 0.7% abundance across the reserve) was less abundant than *D. cinerea*. *A. nilotica* was the least abundant species of all the target species (0.82 ± 0.4% abundance across the reserve) (Fig. 3).
Fig. 3. Percentage abundance of each of the seven target species. Bars represent 1±S.E. *A. karroo =* *Acacia karroo, A. nilotica =* *Acacia nilotica* and *D. cinerea =* *Dichrostachys cinerea* (the three principal species). *S. pentheri =* *Searsia pentheri* (formerly known as *Rhus pentheri*), *E. natalensis =* *Euclea natalensis*, *P. africanum =* *Peltophorum africanum* and *G. buxifolia =* *Gymnosporia buxifolia* (the four avoided species).

**QUALITY OF PLANTS**

Overall, the MANOVA was significant for all main effects and all interaction effects (Table 2). All individual nutritional parameters were significant (see supplementary material in Appendix 2). Therefore, I ran a principal component analysis (PCA) as a dimension-reduction technique. I found the first PC axis eigenvalue was 3.658 and explained 40.6% of the variance. The second PC axis eigenvalue was 2.801 and explained 31.1% of the variance. The cumulative variance explained by the first two axes of the PCA was 71.8%. Thus, I focused on these two axes. Most of the variance in PC1 was explained by total polyphenols (TP) (component= -0.891), the CP:TP ratio (component= 0.775), and the reciprocal of
ADF:TP ratio (component=0.739) (Table 3). Note that there is a negative relationship with total polyphenols and a positive relationship with the ratios. The CP:TP result is consistent with what Shrader et al. (2012) found. Most of the variance on PC2 was explained by CP:ADF ratio (component = 0.841), followed by crude protein (component = 0.803), and CP:NDF ratio (component = 0.756). Therefore, I focused on these six factors on the first two axes highlighted by the PCA, noting that the first axis (by definition) explains most of the variance (Flury & Riedwyl 1988). Furthermore, I focused on the principal species only as they are the species used by the elephants.
Table 2. MANOVA statistics of the effects of season, area, species and their interactions on the seven target species to determine forage quality. Forage quality was measured for: crude protein, acid detergent fibre (ADF), neutral detergent fibre (NDF) and total polyphenols (TP). Additionally, ratios of some of these parameters were also considered.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Wilks Lambda</th>
<th>DF</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>0.397</td>
<td>218</td>
<td>0.0001</td>
</tr>
<tr>
<td>Area</td>
<td>0.649</td>
<td>617.1</td>
<td>0.0001</td>
</tr>
<tr>
<td>Species</td>
<td>0.069</td>
<td>960.1</td>
<td>0.0001</td>
</tr>
<tr>
<td>Season*Area</td>
<td>0.669</td>
<td>617.1</td>
<td>0.0001</td>
</tr>
<tr>
<td>Season*Species</td>
<td>0.220</td>
<td>960.1</td>
<td>0.0001</td>
</tr>
<tr>
<td>Area*Species</td>
<td>0.271</td>
<td>1256.5</td>
<td>0.0001</td>
</tr>
<tr>
<td>Season<em>Area</em>Species</td>
<td>0.290</td>
<td>1256.5</td>
<td>0.0001</td>
</tr>
</tbody>
</table>
Table 3. Component weightings for the principal components analysis (PCA) for log$_{10}$ crude protein (CP), log$_{10}$ total polyphenols (TP), acid detergent fibre (ADF), neutral detergent fibre (NDF), the log$_{10}$ ratio of crude protein:total polyphenols (CP:TP), log$_{10}$ crude protein:ADF ratio (CP:ADF), log$_{10}$ crude protein:NDF ratio (CP:NDF), log$_{10}$ reciprocal of acid detergent fibre: total polyphenol concentrations (ADF:TP) and log$_{10}$ reciprocal of neutral detergent fibre:total polyphenol concentrations (NDF:TP). Note that it is the absolute value that determines importance.

<table>
<thead>
<tr>
<th>Factors</th>
<th>1</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>log$_{10}$ CP</td>
<td>-0.251</td>
<td>0.803*</td>
</tr>
<tr>
<td>log$_{10}$ TP</td>
<td>-0.891*</td>
<td>-0.43</td>
</tr>
<tr>
<td>ADF</td>
<td>0.475</td>
<td>-0.219</td>
</tr>
<tr>
<td>NDF</td>
<td>0.592</td>
<td>-0.081</td>
</tr>
<tr>
<td>log$_{10}$ CP:TP</td>
<td>0.775*</td>
<td>0.038</td>
</tr>
<tr>
<td>log$_{10}$ CP:ADF</td>
<td>-0.482</td>
<td>0.841*</td>
</tr>
<tr>
<td>log$_{10}$ CP:NDF</td>
<td>-0.607</td>
<td>0.756*</td>
</tr>
<tr>
<td>log$_{10}$ ADF:TP</td>
<td>0.739*</td>
<td>0.562</td>
</tr>
<tr>
<td>log$_{10}$ NDF:TP</td>
<td>0.691</td>
<td>0.565</td>
</tr>
</tbody>
</table>

*most important*
The season X area X species interaction showed that during the wet season two out of three principal species (*A. karroo* and *D. cinerea*) had lower total polyphenol concentrations in the SE of IGR (Fig. 4). The eastern section of IGR is a common wet-season foraging area. *A. karroo* had increased CP:TP ratio, CP:ADF ratio and crude protein during the wet season in the SE of IGR (Figs. 5, 6 and 7). *D. cinerea* was the only species with increased reciprocal of ADF:TP in the SE during the wet season (Fig. 8). All three principal species showed no significant differences between areas during the wet season for CP:NDF ratio (Fig. 9).

During the dry season, elephants preferred to forage in the west (Fig. 1). *A. karroo* was the only species with lower total polyphenols during this time in the SW. All three principal species had increased levels of CP:TP ratio, CP:ADF ratio and crude protein in the SW during the dry season (Figs. 5, 6 and 7). *D. cinerea* and *A. nilotica* had a higher reciprocal of ADF:TP ratio during the dry season in the NW (and SW for *A. nilotica* only) (Fig. 8). Only *A. karroo* had higher CP:NDF during the dry season in the SW relative to the other two principal species (Fig. 9).

There was a decline in mean total polyphenol concentrations in *A. nilotica* between the wet season and dry season, which is consistent with the change in preference for this species between wet and dry seasons (2.9% in the wet season and 39.3% in the dry season - Shrader *et al.* 2012). Similarly, the CP:TP ratio, the reciprocal of ADF:TP ratio and CP:ADF ratio all had higher values for *A. nilotica* in the dry season than in the wet season (Figs. 5, 6, 8).

Overall, total polyphenol concentrations were higher in principal species (mean ± S.E. ratio (log10) -0.64 ± 0.07) than avoided species (mean ± S.E. ratio (log10) -0.91± 0.06) (Fig. 4). However, principal species had higher ratios of CP:ADF (principal (mean ± S.E. ratio (log10)): -1.00 ± 0.06; avoided: -0.80 ± 0.05) and CP:NDF (principal (mean ± S.E. ratio (log10)): -0.91 ± 0.09; avoided (mean ± S.E. ratio (log10)): -0.77 ± 0.07) (Figs. 7, 9).
Elephant numbers were determined from Global Positioning System (GPS) satellite data. I counted elephant numbers in each area for both wet and dry seasons from the mapped GPS data. The contingency table analyses indicated that the CP:TP ratio was the only significant parameter within both the wet ($\chi^2 = 12.40; p= 0.0001$) and dry seasons ($\chi^2 = 10.88; p= 0.0001$). A significant result indicates that the elephants utilized that section more frequently than by chance alone. The SW had the highest CP:TP ratio in the dry season which is consistent with the highest elephant numbers in that quadrant (391 sightings from June-August). However, the NW had similarly high elephant numbers (314 sightings from June-August). The SE section had the highest CP:TP ratio during the wet season with lower elephant numbers (307 sightings from December-February) than the NE (368 sightings from December-February) (Table 4).
Fig. 4. The seasonal values of log_{10} total polyphenol concentrations for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. GAE = gallic acid equivalents. Full names as for Fig. 3.
Fig. 5. The seasonal values of the log$_{10}$ crude protein:total polyphenol (CP:TP) ratios for a) principal and b) avoided species. Bars represent ±S.E. Dashed line is the overall mean. Full names as for Fig. 3.
Fig. 6. The seasonal values of the log_{10} CP:ADF ratios for a) principal and b) avoided species. CP = crude protein; ADF = acid detergent fibre. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.
Fig. 7. The seasonal values of the log_{10} crude protein values for a) principal and b) avoided species. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.
Fig. 8. The seasonal values of the log$_{10}$ reciprocal of ADF:TP ratios for a) principal and b) avoided species. TP= total polyphenol concentrations. High values indicate high quality vegetation. Bars represent 1±S.E. Dashed line is the overall mean. Full names as for Fig. 3.
Fig. 9. The seasonal values of the log_{10} CP: NDF ratios for a) principal and b) avoided species. CP = crude protein; TP = total polyphenol concentrations. Bars represent 1±SE. Dashed line is the overall mean. Full names as for Fig. 3.
Table 4: Contingency table analyses of total polyphenols (TP), the ratio of crude protein to total polyphenols (CP:TP), reciprocal of Acid Detergent Fibre:total polyphenol ratio (ADF:TP), crude protein:ADF ratio (CP:ADF), crude protein (CP), crude protein:Neutral Detergent Fibre ratio (CP:NDF) and elephant numbers between the four sections in the wet and dry seasons. Predictions are based on elephant numbers found in each quadrant in each season. Elephant numbers were based on satellite observations in 2011.

<table>
<thead>
<tr>
<th>Elephant no.</th>
<th>NW WET</th>
<th>NW DRY</th>
<th>NE WET</th>
<th>NE DRY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elephant no.</td>
<td>42</td>
<td>314</td>
<td>368</td>
<td>0</td>
</tr>
<tr>
<td>TP</td>
<td>0.28</td>
<td>0.25</td>
<td>0.37</td>
<td>0.30</td>
</tr>
<tr>
<td>CP:TP</td>
<td>110.01</td>
<td>50.60</td>
<td>63.82</td>
<td>64.56</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>0.12</td>
<td>0.14</td>
<td>0.10</td>
<td>0.13</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>0.36</td>
<td>0.36</td>
<td>0.30</td>
<td>0.35</td>
</tr>
<tr>
<td>CP (%)</td>
<td>16.69</td>
<td>11.07</td>
<td>13.76</td>
<td>12.67</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>0.49</td>
<td>0.36</td>
<td>0.45</td>
<td>0.39</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Elephant no.</th>
<th>SW</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elephant no.</td>
<td>5</td>
<td>391</td>
</tr>
<tr>
<td>TP</td>
<td>0.219</td>
<td>0.25</td>
</tr>
<tr>
<td>CP:TP</td>
<td>132.14</td>
<td>177.48*</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>0.25</td>
<td>0.77</td>
</tr>
<tr>
<td>CP (%)</td>
<td>15.00</td>
<td>32.14</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>0.42</td>
<td>0.54</td>
</tr>
</tbody>
</table>

*significant difference
PLANT PARTS

It is often assumed that branches only add fibre to the diet and are less chemically defended (Owen-Smith & Chafota 2012). The ranked MANOVA between leaves and branches was significant (Wilks’ lambda = 0.284; df= 546; p<0.01). Crude protein (mean ± S.E. ratio (log$_{10}$)) leaf: 1.10 ± 0.02; branch: 0.77 ± 0.02) and the CP:TP ratio (mean ± S.E. ratio (log$_{10}$)) leaf: 1.90 ± 0.04; branch: 1.53 ± 0.04) were significantly higher in leaves than branches. ADF (mean ± S.E. ratio) leaf: 50.48 ± 1.53; branch: 61.99 ± 0.87) and NDF (mean ± S.E. ratio) leaf: 44.71 ± 3.13; branch: 66.30 ± 1.63) were significantly higher in branches than leaves. Similarly, the reciprocal of ADF:TP (mean ± S.E. ratio (log$_{10}$)) leaf: -0.88 ± 0.03; branch: -1.02 ± 0.03) and the reciprocal of NDF:TP ratios (mean ± S.E. ratio (log$_{10}$)) leaf: -0.83 ± 0.05; branch:-1.06 ± 0.05) were significantly higher in branches than in leaves. In contrast, there was no significant difference in total polyphenol concentration between leaves and branches (mean ± S.E. ratio (log$_{10}$)) leaf: -0.80 ± 0.03; branch: -0.76 ± 0.03) (Table 5).
Table 5. MANOVA statistics from the ranked comparisons of leaf and branch for the different plant quality parameters. CP = crude protein; TP = total polyphenol concentrations; ADF = acid detergent fibre; NDF = neutral detergent fibre.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Part</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>484.365</td>
<td>0.0001</td>
</tr>
<tr>
<td>TP</td>
<td>0.580</td>
<td>0.446</td>
</tr>
<tr>
<td>ADF</td>
<td>124.262</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:TP</td>
<td>113.097</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>719.450</td>
<td>0.0001</td>
</tr>
<tr>
<td>NDF</td>
<td>420.894</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>909.516</td>
<td>0.0001</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>99.515</td>
<td>0.0001</td>
</tr>
<tr>
<td>NDF:TP</td>
<td>345.040</td>
<td>0.0001</td>
</tr>
</tbody>
</table>
Chapter 4: Discussion

The distribution of forage in an environment is heterogeneous in time and space (Senft et al. 1987; Shipley 2007; Holdo et al. 2009). As a result, herbivores alter their foraging behaviour to compensate for these changes, e.g. by changing diet breadth, or habitat usage (Senft et al. 1987; Bailey et al. 1996). Numerous studies have shown that elephants do not homogenously consume vegetation but are selective at both small and large scales (Boundja & Midgley 2009; Loarie et al. 2009b; Pretorius et al. 2012; Shrader et al. 2012). Therefore, I predicted that elephants would alter their seasonal movement patterns in response to either 1) changes in the availability of principal species, and/or 2) changes in forage quality.

In contrast to my prediction that principal species will determine seasonal use of elephants in IGR, I found no difference in the seasonal percentage abundance and spatial distribution of principal tree species across the reserve. The high proportion of *D. cinerea* in both wet and dry season diets may be as a result of the higher abundance of this principal species across the reserve as compared with the other two principal species sampled. This choice is as a result of foraging preferences being based on both the abundance and quality of the most preferred food type (Senft, Rittenhouse & Woodmansee 1985).

Plant quality has been shown to be an important determinant of herbivore foraging decisions (Cooper & Owen-Smith 1985; Jia et al. 1997; Frye et al. 2013). Holdo (2003) showed that elephant damage was more prominent in species with higher levels of protein, calcium, magnesium and potassium. Furthermore, secondary metabolites have also been shown to alter foraging choices (Cooper & Owen-Smith 1985; Cipollini & Levey 1997; Frye et al. 2013). Consistent with my predictions, I found plant quality to differ seasonally and across the reserve. In line with previous studies (Pretorius et al. 2011; Pretorius et al. 2012; Shrader et al. 2012), I found that the inclusion of plant species into their diets (i.e. at small
spatial-scales), the elephants in IGR are selective. Specifically, the increased inclusion of *A. nilotica* in the dry season (2.9% in the wet season and 39.3% in the dry season - Shrader *et al.* 2012) can be explained by the seasonal decline in total polyphenols from the wet to the dry season and an increase of the digestion-enhancing: digestion-reducing ratios during the dry season.

Elephants in IGR avoided species with higher digestion-reducing substances, including fibre and total polyphenols. However, total polyphenol concentrations were higher in principal species than in avoided species. Nevertheless, the avoided species are known to contain high levels of plant toxins. For example, *Euclea* spp. contain naphthaquinones and triterpenoids (*Gordijn et al.* 2012; Shrader *et al.* 2012). *Searsia* spp. contain inositol, malic and nonanoic acids (*Gordijn et al.* 2012). I measured total polyphenol concentrations, which include tannins, because these are the most common digestion-reducing compounds (*Cooper & Owen-Smith* 1985; *Freeland* 1991; *Waterman & Mole* 1994) and did not focus on specific compounds. Similar to the results of Shrader *et al.* (2012), I found that the digestion-enhancing: digestion-reducing ratio was the most important factor influencing foraging decisions. The PCA ranked four of the six most important factors to be digestion-enhancing: digestion-reducing ratios, explaining 71.8% of the variability. The remaining two factors were total polyphenols and crude protein. Thus, elephants in IGR are selective in their small-scale foraging decisions. The elephants may be selecting plant species, and areas, with lower secondary metabolites (see negative value for total polyphenols - Table 3) and higher crude protein concentrations (note positive value for crude protein - Table 3). Similarly, elephants in Timbavati Private Reserve (Mpumalanga) utilised patches that had higher leaf-nitrogen contents on nutrient-enriched soils (*Pretorius et al.* 2011). However, on soils that were not enriched by fertilizers, elephants pushed over trees to get to the higher quality roots (*Pretorius* 2011).
et al. 2011). This indicates that elephants are selecting food based on their quality and will
even utilise specific plant parts with higher nutrients.

Little is known about how woody matter adds to the diet of elephants. It is often
assumed that branches only add fibre to the diet and are less chemically defended (Owen-
Smith & Chafota 2012). As expected, leaves had an overall higher quality than branches with
increased crude protein and fewer digestion-reducing substances. I found that there was no
significant difference in total polyphenols between leaves and branches. Owen-Smith and
Chafota (2012) found that the part of the plant that elephants forage on is more important
than species per se. These authors attributed this to lower chemical defences. However, these
authors never tested these hypotheses directly. Moose (Alces alces) are known to also forage
on branches (Bergstrom & Danell 1987; Bergström & Danell 1995; Jia et al. 1997). Jia et al.
(1997) studied moose feeding behaviour with different quality of birch (Betula pendula)
clones to test the effects of quality on foraging and found differences in total polyphenol
concentration between birch clones. Contrary to common assumptions, they found moose
were more likely to reduce fibre intake than total polyphenol intake by feeding on younger
shoots (Jia et al. 1997). This is not inconsistent with my results, which show that leaves had
higher levels of crude protein than their branches. Elephants also preferred leaves which had
lower levels of fibre.

ELEPHANT MOVEMENT IN IGR

Small-scale foraging decisions, i.e. changes in plant quality, have also been linked with
changes in large-scale foraging patterns, such as migrations. However, the small-scale
changes in foraging by the elephants in IGR do not seem to explain all of their broader-scale
foraging choices. During the wet season the elephants used the east, mainly the NE (Fig. 1).
However, the section with the highest nutritional quality, at least for *A. karroo*, was the SE where there was increased CP:TP ratio, CP:ADF ratio and crude protein. Total polyphenols were also lower in the SE for *A. karroo* and *D. cinerea*. Nonetheless, elephants clearly preferred the eastern section of the reserve over the west during the wet season, which is consistent with my results.

Where my results do help to explain elephant movement in IGR is during the dry season when the elephants move into and forage in the west (Fig. 1). During this time, the SW had higher CP:TP ratios, CP:ADF ratios and crude protein for all three principal species. *A. nilotica* and *D. cinerea* had higher reciprocal of ADF:TP ratio in the NW (and SW for *A. nilotica*) while *A. karroo* had higher CP:NDF ratios in the SW. *A. karroo* also had lower total polyphenols in the SW during the dry season. Similarly, the contingency table analysis showed the SW had higher CP:TP ratios than the other sections (Table 4). Therefore, this increase in plant quality in the west, compared with a reduction in the east at this same time, appears to influence these seasonal movements of the elephants back into IGR.

It is clear that plant quality is an important factor in the movement patterns of IGR elephants. The elephants are moving back into IGR and are utilizing the west when the best forage quality is found there. However, it is not clear why the elephants are utilizing the east during the wet season. It is possible that I found this pattern of movement because of behavioural learning. That is, when animals are released into a new environment they have no knowledge of the environment (Owen-Smith 2003). They need to learn where the best quality forage is distributed seasonally. Other factors influencing re-introduced individuals are the distribution of water and areas of predation risk. For an individual to learn the optimal distribution of an environment takes time (Owen-Smith 2003). For example, the Arabian oryx (*Oryx leucoryx*) were released in two groups into the central desert region of the Oman during the 1980s (Owen-Smith 2003). The animals were housed in an enclosure for
acclimation to occur prior to release. Animals in the first release found an area where there were no conspecifics and had larger home ranges. After the rains they temporarily utilised more areas. However, when drought followed, the oryx returned to their release site where supplementary fodder was provided (Owen-Smith 2003). These oryx had smaller home ranges, as a result of the presence of conspecifics. About 6-8 years after the release of the oryx they had established where they could find needed resources and consequently utilised less space (Owen-Smith 2003). Similar patterns were found for Asiatic wild asses (*Equus hemionus*) (Saltz & Rubinstein 1995).

The elephants at IGR were released into the southwestern section of IGR. Over time, they may have utilised more areas of the reserve and learned that the western section has a higher nutritional quality during the dry season. In translocation studies on elephants it has been shown that elephants do not utilise vegetation uniformly once released but will congregate in areas of refuge as they slowly learn about their environments (Dublin & Niskanen 2003). Furthermore, the elephants at IGR may have slowly explored the reserve (Appendix 1). Thus, when resources declined at the onset of the dry season, the elephants returned to the west where forage quality was known to be better.

A second, and perhaps less important, factor influencing elephant movement back into the reserve during the dry season may be related to increased human interactions. Elephants are known to avoid unnecessary human interaction (Dublin & Niskanen 2003). To the north of the Pongola River there are communal areas with large numbers of people and cattle. During the dry season, when water availability is reduced, the people may more frequently come to the river to collect water, resulting in increased potential contact and interference with the elephants. As a result, they may move to avoid this increased human presence along the Pongola River.
MANAGEMENT AND FUTURE STUDIES

There were about 56 elephants in 2000 (Wiseman et al. 2004) and about 130 individuals in 2008 (van Rooyen & van Rooyen 2008; Shrader et al. 2012). I expect that these increasing numbers are the reason for increased utilization of the reserve during the dry season. Primarily, the elephants use the SW section with the best quality during the dry season. However, they are also utilizing the NW section, where quality is not as high. This may be as a result of these increasing elephant numbers and possible intraspecific competition.

Wiseman et al. (2004) noted that an increase in elephant numbers is a potential problem in IGR. They calculated the “carrying capacity” of elephants in IGR to be about 50 elephants. Furthermore, they found that elephants did not utilise 50% of the space due to topography (Wiseman et al. 2004). Elephants are known to avoid costly “mountaineering” (Wall, Douglas-Hamilton & Vollrath 2006). In this study, elephants used the roads to access forage in the steeper areas (pers. obs.). More than 20% of the reserve had gradients greater than 40°, reducing access for large mammals, such as elephants (Wiseman et al. 2004). Thus, the total area available to elephants is considerably less than expected based on total reserve size.

The density of elephants that Wiseman et al. (2004) calculated in 2000 in IGR was 0.19 elephants/km², which was lower than the stocking density for elephants in valley bushveld (0.4 elephants/km² (Penzhorn, Robbertse & Olivier 1974)). This stocking density is also below the optimal stocking density for dry savannas of 0.5 elephants/km² (Fowler & Smith 1973), which is considered to be the threshold where elephants can cause serious plant damage (Fowler & Smith 1973; Wiseman et al. 2004). Currently, the density of elephants in IGR is 0.43 elephants/km², exceeding the recommended stocking density for elephants in valley bushveld and approaching the recommended stocking density for elephants in dry savanna. This original stocking density for IGR may have been calculated on the basis of a
standard model for grazers (Meissner 1982). This calculation would then be exaggerated
if elephants are largely browsers and because neither nutritional yield (Hobbs & Swift 1985)
nor secondary plant compounds (Windels & Hewitt 2011) were incorporated into the
calculations. Furthermore, the densities of elephants in IGR includes areas that the elephants
cannot use because they are too steep to access (see above). Additionally, even if there is
sufficient vegetation to allow for increased elephant numbers it is important to allow the
vegetation time to recover (e.g. Horsley, Stout & DeCalesta 2003; Holdo et al. 2011).

There is no clear reason for the elephants to leave the reserve as there is sufficient
food available to them. Although the density of elephants is increasing in IGR, this is not the
primary reason for the movement patterns we are seeing. If density was the main determinant
we would expect to see elephants searching for extra sources of forage during the forage-
limited dry season. However, elephants are leaving during the wet season. Additionally, food
selection would change. We would expect to see elephants feeding less selectively, using a
range of habitat types and species. There are 26 possible habitat types in IGR; during the wet
season, elephants utilized 9 habitat types while they only utilised 8 habitat types during the
dry season (Shrader et al. 2012). Furthermore, two or three principal species made up ca.
80% of the diet in each season (Table 1). Nevertheless, we can see that they are slowly
exploring further and further out of the reserve each wet season (Appendix 1). The reasons
for this pattern are somewhat unclear. They may be accessing a greater spatial distribution of
resources (Owen-Smith 2003) because of increased population densities. There may also be
another food-related reason that I did not test that is influencing their movement. For
example, elephants have shown that selection of plant parts was more important rather than
species per se (Owen-Smith & Chafota 2012). This may be as a result of different growth
forms, i.e. shoots vs. leaves vs. branches, and/or having varied physical and chemical
defences (Rehill et al. 2006). Further research at IGR may reveal the interactions of species
selection and plant-part selection. The digestion-enhancing: digestion-reducing ratios may explain more about why the elephants are utilizing the eastern section during the wet season. However, this extremely fine-scale decision making by elephants is not realistic for managers to monitor.

Further findings from this study include the fact that the digestion-enhancing: digestion-reducing ratio was of importance. This finding is important as the quality of a plant is not only determined by the crude protein but also the defences that the plant invests in, including chemical or physical defences. These findings were analogous with those of Shrader et al. (2012). Interestingly, physical defences appear not to be related to the choices that elephants make because the three principal species (A. karroo, A. nilotica and D. cinerea) are thorny while three of the four avoided species (E. natalensis, P. africanum and S. pentheri) have no physical defences. Therefore, future research on elephants must include both measures of the palatability as well as the digestion-reducing substances the plant uses when determining forage quality.

Of potential concern is that the high utilization of A. nilotica in the dry season may ultimately negatively affect the survival of this species in the reserve. Although we did not explicitly test this, Wiseman et al. (2004) found A. nilotica to be markedly reduced during an eight-year period in IGR. The largest size class of A. nilotica declined due to high browsing pressure by megaherbivores and low recruitment rates (Wiseman et al. 2004). This may explain the very low abundance of A. nilotica in IGR, which will further be influenced by the high utilization by elephants. Similarly, Bond and Loffell (2001) found that Acacia davyi had been extirpated in IGR, although they ascribed this to the introduction of giraffes (Giraffa camelopardalis). Furthermore, Gordijn et al. (2012) highlighted the change in species in IGR toward an increase in more unpalatable species, including Searsia spp. and Euclea spp., as a result of avoidance by megaherbivores. These authors also found that there was an overall
decline in more palatable species as a result of heavy utilization by megaherbivores (Gordijn et al. 2012).

Ultimately, I wanted to know if the elephants are making small-scale decisions and if these decisions explain the elephant’s large-scale movement patterns. At small spatial scales the elephants select for more nutrient-rich and less defended species. At large spatial scales the elephants are moving into the reserve during the dry season as a result of increased nutrients in their principal species. However, it is unclear why the elephants are moving out of the reserve during the wet season.
References


University of Idaho, Moscow, ID, U.S.A.


Appendix 1.

Appendix 1a. Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2008 in Ithala Game Reserve between seasons wet (black triangles) and dry seasons (grey stars). Straight lines indicate the quadrants (NW, SW, SE, NE) where I measured tree abundances and nutrient quality.
Appendix 1b. Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2009 in Ithala Game Reserve between seasons wet (black triangles) and dry seasons (grey stars). Straight lines indicate the quadrants (NW, SW, SE, NE) where I measured tree abundances and nutrient quality.
Appendix 1c. Global positioning system points (determined by satellite observations) of the elephants’ distributions from 2010 in Ithala Game Reserve between seasons wet (black triangles) and dry seasons (grey stars). Straight lines indicate the quadrants (NW, SW, SE, NE) where I measured tree abundances and nutrient quality.
Appendix 2.

MANOVA statistics between plant quality data and the factors (season, area, species and higher-order interactions). Error degrees of freedom = 1005. CP = crude protein; TP = total polyphenol concentrations, ADF = acid detergent fibre; NDF = neutral detergent fibre.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Season</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>0.023</td>
<td>0.88</td>
</tr>
<tr>
<td>TP</td>
<td>19.999</td>
<td>0.0001</td>
</tr>
<tr>
<td>ADF</td>
<td>290.09</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:TP</td>
<td>12.217</td>
<td>0.001</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>37.809</td>
<td>0.0001</td>
</tr>
<tr>
<td>NDF</td>
<td>51.576</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>12.001</td>
<td>0.001</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>0.758</td>
<td>0.385</td>
</tr>
<tr>
<td>NDF:TP</td>
<td>2.122</td>
<td>0.147</td>
</tr>
</tbody>
</table>

<p>| <strong>Area</strong>   |      |         |
| CP         | 9.368 | 0.0001  |
| TP         | 8.172 | 0.0001  |
| ADF        | 13.244| 0.0001  |
| CP:TP      | 13.703| 0.0001  |
| CP:ADF     | 6.846 | 0.0001  |
| NDF        | 7.89  | 0.0001  |
| CP:NDF     | 6.555 | 0.0001  |
| ADF:TP     | 7.084 | 0.0001  |
| NDF:TP     | 7.538 | 0.0001  |</p>
<table>
<thead>
<tr>
<th>Parameter</th>
<th>F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>31.547</td>
<td>0.0001</td>
</tr>
<tr>
<td>TP</td>
<td>30.024</td>
<td>0.0001</td>
</tr>
<tr>
<td>ADF</td>
<td>71.564</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:TP</td>
<td>24.384</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>28.84</td>
<td>0.0001</td>
</tr>
<tr>
<td>NDF</td>
<td>22.085</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>36.012</td>
<td>0.0001</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>27.031</td>
<td>0.0001</td>
</tr>
<tr>
<td>NDF:TP</td>
<td>19.181</td>
<td>0.0001</td>
</tr>
<tr>
<td><em><em>Season</em> Area</em>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>4.260</td>
<td>0.006</td>
</tr>
<tr>
<td>TP</td>
<td>5.333</td>
<td>0.001</td>
</tr>
<tr>
<td>ADF</td>
<td>2.910</td>
<td>0.035</td>
</tr>
<tr>
<td>CP:TP</td>
<td>0.435</td>
<td>0.728</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>4.087</td>
<td>0.008</td>
</tr>
<tr>
<td>NDF</td>
<td>1.697</td>
<td>0.169</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>2.289</td>
<td>0.079</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>5.164</td>
<td>0.002</td>
</tr>
<tr>
<td>NDF:TP</td>
<td>8.598</td>
<td>0.0001</td>
</tr>
<tr>
<td><em><em>Season</em> Species</em>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>7.884</td>
<td>0.0001</td>
</tr>
<tr>
<td>TP</td>
<td>13.918</td>
<td>0.0001</td>
</tr>
<tr>
<td>ADF</td>
<td>5.958</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:TP</td>
<td>17.296</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>4.945</td>
<td>0.018</td>
</tr>
<tr>
<td>NDF</td>
<td>9.931</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>4.684</td>
<td>0.0001</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>11.997</td>
<td>0.001</td>
</tr>
<tr>
<td>NDF:TP</td>
<td>7.400</td>
<td>0.0001</td>
</tr>
<tr>
<td>Parameter</td>
<td>F</td>
<td>P-value</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>------</td>
<td>---------</td>
</tr>
<tr>
<td><em><em>Area</em> Species</em>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>2.358</td>
<td>0.002</td>
</tr>
<tr>
<td>TP</td>
<td>2.597</td>
<td>0.001</td>
</tr>
<tr>
<td>ADF</td>
<td>4.218</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:TP</td>
<td>2.512</td>
<td>0.001</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>2.164</td>
<td>0.005</td>
</tr>
<tr>
<td>NDF</td>
<td>2.696</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>2.129</td>
<td>0.006</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>2.229</td>
<td>0.004</td>
</tr>
<tr>
<td>NDF:TP</td>
<td>2.842</td>
<td>0.0001</td>
</tr>
<tr>
<td><em><em>Season</em> Area</em>Species**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>3.625</td>
<td>0.0001</td>
</tr>
<tr>
<td>TP</td>
<td>2.337</td>
<td>0.002</td>
</tr>
<tr>
<td>ADF</td>
<td>3.064</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:TP</td>
<td>3.948</td>
<td>0.0001</td>
</tr>
<tr>
<td>CP:ADF</td>
<td>3.01</td>
<td>0.0001</td>
</tr>
<tr>
<td>NDF</td>
<td>1.923</td>
<td>0.015</td>
</tr>
<tr>
<td>CP:NDF</td>
<td>2.045</td>
<td>0.009</td>
</tr>
<tr>
<td>ADF:TP</td>
<td>2.622</td>
<td>0.001</td>
</tr>
<tr>
<td>NDF:TP</td>
<td>1.943</td>
<td>0.014</td>
</tr>
</tbody>
</table>