

How decisions lead to conflicts –
The roles of elephant behaviour and
agricultural practices in elephant crop
consumption

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Abstract

How decisions lead to conflicts- The roles of elephant behaviour and agricultural practices in elephant crop consumption

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Elephant crop consumption can have negative direct and indirect consequences for subsistence farmers (e.g. crop losses, livelihood vulnerability, fear) and can result in a reduction in support for the conservation of elephants, which are IUCN classified as vulnerable, and can even result into physical conflicts that can lead to injuries and death of people and elephants. In this thesis, I examine how decisions that elephants make in their movements and foraging behaviour, and farmers make in their mitigation methods, influence elephant crop consumption in the eastern panhandle of the Okavango Delta, Botswana. **Chapter 2** shows that elephant corridors are important for exploratory movements of elephants towards the river, and that sexual segregation occurs in elephants' responses to agricultural fields. Female elephants showed encamped movements in agricultural fields at night and during the dry season, supporting the predation-risk hypothesis, as crop consumption was safest for elephants at these times. **Chapter 3** and **Chapter 4** suggest that the local natural diet of elephants may be deficient in micronutrients – in particular phosphorus - which indicates that elephants need to consume large amounts of vegetation in order to satisfy their micronutrient levels. This makes crops an optimal alternative, due to their higher levels of absolute phosphorus and dry matter intake. **Chapter 5** reveals that one-off inputs of materials to support farmers to deter elephants from their fields do not result in the sustainable

mitigation method use desired by providers of materials. In order to empower farmers to live with elephants, external bodies such as government and non-governmental organisations could increase logistical support, and facilitate the improvement of the supply-chain of materials for mitigation methods. Crop consumption mitigation could be improved if sexual segregation in crop consumption patterns are taken into account and crops are harvested earlier (**Chapter 2**), if alternative micronutrient sources are provided in elephant corridors (**Chapter 3** and **Chapter 4**) and farmers are included in the development and implementation of mitigation method interventions (**Chapter 5**).

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Dominus illuminatio mea,

Oxford, October 2018

Author contributions

I declare that this thesis, *How decisions lead to conflict- The roles of elephant behaviour and agricultural practises in elephant crop consumption* is my own work.

The contributions by other authors to any of the manuscripts are clearly stated below.

None of the work included has been submitted, in whole or part, in any previous application for a degree.

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Figure 4 of Chapter 1 is by M. Windler, remaining photographs and drawings are by S.M. Vogel.

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List of abbreviations

ADF	–	Acid Detergent Fibre
C	–	Calcium
DE	–	Digestible energy
DMI	–	Dry Matter Intake
EDM	–	Ethnographic Decision Model
FGD	–	Focus Group Discussion
GLM	–	Generalized Linear Model
GLMM	–	Generalized Linear Mixed Model
HEC	–	Human-Elephant Conflict
HMM	–	Hidden-Markov model
K	–	Potassium
MCMC	–	Markov Chain Monte Carlo
Mg	–	Magnesium
N	–	Nitrogen
Na	–	Sodium
NDF	–	Neutral Detergent Fibre
NGO	–	Non-governmental organisation
P	–	Phosphorus
RMT	–	Right-angle Mixture Triangle

The blind men and the elephant

Originating back to ancient Buddhist and Hindu texts from India (~1500 BC), the story of the blind men and the elephant is a parable that challenges us to humbleness, as it emphasized the limits of our perceptions and the importance of a complete context. In the parable a group of blind men tries to understand what an elephant is, each by investigating only part of the elephant, just as each part of my thesis is only one perspective on elephant crop consumption. Therefore, each of the data chapters are accompanied with part of the poem that British author John Godfrey Saxe wrote in 1872, describing the ancient sage of the blind men and the elephant. I adapted the order of the blind men to better match chapter topics and left out some verses. The full poem can be found at the end of the supplementary information.

1 | Introduction

*It was six men of Indostan
To learning much inclined,
Who went to see the Elephant
(Though all of them were blind),
That each by observation
Might satisfy his mind.*

Chapter 1. Introduction

1. Problem statement

1.1 Wildlife crop consumption

Conservation of wildlife outside of protected areas comes with the challenge of co-existence between humans and wildlife (Trimble & van Aarde, 2014; Redpath et al. 2005). This challenge is especially prevalent where people depending on rural livelihoods and wildlife species share the same areas (Sitati et al., 2003) and depend on the same natural or agricultural resources (Webber et al., 2007). This sharing of mosaics of human-modified landscape fragments can cause high frequencies of human-wildlife encounters, and can result in negative interactions between wild animals and people (Meijaard et al., 2011; Hartter et al., 2011). The most common examples of these interactions are the impact of wildlife on livestock and cultivated crops by consuming or damaging them (Trimble and van Aarde, 2014; Redpath et al. 2005). Sometimes these interactions are classified as ‘human-wildlife conflicts’, yet we consider this term inaccurate as these behaviours in itself are not conflicts, and wildlife cannot be considered to be consciously into conflict with humans (Peterson et al., 2010; Madden & McQuinn, 2014; Redpath et al., 2014). Furthermore, these situations often evolve out of deeper conflicts between humans (Madden & McQuinn, 2014), such as disagreements over land rights and resource use between nature conservation organisations, governments and local communities (Laudati, 2010) or loss and fragmentation of animal habitat (Ogra & Badola, 2008). Whenever the word ‘conflict’ is used in this thesis, I either refer to conflict in this broader sense, thus including social, political and historical aspects that lead to a sentiment of farmers being in ‘conflict’ with elephants or elephant conservation -as in the title of this thesis, or to actual

physical conflicts between elephants and humans, where they attack each other and injure or kill. Arguments have also been put forward against using the term ‘crop raiding’ to describe wildlife impact on crops (Sitati et al., 2003; Naughton-Treves & Treves, 2005; Nyhus, 2016; Seoraj-Pillai & Pillay, 2017), because the consumption or trampling of crops cannot be assumed to be equivalent to an act of conscious raiding (Hill, 2018). Therefore I use the term ‘crop consumption’ to describe elephants entering agricultural fields and consuming crops cultivated by farmers, and in the process potentially trampling and destroying crops.

1.2 Elephant crop consumption

Across Asia and Africa, elephants (respectively *Loxodonta* spp. and *Elephas* spp.) are well known for their crop consumption behaviour (Sitati et al., 2003; Hoare, 2012). However, some studies mention that elephants cause less destruction of crops compared to other crop loss sources, yet studies referred to lack unambiguous evidence in support of this claim (Harich et al., 2013; Gross et al., 2017). For example, in Cameroon Arlet & Molleman (2007) showed that rodents consumed crops at a higher frequency, and affected a higher amount of fields and plants than elephants, but lack of elephant crop damage in this study was attributed to their rareness in the area. In Kibale National Park, Uganda, elephants were less rare, and again smaller animals such as primates and livestock caused a higher frequency of crop damage events with a median of 72% of farms damaged, compared to elephants damaging only 8% of farms. Yet, per event elephants caused between 84 and 99% higher m² damage per event, and they caused the second highest total percentage of area damaged after baboons (21% compared to 24%) (Naughton-Treves & Naughton-Treves, 1998; Naughton-Treves, 1997). This higher scale and impact of elephant crop consumption can make the issue less manageable and

more threatening than losses to smaller mammals (Songhurst, 2012). Moreover, the perceived crop loss by elephants can be higher than the actual loss, due to social influences like power struggles between people and organisations, and the lack of ability of farmers to cope with the losses (Naughton-Treves & Treves, 2005; Dickman, 2010). Nevertheless, there are areas in which crop consumption by elephants can seriously threaten local food security (Mackenzie & Ahabyona, 2012). Issues with crop consumption are prevailing in areas with both high concentrations of elephants and subsistence farmers, such as in northern-Botswana (Osborn, 2004; Songhurst, 2012; Pozo et al., 2017). Here, entire harvests can be destroyed by elephants, posing a threat to the nutrition and livelihood of local farmers (Gupta, 2013). Moreover, when elephants are in close proximity to or in agricultural fields people are sometimes injured or killed by elephants (Department of Wildlife and National Parks Botswana, 2003). Besides these impacts of elephants on peoples' lives and livelihoods, crop consumption can also result in a reduction in support for elephant conservation, and the killing of elephants in retaliation (Tchamba, 1996; Redpath et al., 2013). This can threaten a species already vulnerable (*Loxodonta africana*) or even endangered (*Elephas maximus*) according to the IUCN red list (Blanc, 2008).

1.3 Factors influencing elephant crop consumption

In general, we know that elephant behaviours associated with crop consumption, i.e. foraging and movement, are influenced by factors such as the presence of water sources (Shannon et al., 2009; de Boer et al., 2013), time of day (Sukumar, 1990; Hoare, 1999; Sitati, Walpole & Leader-Williams, 2005; Barnes et al., 2006; Jackson et al., 2008) and rainfall (Hoare, 1999; Osborn, 2004; Barnes et al., 2006; de Boer et al., 2013). They are also influenced by vegetation characteristics such as the structure and heterogeneity of

habitat (Duffy et al., 2011), available ecological niches (Ludwig et al., 2008; de Knecht et al., 2011), Normalized Difference Vegetation Index (NDVI) (Wall et al., 2013; de Boer et al., 2013), Net Primary Production (NPP), plant biomass (de Boer et al., 2013) and Acid Detergent Fibre (ADF), crude protein, energy content and digestibility (Rode et al., 2006). Likewise, the occurrence and frequency of the consumption of crops by elephants is affected by ecological conditions both within elephant habitat and on agricultural lands (Barnes et al., 2006) and social factors such as social cohesion and human activity (Osborn et al., 2003; Guerbois et al., 2012). From the elephant's perspective, studies have aimed to understand how these ecological conditions influence elephant behaviour in agricultural areas. For example, by analysing elephant distribution patterns in these areas (Jackson et al., 2008; Graham et al., 2009; Von Gerhardt et al., 2014; Songhurst, McCulloch, et al., 2015) or how nutritional quality of forage influences the occurrence and timing of crop consumption by elephants (Osborn, 2004; Chiyo et al., 2005; Rode et al., 2006; Webber et al., 2011). From the human perspective, anthropogenic factors that are expected to have an influence on crop consumption are human population density, land-use changes, distance from roads, and the proximity of farmers to elephant daytime refuges or elephant pathways (Jackson et al., 2008; Songhurst & Coulson, 2014). To understand the human role in the occurrence and frequency of elephant crop consumption incidences, the focus of much research has been on how people behave towards elephants and how they protect their fields (Sitati et al., 2005; Graham & Ochieng, 2008; Davies et al., 2011; Noga et al., 2015).

1.4 Mitigating elephant crop consumption

Efforts to reduce, or mitigate elephant crop consumption are extensive (Fernando, 2008; Hoare, 2012). Mitigation measures that farmers can apply to protect their fields can be divided into four classes: passive methods, active methods, innovative methods and adapting agricultural choices in order to reduce the likelihood for animals to enter a field (Parker et al., 2007; Hockings & Humle, 2009). Passive methods are traditionally very common, with fences such as (barbed) wire barriers (Osborn & Parker, 2002; Sitati et al., 2005; Sitati & Walpole, 2006), pole barriers (Sitati et al., 2005) and more recently electric fencing (Kioko et al., 2008; Davies et al., 2011). Most innovative methods are also passive, such as trip-alarms and play-backs of elephant warning calls (O’Connell-Rodwell et al., 2000) or bees (King et al., 2007), thunder flashes (Sitati & Walpole, 2006), virtual fences (Jachowski et al., 2014), beehive fences (King et al., 2009) and novel chilli-rope fences (Sitati & Walpole, 2006; Graham & Ochieng, 2008; Hedges & Gunaryadi, 2009; Davies et al., 2011). Chilli is also used in active methods to deter elephants from fields, such as chilli-smoke (briquettes) (Osborn & Parker, 2002; Graham & Ochieng, 2008; Davies et al., 2011) or even firing chilli catapults at elephants (Le Bel et al., 2010). More traditional active measures are the use of noisemakers such as shouting, drums and fire crackers or cowbells (Osborn & Parker, 2002; Sitati et al., 2005; Davies et al., 2011) and bangers and banger-sticks (Graham & Ochieng, 2008). Fire is also commonly used to deter elephants (Osborn & Parker, 2002; Sitati et al., 2005; Davies et al., 2011), with spotlights like solar powered torches as their more modern variant (Graham & Ochieng, 2008; Davies et al., 2011). Active guarding commonly takes place (Sitati et al., 2005), sometimes from watchtowers (Graham & Ochieng 2008, Sitati & Walpole 2006, Osborn & Parker 2002). Finally, there are some accounts of throwing rocks with catapults (Osborn & Parker 2002), and

elephant drives (O'Connell-Rodwell et al., 2000; Davies et al., 2011). Besides these methods, there is an increasing interest in methods that address the issue of crop consumption more sustainably, by adapting land-use planning and making agricultural choices that are more 'elephant sensitive' by incorporating information on elephant behaviour (Parker et al., 2007; Songhurst, McCulloch, et al., 2015; Gunaryadi et al., 2017), which we will group under 'elephant conscious farming' (Hockings & Humle, 2009). Examples of these are buffer regions around fields or dry vegetation (Sitati et al., 2005), cleared vegetation (Osborn & Parker 2002), the use of alternative or buffer-crops (Gross et al., 2016, 2017). Beyond individual farmer's decisions, this also includes larger scale land use planning, such as to set aside specific regions or corridors for elephants to roam (Jachowski et al., 2013; Songhurst, McCulloch, et al., 2015; Adams et al., 2016). These elephant conscious farming methods and land-use change measures are especially promising as long-term sustainable mitigation methods, as they aim to take into consideration the underlying causes and triggers of crop consumption instead of focussing on reducing the symptoms of the problem, elephants entering fields, as most other mitigation strategies do (Barnes, 2002).

2. Case-study

2.1 Study-site

The eastern panhandle of the Okavango Delta in Botswana is an ideal study system to examine the role of elephant and human decisions in elephant crop consumption, due to the high elephant population and intensity of human-elephant interactions (Songhurst, Chase, et al., 2015). Botswana maintains the largest population of African elephants in the world, with 37% of the total population and on average 1.28 elephants per km² (Chase et al., 2016). In Botswana elephants are protected by law, yet over 80% of the elephant population roams outside of protected areas (Thouless et al., 2016). In the past, poaching has been relatively low compared to its surrounding countries, yet poaching appears to be increasing (Chase et al., 2016). The study-area is an 8,732 km² triangle-shaped area enclosed by the Namibian border, the northern buffalo fence and the Okavango river and is home to about 18,000 elephants (Songhurst, 2016).

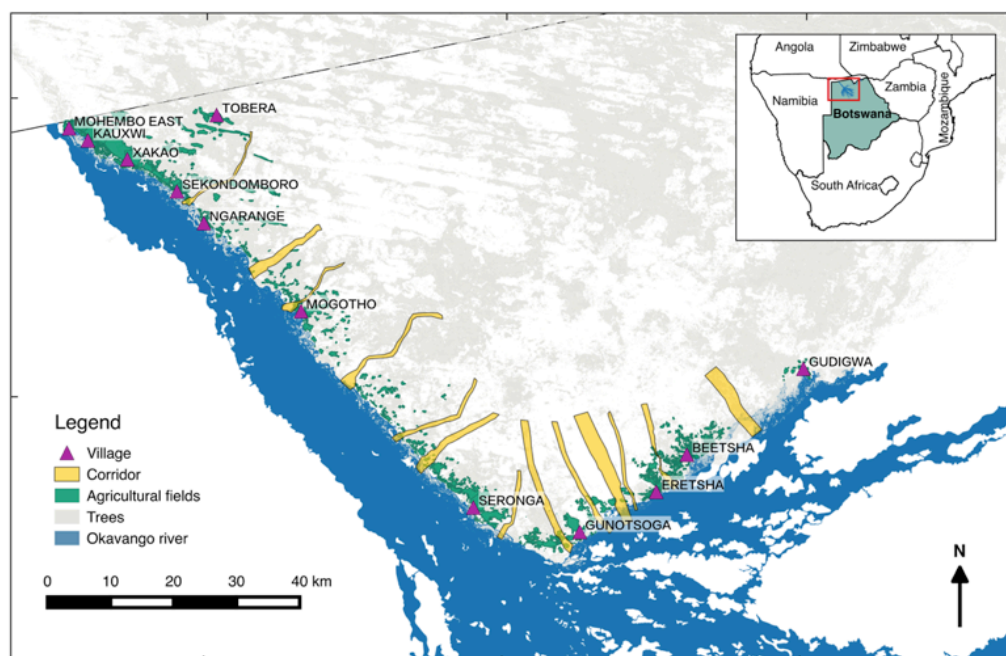


Figure 1. Study site of the eastern panhandle of the Okavango delta, Botswana including habitat features used in this study. The green areas represent agricultural

fields, with the purple triangles representing the location of the villages, with highly used elephant corridors in yellow markings running through them towards the Okavango River in blue. White and grey areas represent savanna and tree groups, respectively.

The mean monthly maximum temperature ranges from 26.1 to 35.1 °C (Statistics Botswana, 2016). There is a dry and a wet season in the area, which can be divided into early dry (May-July), late dry (August-October), early wet (November-January) and late wet (February-April) seasons (Jackson et al., 2008). During the wet season on average 503 mm of rain falls (Statistics Botswana, 2016), with most rain tending to fall around January (Statistics Botswana, 2016).

2.2 Landscape

The vegetation in the study-site can be divided into seven types (Songhurst, 2012; Mendelsohn & Obeid, 2004). Near the Okavango River, the floodplain is dominated by grasses such as swamp savanna grass (*Miscanthus junceus*) and mat sedge (*Schoenoplectus corymbosus*), which grow along the edges of water sources. Other grasses often seen higher up from the waterline are African bristlegrass (*Setaria sphacelata*) and drop seed (*Sporobolus fimbriatus*). In these floodplains there are groups of large often berry carrying tree species that function as forage for elephants, for example jackal berry (*Diospyros mespiliformis*) and water berry (*Syzygium spp.*), mixed with shrubs like red star apple (*Diospyros lycioides*) and magic guarri (*Euclea divinorum*). These thickets of vegetation grow on old termite mounds and can form large patches evolving into riverine forest.



Figure 2. Example of floodplain and tree groups in between Gunotsoga and Eretsha, eastern panhandle of the Okavango Delta, Botswana.

Beyond this inhabited strip along the river, there are four dry bush vegetation types.

Mopane woodland is dominated by mopane (*Colophospermum mopane*), often browsed to a short height by elephants and cattle, and combined with species like sand camwood (*Baphia massaiensis*) forming mixed mopane woodland. Acacia woodland consists of thorny trees and bushes, with species such as camel thorn (*Acacia erioloba*), knobthorn (*Acacia nigrescens*), flame thorn (*Senegalia ataxacantha*), and buffalo thorn (*Ziziphus mucronata*). Much of the dry bush area contains deeper sandy soils covered with the mixed silver terminalia (*Terminalia sericea*) vegetation type, often occurring with taller trees. During the wet season, grasses such as silky bushman grass (*Stipagrostis uniplumus*) and love grasses (*Eragrostis porosa*, *Eragrostis rotifer*, *Eragrostis lehmaniana*) grow amongst shrubs and trees in the dry bush, and on the edges of the roads. Grasses common throughout the area are couch grass (*Cynodon dactylon*), phuka

(*Urochloa brachyuran/trichopus*), and false signal grass (*Brachiaria deflexa*). In the dry season these grasses dry out and make way for sandy plains. In all areas herbs like white bauhinia (*Bauhinia petersiana*) and shrubs like Kalahari currant (*Commiphera rhus*) and grewia species (*Grewia spp.*) occur. Finally, the dry bush includes forest patches of the false mopane (*Guibourtia coleosperma*), Zambezi teak (*Baikiaea plurijuga*) and wild syringa (*Burkea africana*) woodland.



Figure 3. Example of elephants in dry bush vegetation with Acacia woodland species, Okavango Delta, Botswana.

On agricultural fields in the inhabited river area, farmers plant crops, including cereals such as millet (*Pennisetum glaucum/ Eleusine coracana*), sorghum (*Sorghum bicolor*), maize (*Zea mays*) and sweet reed (*Sorghum vulgare*) and other crops such as watermelon (*Citrullus lanatus*), beans (*Vigna aconitifolia/ Phaseolus vulgaris*), groundnuts (*Arachis hypogaea*), melons (*Citrullus lanatus*) and pumpkin (*Cucurbita spp.*) (Songhurst, 2011; Heath & Heath 2009).

2.3 People and elephants

Close to the Okavango River there are 14 human settlements, and from the northern elephant rangelands to the inhabited river area there are several elephant pathways, some near villages, see Figure 1. According to the 2011 census, 16,306 people live in the study area, within and between the 14 villages. Most of these people rely on dry land farming on the floodplains, or *molapo* farming, for their subsistence, in which they time the preparation of fields and planting based on patterns of rainfall and the receding Okavango river. Most of the planting occurs between November-January while harvesting takes place when the crops are mature between April to June (Songhurst, 2012; Songhurst, McCulloch, et al., 2015).



Figure 4. Example of agricultural field with watch hut and homesteads, Eretsha village, eastern panhandle, Okavango Delta, Botswana.

The elephant population in this area is estimated to be around 18,000 individuals (Songhurst, 2016), with an above average rate of increase of 9.5% per year (Songhurst, Chase, et al., 2015). Crop consumption by elephants is common in the entire area, and

most crop consumption occurs from January to April (Jackson et al., 2008; Songhurst, 2012). Besides crop consumption, there are also records of humans being killed by elephants, which occurs mainly during the period of August until January (Songhurst, 2012) and elephants being killed by humans, mainly towards the end of the crop season (April to October). During the wet season, elephants move further away from the Okavango River as there are sufficient alternative water sources available, but when these dry up in the transition to the dry season, elephants generally remain within a 10 km range of the river (Jackson et al., 2008). When close to the river, elephants show daily movements towards the river at dusk, returning at dawn after visiting the river to drink and rest. To get to the river, elephants need to pass through the inhabited strip of land, which includes villages and agricultural fields (Jackson et al., 2008; Songhurst, McCulloch and Coulson, 2015).



Figure 5. Example of elephants using the largest corridor of the eastern panhandle, Okavango Delta, Botswana, located in between Gunotsoga and Eretsha with short browsed Mopane vegetation.

As elephants in the area tend to avoid contact with humans when possible, fields further away from villages are more susceptible to elephant visits (Songhurst & Coulson, 2014). In the area, 106 pathways have been identified from the northern uninhabited region towards the river, out of which 13 are so often used that they can be labelled as elephant corridors (Songhurst, McCulloch, et al., 2015).

3. Thesis outline

3.1 Aims and objectives

This thesis aims to contribute to the development and improvement of strategies that address the underlying causes of elephant crop consumption instead of focussing on the symptoms (Barnes, 2002; Hill, 2018). To do so, I focus on increasing understanding in the reasons for elephants to include crops into their diet, and the reasons farmers have for their responses to elephant crop consumption in their farming practises. Therefore, the overall aim of the thesis is *‘To analyse the decisions that elephants and humans make in agricultural fields, and how these decisions influence the occurrence of elephant crop consumption.’* I focus on decision-making to avoid reducing the role of either elephants or people to that of perpetrators or victims (Hill, 2018). By doing so, I want to recognise that both species contain autonomous and diverse individuals, with reasons behind their behaviour, and agency to shape their co-existence and interactions, and potential competition over space and resources (Chiyo et al., 2012; Barua, 2014b; Evans & Adams, 2016, 2018). From the elephants’ perspective, I use novel spatial approaches to increase understanding of the influence of agricultural fields on elephant movement decisions (**Chapter 2**) and analyse foraging decisions and timings to understand the role of crops in elephant diet (**Chapter 3 & 4**). To increase understanding in the role of human decisions in elephant crop consumption, I focus on

farmers' reasoning behind using (or not using) mitigation methods and elephant conscious farming (**Chapter 5**). I conclude the thesis with a general discussion in the form of a synthesis, and conclusion in **Chapter 6**.

3.2 Movement decisions

To understand the influence of agricultural fields on elephant movement behaviour, I used multi-state hidden-Markov models (HMM) to analyse two years of hourly GPS-locations of 11 elephants. These models categorize animal movements into movement types ('states'), based upon the distances travelled between two consecutive GPS fixes, 'step sizes', and the relative turning angle between these points (Morales et al., 2004). Hidden-Markov models are machine-learning models that assign a label to each observed value in a sequence that describes the unobserved (hidden) state at that value. This type of model assigns the sequences of unobserved states by calculating a probability distribution of possible label sequences, given the sequence of observed values and choosing the best one. To discover these hidden states, it is necessary to decode the state sequence. This can be done with a number of algorithms, but the most common one is the Viterbi algorithm. This algorithm is dynamic and tries to find the most likely sequence of states based upon the observation sequence by maximising the likelihood of the observation at each step of the sequence (Jurafsky & Martin, 2014; Michelot et al., 2016; Patterson et al., 2016). Translated to the animal movement situation, this means that the model will calculate for each observed combination of turning angle and step size, which state the elephant is in at that point in time, given the full pathway of the animal (Michelot et al., 2016; Patterson et al., 2016). When combining this type of model with habitat features, such as agricultural fields, we can find out which movement behaviour elephants show in certain habitats, and if they

switch their behaviour when encountering these areas (Morales et al., 2004). Since I am interested in whether elephants target agricultural fields purposefully, in **Chapter 2** I use this method of determining behavioural states and switches between states to understand how elephants' movement decisions respond to agricultural fields. I used this method to analyse the role that environmental factors play on the switching between rapid directional movements associated with an 'exploratory mode' towards a goal, and more irresolute sedentary movements, or the 'encamped mode' corresponding to behaviour common in attractive habitat, e.g. foraging (Morales et al., 2004; Fryxell et al., 2008). **Supplementary information A.1** explains how these multistate hidden Markov models relate to other types of animal movement models.

3.2 Foraging decisions and timing

Even though elephants are generalist feeders, they show a forage preference for certain vegetation species (Sukumar, 1990; De Boer et al., 2000). They also have specific preferences about which parts of a plant they eat (Sukumar, 1990; Osborn, 2004; Chiyo et al., 2005). Regarding crops, elephants tend to prefer mature crops over intermediate and early growth stages (Hoare, 1999; Barnes et al., 2006). Only a few studies give insights in the role crops play in elephant diet, and how changes in crop characteristics and natural forage might stimulate elephants to consume crops (Chiyo et al., 2005; Rode et al., 2006). Studies that focus on this topic rarely include actual measures of vegetation quality, and instead rely on estimated forage quality indices (Rode et al., 2006). Rode et al. (2006) and Chiyo et al. (2005) analysed crop consumption by forest elephants in Kibale National Park, Uganda, but stress that their findings will probably differ from those in savanna landscapes (Rode et al., 2006). Therefore, in **Chapter 3** I analyse how nutritional content influences foraging preferences and differ between

natural forage and crops differs between these sources, change over season, and the roles they indicate that crops have in elephant diet. Crop consumption by animals can be just a form of foraging optimization (Lambert & Rothman, 2015; Hill, 2018) or because crops are a fall-back food when wild forage is low in quantity (Hill, 2018) or quality (Lambert & Rothman, 2015). The latter is important; as elephant diets are known to be deficient in micronutrients (Sukumar, 1990; Osborn, 2004; Chiyo et al., 2005; Rode et al., 2006), which can cause a nutrient drive in foraging decisions in which elephants select those plant species that contain high levels of the nutrients in which they are deficient (Pretorius et al., 2012). This could potentially stimulate elephants to consume crops to satisfy their nutrient requirements. There are indicators that in savanna landscapes, nutritional stress plays an important role in stimulating crop consumption by elephants (Chiyo et al., 2005). **Supplementary information B.1** gives more detailed information on the functions of micronutrients important in herbivore diets, and the occurrence of deficiencies. In this chapter we focus on comparing the nutritional balance of the different food sources available for elephants. To do this we used a nutrition geometry framework in which we plotted relative nutrient concentrations in multi-dimensional two-axes plots to understand the relative contribution of each food source in reaching elephant nutritional requirements. This allowed us to discover the role crops currently play in the elephant diet in this region, and the trade-offs that elephants make. This helped us to understand whether crops are complementary to the elephant diet, a substitute for natural forage, or a necessary component to fulfil elephant dietary needs (Raubenheimer & Simpson, 1999; Raubenheimer, 2011). **Supplementary information B.2** gives a hypothetical example of this method.

Chapter 4 builds on the information on foraging decisions described in **Chapter 3**, by including the monthly quantities of browse and grass included in elephant diet, allowing

for absolute dietary calculations. In general, elephants switch between browsing and grazing behaviour over seasons, depending on availability and quality of foraging types (J. Codron et al., 2012). Osborn (2004) suggests that there could be a relationship between the switching from grass to browse in the early dry season and crop consumption. Using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes of elephant faeces we derive the monthly percentages of browse and grass in elephant diet in the study area and analyse its relation to elephant crop consumption. We also calculate absolute nutritional intake by elephants, in order to reveal information on potential deficiencies. Together these two chapters will give insights in potential effectiveness of mitigation measures such as artificial salt licks (Zhang & Wang, 2003).

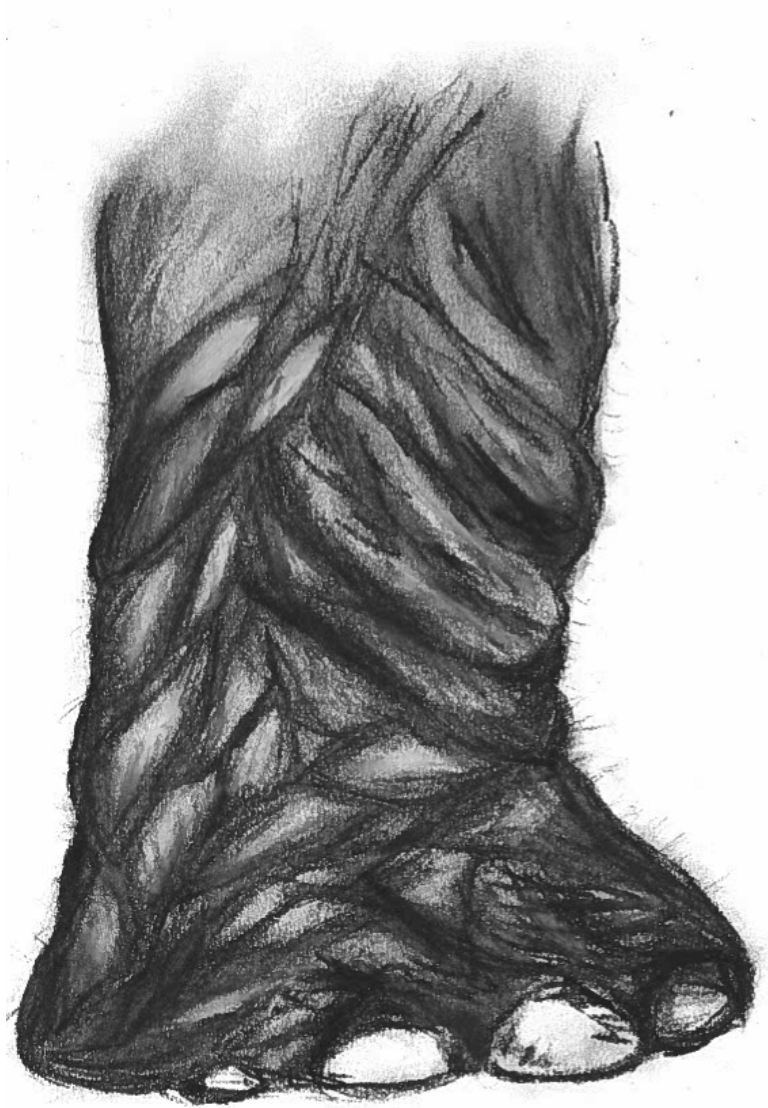
3.3 Mitigation method decisions

Although the government and nongovernmental organisations (NGOs) have tried to convince farmers to adopt mitigation methods in the Okavango Delta of Botswana, there is no evidence of a long-term use of an effective method to mitigate elephant crop consumption (Noga et al., 2017). In **Chapter 5** I analyse this situation by combining a political ecology perspective on local elephant crop consumption and Ethnographic Decision Models, a method used in analyses of farmer decision strategies.

Supplementary information D.1 provides an overview of both of these topics. From a political ecology perspective, local decisions and strategies of individuals are influenced by larger scale political and economic forces, and we need to put individual decisions in these larger context (Miller et al., 2014; Robbins et al., 2015). Ethnographic decision models have an extensive track record of previous applications in farmers' decision-making research (Gladwin 1989c; Gladwin 1989b). Examples are farm trial designs (Gladwin, 1983), changing cropping system (Gladwin 1989c) and coping with natural

hazards such as drought (Keshavarz & Karami, 2014; Miller et al., 2014). Concerning conservation, scholars have looked at adopting methods for soil conservation (Morera & Gladwin, 2006; Roth & Botha, 2009; Clark, 2013), agroforestry (Thangata et al., 2002; Djalilov et al., 2016), organic farming methods (Fairweather, 1999; Locke, 2006; Bravo-Monroy et al., 2016), gold mining in tropical rainforest (Heemskerk, 2002) and applying conservation agriculture methods (Bell et al., 2018). An issue that reoccurs in these studies, is that while a first round of interviews is used to construct the decision trees, they subsequently need to be tested on an independent second subset of the population, to verify if indeed it is possible to use the constructed hierarchical tree to predict farmers' decision and validate the decision tree. This step is often minimized or omitted in reports (Fairweather, 1999; Roth & Botha, 2009; Miller et al., 2014; Bravo-Monroy et al., 2016), making the resulting trees only descriptive rather than predictive (Gladwin 1989a). As we sought to predict farmers' mitigation decisions, we include two rounds of interviews, one to construct and one to test the decision trees.

2 | Movement decisions



*The First reached out his eager hand,
And felts about the knee.
“What most this wondrous beast is like
Is mighty plain,” quoth he;
“ ’T is clear enough the Elephant
Is very like a tree!”*

Chapter 2. Exploring movement decisions: can Bayesian movement-state models explain crop consumption behaviour in elephants (*Loxodonta africana*)?

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Abstract

1. Animal movement characteristics, and the influence of habitat features on these characteristics, can reveal animals' intrinsic motivations behind movement. However, it is hard to tease apart the influence of different habitat features on movements and consequently on intrinsic motivations.
2. We use Bayesian hidden-Markov models and hourly GPS-fixes to distinguish animal movements into movement states and analyse the influence of environmental variables on being in a state and switching between states. Specifically, we apply our models to understand elephant movement decisions surrounding agricultural fields and crop consumption. It is unclear what the role of habitat features are on this complex issue, so we analyse whether elephants target agricultural crops for consumption, or simply pass through them in search of water.
3. Our hidden-Markov models divide elephant movements into two states: exploratory movements that are fast and directional, and encamped movements that are slow and meandering. For 11 elephants with each 19,391 GPS fixes, we ran 16 models for each possible combination of habitat features (river, elephant corridor, agricultural field, trees), and repeated these analyses including interaction effects with both season and the time of day. We used cross-validation to select the best performing model, and GLMMs to analyse the influence of habitat features on being in and switching to a state.
4. Our results show that in corridors, exploratory movements are dominant. Elephants mainly showed encamped movements at the river during the dry

season, when temporary water sources have dried out and elephants rely on this permanent water source. In fields, males most often exhibited exploratory movements and their encamped movements were higher during the day than at night, while females showed an increase in the frequency of encamped movements at night. Both males and females increased their encamped movements during the dry season, but this increase was stronger for females than for males.

5. The predation-risk hypothesis could explain why females increased their frequency of encamped movements in fields at night, since foraging in fields might be less risky under the cover of darkness and during the dry season when farmers are absent from fields. This sexual segregation in elephant movement decisions highlights the importance of risk in movement patterns, while the increase in encamped movements in the dry season suggests the importance of agricultural timing. Taking this into account could increase efficiency of elephant crop consumption mitigation.

Keywords

Hidden-Markov models, crop raiding, conservation, human-elephant conflict

1. Introduction

For decades we have tried to understand why animals move, yet we still do not fully understand their internal motivations (Nathan et al., 2008). Movement is driven by the search for resources. It can provide benefits, as intra-specific competition may decrease, risk factors are avoided, and new or better resources and mates can be found. However, moving comes with an energy cost and mortality risk (Bowler et al., 2005; Fahrig, 2007). This cost increases with the duration of movement and the mortality risk associated with the habitat (Fahrig, 2007). While some habitats may contain more attractive forage than others, the costs of moving in a habitat –in time, energy and risk– could reduce its attractiveness (Senft et al., 1987).

Herbivores show different movement types in different habitats. They move slowly and turn frequently in more productive and heterogeneous habitats, and move rapidly and turn less in areas with less attractive forage (Senft et al., 1987; Fryxell et al., 2008; Venter et al., 2015). However, quick and straight movements are also associated with animals moving through risky habitat (Fahrig, 2007). Therefore, movement goals or targets are based upon responses to habitat characteristics e.g. maximization of resources, risk avoidance, or social factors, e.g. learning and reproducing (Nathan et al., 2008). These different types of movements are associated with certain animal behaviours, e.g. exploring or foraging (Morales et al., 2004; Fryxell et al., 2008).

Understanding the movement responses of animals to different habitat types can reveal information about their internal goals (Nathan et al., 2008).

We can use insights about animal movement goals to understand and address situations where animals and humans share space and resources, which can lead to high frequencies of human and wildlife encounters and potential conflicts between them. For

example, anthropogenic features, such as roads, result in an increase in speed and directionality in the movements of Florida black bears (*Ursus americanus floridanus*, Karelus et al. 2017). Similarly, at night, pumas (*Puma concolor*) are more active and travel greater distances in suburban areas compared to in other habitats (Wang et al., 2017). Finally, smaller travel distances show that urban wild boar (*Sus scrofa*) have higher tolerances to human presence than rural conspecifics (Stillfried et al., 2017). These studies provide useful insights that can predict encounters and potential conflict between wildlife and humans, and inform the development of mitigation methods (Karelus et al., 2017; Wang et al., 2017).

In this paper we analyse elephant movement to gain insights into elephant crop consumption in northern Botswana, addressing an issue of both conservation and farmer livelihood concern (Osborn, 2004; Songhurst, 2012; Mackenzie & Ahabyona, 2012; Gupta, 2013; Songhurst & Coulson, 2014; Pozo et al., 2017). Elephant crop consumption depends upon both the distribution of agricultural fields and elephant movement patterns (Sitati et al., 2003; Songhurst & Coulson, 2014; Cook et al., 2015). Rainfall generates seasonal changes in both the movements of elephants (Hoare, 1999; Osborn, 2004; Barnes et al., 2006; de Boer et al., 2013), and crop consumption (Sukumar, 1990; Hoare, 1999; Chiyo et al., 2005; Jackson et al., 2008). An explanation for this pattern could be that rainfall stimulates the growth of crops as well as vegetation around agricultural fields, attracting elephants towards farms because of the high nutrient grass and browse surrounding it (Barnes et al., 2006). In addition, the presence and distribution of (artificial) water sources can play a role in elephant movements and crop consumption (Shannon et al., 2009; de Boer et al., 2013). Elephants tend to increase their speed when approaching water sources (Chamaillé-Jammes et al., 2013) and show more directional, less tortuous, movements when they are traveling towards

them (Duffy et al., 2011). In contrast, vegetation patches with a high density, like groups of trees in a savanna landscape, result in shorter and more tortuous steps (de Knegt et al., 2007; Duffy et al., 2011). These tree groups could provide elephants with higher forage quality than savanna grasses, making it a preferred habitat for elephants to forage in (Ludwig et al., 2008). Elephants are also known to move along well-worn pathways or corridors (Gerhardt-Weber, 2011; Guerbois et al., 2012; Jachowski et al., 2013; Von Gerhardt et al., 2014; Songhurst, McCulloch, et al., 2015), and proximity to these pathways is an important factor influencing the likelihood of crops to be consumed by elephants (Songhurst & Coulson, 2014). Finally, most crop consumption takes place at night between dusk and dawn (Sukumar, 1990; Hoare, 1999; Sitati et al., 2005; Barnes et al., 2006; Jackson et al., 2008), with males more often recorded consuming crops than females (Hoare, 1999; Chiyo et al., 2005; Von Gerhardt et al., 2014; Songhurst, 2017).

Teasing apart the influence of habitat features on elephant movements is a challenge, as resources often coincide in space, such as in the case of forage and water sources. This makes it difficult to determine whether changes in movement speeds and directions are driven by an urge for water or for good quality forage (Duffy et al., 2011; Chamaillé-Jammes et al., 2013). Farmers tend to grow agricultural crops near water sources, causing ambiguity on whether elephants deliberately target agricultural fields to forage crops, or crops are a side benefit of passing through the fields while heading towards the water (Jackson et al., 2008; Songhurst, McCulloch, et al., 2015). A solution to this issue is to use models that classify movements into different movement types. These models use mixtures of random walks to categorize consecutive GPS fixes into distinct behaviours (Morales et al., 2004) and can be used to associate the probability of switching between movement states with habitat types (Fryxell et al., 2008; Nathan et

al., 2008). In our study we apply the concept of multiple movement states to explore if this method can tease apart the elephant's reactions to the presence of crops and water.

2. Methods

2.1 Study site

We collected data in the eastern panhandle of the Okavango delta, an 8,732 km² area between the Namibian border fence, the northern buffalo fence and the Okavango River (Figure 1, **Chapter 1**). The elephant population in this area is estimated to be around 18,000 individuals (Songhurst, 2016), with an above average growth rate of 9.5% per year (Songhurst, Chase, et al., 2015). Along the Okavango River there are 14 villages, and the total population of these villages and the area in between them consists of ca. 16,000 people (CSO, 2011).

In the study site, elephants move away from the river during the wet season when waterholes in the north of the area are filled with rainwater. During the dry season, they typically stay within a 10 km range of the river. When near the river, elephants show daily movement patterns towards the river at dusk and away from it at dawn (Jackson et al., 2008). When moving towards the river, elephants make use of elephant corridors, from the elephant rangeland through rural villages and fields, towards the grassy floodplains and river, and back (Songhurst, McCulloch, et al., 2015). During this time, fields are at risk of being visited and crops of being consumed (Songhurst & Coulson, 2014). Within the study area, 106 elephant pathways from the northern uninhabited region towards the river swamps and floodplains are identified, out of which 13 are so often used that they are now designated elephant corridors (Songhurst, McCulloch, et al., 2015). In this area incidents of negative impacts of elephants on people are high, as elephants damage crops; break fences; damage property; and chase, injure, and

sometimes kill livestock and humans. Meanwhile, human residents modify elephant habitat through cultivating land and developing new settlements; and also chase, injure, and occasionally kill elephants (Songhurst, 2017).

2.2 GPS data collection

We collected GPS data over the period of April 2014 to July 2016 from 6 male elephants with an average age of 33.7 years (s.d.=4.3) and 5 female elephants with an average age of 23.0 years (s.d.=4.4) and each associated with a different family group of on average 7 individuals (s.d.=2.12), collared with Vectronic GPS collars. The collars produced hourly fixes of elephants' locations, resulting in 19,391 fixes per elephant. We downloaded data using the Vectronic GPS PLUS X Collar Manager. We created NA fixes on missing points due to GPS reception issues, to avoid gaps in the series of fixes. Elephants included in the study contained less than 25% NAs.

2.3 Remote sensing data collection

For the creation of habitat feature shape files we used the Semi-automatic Classification Plugin (Congedo, 2014) available in the open source Quantum GIS Geographic Information System program (Quantum GIS Development Team, 2016). We downloaded Landsat 8 images using this plug in and created different bandset combinations in order to highlight habitat features to create cultivated fields and tree agglomerations shapefiles. We calculated overlaps between downloaded GPS coordinates and habitat features using the 'NNJoin' QGIS Plugin (Tveite, 2015), resulting in dummy variables for each of the covariates per hourly GPS fix. Inputs included four different shapefiles: the Okavango river, elephant corridors (determined by Songhurst et al., 2015), agricultural fields and tree agglomerations. For both river

and fields we also calculated a buffer zone of each 300m, since this allowed us to account for seasonal variation at borders, and research has shown that elephant movements change within those radii of these types of landscape features (Saj et al., 2001; Naughton-Treves & Treves, 2005; Chamaillé-Jammes et al., 2013). Other vegetation such as grasses and herbs in the area are highly dependent on the rainfall and therefore non-permanent, therefore we left those out of the analyses.

2.4 Preparing the data

We combined the datasets of all 11 elephants into one large dataset and converted the northing and easting coordinates into kilometres, and transformed the GPS coordinates into step sizes and relative turning angles using the `adeHabitatLT` R package in R Statistical software (Calenge et al. 2016; R Core Team, 2017). For the calculation of the step length the program uses two subsequent GPS fixes, while the relative turning angle requires three fixes. Due to an error in the GPS data we had to discard 11,731 extra fixes (of the total 213,301 fixes for all elephants) because they located the elephant over 4000 km outside of their home ranges. We constructed a season variable in order to calculate interaction effects, with the wet season ranging from November-April and dry season from May-October. We also created a time of day variable to calculate interaction effects, we consider day to be from 6.00-19.00 and night from 20.00-5.00, including dusk and dawn, when most movements in fields and river take place.

2.5 Movement model specification

We described elephant movements with two states, the first state with rapid directional movements associated with an ‘exploratory mode’, identifiable by small turning angles and large distances between fixes. The second state shows more tortuous sedentary

movements with smaller distances and larger turning angles between fixes which we call the ‘encamped mode’, expected to correspond to behaviour common in attractive habitat, e.g. foraging (Morales et al., 2004; Fryxell et al., 2008). We used hidden-Markov models (HMMs) to retrieve unobserved (hidden) movement states, from the observed combinations of step sizes and turning angles (Patterson et al., 2016). Recently, R software packages like moveHMM and momentuHMM have been released, making Hidden-Markov models easily accessible to the animal movement community (McClintock & Michelot, 2017; Michelot et al. 2016). Whilst these packages implement maximum likelihood estimation, here we use a Bayesian approach, since this provides uncertainties in estimated the latent states, switching probabilities and parameters characterising movement in each state.

We wrote the movement models in the Stan language and ran Markov chain Monte Carlo (MCMC) from R using the RStan interface (R Stan Development team 2017), a full model specification is available in **Supplementary material A.2**. As step sizes are strictly positive and continuous, we specified a Gamma distribution with shape parameter a and scale parameter b to model the step sizes x , as is common in movement state analyses (Patterson et al. 2016):

$$\gamma(x|a, b) = \frac{1}{b^a \Gamma(a)} x^{a-1} e^{-\frac{x}{b}} \quad \text{with } \Gamma(x) = \int_0^{\infty} t^{x-1} e^{-t} dt, \quad x > 0, a > 1, b > 0$$

We used separate priors for the parameters of the gamma for each movement state, with $a_1 \sim N(1.5, 0.5)$ and $b_1 \sim N(2, 0.5)$ for the exploration state (state 1); in the encamped state (state 2) the smaller step sizes were better described by an exponential distribution (a gamma distribution with $a_2=1$), and we used a normal prior for the scale parameter, $b_2 \sim N(3.5, 0.5)$. Following Morales *et al.* (2004) we used the wrapped-Cauchy

distribution to allow turning angles between $-\pi$ and $+\pi$, with μ as the location parameter and ρ controlling the spread of turning angles (Kato & Jones, 2013),

$$C(\phi|\mu, \rho) = \frac{1}{2\pi} \frac{1 - \rho^2}{1 + \rho - 2\rho \cos(\phi - \mu)} \quad -\pi \leq \phi \leq \pi, -\pi \leq \mu \leq \pi, 0 \leq \rho \leq 1$$

For the turning angle distributions, we did not have a strong *a priori* belief that μ would vary significantly between movement states and set $N(0,0.5)$ priors on each state of the parameter; for the exploration state we specified $\rho_1 \sim N(0.6, 0.1)$, and for the encamped state $\rho_2 \sim N(0.1, 0.1)$, the latter representing a higher variance in the distribution of ϕ .

Together, the distributions for the step sizes and turning angles result in the following likelihood distribution for a given vector of unobserved states ($\mathbf{Z}$),

$$p(\mathbf{x}, \boldsymbol{\phi} | \mathbf{a}, \mathbf{b}, \boldsymbol{\mu}, \boldsymbol{\rho}, \mathbf{Z}) = \prod_{t=1}^T \gamma(x_t | a_{Z_t}, b_{Z_t}) C(\phi_t | \mu_{Z_t}, \rho_{Z_t}),$$

where $Z_t = \{1, 2\}$, indicates the (unobserved) movement state at time t , and bold typeface indicates a vector (as opposed to a scalar). We seek a posterior distribution over movement parameters and state vector,

$$p(\mathbf{a}, \mathbf{b}, \boldsymbol{\mu}, \boldsymbol{\rho}, \mathbf{Z} | \mathbf{x}, \boldsymbol{\phi}) \propto \prod_{t=1}^T \gamma(x_t | a_{Z_t}, b_{Z_t}) C(\phi_t | \mu_{Z_t}, \rho_{Z_t}) \times \prod_{t=2}^T p(Z_t | Z_{t-1}) \times p(Z_1) \times p(\mathbf{a}, \mathbf{b}, \boldsymbol{\mu}, \boldsymbol{\rho}),$$

where the 1st order Markov property of the state sequence is represented by the $p(Z_t | Z_{t-1})$ term, since the next movement state only depends on the current movement state. In this formula, $p(\mathbf{a}, \mathbf{b}, \boldsymbol{\mu}, \boldsymbol{\rho})$ represents the (independent) priors on the movement parameters, and we set $p(Z_1 = 1) = 0.5$ as a prior for the initial state. For the transition probabilities, we specify the following state equation,

$$p(Z_t = i | Z_{t-1} = j) = p_{i,j},$$

which represents the probability of the elephant transitioning from movement state j at time $t-1$, to state i at time t . In the model with no covariates, independent continuous uniform priors between 0 and 1 were set on $p_{1,1}$ and $p_{2,2}$. In the model with covariates, these transition probabilities were specified by,

$$p_{i,j}(t) = \frac{\exp(\beta_0^{i,j} + \boldsymbol{\beta}_1^{i,j'} \mathbf{X}(t))}{\sum_{k=1}^2 \exp(\beta_0^{i,k} + \boldsymbol{\beta}_1^{i,k'} \mathbf{X}(t))},$$

where $\mathbf{X}(t)$ represents a vector of landscape covariates, and $(\beta_0^{i,j}, \boldsymbol{\beta}_1^{i,j'})$ is a vector of parameters which differ for each possible state transition. We specified independent $\beta_l^{i,j} \sim N(0,2)$ priors for all possible combinations of $i, j \in \{1,2\}$.

We computed the probability for the elephant to be in a given hidden states at each time fix using the forward algorithm (Rabiner, 1989). By marginalising out the hidden state sequence from the forward probability distribution of the final GPS data point, this algorithm determines the overall likelihood of the observed data. We used the Viterbi algorithm to determine the sequence of hidden states with the highest probability for each posterior draw of the set of parameters (Rabiner, 1989; Lambert, 2018). To determine if multiple elephant movement states were appropriate, we first fit a one-state model to the GPS data for each elephant, separately. Next, for each elephant we fit 48 separate two-state models incorporating all possible combinations of covariates, divided into three groups of models. The first group of 16 movement models consists of baseline models with all possible combinations of the four covariates: Okavango River, agricultural fields, tree groups and elephant corridors. The second group of models also included an interaction effect with season, distinguishing the effect of the dry and wet

season on the role of covariates in influencing the movement states. For the third group of models we supplemented the baseline models with an interaction effect of a day-night dummy variable with the covariates.

2.6 Model fitting and comparison

We used Stan’s No-U-Turn sampler to undertake Markov chain Monte Carlo (MCMC) sampling from the posterior distribution (Hoffman & Gelman, 2011; Stan Development Team, 2017). We ran models for 400 iterations across each of four chains, with 200 of the initial observations discarded as warm-up, resulting into 800 iterations in total. We determined convergence when the potential scale reduction factor on split chains approached one ($\hat{R} < 1.1$) (Gelman et al. 2014). We compared the predictive fit of competing models using cross-validation, where the models were trained on a portion of the data and used to predict observations in a ‘test’ set. For each elephant, the model was trained on the first 17,391 observations, which was then used to predict the distance and angle observations for the last 2000 observations. To calculate the probability of the test set observations, we used the forward-backward algorithm (Rabiner, 1989) to first determine $p(Z_T | x_{1:T}, \phi_{1:T})$, where T is the final time point in the training data. We then used the forward algorithm initialised with the state probabilities at time T to determine the probability of the test set observations. For each test set, we determined the log-likelihood for each data point, for each of the posterior parameter samples. We used this to estimate the average log-likelihood of each data point across all posterior samples for each elephant-model combination. The model with the highest average log-likelihood indicated to be the most predictive model, which we term the ‘best performing movement model’. To determine whether the most predictive model performed significantly better than each of the other models, we use the method outlined in

Gelman, Hwang and Vehtari (2014) based on a normal approximation, which better accounts for the uncertainty in parameter values and the underlying fit to the data than measures like the Akaike-Information Criteria (AIC) (Gelman et al., 2014). In our post-model analyses, we grouped our results into males and females, which we analysed separately in terms of their predictive fit.

2.7 Analysing the covariates

We used the best performing movement model of each model type (simple, wet-dry and day-night) to analyse how environmental variables influenced the choice of movement state, and the probability of switching between these states. To analyse how the habitat type influenced the probability of being in either the encamped state compared to the exploratory state, we estimated logistic regression GLMMs with a binomial error structure using the lme4 package (lme4 version 1.1-16, Bates et al. 2015) in R Statistical Software (R Development team 2017). To differentiate these results from the movement models, we will refer to these models as ‘state models’ in our results. Since in each model we included only one random effect, namely elephant id, we used the Laplace method (Gauss-Hermite quadrature with one point per axis) to approximate the likelihood to estimate parameters (Bolker et al., 2008; Douglas et al., 2018). In these models, the response variable was the list of estimated movement states at a given time for the model that performed best overall. For the ‘simple’ GLMM we included habitat types of the best performing model, gender and their interaction as fixed effects. For the results of the ‘interaction movement models’ with season and time of day, we included these fixed effects and the two and three-way interactions with them and habitat type and gender. Due to issues with duration and convergence of bootstrap methods, we tested the significance of the fixed effects of the model with the Likelihood Ratio Test

(ANOVA). We conducted pairwise comparisons between the full model and reduced models, with each of these models reduced on one fixed effect, where the reduced model consisted of the full model without a fixed effect of interest. For the ANOVA we used the Chi-Square test, as our models were not overdispersed (Bolker et al. 2008; Bolker, 2018, <http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html>, accessed 8/4/2018). Unfortunately, it was not possible to run the GLMMs with dummy variables for the presence of different habitat types to reveal their individual importance due to the problem of multicollinearity (dummy variable trap). Therefore, we also reported the Wald-z scores of the GLMM output for the different habitat levels. Finally, we analysed how the covariates influenced the switching between states from 1 to 2 and vice versa, we did this by comparing the significance of the overlap of the confidence intervals posterior switching probability distributions.

We expected that a model including two movement states explains movement patterns better than a one-state model (Schick et al., 2008). We expected a higher probability of being in and switching to an exploratory state in corridors (Jachowski et al., 2013; Songhurst, McCulloch, et al., 2015), and a higher probability of being in and switching to an encamped state in tree groups (de Knecht et al., 2007; Ludwig et al., 2008). When approaching the river, we expected elephants to switch to and remain in an encamped state (Shannon et al., 2009; de Boer et al., 2013). If elephants target fields deliberately, we expected that upon approaching the fields elephants would show a high probability of switching from exploring to and remaining in an encamped movement state. If elephants do not target fields deliberately, or physical stressors of fields result in minimization of time spent in the fields, we expected they will have a high probability of remaining in an exploring state towards the water (Nathan et al., 2008; Duffy et al., 2011; Chamaillé-Jammes et al., 2013). Finally, we expected these patterns to vary

between day and night and wet and dry season (Jackson et al., 2008), and between males and females (Hoare, 1999; Chiyo et al., 2005; Von Gerhardt et al., 2014).

3. Results

3.1 Determining the states

Elephants in the dataset moved 0.46 km per hour and turned 1.28 radians on average. Males moved 1.2 times faster and had 1.06 times bigger turning angles than females. On average, elephants moved faster in the wet, than in the dry season (0.51 km/h compared to 0.42 km/h) and during the day compared to night, with 0.50 km/h and 0.41 km/h respectively. Overall, when amongst tree groups and near the Okavango River, elephants had the lowest speed and highest turning angle (Trees: speed=0.45 km/h, angle=1.32 radians; River: speed=0.44 km/h, angle=1.35 radians). In the corridors elephants walked fastest and showed the lowest turning rate (Corridor: speed=0.57 km/h, angle=1.25 radians), and while on average elephants showed the same rate of turning in agricultural fields, they were considerably slower (Fields: speed=0.48 km/h, angle=1.25 radians).

All of our two-state movement models out-performed the one state movement model (Table 1). Figure 2 shows the distribution of step sizes (left) and angular displacement (right) for the two estimated movement states. State 1 in our two-state model corresponds to exploratory movements, with relatively larger step sizes (faster movements between hourly fixes) of on average 0.77 km per hour and small turning angles with a standard deviation from the mean ($\mu=0$) of 0.94 radians. State 2 corresponds to encamped movements, with elephants in state 2 having an average movement of 0.16 km per hourly fix. For this second state there is a larger turning angle standard deviation of 1.55 radians.

Table 1. The log-likelihood scores for the most predictive models for each of the three model categories, from the 16 possibilities of covariate combinations. Note that the log-likelihoods were estimated from an independent test data set of 2000 observations, and represent averages across all posterior samples.

Model	Sex	Field	River	Corridor	Trees	Log Likelihood
One State	Female	-	-	-	-	-13521.11
	Male	-	-	-	-	-17226.47
Simple	Female	1	1		1	-12434.02
	Male	1	1	1		-15976.12
Day- Night	Female	1	1		1	-12376.35
	Male	1	1	1		-15877.02
Wet-Dry	Female	1	1			-12441.94
	Male	1	1	1		-15973.13

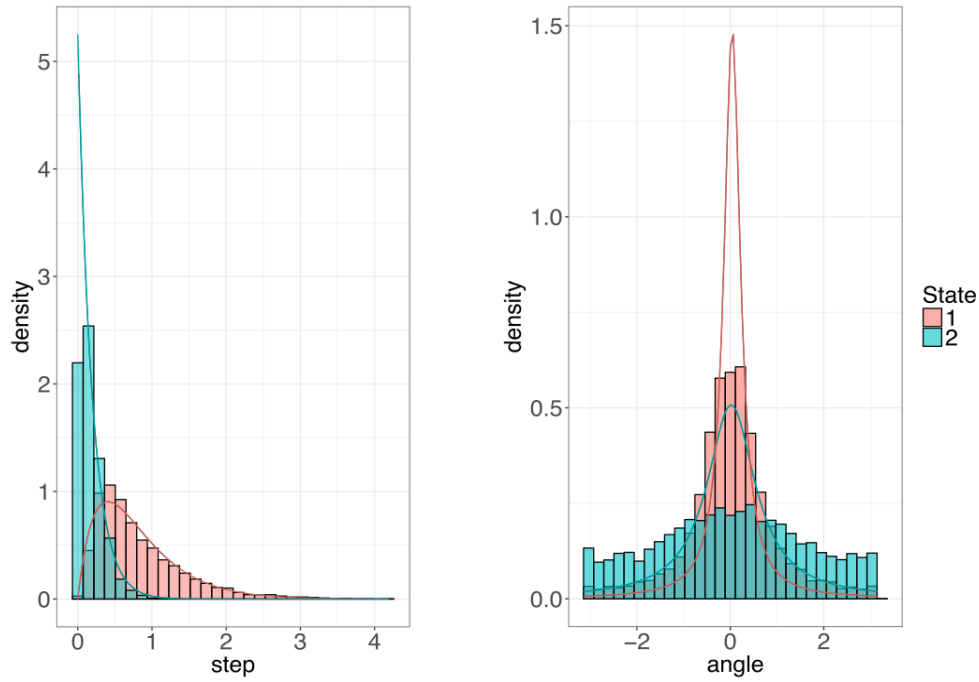


Figure 2. Distribution of the step sizes (km) and turning angles (π radians) of both estimated movement states of a single male elephant. State 1 (in orange) corresponds to exploratory movements with longer step sizes and less turning than state 2 (in blue), which corresponds to encamped movements that are smaller in step size and more winding.

Figure 3 illustrates the model estimates of the movement states for a single male elephant and is indicative of the model's mechanism for the other elephants and times.

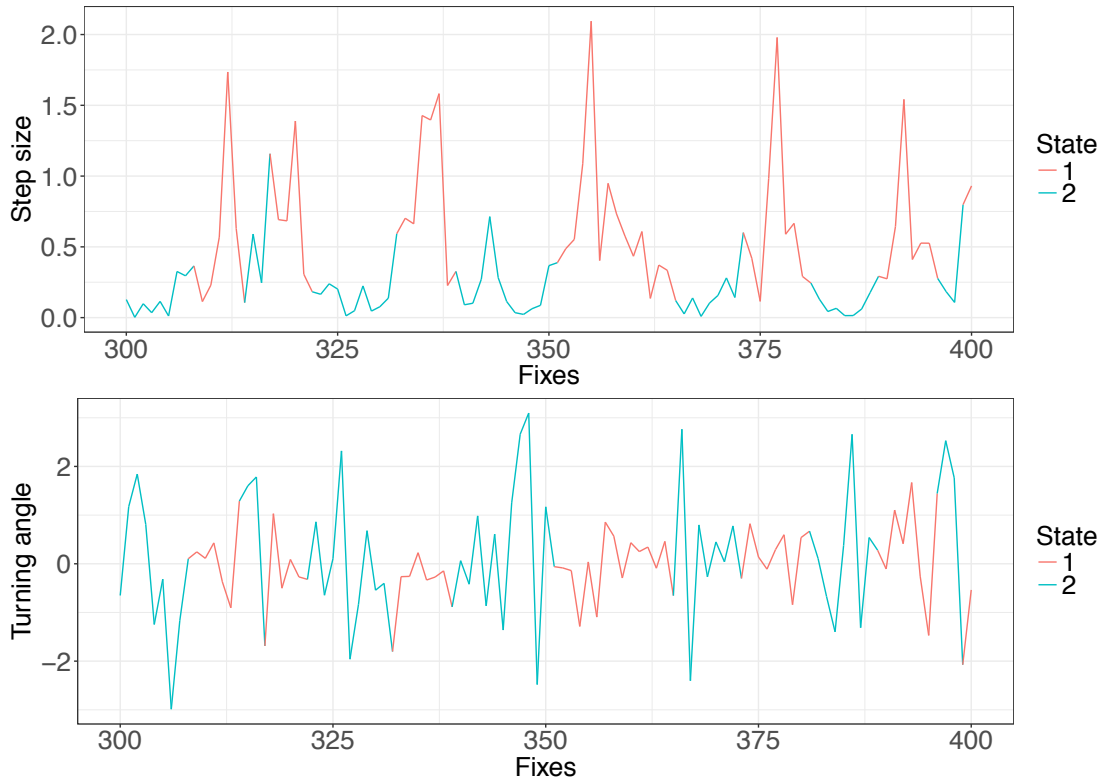


Figure 3. The results of the state calculations for the model without any covariates and interaction effects, projected on the step sizes and turning angles of 100 GPS fixes of a single male elephant.

3.2 Comparing the models

Of the simple models without interactions with season or time of day, the model for females including field, river and trees explained the elephants' movement states best, performing significantly better than 73% of the other models. For males the most predictive model included field, river and corridor, although this model only scored significantly better than 40% of the other models and did not show a significant difference from a model that included no covariates ($p=0.069$). When we included seasonality into the model, for females the model including field and river was most

predictive, significantly outperforming 87% of the models. For males, the most predictive model again included field, river and corridor, being significantly better than 73% of the other models. Including time of day as an interaction effect in the models improved the predictive fit for both the females and males. For females, the model including field, river and corridor better predicted the observations than 67% of the other models, while for male elephants the model including only field and river performed better than 80% of the other models. Overall, the models appear to be better able to explain the movement states for females than for males, see Table 1 for an overview and average log likelihoods on the test data set. For both sexes the best performing models were those including day and night interaction effects. Without differentiating between males and females, the most predictive of the simple and wet-dry models included fields and rivers, while the most predictive day-night model included fields, rivers and corridors.

3.3 Analysing the covariates, states

We now take the states each elephant is in from each of our movement models, and analyse these as a function of covariates. Figure 4 shows a visual representation of the GPS fixes and their states for one female and one male elephant.

3.3.1 Simple model

Including elephant sex did not significantly improve our ability to predict whether an elephant was in an encamped state versus exploratory state (ANOVA, $\chi^2_3=7.78$, $p=0.05$). Nevertheless, the habitat types did play a significant role (ANOVA, $\chi^2_4=52.74$, $p<0.0001$).

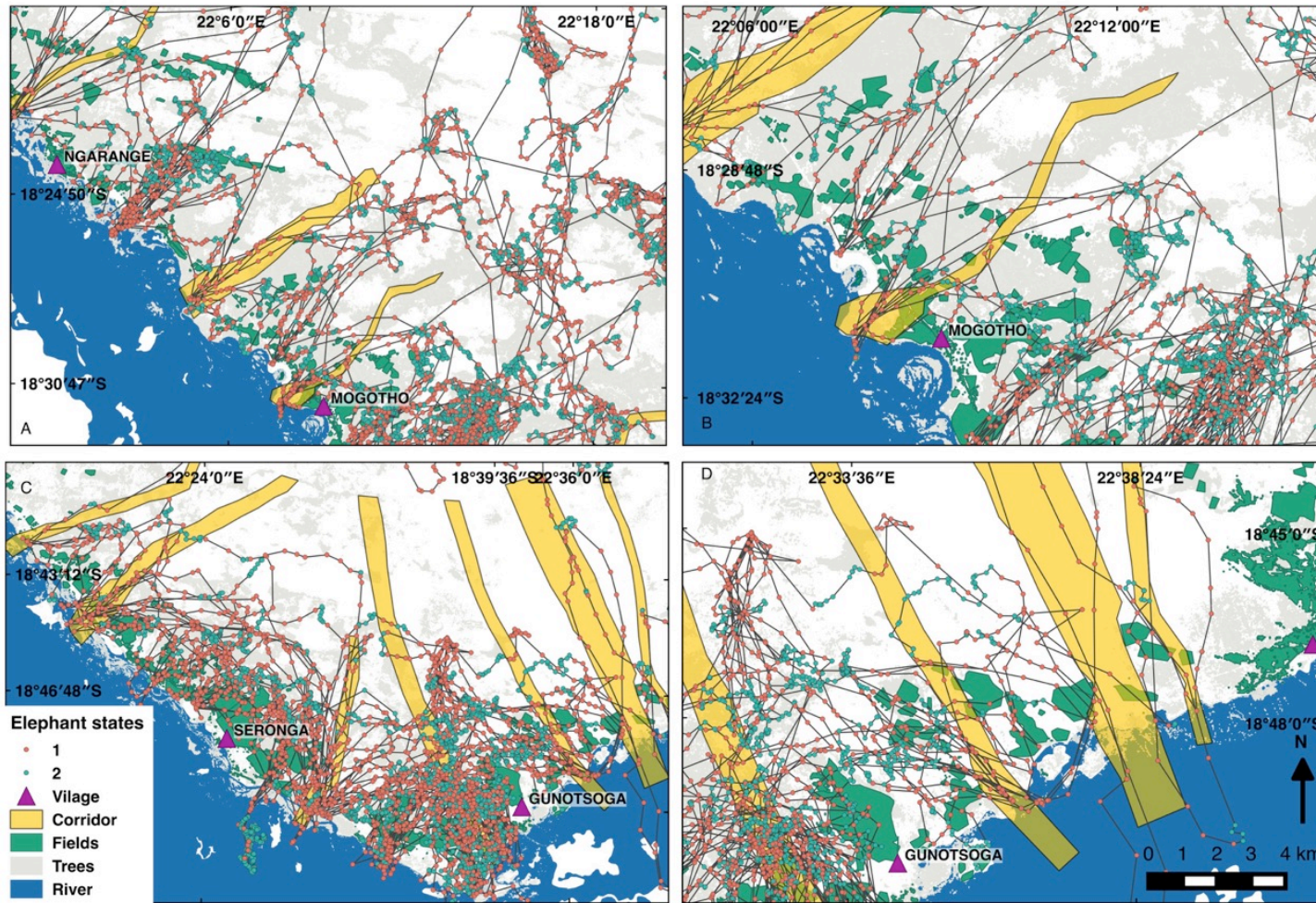


Figure 4. Visual representation of encamped (1) and exploratory (2) movement states of female elephant 'Mbamba' (A & B) and male elephant 'Centurion' (C & D) of all GPS hourly fixes from 2015, figures A & C display an overview while B & D are zoomed in.

Effect of river on states

Both females and males were most often in the encamped state in the river compared to the other two habitat types (GLMM with binomial error structure, females: Wald- $z=2.13$, $p<0.05$; males: Wald- $z=2.52$, $p<0.05$, Table 2).

Effect of fields on states

While in fields, females were equally likely to be in an encamped or exploratory state, yet the probability to be in encamped state was smaller in fields than in savanna or river habitat (GLMM with binomial error structure, Wald- $z=-2.14$, $p<0.05$). The presence of fields did not have a significant effect of whether the elephants were in encamped movement state (Wald- $z=-0.95$, $p=0.34$).

3.3.2 Interaction with time of day model

For the models including a time of day interaction effect, elephant sex (ANOVA, $\chi^2_8=139.28$, $p<0.0001$), habitat types (ANOVA, $\chi^2_8=139.28$, $p<0.0001$) and the effect of the day and night dichotomy (ANOVA, $\chi^2_8=5837.30$, $p<0.0001$) had a significant effect on the states elephants were in.

Effect of river on states

Both males and females increased in the probability to be in an encamped state near the river at night compared to daytime (GLMM with binomial error structure, Wald- $z_{\text{female}}=-20.30$, $p_{\text{female}}<0.0001$; Wald- $z_{\text{male}}=3.510$, $p_{\text{male}}<0.001$, Table 2). Although it appears that during the day for both sexes the probability to be in an encamped state is highest in the river than in any other habitat type, this effect is only significant for females (Wald- $z_{\text{female}}=13.61$, $p_{\text{female}}<0.0001$; Wald- $z_{\text{male}}=0.21$, $p_{\text{male}}=0.83$).

Effect of corridor on states

In corridors, female elephants were more likely to be in an exploratory state than in an encamped state, regardless of time of day (GLMM with binomial error structure, Wald- $z_{\text{day}} = 2.78$, $p_{\text{day}} < 0.01$; Wald- $z_{\text{night}} = -14.63$, $p_{\text{night}} < 0.0001$). For males, corridors did not significantly impact which state an individual was in, either during the day or at night (Wald- $z_{\text{day}} = 1.06$, $p_{\text{day}} = 0.29$; Wald- $z_{\text{night}} = 1.25$, $p_{\text{night}} = 0.21$).

Effect of fields on states

During the night, female elephants were more likely to be in an encamped state in fields compared to during the day, while for male elephants the probability to be in the encamped state in fields decreased at night (GLMM with binomial error structure, Wald- $z_{\text{female}} = -11.45$, $p_{\text{female}} < 0.0001$; Wald- $z_{\text{male}} = -3.16$, $p_{\text{male}} < 0.01$).

3.3.3 Interaction with season model

When including the interaction with seasons, elephant sex was again important in determining the state elephants were in (ANOVA, $\chi^2_6 = 388.48$, $p < 0.0001$). Habitat type and seasonality also significantly improved the explanation of elephant states (ANOVA, habitat: $\chi^2_8 = 412.89$, $p < 0.0001$; season: $\chi^2_6 = 2031.80$, $p < 0.0001$). In all habitat types, for both sexes, the probability of being encamped increases in the dry season compared to the wet season (Table 2).

Effect of river on states

Compared to all other scenarios for females, the probability of being in an encamped state is lowest during the wet season in rivers (GLMM with binomial error structure, Wald- $z = 15.02$, $p < 0.0001$). Males are also less likely to be in an encamped state in the wet season compared to the dry season (Wald- $z = -6.08$, $p < 0.0001$).

Effect of fields on states

During the wet season (the time when crops are grown), there is a low probability to be in an encamped state in fields has a low probability for both females and males (GLMM with binomial error structure, Wald-z_{female}= 3.62, p_{female}<0.001; Wald-z_{male}=-2.46, p_{male}<0.05). In the dry season, the probability of being in an encamped state in fields increases for both sexes and is especially high for females (Wald-z_{female}= -7.30, p_{female}<0.0001; Wald-z_{male}=3.53, p_{male}<0.001).

Table 2. Probabilities of being in the encamped versus the exploratory state, for each of the covariates of the winning models, calculated from the estimated parameters from the logistic regression binomial GLMM, using the log link formula.

Sex	Covariate	Simple	Interaction Time		Interaction Season	
			Day	Night	Wet	Dry
Female	Savanna	0.51	0.40	0.66	0.45	0.59
	River	0.53	0.51	0.53	0.24	0.59
	Field	0.50	0.43	0.51	0.33	0.53
	Corridor	-	0.43	0.49	-	-
Male	Savanna	0.50	0.41	0.60	0.47	0.52
	River	0.53	0.51	0.54	0.42	0.56
	Field	0.47	0.48	0.43	0.42	0.48
	Corridor	-	0.42	0.44	-	-

3.4 Analysing the covariates, switching

Because of a large uncertainty in the estimated switching probability distributions, only a few distributions were significantly different from one another (Figure 5). For example, for males the probability to switch from encamped to exploratory movements in savanna habitat is higher than *vice versa* (Overlap of posterior distributions, $p < 0.001$).

In the dry season, males in fields had a significantly lower probability of switching from exploratory to encamped movements than in savanna landscape (Overlap of posterior distributions, $p < 0.05$). In general, there was a decrease in the probability of switching from encamped to exploratory movements for both females and males in the dry season compared to the wet season. In the wet season, for males this probability to switch from encamped to exploratory movement is higher than from exploratory to encamped movement (Overlap of posterior distributions, $p < 0.05$).

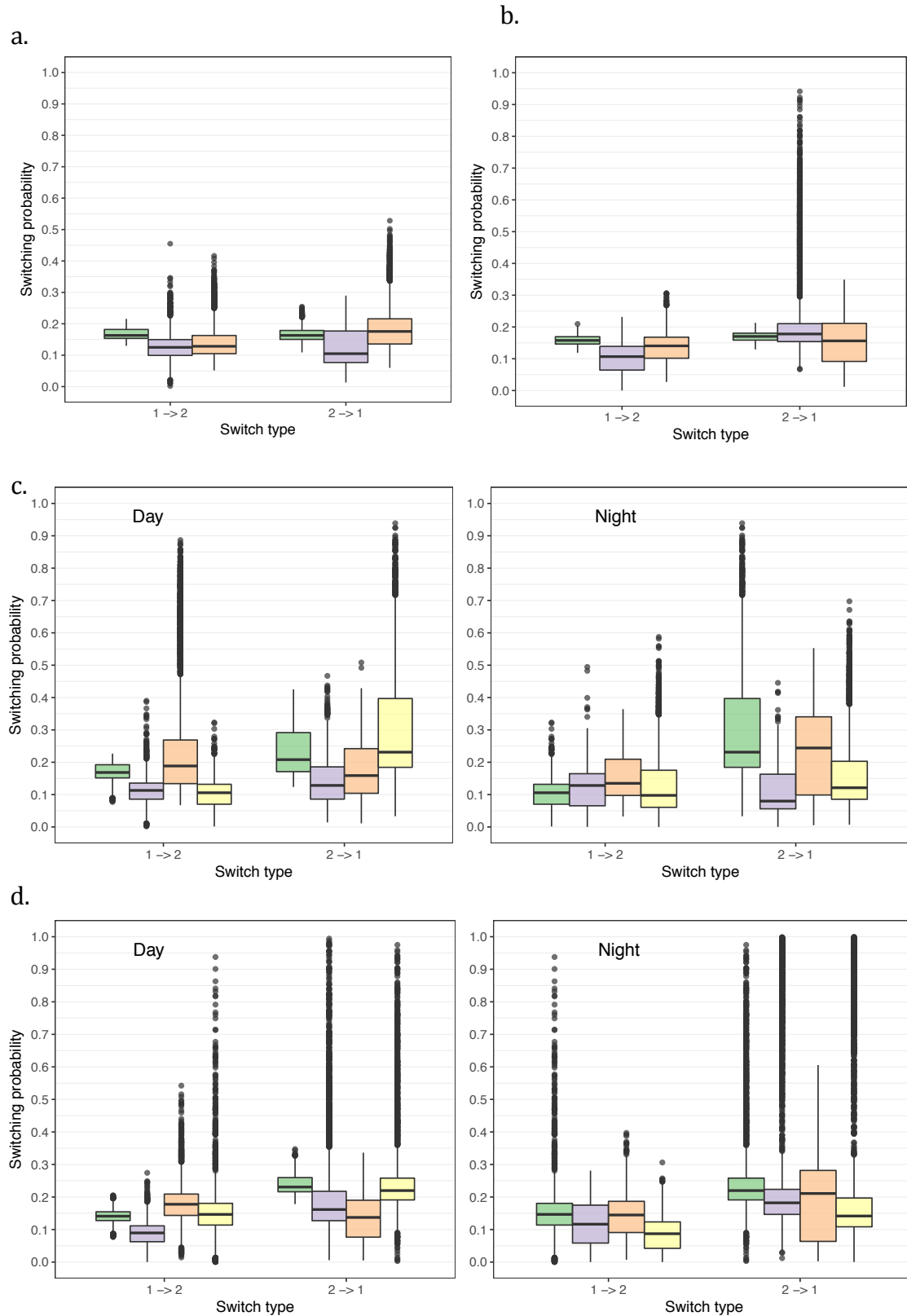


Figure 5. Continues on page 63.

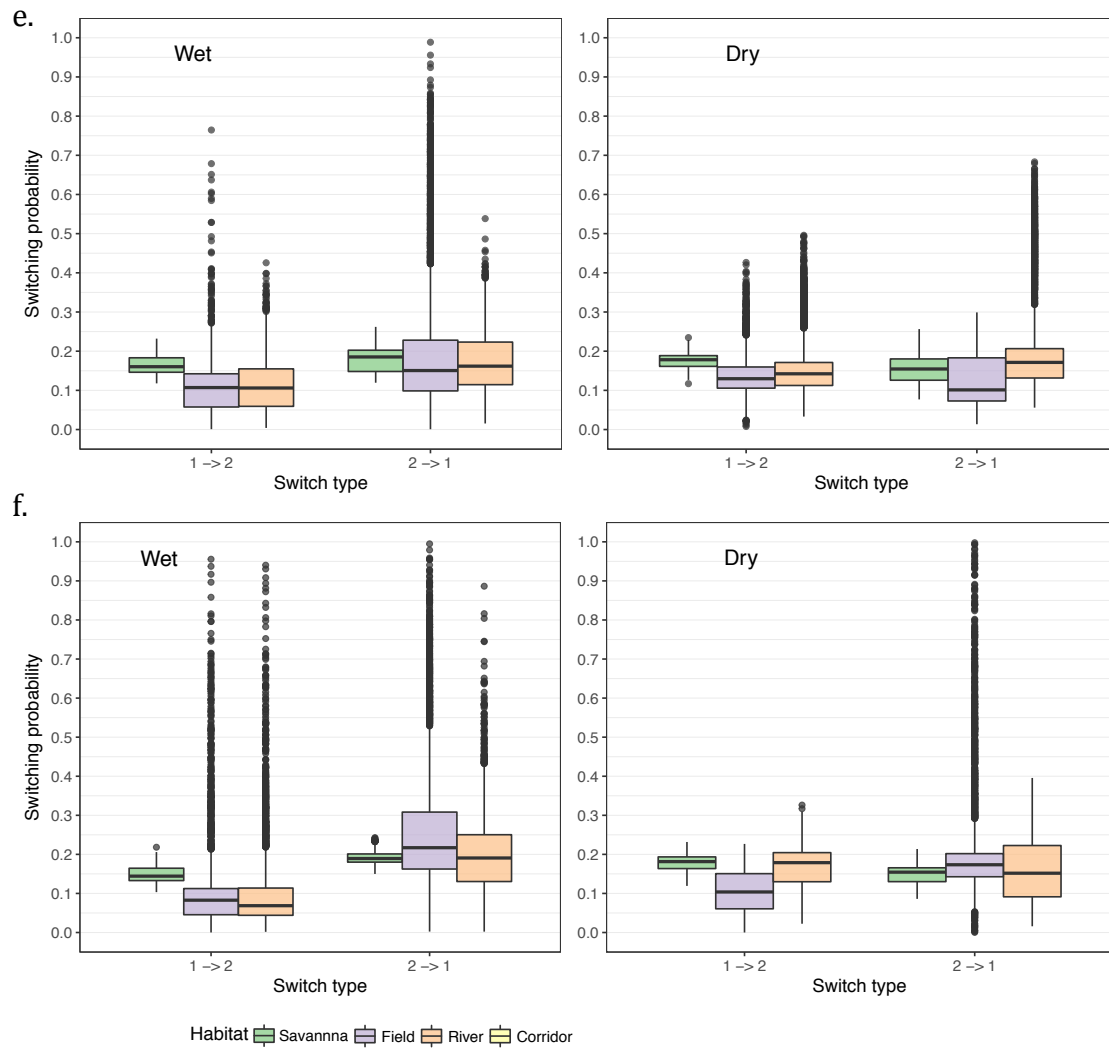


Figure 5. Switching probabilities between the different movement states, state 1 corresponds to the exploratory movements, while state 2 corresponds to the encamped movements. Figure a & b represent the simple models, c & d the models with time of day interaction and e & f the models with seasonal interaction. Figure a, c, e are females and b, d, f male elephants.

4. Discussion

Our comparison between the two and one-state movement models and the characteristics of the exploratory and encamped states reveal that elephant movements can be divided into two movement types. By simultaneously analysing speed and turning angle and classifying these combinations into movement states, we could provide more detailed insights into the influence of water and nearby vegetation on elephant movement decisions, than studies that only analyse average speed and turning angles (Duffy et al., 2011; Chamailé-Jammes et al., 2013). In our movement models, agricultural fields and the Okavango River were the main important factors explaining movement type. In particular, the effect of day and night appeared important in determining movement states.

As we expected, exploratory movements were dominant in corridors, and encamped movements near the river at night, which corresponds to elephants' nightly resting and drinking behaviour around the river. There was a difference between male and female movement state in fields at night, with a higher probability for females to be in an encamped state and a decreased probability for males. This behaviour could be explained by the predation-risk hypothesis - males and females differ in their habitat use because they have different roles in reproduction. As female reproduction success largely depends on the survival of their offspring, females and calves prefer safe habitats, while males can afford to take higher risk and forage on more dangerous habitats (Mysterud, 2000; Conradt et al., 2001; Kanallakan et al., 2005; Pérez & Pacheco, 2006; Shannon et al., 2008; Chiyo et al., 2014). Most crop consumption takes place at night when it may be easier and safer for elephants to enter fields under the cover of darkness and consume crops (Gunn et al., 2013).

Including seasonality did not improve the negative log likelihood scores of our models, nevertheless seasons did play a significant role in determining the state an elephant is in. Including seasonality revealed important information about the influence of habitat features on movement states. In the wet season when there are sufficient water sources away from the river, both males and females have a lower possibility of encamped movements in river and field habitat than in the dry season. In the wet season when the crops are growing and farmers guard their fields, both sexes show a reduced probability of encamped movements in fields, indicating either risk-avoiding behaviour or that fields are not foraging targets. Since the likelihood of encamped movements increases during the dry season, the former seems most probable, as by this time residues are left after the crop harvest and farmers are less likely to be at their fields.

Interpreting the switching behaviour of elephants is challenging, as the possibility to remain in a state is higher than to switch, especially at night. The low probabilities to switch to exploratory movements, and high probabilities to switch to encamped movements in the dry season could be related to differences in migratory patterns of elephants between these seasons. During the day elephants had a high probability to switch to encamped movement in corridors, suggesting foraging and resting behaviour. In the dry season, elephants are concentrated around the riverine habitat, while in the wet season they need to perform larger movements in the north searching for alternative water sources.

It is important to keep in mind that our data has a one-hour resolution, and in this time frame elephants can show several behaviour types (Patterson et al., 2016). However, we focus on a two-state model and take caution not to oversimplify the expected corresponding behaviours. Therefore, we do believe that we are capable to give our

states ecological meaning, while refraining from a too detailed sampling method to reduce autocorrelation risks associated with oversampling (Turchin, 1998). We did not include differences in developmental stage, body size and condition (Bowler et al., 2005), nor social interactions and internal drivers in our analyses (Getz & Saltz, 2008; Nathan et al., 2008). Such factors could be included in future studies of elephant movements.

5. Conclusion

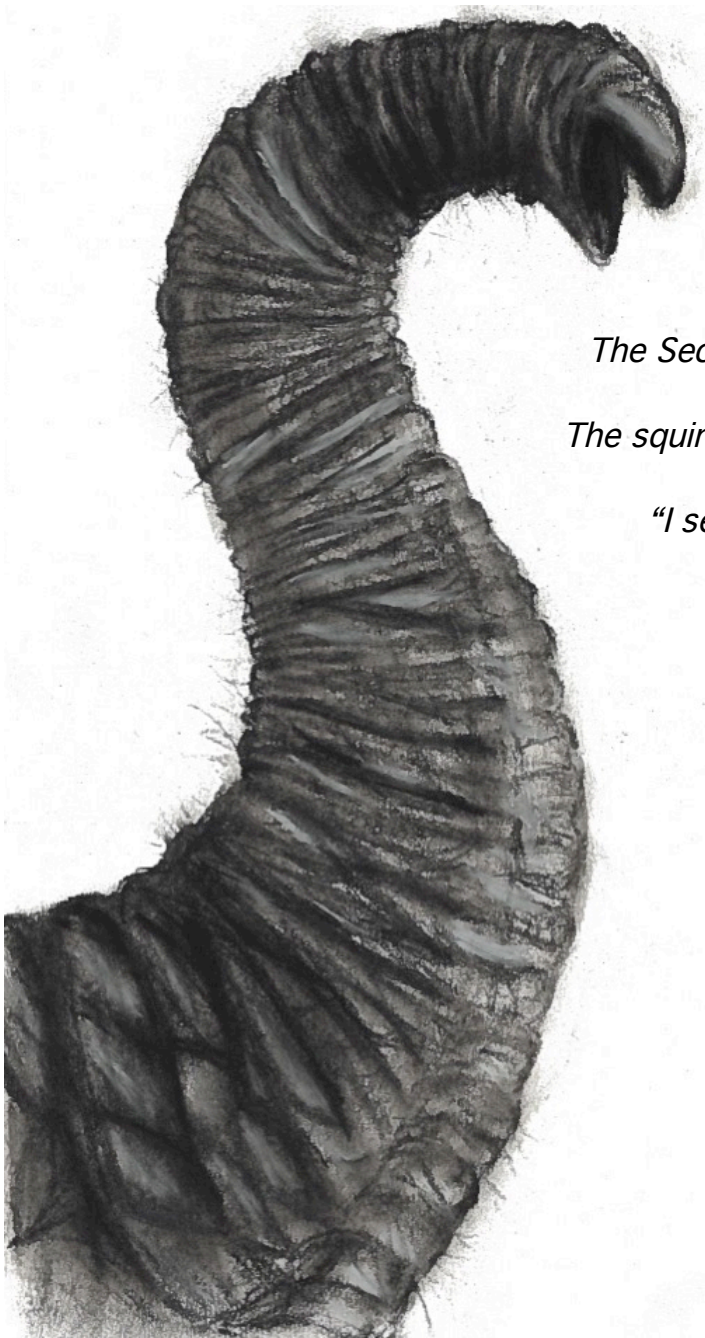
Our study shows that elephant movements can be divided into two movement types and that Bayesian movement models can provide valuable insights in the influence of habitat features on movement type and switching to a different movement state. Our results indicate sexual segregation in movement states, and that movements are influenced by both accesses to resources (e.g. water and forage) and anthropogenic features such as agricultural fields and farmer presence. Our results underline the importance of corridors for both commuting and as a place of refuge during the day, while seasonal changes in water source distribution seem to drive movements around the riverine habitat. In fields, sexual segregation in movement states supports the predation-risk hypotheses, as females appear to purposefully target fields for foraging when this is least risky during the night and dry season. Males however, are more likely to stay in exploratory mode towards the river, potentially consuming crops on their way. This sexual segregation indicates that (perceived) risk plays an important role in female movements and that sexes may respond differently to mitigation measures protecting agricultural fields. This requires further research and underlines that successful mitigation requires combinations of different methods (Hoare, 2012). Our results also have important ramifications with regard to management decision-making, especially in terms of landscape level management, allowing elephants free passage along corridors

and taking advantage of elephants avoiding risk and reinforcing ‘risky’ boundaries with field areas, which can be done with careful, appropriate land use planning and well placed effective mitigation techniques. Finally, the arrival of the dry season marks a very different scenario in terms of the likelihood of elephants moving into and being encamped around fields, which points to the importance of cultivation timing and crop harvest, which can be adapted to avoid this. Taking this into consideration when applying mitigation measures could increase their efficiency.

6. Acknowledgements

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3 | Foraging decisions



*The Second approached the animal,
And happening to take
The squirming trunk within his hands,
Thus boldly up and spake:
“I see,” quoth he, “the Elephant
Is very like a snake!”*

Chapter 3. Do African savanna elephants (*Loxodonta africana*) eat crops because they crave micronutrients?

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Abstract

1. Elephants consuming agricultural crops can have negative consequences for both humans and elephants. It is unclear to what extent savanna elephants consume crops because of the high digestibility of crops or their high micronutrient content. Therefore, we analysed the role of vegetation quality on elephant crop consumption. We particularly focused on the role of micronutrients, as natural elephant diets are suggested to be insufficient in elements such as sodium, which can influence their consumption decisions.

2. For 12 months across four seasons we collected elephant forage data along with tree, grass and crop samples. We investigated how the quality and availability of these items influenced elephant dietary choices across months and seasons. Subsequently, we compared levels of fibre, digestible energy, dry matter intake, and micronutrients in which elephants are reported to be potentially deficient, together with secondary compounds (tannins) across the three vegetation groups. As elephants do not make dietary choices based on one component, we also analysed the nutrient balance of food items with right-angle mixture models.

3. The levels of phosphorus, magnesium and dry matter intake corresponded to foraging preference. Compared to trees and grasses, crops contained significantly higher amounts of digestible energy content, dry matter intake, nitrogen, phosphorus, potassium, calcium and magnesium. Crops especially distinguished themselves by their phosphorus and magnesium levels. The right-angle mixture models indicated that except for one tree species, all food items foraged upon by elephants were relatively deficient in phosphorus.

4. The combined results of these analyses suggest a phosphorus deficiency in the elephant diet. Crops with their high absolute phosphorus levels and dry matter intake could provide an alternative source of phosphorus to reduce this deficiency, and as such explain the high intensity of crop consumption in the wet season. A potential mitigation measure against elephant crop consumption might consequently be to provide supplementary phosphorus sources.

Keywords

Human-wildlife conflict, crop raiding, foraging preference, vegetation quality, micronutrient, nutritional geometry

1. Introduction

The consumption and destruction of crops by wildlife, often described as ‘crop raiding’, can impede co-existence of wildlife and people (Nyhus, 2016). Many rodent and mammal species, such as ungulates and primates, are known to consume crops (Naughton-Treves, 1998; Pérez & Pacheco, 2006; Arlet & Molleman, 2007; Anand & Radhakrishna, 2017). More specifically, large primates, such as baboons (*Papio* spp.) and chimpanzees (*Pan* spp.), are notorious crop consumers, causing severe damage, and, additionally, on occasion attacking farmers (Hill et al., 2002; Hockings et al., 2010). Across Asia and Africa, elephants (respectively *Elephas* spp. and *Loxodonta* spp.) are also well known for their crop consumption behaviours (Sitati et al., 2003; Hoare, 2012). African elephants consume between 100 - 300 kg of wet mass vegetation per day (Laws, 1970) and are generalist, mixed- feeders, being both browsers and grazers (Codron et al., 2011). Cultivated crops are commonly included in the diet of elephants that roam human inhabited areas (Sitati et al., 2003).

Crop consumption by elephants can threaten local human food security (Mackenzie & Ahabyona, 2012). This sharing of limited resources, and the associated close proximity of humans and elephants, can result into deaths and injuries to both species (Sitati et al., 2003; Galanti et al., 2006; Kioko et al., 2008; Le Bel et al., 2010). Elephant crop consumption is prevalent in areas with high concentrations of both elephants and subsistence farmers, as in northern Botswana (Osborn, 2004; Pozo et al., 2017; Songhurst, 2017). Here, entire harvests can be destroyed by elephants, posing a threat to the livelihood and nutrition of local farmers (Gupta, 2013). As a response, the Government of Botswana and nongovernmental organizations such as Ecoexist, provided farmers with several agricultural and mitigation strategies, and conduct research projects, of which this study is part. Mitigation studies often address the

symptoms of crop consumption, aiming to find ways to keep elephants out of fields. However, it is imperative that management strategies also focus on the causes of the behaviour i.e. the reasons why elephants include crops in their diet (Barnes, 2002; Jackson et al., 2008). Most studies examining elephant crop consumption from the animal perspective focus on spatial and temporal patterns of the behaviour (Jackson et al., 2008; Von Gerhardt et al., 2014; Songhurst & Coulson, 2014; Wilson et al., 2015). Instead, we aim to analyse dietary factors associated with elephant crop consumption, in order to increase understanding in how elephants make foraging decisions, and gain insights in the reasons behind crop consumption.

Given their large size, elephants are expected to be flexible in their dietary decisions - according to the Jarman-Bell principle larger herbivores have higher digestive efficiency and a high tolerance to low quality forage (Bell, 1971; Jarman, 1974; Müller et al., 2013). Elephants appear to consume grass species relative to their availability, hence elephants do not show clear preferences for certain species (De Boer et al., 2000). However, elephants feed selectively on the woody species available, neglecting or rejecting abundant forage species, and this selectiveness varies across the seasons (De Boer et al., 2000; Kos et al., 2011; Owen-Smith & Chafota, 2012). Elephants are also known to show low tolerance of secondary chemicals such as tannins and tend to avoid phenolic-rich leaves that smaller ruminants eat (Owen-Smith & Chafota, 2012). Plants develop chemical defences as tannins and other secondary chemicals to deter animals from consuming them (Molyneux & Ralphs, 1992; Kanallakan et al., 2005). These chemical plant defences are particularly present in areas with nutrient-deficient soils as in northern Botswana (Owen-Smith & Chafota, 2012).

Seasonal patterns in crop consumption indicate that both crop and natural forage (i.e. browse and grass) quality and quantity could play a role in driving crop consuming patterns (Chiyo et al., 2005; Rode et al., 2006). During the dry season grass matures and decreases in nutritional quality, while the quality of browse changes due the availability of flowers, fruits and young leaves (De Boer et al., 2000; Kos et al., 2011; Pretorius et al., 2012; Shannon et al., 2013). During this time we expect elephants to transition from grazing to browsing, there is a window of opportunity in which crop consumption is an attractive alternative to browsing (Osborn, 2004). Indeed, temporal variation in crop consumption appears to correlate with crop availability at certain phenological stages (Sukumar, 1990; Tchamba, 1996; Chiyo et al., 2005; Sitati & Walpole, 2006).

Agricultural crops offer high intake rates, retain high micronutrient value and a low fibre content at maturation, and contain few chemical or physical defences (Sukumar, 1990; Osborn, 2004). Therefore, elephant crop consumption is in line with optimal foraging theory, as according to optimization models animals will select the best available food items from a set of foraging alternatives, based on the energy gain and costs of each choice (Krebs, 1977; Stephens & Charnov, 1982; Lambert & Rothman, 2015). In particular, the high levels of sodium and other micronutrients in crops, in combination with a high digestibility due to low fibre content and deterrent chemicals, are suggested to contribute to crop-consumption behaviour (Rode et al., 2006).

Nevertheless, it is unclear to what extent elephants consume crops because of their high digestibility (i.e. low levels of fibres and secondary compounds) or their micronutrient content. Crops could simply be a better alternative to their natural forage, or a necessity for elephants in order to avoid dietary deficiencies in micro-nutrients (Chiyo et al., 2005). Consuming crops could be a way to satisfy or maximize micronutrient intake, as natural diets of elephants are prone to micronutrient deficiencies (Sukumar, 1990;

Osborn, 2004; Chiyo et al., 2005; Rode et al., 2006). The suggestions of micronutrient deficiencies in elephant diet are based on their consumption patterns (Weir, 1969; Sukumar, 1990; Holdø et al., 2002) and the occurrence of diseases associated with micronutrient deficiencies (Wang et al., 2007). Research in Kibale National Park in Uganda suggests that elephants in the area are limited by minerals, rather than other factors such as energy and protein (Rode et al., 2006). For mammals, the essential major mineral elements are calcium (Ca), sodium (Na), phosphorus (P), potassium (K), chlorine (Cl), sulphur (S) and magnesium (Mg). These elements are known to have a metabolic role in the body, and a lack of such elements can cause symptoms of deficiency that can only be countered by adding the mineral to the diet (McDonald et al. 2011, McDowell, 2003). Nutrients in which elephants are potentially deficient are sodium (Na), phosphorus (P), nitrogen (N), potassium (K), magnesium (Mg) and calcium (Ca) (Pretorius et al., 2012). Elephants can obtain their required nutrients through efficient foraging and water sources, or by consuming soil, also known as geophagy (Klaus et al., 1998; Holdø et al., 2002). Common types of elephant geophagy are the consumption of salt licks and salt deposits on cave walls consisting of concentrations of micronutrients (Weir, 1969; Howell et al., 1996). Another way elephants avoid deficiency in micronutrients is to select those plant species that contain high levels of the nutrients in which they are deficient (Pretorius et al., 2012).

Previous research on the role of digestibility and micronutrient content in crop consumption focused either on forest elephants in forest landscapes, and used estimated forage quality proxies instead of measures, or did not include micronutrient concentrations (Osborn, 2004; Chiyo et al., 2005; Rode et al., 2006). Forest elephant crop consumption appears to be mainly driven by agricultural crop availability, while it is suggested that in savanna habitats seasonal fluctuations in natural forage quality, and

therefore the risk of nutrient deficiency, may play a more important role (Chiyo et al., 2005). To examine this hypothesis, we analysed year-round levels of micronutrients, tannins, and fibre measures (i.e. digestible energy and dry matter intake) of browse, grass and crop. First, in order to gain insight in the role of these vegetation quality measures on foraging decisions, we analysed how each of them influenced elephant foraging choices in browse and how this changed over the year (De Boer et al., 2000; Kos et al., 2011; Owen-Smith & Chafota, 2012). Secondly, we compared the levels of the vegetation quality measures between the crops, trees and grasses included in the diet of elephants in the area. We did this to examine whether crops are a better forage alternative than grass and browse, in particular on those quality measures that showed to be important in foraging choices according to our first analyses. Finally, since animals do not make their dietary choices based on merely individual nutrient levels, but need to maintain the intake of multiple nutrients at the same time, we analysed elephant foraging options with Right-Angle Mixture Triangles (Simpson & Raubenheimer, 1993). This method is an element of nutritional geometry, in which dietary choices are considered to be based on the levels of multiple elements (Raubenheimer & Simpson, 2003; Simpson et al., 2004; Raubenheimer et al., 2014). We used the combination of these methods to understand to what extent crop consumption is related to nutrient deficiency or to opportunistic foraging behaviour. Together, the results of these analyses provide insights into the importance of micronutrients in crop consumption behaviour, and the potential effectiveness of mitigation measures such as artificial salt licks (Zhang & Wang, 2003).

2. Methods

2.1 Study site

We studied the role of crop consumption in the diet of elephants in the eastern panhandle of the Okavango Delta (Figure 1, **Chapter 1**). This is an area of approximately 8,000 km² in northern Botswana, north of the Okavango River (Songhurst et al., 2015a). The soil in the area mainly consists of nutrient-poor Kalahari sands (Dougill & Thomas, 2004). Annually, there is one main wet season, which has on average 503 mm of rain (2011-2015, Statistics Botswana, 2016). This rainfall can be divided into the early wet season from November until January and the late wet season from February until April, with most rain tending to fall around January (Statistics Botswana, 2016). The crop season starts with the germinating of crops around January and crop maturation continues until harvest in April-May (Songhurst, 2012). From May until July the weather becomes dry, with the late dry season from August until October. In the eastern panhandle of the Okavango delta, mean maximum temperatures vary over these seasons from 26°C in July to 36°C in October (2000-2015, Statistics Botswana, 2016). Within this area live approximately 18,000 elephants (Songhurst et al., 2015a).

The area consists of floodplains, dry bush and agricultural fields, with seven distinguishable tree vegetation categories (Ben-Shahar, 1993; Songhurst, 2012). Around the river the floodplain vegetation type occurs, with floodplain grassland and riverine woodland with large fruit-bearing trees and small shrubs. Parts of the dry bush are dominated by mopane trees (*Colophospermum mopane*), heavily browsed by elephants, sometimes combined with other species into mixed mopane woodland. The dry bush also consists of acacia woodland with thorny browse species, areas with mixed silver terminalia (*Terminalia sericea*) vegetation and finally tree groups named the false

mopane (*Guibourtia coleosperma*), Zambezi teak (*Baikiaea plurijuga*) and wild syringa (*Burkea Africana*) woodland. During the wet season grasses occur throughout the dry-bush area, **Supplementary information B.3** gives a more detailed overview of tree and grass species per vegetation type. In this area 106 pathways were identified that elephants use to walk from the uninhabited area through human dominated areas towards the river (Songhurst et al., 2015). Of these pathways, 13 are used most frequently and have been zoned as elephant corridors in land use plans (Songhurst et al., 2015). In the same area along the river and Delta there are 13 villages with around 16,000 inhabitants (CSO, 2011). Around these villages there are (subsistence) agricultural fields including cereals like millet, sorghum and maize (*Pennisetum glaucum/ Eleusine coracana*, *Sorghum bicolor*, *Zea mays*, Songhurst, 2011; Alison Heath & Roger Heath 2009). It is evident from Figure 1 in **Chapter 1**, that these villages and crops are positioned on the route of elephants from the dry land to the Okavango River, making crops susceptible to be consumed by elephants.

2.2 Data collection

Data were collected with permission of the Republic of Botswana Ministry of Environment, Wildlife and Tourism, research permit EWT 8/36/4 XXXI (49). First, we constructed a vegetation focal list including the mean browse and grass species included in the local elephant diet. Subsequently, we followed fresh elephant feeding trails to record tree and shrub species available to, and consumed by, elephants and collected tree, grass and crop samples for nutritional content analyses.

2.2.1 Constructing vegetation focal list

From August until September 2015 we constructed a vegetation focal list of species that

were previously reported as elephant forage and reported to occur in our study site, and we verified them with foraging evidence on one of seven elephant feeding trails (less than 24 h old) in each of the seven vegetation categories (Stokke, 1999; De Boer et al., 2000; Greyling, 2004; Chiyo et al., 2005; Rode et al., 2006; Kos et al., 2011; Owen-Smith & Chafota, 2012; Pretorius et al., 2012). The focal list can be found in **Supplementary information B.4**. Grass identifications were verified at Wageningen University, and browse identifications were verified and included in a reference specimen collection at the Okavango Research Institute (ORI) herbarium in Maun.

2.2.2 Acceptance and availability plots

From October 2015-September 2016 we followed 7-10 fresh (with spoor less than 24 h old) elephant feeding trails, during the first week of each month for 11 months (excluding April due to logistical reasons), between 6.00 AM and 6.00 PM. We took a stratified random selection of seven of the 106 pathways to focus our search effort for fresh spoor on, spread over the entire region, and incorporating all dominant vegetation types in the area. We collected the feeding trail information following acceptance and availability methods developed and adapted by Owen-Smith and Cooper (1987), Stokke (1999), and Greyling (2004). At the first tree with fresh elephant impact, we created a 5 m radius circular ‘food plot’ in order to record which trees were available to the elephant and which trees were consumed by the elephant. In each of these food plots we recorded each tree >20 cm tall within the 5 m radius circle on species, height, DBH, type of elephant impact (no damage, leaves removed, twigs and leaves removed, branch broken, debarked, main stem broken, uprooted) and percentage of the tree impacted, **Supplementary information B.5** gives an overview of measurement classifications. We repeatedly continued 50 m along the feeding trail and collected

another food plot until in every feeding trail we collected six food plots. At every other food plot we created a 'control plot' similar to the food plot but 50 m perpendicular to the feeding trail, randomly to the left or right, in order to record available trees in close proximity of the feeding trail. We followed a total of 103 feeding trails, 74 from female individuals of breeding herds and 27 from male elephants. We aimed to collect equal amounts of samples from female and male elephants but this did not appear feasible, as male elephant spoor was more difficult to encounter. We collected information on 594 food plots and 293 control plots. Each of these plots contained approximately 13 trees; as a result we measured 13461 trees in total, of which 9017 in food plots and 4444 in control plots.

2.2.3 Vegetation content analyses

In the last month of each season (October, January, April and July) we collected vegetation samples of all tree species on the focal list, and each month of the crop season (February, March, April) we collected samples of all grass species with signs of elephant impact and crop species available. We included 27 tree species for year-round dietary choices analyses (108 trees in total), and in the vegetation content analysis we included 27 tree species (additionally a total of 81 trees), 15 grass species (45 grass samples in total) and 7 crop types (21 crop samples in total) throughout the crop season for comparisons between vegetation types.

Along the feeding trails, we collected browse species by including a mixture of leaves and twigs, of a variety of quality and location on the tree, of different trees from different regions of the study site. For grass samples we combined the same species from different sites when available, and we mixed crop samples from four different farmers, using different agricultural techniques (e.g. fertilization method). Vegetation

samples were air-dried in a cabinet and dried for a further 24 h at 70°C in the laboratory and ground to fit through a 1 mm mesh. We extracted condensed tannins using a butanol-HCl-iron assay run with 50% aqueous acetone and measured using a spectrophotometer. We calculated the Dry Matter Intake (DMI) of the samples by measuring the Neutral Detergent Fibre (NDF), and the Digestible Energy (DE) from the concentration of Acid Detergent Fibre (ADF) in the samples. We measured the NDF and ADF by measuring sample weight differences after subsequently applying the ANKOM Fiber Analyzer vessel according to NDF and ADF guidelines (ANKOM Technology). Finally, we measured the concentration of the nutrients phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), and nitrogen (N) using a continuous flow analyser after destruction of the samples with salicylic acid, sulphuric acid-selenium and hydrogen peroxide. **Supplementary information B.1** gives an overview of information available on potential micronutrient deficiencies in the diet of herbivores and elephants in particular.

2.3 Data analyses

For our data analyses we used R (R Core Team, 2017). To construct our study site map, we used QGIS (Quantum GIS Development Team, 2015), the Semi-Automatic Classification plugin (Congedo, 2016) and Landsat 8 data, courtesy of the U.S. Geological Survey.

2.3.1 Control plots

In order to test whether control plots and food plots consisted of similar vegetation, we modelled the proportion of plots in which a browse species was present versus the proportion it was absent, using a generalized linear model with a binomial error

structure. Plot type (control or feeding trail) and month were fitted as explanatory variables.

2.3.2 Acceptance/availability indices

We used the data from the food plots to calculate an index for the availability of each browse species and an index for consumption -or acceptance- of each species, per season and averaged over feeding trails. We calculated the availability index by dividing the frequency at which a species was present with the number of food plots, per season, and the acceptance index by dividing the frequency a species was accepted by their availability to elephants, per season. Plotting these acceptance and availability indices against each other for the four seasons (early dry, late dry, early wet, late wet) reveals the feeding trail-based foraging preferences and avoidances (Greyling, 2004; Owen-Smith & Chafota, 2012).

2.3.3 Analysing dietary choices

In order to compare how elephants' dietary choices were influenced by vegetation characteristics, we constructed a generalized linear model with a binomial error structure with the seasonal proportion a species was accepted and those in which it was present as the response variable. To remove pseudo-replication, we averaged the acceptance ratio's and vegetation characteristics over the food plots per feeding trail. As explanatory variables, we used the following vegetation characteristics: nutrient levels (N, Na, P, K, Mg, Ca), tannin levels, digested energy and dry matter intake percentages. Models were simplified using a backward selection procedure until variable removal significantly reduced the variance explained by the model.

2.3.4 Comparing vegetation characteristics between vegetation types

For comparisons between trees, grasses and crops we used the data collected during the three phases of the crop season: early (February), mid (March) and late (April), as crops and grasses are predominantly present in these months. We used the NDF and ADF estimates to calculate two proxies of the intake rate and energy content of the vegetation, respectively Dry Matter Intake and Digestible Energy intake. NDF is a measure of the fibre content of a plant, and a plant's NDF content determines how much of the plant an elephant can consume (van Soest & McQueen, 1973; van Soest, 1978). We use these NDF levels to calculate the daily Dry Matter Intake (DMI) for elephants: $\% \text{ of DMI per kg body mass} = 120/\% \text{ NDF}$, for each of the vegetation samples (Moore & Undersander, 2002). ADF can be used to calculate proxies for the energy content of vegetation. We used the ADF levels to calculate digested energy for elephants, following the formulas used by Pretorius et al. (2012): $\text{digested Energy} = 64.850 \times \text{digested ADF}^{-0.205}$, with $\text{digested ADF} = 6.665e^{0.0246(\text{ADF diet})}$. We compared whether vegetation characteristics differed between trees, grasses and crops using one-way ANOVAs. If residuals were not normally distributed or we observed evidence of heteroscedasticity, we used non-parametric Kruskal-Wallis tests. Due to the high number of dimensions and complexity of relationships, we used a Principle Component Analyses (PCA) in order to visualise how the different vegetation types (grass, browse, crops) are distinguishable based on the different vegetation quality measures (nutrients, fibre and tannin) and how this changes throughout the crop season.

2.3.5 Right-angle mixture model

In dietary choices, animals aim to not only avoid nutrient deficiencies, but also nutrient excess, resulting in a rule of compromise in which the costs of under and over consumption of certain nutrients are taken into account (Raubenheimer & Simpson, 1999; Simpson et al., 2004). We can analyse this nutrient balance visually by plotting the different relative nutrient levels as dimensions of a graph, resulting in a multidimensional space in which we plot both required and available food items (Simpson & David Raubenheimer, 1993). By subsequently analysing the position of different food items in this multidimensional nutrient space compared to the required balance, it is possible to understand the role of these food items in achieving a balanced diet (Raubenheimer & Simpson, 1993). This results into a Right-angle Mixture Triangle (RMT); a two-dimensional plot with three axes, each representing a vegetation quality measure (e.g. sodium). These axes show the percentages in which different components are present in a dietary composition (Raubenheimer, 2011). If each of the species that elephants include in their diet is considered to be a composition of the elements of these three axes (e.g. sodium, phosphorus, magnesium), it is possible to calculate their relative percentage based on their concentration in the vegetation samples. The RMT thus reveals the nutritional balance of each vegetation species, and can be compared to the ideal nutrient balance, which we calculated as a nutrient space from estimated minimum and average elephant dietary requirements (phosphorus: $\%P_{\min}=0.15$, $\%P_{\text{av}}=0.2$, potassium: $\%K_{\min}=0.5$, $\%K_{\text{av}}=0.7$, magnesium: $\%Mg_{\min}=0.1$, $\%Mg_{\text{av}}=0.3$, Pretorius et al., 2012). Instead of capturing how food sources contribute to reaching these requirements, RMTs demonstrate how balanced different food items are in their micronutrient composition, and how the elephant could combine food items to achieve the balanced diet that the elephant requires (Raubenheimer & Simpson, 1999; Simpson

et al., 2004). When plotting all species included in elephant diet on these three axes, it is possible to compare the position of these vegetation species between vegetation type (browse, grass, crops), and compare it to a minimum and average dietary input of micronutrients. The nutrient space of the RMT then demonstrates nutrient balances and enables us to consider the role and importance of different vegetation types in reaching minimum nutrient input required by elephants.

The use of RMTs has proven useful in understanding the dietary choices animals make (Chambers et al., 1995; Hewson-Hughes et al., 2013; Raubenheimer et al., 2015; Cabana et al., 2017). Hence, we selected those vegetation characteristics that appeared most important in the first two analyses, and plotted these elements of the three types of vegetation against the required compositions of elephant diets. Since we are mainly interested in understanding the role and potential deficiency of micronutrients in elephant diet, we focus on these instead of macronutrients as conventional in RMT analyses (Raubenheimer & Simpson, 1999; Raubenheimer et al., 2015).

3. Results

3.1 Summary of results

The analyses of browsing preference indicated that elephant foraging choices are positively associated with magnesium, phosphorus and dry matter intake, and negatively associated with potassium. The subsequent analyses comparing vegetation types revealed that crops have higher concentrations of most nutrients, digestible energy and dry matter intake and a lower tannin concentration than browse. Finally, right-angle mixture triangles showed that elephant diet is unbalanced in phosphorus. Although crops do not have an ideal nutrient balance, their high dry matter intake and absolute phosphorus levels could make them a strategy to reduce phosphorus deficiencies. We now explain how these findings emerged from the statistical analyses we conducted.

3.2 Dietary choices

3.2.1 Control plots

Over all feeding trails and months, food plots had a 9% higher occurrence of vegetation species compared to control plots (Linear model, $F_{1,532}=19.58$, $p<0.0001$).

3.2.2 Acceptance/availability plots

The acceptance and availability plots reveal that changes in species elephants select are influenced by the quality of vegetation, as elephant tree preferences change over the dry and wet seasons (Figure 2).

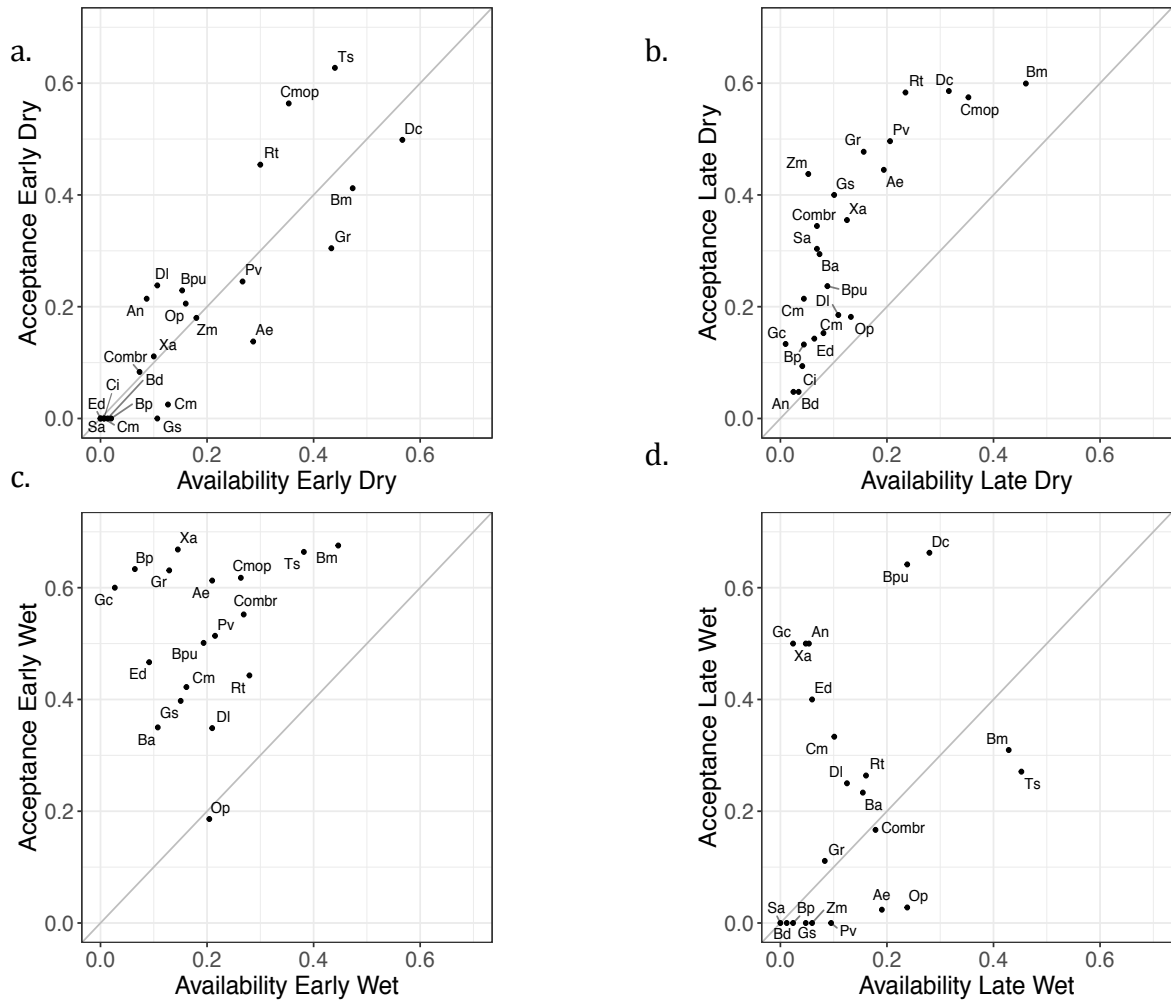


Figure 2. Acceptance versus availability plots divided in different seasons: a. early dry, b. late dry, c. early wet and d. late wet. Species abbreviations: Bm= *Baphia* mossaiensis, Ts=*Terminalia sericea*, Cm=*Croton megalobotrys*, Dl=*Diospyros lycioides*, Rt= *Rhus tenuinervis*, Op= *Ochna pulchra*, Ba= *Burkea africana*, Gs= *Gymnosporia senegalensis*, Gc= *Guibourtia coleosperma*, Cmop= *Colophospermum*

mopane, *Combr*= *Combretum* spp., *Gre*= *Grewia* spp., *Xa*= *Ximenia Americana/caffra*, *Ae*= *Acacia erioloba*, *Bpu*= *Bauhinia petersiana*, *Ed*= *Euclea divinorum*, *An*= *Acacia nigrescens*, *Cm*= *Combretum mossambicense*, *Zm*= *Ziziphus mucronata*, *Bd*= *Berchemia discolor*, *Ci*= *Combretum imberbe*, *Bp*= *Baikiaea plurijuga*, *Pv*= *Philenoptera violacea*, *Sa*= *Senegalia ataxacantha*.

Species that were above the 1:1 line through the origin, i.e. preferred species, were *Terminalia sericea*, *Colophospermum mopane*, *Ximenia Americana/caffra*, *Guibourtia coleosperma*, *Acacia nigrescens*, *Burkea africana* and *Rhus tenuinervis*. Species for which elephants show a moderate to low preference were *Diospyros lycioides*, *Euclea divinorum*. For species such as *Dichrostachys cinerea*, *Combretum mossambicensis*, *Ziziphus mucronata*, *Baikiaea plurijuga* and *Grewia* spp. elephants show preference in some seasons, while in other seasons elephants avoided them. Elephants either avoided *Ochna pulchra*, or consumed it relative to the availability of the species. Note that in some seasons, our feeding trails did not include sufficient quantities of each species in order to include them into our analyses. Not only did the level of selection by elephants change, so did the patterns of species distribution on the plots of Figure 2. During the early dry season elephants had few preferred tree species, as most species were grouped along the line or even below it, revealing aversion. In the late dry season elephants start to show clear preference and avoidance for certain species. This preference becomes more pronounced in the early wet season, but during the late wet season elephant general tree preferences become less strong, returning to the 1:1 ratio line.

3.2.3 Explaining dietary choices

Elephant dietary choices were influenced by season, the levels of phosphorus, magnesium and potassium, and the dry matter intake. The number of plots in which a

species was eaten versus the number of plots in which it was not eaten per feeding trail, differed significantly between seasons (GLM binomial logistic regression: $\chi^2_3=154.83$, $P<0.0001$, parameter estimates: Early Dry $\mu=-2.61$, $SE=0.42$; Late Dry: $\mu=0.48$, $SE=0.18$; Early Wet $\mu=0.50$, $SE=0.19$; Late Wet $\mu=-0.50$, $SE=0.22$, Table B.5 in **Supplementary information B.6** and Figure B.4 in **Supplementary information B.7**).

This corresponds to the acceptance/availability plots in Figure 2, where there is a clear difference in pattern across the seasons in acceptance and availability. During the early wet and late dry when acceptance is based on availability or preference are positive, compared to the parameter estimates in the early dry and late wet seasons, when elephants are more selective and avoid certain species. Of the nutrient levels we included in the initial model, only phosphorus, potassium and magnesium remained in the final simplified model. Of these, phosphorus and magnesium were significant in explaining the variance in the data (GLM binomial logistic regression, phosphorus: $\chi^2_1=131.09$, $P<0.0001$, parameter estimates $\mu=5.53$, $SE=1.08$; magnesium: $\chi^2_1=124.52$, $P<0.05$, parameter estimate $\mu=0.34$, $SE=0.16$). In particular, phosphorus appears to be important in determining the ratio between numbers of plots where a tree is eaten compared to not eaten, with a strongly significant positive parameter estimate. On the contrary potassium appears to have the opposite effect with a negative parameter estimate, yet this effect was insignificant ($\chi^2_1=128.37$, $P=0.10$, parameter estimates $\mu=-0.40$, $SE=0.16$). Finally, dry matter intake, which is the variable we calculated based on the NDF content of the vegetation, appears to have a positive influence on the eaten/not eaten ratio in this final model ($\chi^2_1=111.89$, $P<0.0001$, parameter estimate $\mu=0.56$, $SE=0.16$).

3.3 Comparing vegetation characteristics between vegetation types

The three vegetation types of grasses, trees and crops differed on each of the vegetation characteristics when averaged across the crop-growing season, and crops particularly distinguished themselves from the other vegetation types by their high DMI, phosphorus and magnesium values (Table B.6 in **Supplementary information B.6**). During the crop season, there was a steady increase in both ADF and NDF for grasses, while crops and trees remained relatively stable in their levels (ANOVA: NDF: $\chi^2_2=109.60$, $p<0.0001$, ADF: $\chi^2_2=40.39$, $p<0.0001$). Regardless of their phenological state throughout the season, crops scored highest for digestible energy content, and dry matter intake (DE: ANOVA, $\chi^2_2=41.52$, $p<0.0001$, DMI: Kruskal-Wallis test, $F_2=156.52$, $p<0.0001$, Figure 3).

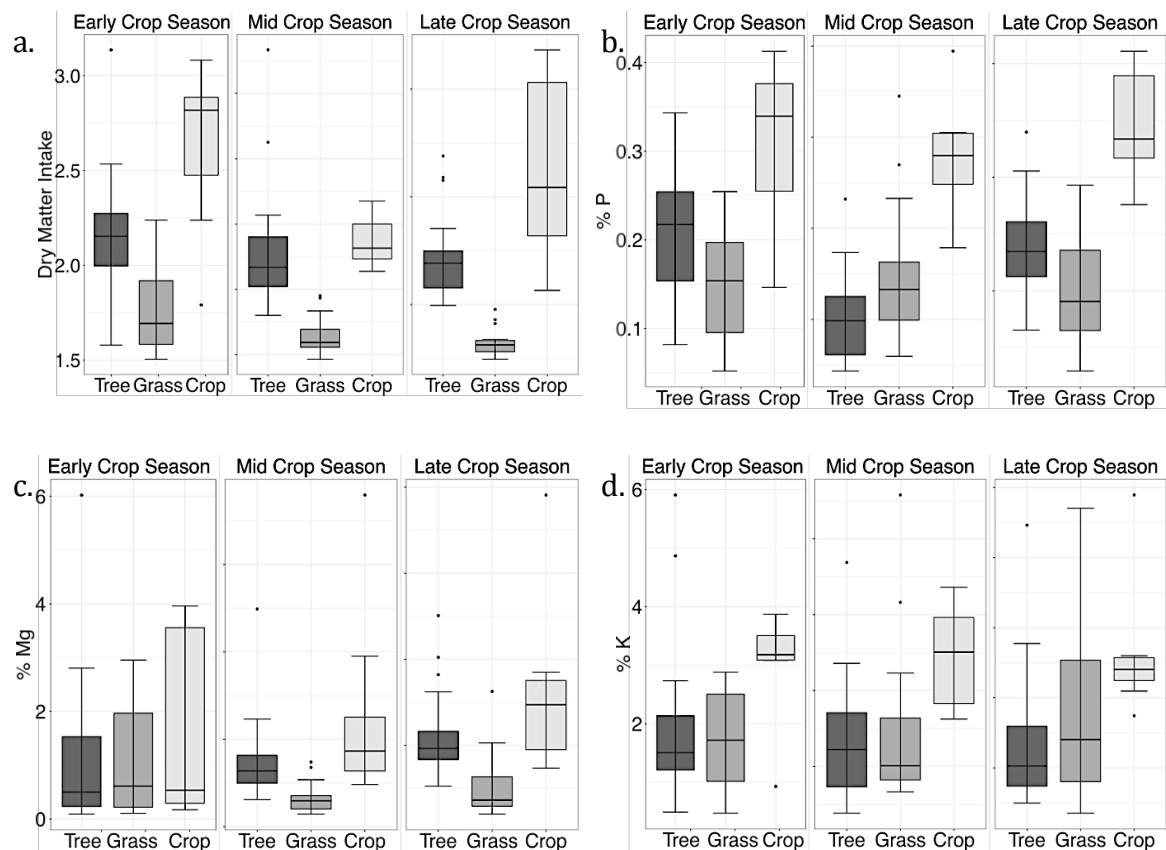


Figure 3. Boxplots comparing the differences in the vegetation characteristics a. Dry Matter Intake, b. Phosphorus (P), c. Magnesium (Mg) and d. Potassium (K) between trees, grasses and crops, and their changes over the crop season.

In the late crop season just before crops are harvested, crops had higher concentrations of nitrogen, phosphorus, calcium and magnesium compared to trees and grasses (ANOVA: nitrogen: $\chi^2_2=72.98$, $p<0.0001$, phosphorus: $\chi^2_2=38.89$, $p<0.0001$, Kruskal-Wallis test: potassium: $\chi^2_2=26.52$, $p<0.0001$, calcium: $\chi^2_2=42.51$, $p<0.0001$, magnesium: $\chi^2_2=23.78$, $p<0.0001$, sodium: $\chi^2_2=1.85$, $p=0.4877$). During the different phenological crop stages, this difference between crops and the other vegetation types increased for calcium, magnesium and phosphorus, while it remained steady for nitrogen. The potassium levels in grasses were similar to crops, while sodium levels were highest for grasses, and maturation reduced sodium levels in crops. Tannin levels

were over ten times higher for trees than for crops and grasses, and the levels remained stable across seasons (Kruskal-Wallis test: tannin: $\chi^2_2=96.29$, $p<0.0001$),

Supplementary information B.7.

In the early crop season the first three components of the PCA explained 80% of the total variation, **Supplementary information B.8**. The first component explained over half of the variance in the data, and was loaded with each of the vegetation characteristics besides tannin. For this first component, especially digestible energy appeared to have a positive correlation, while % ADF had a similar negative influence. The second components appeared to be dominated negatively by tannin and positively by phosphorus (Figure 4). During the mid crop season, there was a small change in the percentages of variance explained in the first and second component, while the construction of the components remained the same as in the early season. During the late crop season when crops were maturing, the first component of the PCA increased again in the percentage of variance it explains, while the second reduced. The first component did not change, except tannin was no longer loaded, yet the reloading on the second component changed considerably. Nitrogen, which at first only played a role in the first component, loaded most strongly, and phosphorus remained important in the first component yet strongly reduced in its importance for the second component.

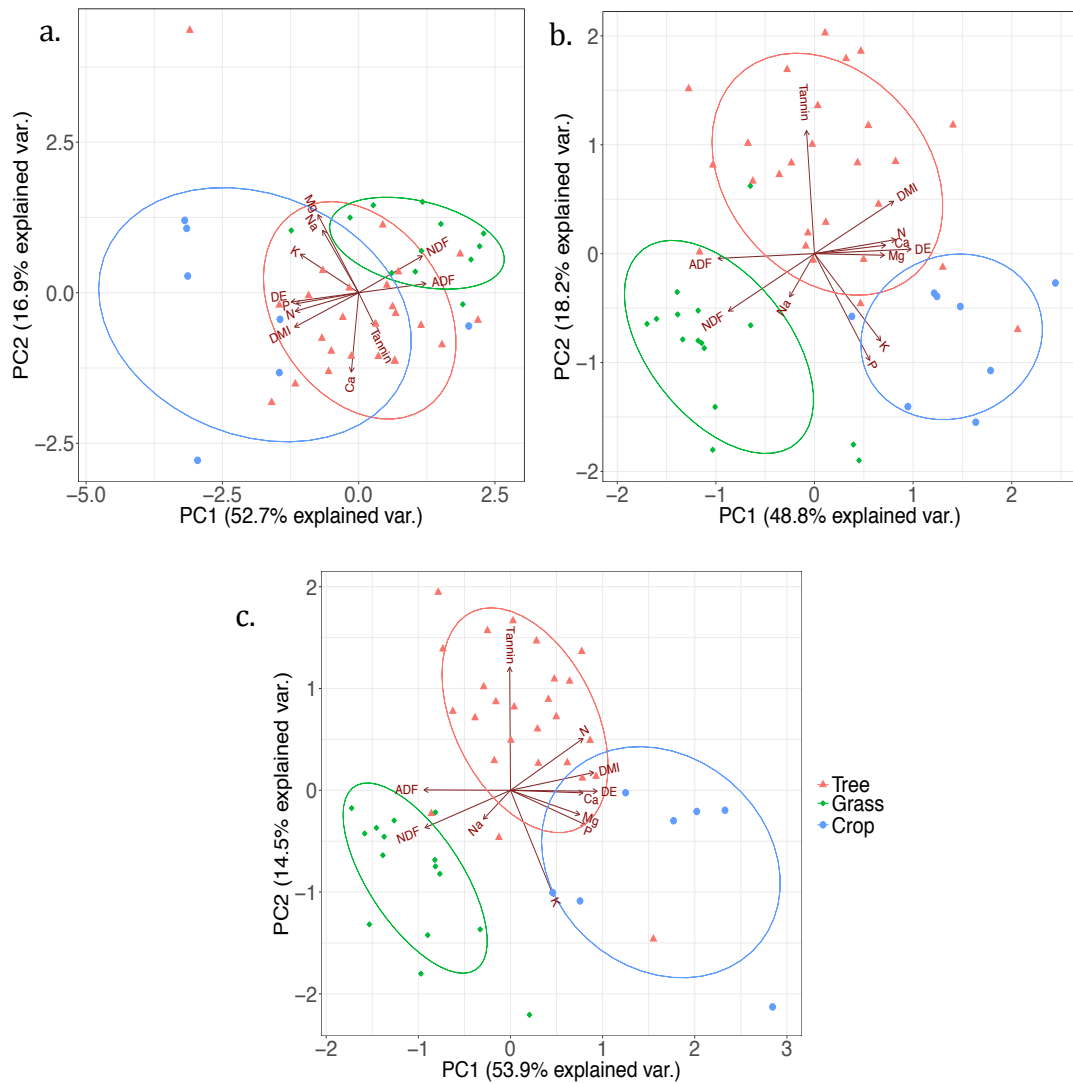


Figure 4. Biplots of PCAs for the a. early, b. mid and c. late crop season, revealing the clusters of groups of trees, grasses and crops.

The PCA biplots (Figure 4) showed three distinctive groups; with the grasses data grouped around the fibre measurements ADF and NDF, whereas crops were grouped among most of the nutrient variables. Sodium (Na) was more associated with grasses than with crops. Finally, trees were centred in the middle, grouped around tannin. With progression of the crop season and rainfall stimulating crop and grass growth, the differences between trees, grasses and crops increased. Crops seemed to be centred and

especially distinguished from the other two vegetation types by their higher levels of phosphorus and magnesium.

3.4 Right-angle mixture models

Since our final model on foraging preferences included phosphorus (P), magnesium (Mg) and potassium (K), we used these three micronutrients as our RMT axes, with P on the x-axis, Mg on the y-axis and K on the tertiary axis. Because P and Mg levels were all below 60% and K levels above 40%, our axes start at these values, with the tertiary axis of 40% at the base of the triangle, and reaching 100% in the origin of the plot (Figure 5). Grey lines indicate the nutrient space between the minimal and average required nutrient balances for elephants for each of the three micronutrients. For example, food sources within the horizontal grey lines constitute of the required concentration of Mg, while those above the lines have a relative surplus of Mg and those below a relative deficiency in Mg. The parallelogram created by these six grey lines represents the nutrient space in which food items are optimally balanced in these three micronutrients. If a food source lies within this nutrient space, elephants can reach a diet balanced in these three micronutrients by only consuming that food item.

Nevertheless, it is also possible to reach this dietary balance by combining food sources, and thus consuming food items with matching surpluses and deficiencies in other to reach a balance on average (Raubenheimer et al., 2015). Our RMT plots indicate that the ratio between P:Mg:K varies over the seasons, with in the early and mid crop season excessive ratios of Mg and K, and in each of the seasons a relative imbalance in phosphorus (Figure 5). Only one tree species *Ochna pulchra* reached the required P level in the late crop season with 19%. It is striking that in the late crop seasons when crops are mature, the P:Mg:K ratios of trees, crops and grasses are clustered, similar to

the pattern depicted in the PCA graphs. In the last example of the RMT plots (Figure 5.d), we included the dry matter intake levels based on the NDF (Figure 6a) and relative condensed tannin (Figure 6b).

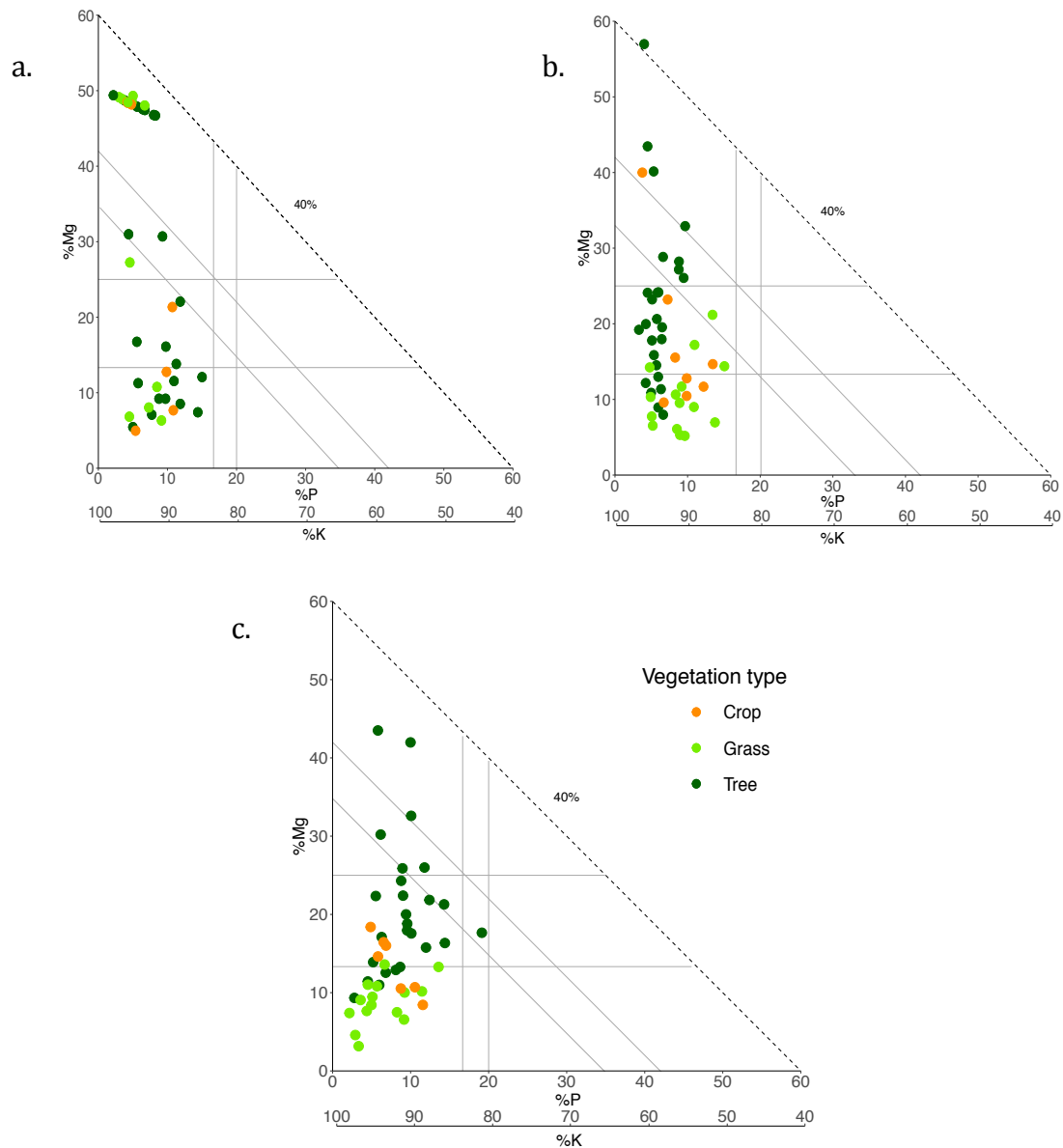


Figure 5. Right-angle Mixture Triangles, plotted with phosphorus on the X-axis (P), magnesium on the Y-axis (Mg) and potassium on the diagonal Z-axis (K). Plot a, b and c show the P:Mg:K ratio for respectively the early, mid and late crop season, for crops, grass and trees. The axes are scaled from 0-60% and 100-40%, none of the points contained a percentage of Mg or P higher than 60%, and only one a percentage of K lower than 40%.

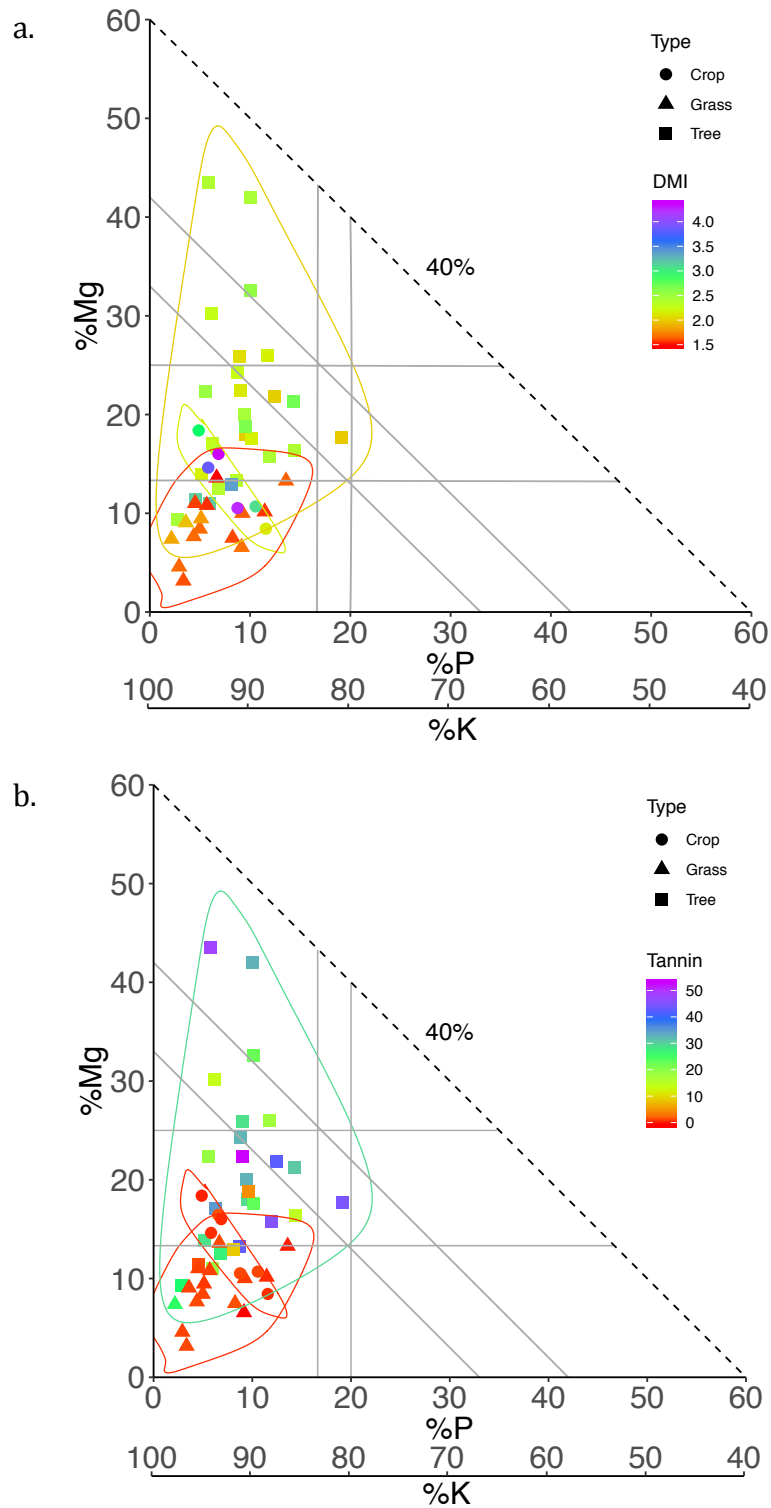


Figure 6. Plots shows the same data as plot c in Figure 5, however the colour of the food items indicates the dry matter intake levels (a) or condensed tannin (b). The axes are scaled from 0-60% and 100-40%, none of the points contained a percentage of Mg or P higher than 60%, and only one a percentage of K lower than 40%.

4. Discussion

Our results suggest that in our study site micronutrient concentrations and dry matter intake are the main motivators for elephants to include crops into their diet. The acceptance/availability plots indicate that foraging preferences vary over the season. Our analyses of foraging preference indicates that elephants select browse species based on the dry matter intake value and concentrations of phosphorus and magnesium, and potentially potassium. Phosphorus and magnesium had a positive effect on browse preference. Dry matter intake appeared to also have a positive influence on dietary preferences towards tree species. This appears contrary to previous research that showed fibre measures were unrelated to elephant food intake (Meyer et al., 2010).

Our comparison between crops, grasses and trees on nutrient and fibre measurements showed that grasses were highest in ADF and NDF fibre contents, and that these levels increased towards maturation when the fresh green grass started to dry. On the contrary, the digestible energy and dry matter intake were higher in crops; thus consuming crops increases energy levels faster than consuming grass or trees. This concurs with previous research that showed that digestible energy is an important factor in elephant dietary optimisation (Pretorius et al., 2012). Tannin levels were significantly higher in trees than in crops and grasses, indicating that crops and grasses should be preferred over browse (Owen-Smith & Chafota, 2012). However, our analysis indicated that tannin levels do not appear to influence elephant dietary preferences among tree species, suggesting that unless there is a threshold relationship above which tannins do not play a role, tannin levels are not an important driver in forage choice by elephants. Even if there is a threshold relationship tannin cannot explain elephants consuming crops over grasses, as there was no significant difference between them.

During crop maturation, nutrient concentrations in crops became significantly higher than those in browse and grass, except for sodium, which was more available in grasses than crops. This could be because the crop season takes place in the wet season, when fresh grasses start to grow and increase in nutrient contents as well. Therefore, we did not find support for sodium deficiency in elephant diet in our study area or evidence that crop consumption is a response to sodium cravings, contrary to comparable studies in other areas (Sukumar, 1990; Holdø et al., 2002; Rode et al., 2006).

The clustering of trees, grasses and crops in the PCA became increasingly concentrated into separate groups towards the end of the crop season. Nutrients played an important role in explaining the variance within the data, with crops clustered around a correlated group of dry matter intake, digestible energy, phosphorus, magnesium, calcium and potassium. Browse species were mainly concentrated around tannin, nitrogen, and grass around the fibre measures NDF and ADF and sodium levels.

Finally, the RMT graphs displayed how the ratios between the three nutrients were distributed over trees, grasses and crops. Grasses appeared to result in the highest and trees in the lowest potassium percentages, with crops in an intermediate position, especially in the late crop season. Regarding magnesium, crops contained intermediate percentages compared to trees and grasses. At the same time, most trees achieved the required ratio in magnesium, while most grasses had lower values. While there were multiple food sources that fell within the nutrient space indicating balanced magnesium and potassium values, neither natural forage nor crops reached a nutrient balance for elephants regarding phosphorus, revealing a potential deficiency in phosphorus in elephant diet. The intermediate position of crops compared to trees and grasses could also contribute to crops' attractiveness to elephants. For example, by selecting crops,

elephants could balance out the excess of potassium and deficiencies in other nutrients, which in the RMT framework is considered a ‘rule of compromise’. Moreover, the RMT plot including the dry matter values, clearly illustrates the significantly lower dry matter values of crops, meaning that elephants can consume significantly more crops than trees and grasses, thus allowing a higher possibility of consuming sufficient amounts of phosphorus. The RMT plot including tannin levels visualises the higher tannin levels of trees, however we know from the vegetation content comparisons that there was no significant difference between tannin levels of grasses and crops.

5. Conclusion & management implications

Our study suggests that consuming crops could be more than just a better alternative to browse and grass and could be related to micronutrient deficiencies in natural forage. Crops are clearly a better option to browse and grass due to their higher dry matter intake and micronutrient values, and to browse due to their lower tannin values. However, the importance of phosphorus levels in increasing foraging preference, the higher levels of phosphorus in crops compared to other vegetation types, the importance of phosphorus in clustering the vegetation types and furthermore the relative phosphorus deficiency indicated by the RMT models support the idea that crop consuming behaviour in elephants could be related to a phosphorus deficiency. Phosphorus has more known functions than any of the major minerals (McDonald et al., 2011) and plays an important role in the development of cells and tissues (Ihwagi et al., 2011), energy metabolism and is in close association with calcium in bone (McDonald et al., 2011). Deficiencies in phosphorous are widespread, since most soils worldwide are deficient in this element, especially in (sub-) tropical regions (McDonald et al., 2011, McDowell 2003, O’Halloran et al., 2010). Deficiencies in phosphorus can have a direct

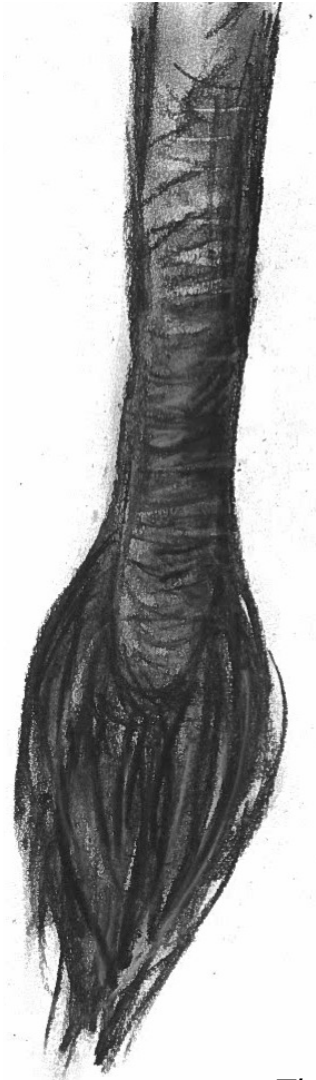
impact on fertility and reproduction (McDonald et al., 2011). Elephants can crave phosphorus, and therefore debark trees, due to the relatively high concentrations of phosphorus in bark (Ihwagi et al., 2011). Elevated levels of phosphorus can also be found in soil licks (Klaus et al., 1998) and in vegetation on termite mounds (Grant & Scholes, 2006). Further research including absolute dietary input is needed to confirm the role of phosphorus deficiency in stimulating elephant crop consumption, taking into account not only the quality but also the quantity of forage elements. Our study also reveals the importance of including information on feeding ecology into addressing crop consuming behaviour, as these influences can be site specific. Incorporating knowledge on crop consumption drivers into mitigation measures can increase efficiency and effectiveness of them; for example, supplementary licks providing a phosphorus source away from crop fields warrants further investigation as a crop consumption mitigation technique.

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4 | Foraging timing



*The Third no sooner had begun
About the beast to grope,
Than, seizing on the swinging tail
That fell within his scope,
“I see,” quoth he, “the Elephant
Is very like a rope!”*

Chapter 4. Timing of elephant dietary switches and crop consumption reveals the importance of crops in elephant nutrition

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Abstract

Tree and grass quality in African savannas shows seasonal variation, which drives mixed-feeding herbivores to switch between browsing and grazing. When elephants switch from grazing to browsing, crop consumption could potentially become an attractive alternative to browsing. We analysed elephant diet variability in the Okavango Delta, Botswana, using stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in faeces. We used frequencies of elephant crop consumption reported by farmers to determine the extent to which crop consumption is related to this potential switch. Although there was a seasonal trend in proportions of browse and grass in elephant diet, browse dominated the annual diet. In February, grass and browse had similar contributions to the elephant diet, after which the proportion of grass in the diet dropped considerably and was still decreasing in April when most crop consumption was reported. Generalized Linear Model results suggested that the proportion of browse compared to grass in elephant faeces increased with increasing crop consumption intensity and nutritional quality of both grass and browse. As crop consumption could also be related to nutrient deficiencies in elephant diet, we calculated the total dietary input of nutrients to reveal potential deficiencies. These calculations revealed that elephant diet continuously contained insufficient levels of sodium, and insufficient phosphorus concentrations from February to July. As this coincides with the timing of crop consumption, we consider our results an indication that phosphorus –and potentially sodium- deficiencies, play an important role in elephant dietary choices that could lead to crop consuming behaviour, and that supplying elephants with these nutrient sources could reduce this deficiency, attract elephant away from fields and ultimately play a role in reducing elephant crop consumption.

1. Introduction

Herbivores make foraging decisions based on the changing quality and quantity of vegetation in order to reach their nutrient requirements (McNaughton, 1990; O'Connor et al., 2007). Savanna landscapes in Africa are characterised by vast grasslands scattered with trees and shrubs, the nutrient quality of which changes with rainfall patterns (Ludwig et al., 2008; Bonnet et al., 2010). Some large herbivores, often described as mixed-feeders, switch between browsing and grazing to cope with this variation in digestibility and quality of browse and grass (Knox et al., 2011; Radloff et al., 2013; Van der Merwe & Marshal, 2014). For example, the intensity of grazing depends on the net biomass accumulation and quality of grass, which partly depends on the amount of rainfall (O'Connor et al., 2007; Bonnet et al., 2010). Savanna landscapes could be deficient in providing sufficient nitrogen and phosphorus for herbivores to obtain a balanced diet (Knox et al., 2011). This can have an impact on elephants, as they are generalist mixed-feeders (J. Codron et al., 2012) with a potential to be deficient in micronutrients (Sukumar, 1990; Osborn, 2004; Chiyo et al., 2005; Rode et al., 2006).

At the beginning of the wet season, grasses sprout and are low in fibre and silica, but high in soluble carbohydrates (Sukumar, 1990) and proteins (Guy, 1976). At this time, young tree leaves contain considerably less protein than they do a few weeks later (Guy, 1976). Until maturation, grass is easier to harvest and handle by herbivores, has fewer toxins and a lower fibre content than browse, and thus provides a higher food intake rate than browse (Osborn, 2004; Codron et al., 2011). However, grasses may lack essential key nutrients, whereas browse contains essential fatty acids and minerals (Sukumar, 1990). Browse usually contains high levels and diversity of nutrients throughout the year; however, it also contains high levels of toxins and lignin (Sukumar, 1990; Osborn, 2004). Tannins can reduce the ability of a herbivore to digest food items and the

quantity of food it can consume, and ultimately affect growth and organ functions (Robbins et al., 1991). Besides, they can limit the amount of nitrogen available to elephants from consumed browse, affecting the carrying capacity of their habitat (Schmitt et al., 2016). Lignin consists of a series of compounds, which are highly resistant to chemical degradation and are the main component of plant fibre. For this reason, plant items that are high in lignin are also low in digestibility (McDonald et al. 1995). When grass matures, it decreases in both digestibility and nutrient content (Osborn, 2004; Codron et al., 2011). As grass becomes dryer, the percentage of fibre increases while the nutritional quality – particularly the amount of phosphorus, and *in-vitro* digestibility- decreases, making browse an attractive alternative (Kos et al., 2011; Shannon et al., 2013).

There is disagreement over the extent to which elephants, and in particularly African savanna elephants, are grazers or browsers (Cerling et al., 1999). The diet of elephants in sub-Saharan Africa includes a mix of browse and grass: elephants mainly consume grass in the wet season when young grasses are abundant, and shift to browsing in the dry season when maturation of the grass decreases its digestibility, nutrient content and quantities (Osborn, 2004; O'Connor et al., 2007; Codron et al., 2011; Kos et al., 2011; Owen-Smith & Chafota, 2012; Shannon et al., 2013). This diet shift may relate to a reduction in protein (Sukumar, 1990) or nitrogen (%N) content in grasses (Guy, 1976; Codron et al., 2011; Pretorius et al., 2012), and the availability of grasses, which tends to be limited to the wet season (O'Connor et al., 2007). As the digestibility of browse tends to be lower than that of grass due to higher fibre and tannin content (**Chapter 2**), the switch from grazing to browsing is only beneficial to elephants once the grass has matured enough for it to become less attractive than browse (Osborn, 2004; Kos et al., 2011; Chapter 2). Switching between grazing and browsing thus allows elephants to

maximise nutrient intake throughout the seasons while minimizing fibre and tannin intake (Shannon et al., 2013). The proportions of browse and graze in elephant diets are flexible and variable across different environments (van der Merwe et al., 1988). Therefore, the importance of the browsing or grazing component in elephant diets tends to differ between areas, and even between herds within an area (Cerling et al., 1999). Furthermore, the importance of browse versus grass appears to differ between individuals across age, size, and sex classes (Codron, Lee-Thorp, et al., 2013; Shannon et al., 2013). For example, males make the switch from browse to grass earlier, spend more time in grassland habitat and include a higher percentage of grass in their diets than females (Shannon et al., 2013). There also tends to be differences between female elephants and their calves in plant part selection, despite their common patterns of variability between browsing and grazing. Calves consume those parts with less fibre and more nutrients, such as leaves, while females select more cellulose rich parts, like bark and branches (Woolley et al., 2011). However, these findings are mainly based on foraging sightings and rough estimates of browse and grass in elephant faeces.

During the transition from grazing to browsing, there is a window of opportunity in which crop consumption could be an attractive alternative to browse (Osborn, 2004). Elephant crop consumption is a common issue where elephants and humans coexist (Sitati et al., 2003), and can pose severe direct and indirect threats to people in local communities, such as human food security (Mackenzie & Ahabyona, 2012). Currently, it is unknown to what extent changes in browse and grass quality stimulate elephant crop consumption in savanna elephants (Osborn, 2004; Chiyo et al., 2005; Rode et al., 2006). Providing insights into the timing of crop consumption incidents and how they relate to switches in natural foraging behaviour could improve responses to address the issue. In this study, we used analyses of stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in faecal

samples to give an indication of the levels of browse and grass in an elephant's diet. The depletion level of carbon within a plant, relative to that of the atmosphere, varies as a function of the photosynthetic pathway used to fix atmospheric CO₂ into carbohydrates within the plant (Cerling et al., 1999). Plants that use the C₃ pathway -mostly dicots such as trees and shrubs and sedges- have lower $\delta^{13}\text{C}$ isotope values than plants using the C₄ pathways, which are mostly monocots like tropical grasses (Vogel, 1978; Cerling, Harris and Leakey, 1999). The $\delta^{13}\text{C}$ isotopic values, and thus the ratio of C₃ and C₄ plants in diet, can be assessed from different animal tissues, such as bone (Vogel et al., 1990), enamel (Cerling et al., 1999, 2003), keratin (Cerling et al., 2003), ivory (Vogel et al., 1990; J. Codron et al., 2012), hair (Sponheimer et al., 2003a; Cerling et al., 2006) and faeces (Sponheimer et al., 2003a; Sponheimer et al., 2003b; Codron et al., 2007; Blumenthal et al., 2012; Codron, Kirkman, et al., 2013; Radloff et al., 2013). These different tissues can give insights into different scales of herbivore diet, as isotopic analyses of body tissues such as hair indicate longer term dietary information, while faecal matter isotope values provide a proxy of short-term dietary switches (Sponheimer et al., 2003a; Codron et al., 2005; Blumenthal et al., 2012). Isotopes in body tissue represent what animals incorporate from their diet in order to synthesize new cells, while faecal isotopes represent what is excreted from the body. The formation of these body tissues can take months or even years, and thus provide a broad measure of isotopic value (Cerling et al., 2003; D. Codron et al., 2012; Codron, Kirkman, et al., 2013), whereas there are indications that faecal isotopes reflect dietary switches within 60 h for hindgut fermenters, the dietary group to which elephants belong (Sponheimer et al., 2003a). Isotopic analyses of herbivore faeces can reveal interspecies dietary variability (Sponheimer 2003a; Codron et al., 2005), intraspecific dietary flexibility (Radloff et al., 2013) and moreover intra-annual dietary shifts (Botha

& Stock, 2005; Blumenthal et al., 2012). Using faecal isotope values to infer dietary switches is a non-invasive method, as it does not require the collection of body tissues, which makes it easier to collect. Finally, faecal isotope analyses have proven reliable in studying elephant diet (Greyling, 2004; Codron & Codron, 2009; Codron et al., 2011; Codron et al., 2013).

Isotopic data has demonstrated that in most regions of Africa, the diets of savanna elephants are dominated by C₃ plants (trees, leaves, fruits and sedges), making them preferential browsers (Codron & Codron, 2009), with the exception of individuals living in the Tsavo-Amboseli region of Kenya where grazing predominated (Cerling et al., 1999). In their study comparing twelve African wildlife refuges, van der Merwe et al. (1988) documented a linear relationship between tree density and the carbon isotopic composition of bone collagen, suggesting a relationship between the availability and consumption of browse. Furthermore, forest elephants tended to have lower $\delta^{13}\text{C}$ values than savanna elephants because forest plants tend to have more negative $\delta^{13}\text{C}$ values than savanna plants (van der Merwe et al., 1988). The type of browse and the homogeneity of the landscape also influences the amount of browsing and grazing and dietary switches in elephant diet, as in mopane (*Colophospermum mopane*) dominated landscapes, elephant grass consumption appears significantly higher (Codron et al., 2006), and dry-season switches to browsing significantly smaller (Codron et al., 2011).

In this study, we first used faecal isotope analyses to estimate the contributions of browse, grass and crops to the diet of the elephants in the eastern panhandle of the Okavango delta, and their intra-annual changes. Next, we determined the extent to which crop consumption was related to these changes in dietary composition. Specifically, we i) analysed whether elephants did indeed switch between browsing and grazing in the study area, ii) used this information to analyse the extent to which crop

consumption reported by farmers was related to this potential switch, and iii) calculated whether local elephant diet could be deficient in micronutrients on the basis of the micronutrient content of grass and browse.

2. Methods

2.1 Study site

We collected elephant faeces and vegetation samples in the eastern panhandle of the Okavango Delta over a period of 12 months (Figure 1, **Chapter 1**). This area comprises 8,732 km² area of nutrient-poor Kalahari sands (Dougill & Thomas, 2004) with a mixture of seven distinguishable semi-open savanna and floodplain vegetation types (Ben-Shahar, 1993; Songhurst, 2012; **Supplementary information B.3**). Mean maximum temperatures range between 26°C in July and 36°C in October (Botswana Statistics, 2016). Around 18,000 elephants (Songhurst et al., 2015a) and 16,000 humans (CSO, 2011) share this area.

Abundant tree species in the dry bush land are mopane (*Colophospermum mopane*), sandcamwood (*Baphia massaiensis*), silver terminalia (*Terminalia sericea*) and thorny trees like camel thorn (*Acacia erioloba*) and sickle bush (*Dichrostachys cinerea*). The riverine woodlands are dominated by large often fruit carrying tree species such as large fever berry (*Croton megalobotrys*), and shrubs like red star apple (*Diospyros lycioides*) and magic guarri (*Euclea divinorum*). In all areas herbs such as white bauhinia (*Bauhinia petersiana*) and shrubs like kalahari currant (*Commiphora rhus*) and Grewia spp. (*Grewia* spp.) occur. Common grasses in the area include couch grass (*Cynodon dactylon*), phuka (*Urochloa brachyuran/trichopus*), drop seed (*Sporobolus fimbriatus*), swamp savanna grass (*Miscanthus Junceus*), mat sedge (*Schoenoplectus corymbosus*) and the lovegrasses (*Eragrostis porosa*, *Eragrostis rotifer*, *Eragrostis lehmaniana*).

While grasses are abundant in the wet season, they die back in the dry season and reveal sandy plains. An average of 503 mm (2011-2015, Statistics Botswana, 2016) of rain falls during the wet season, which can be divided into early and late phases. The early

wet season is from November until January and the late wet season from February to April, with most of the rain falling in January (Statistics Botswana, 2016). People living along the riverine strip grow cereals such as millet (*Pennisetum glaucum/ Eleusine coracana*) and maize (*Zea mays*) and vegetables like watermelon (*Citrullus lanatus*), groundnuts (*Arachis hypogaea*) and pumpkin (*Cucurbita spp.*; Songhurst, 2011; Heath & Heath 2009). Crops start to germinate around January and are ready for harvest in April-May (Songhurst, 2012). During the wet season, elephant home ranges are focused in the north, but in the dry season most elephants stay about 10 km from the Okavango River, and show daily movements to and from the river (Jackson et al., 2008). Villages and crops are often positioned on these routes, making crops susceptible to consumption by elephants (Songhurst, McCulloch, et al., 2015).

2.2 Data collection

Data were collected with permission of the Republic of Botswana Ministry of Environment, Wildlife and Tourism, research permit EWT 8/36/4 XXXI (49). Farmers' reports of elephant crop consumption were collected by community officers of the Ecoexist project; a NGO that aims to facilitate elephant and human coexistence in the eastern panhandle of the Okavango Delta, Botswana.

2.2.1 Collection plant and faeces samples

Between October 2015 and September 2016 (excluding March and May), we collected faecal samples each month. Each month we collected 8-11 fresh faecal samples less than a day old (median n=10) spread across the panhandle, and we aimed to collect equal amounts of female and male samples. We collected a total of 98 faecal samples, 69 samples from females in breeding herds and 27 from lone males. We collected

vegetation samples in the last month of every season (October, January, April, July), of the 13 tree species predominating in the local elephant diet (**Chapter 3**) and 5-11 grass species. These grasses were collected based upon availability of species that showed signs of elephant impact in the vicinity of fresh elephant faeces. We used GPS positions of collared elephants and spoor tracking to locate fresh faeces and identify elephant sex and route. This, together with the short time span of faecal collections (4-7 days) and the large distances (>10 km apart on any one day) between collection sites, minimized the probability to sample the same elephant or herd multiple times per month. At the dung sample location we recorded age and size of the surrounding boluses, footprints, vegetation, and direction of the foraging pathway, by checking spoor and elephant impact on surrounding vegetation. We took great care to not contaminate samples, and only collected samples when these faeces and spoors were from the same day or night before, especially during the wet season when spoor washes out quickly and faeces remain moist for longer. We rejected fresh boluses if they had high levels of dung beetle activity, or sand depositions indicating termite activity. After collection we filtered the faecal samples through a 0.5cm mesh and removed dung beetles and other insects. In order to quantify nutritional content of the elephant diet, we further collected browse, grass and crop samples each season, representative across the study site and analysed these on fibre measures Neutral Detergent Fibre (NDF) and Acid Detergent Fibre (ADF), tannin concentration, and nutrient concentrations of phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), and nitrogen (N; **Chapter 3**). In our analyses we use stable isotopic values from faeces and their association to isotopic values of most likely consumed browse and grass species as proxies for elephant diet. In reality diet content can vary from isotopic content due to issues as fractionation of

isotopes during digestion, this is why we correct the results with fractionation values (Codron & Codron, 2009).

2.2.2 Isotope data processing

We air-dried the faecal and vegetation samples in an air-drying cabinet. After transportation, we dried samples for a further 24 h at 70°C and ground to fit through a 1 mm mesh at the Okavango Research Institute laboratory. Samples were then shipped to the stable isotope laboratory housed in the archaeology department at the University of Cape Town, South Africa. There they were weighed into tin cups to an accuracy of 1 mg on a Sartorius M2P microbalance. Sample weights were 2.5 mg for samples with potentially low nitrogen content, 2.1-2.2 mg for legumes and agricultural samples and 2.3 mg for other sample types. Samples were combusted in a Flash 2000 organic elemental analyser and the gases passed through a Delta V Plus isotope ratio mass spectrometer (IRMS) via a ConFlo IV gas control unit (Thermo Scientific, Bremen, Germany). The in-house standards used were: Sucrose ("Australian National University (ANU)" sucrose), MG (Merck Gel), Acacia (Acacia saligna, Glencairn). All the in-house standards were calibrated against IAEA (International Atomic Energy Agency) standards, either at UCT or by other labs. Nitrogen was expressed in terms of its value relative to atmospheric nitrogen, while carbon was expressed in terms of its value relative to Pee-Dee Belemnite (VPDB).

2.3 Data analyses

For our data analyses we used R (R Core Team, 2017). To construct our study site map, we used QGIS (Quantum GIS Development Team, 2015), the Semi-Automatic Classification plugin (Congedo, 2016) and Landsat 8 data, courtesy of the U.S.

Geological Survey. To calculate the monthly amount of browse and grass in the elephant diet we used two approaches. First, we applied a linear two-source mixing model that allowed us to calculate the percentage of C₄ (grass) and C₃ (trees) plants each month based on the average $\delta^{13}\text{C}$ across faeces. Since this model does not take variation in faeces and vegetation samples into account, we also calculated the monthly dietary contributions of each source with Bayesian tracer mixing models. This approach uses both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of the diet sources to estimate the contribution of different vegetation types in the diet.

2.3.1 Linear two-source mixing model

Following Codron *et al.* 2011, we used the following linear two-source mixing model in order to calculate the percentage of C₃ plants (trees and sedges) and C₄ (other

$$\text{grasses): } \%C_4 \text{ in diet} = \frac{\delta^{13}C_{C_3\text{plants}} + \varepsilon_{\text{faeces-diet}} - \delta^{13}C_{\text{faeces}}}{\delta^{13}C_{C_3\text{plants}} - \delta^{13}C_{C_4\text{plants}}} \times 100$$

In this formula the difference between faeces and diet isotope values ($\varepsilon_{\text{faeces-diet}}$) is -0.9‰ (Codron *et al.*, 2005), while for the other values we used the average values for faeces and C₄ plants, and weighted average for C₃ plants, due to availability of data on proportions of tree species in the elephants' diet (**Chapter 3**). As we were unable to distinguish between trees and sedges $\delta^{13}\text{C}$ values, we included sedges in C₄ plants. We did not process elephant faeces in March and May due to logistic reasons, therefore we used the `interp1` function of the R-package 'pracma' to interpolate proportions of C₃ and C₄ for these months (Borchers, 2018).

2.3.2 Bayesian tracer mixing model

Bayesian mixing models are capable of using multiple tracers, in this case $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, to distinguish between diet sources in under-determined systems, where the

number of possible sources is greater than the number of tracers. Therefore, this approach can be used to potentially quantify feeding on wild C₃ sedges and C₃ browse, as well as crops, which include a mixture of C₃ and C₄ plants. We used the R-package MixSIAR (Stock et al., 2018) with the Bayesian sampling technique of JAGS (Just Another Gibbs Sampler) to calculate probability distributions of the proportions of different food sources within diets. Bayesian mixing models have the advantage of incorporating the isotope data of sources, mixtures (faeces in this case), trophic enrichment factors (isotopic offsets between diet and faeces or other tissues), elemental concentrations (carbon and nitrogen), and the uncertainty in these parameters, as well as prior knowledge of the diet (Moore & Semmens, 2008; Stock et al., 2018b). The sources we included in the initial mixing models were C₄ trees, C₄ grass, C₃ sedge (*Schoenoplectus corymbosus*), C₃ crops: groundnuts (*Arachis hypogaea*), pumpkin (*Cucurbita* spp.) and watermelon (*Citrullus lanatus*); and C₄ crops: maize (*Zea mays*) and millet (*Pennisetum glaucum/ Eleusine coracana*). For these sources we included the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values with their standard deviations (s.d.). Preliminary models revealed a correlation between the C₃ sedge and other browse (between -0.64 and -0.96), owing to similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values, so we combined these sources into ‘non-crop C₃ samples’. Since this group mainly consist of browse we refer to this category for the remainder of the chapter as browse for simplification. For the discrimination values based on faeces-diet fractionation we used $-0.9 \pm 0\text{‰}$ for $\delta^{13}\text{C}$ (Codron et al., 2005) and $1.76 \pm 0.7\text{‰}$ for $\delta^{15}\text{N}$ which we calculated from different herbivore values available in the literature (Steele & Daniel, 1978; Sutoh et al., 1987; Sponheimer, Robinson, Roeder, et al., 2003; D. Codron et al., 2012). We used proportional informative priors based on the Forage Quality Index (FQI) of browse and grasses, which we collected each month while following 6-10 elephant feeding trails

(**Chapter 3**). In the late dry season (August-October) we used the following priors browse 0.78, grass 0.20; in the early wet (November-January): browse 0.73, grass 0.25; in the late wet season (February-April): browse 0.5, grass 0.4; and in the early dry season (May-July) browse 0.58, grass 0.4. For crops we based our prior on both the FQI of agricultural fields, which we observed monthly from January until May, the timings of farmers' reports of crop consumption by elephants and expert opinion on the percentage of crops in the local elephant diet. In months in which crops were neither present nor reported to be consumed by elephants we included a prior of 0.01, and from January-April we used a prior of 0.05 for each crop type (C_3 and C_4). We included residual errors (Parnell et al., 2010) and excluded process errors, as one elephant consumes more than one vegetation sample (Stock et al., 2018b). We ran each model for 3,000,000 iterations.

Since these initial models revealed a high correlation between C_3 crops and browse in some of the months, we reran analyses with C_3 crops separated by species. Except for the change in priors and average values and s.d. for C_3 crops, we used the same settings and again ran the models for 3,000,000 iterations. As we only collected one sample for each of the crop types, we used their measured values as 'average' and the average analytical s.d. of standards used in the isotope analyses as standard deviation. For the late dry, early wet and early dry season we created the new priors by removing 0.02 of the previous grass priors, and distributing these among the new crop types, which resulted in a prior of 0.01 for C_3 crops, groundnuts (*Arachis hypogaea*), pumpkin (*Cucurbita* spp.) and watermelon (*Citrullus lanatus*). In the late wet season priors were 0.2 for each of the C_3 crops, 0.5 for C_4 crops, 0.5 for browse and 0.39 for grass.

2.3.3 Dietary switches and crop consumption

To analyse the interaction in dietary switches between browse and grass in elephant diet, and elephant crop consumption, we used a Generalized Linear Model (GLM) with a quasi-binomial error structure across all collected faecal samples. As the response variable we included the binary denominator of the proportion of browse (as success) and grass (as failure), calculated with the linear mixing model (**Section 2.3.1**). We included a categorical explanatory variable for the presence of elephant crop consumption, with 1 in months in which crops were not present, 2 when crops were present but crop consumption was low and 3 when crop consumption was intense, which was in April 2015, in which 58% of the reported incidents took place in 2015. We also included the concentrations of nitrogen of both C₃ and C₄ vegetation as explanatory variables.

2.3.4 Dietary content calculation

We used the % C₃ vegetation as a proxy for percentage of browse and the % C₄ vegetation as a proxy for percentage of grass in elephant diet, and calculated the total dietary input of the concentration of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), Neutral Detergent Fibre (NDF), Acid Detergent Fibre (ADF) and tannins (**Chapter 3**). Elephants feed selectively on the woody species available, neglecting or rejecting abundant forage species (Owen-Smith & Chafota, 2012), but include grass species in their diet in proportion to availability (De Boer et al., 2000). Therefore, for browse we used the weighted average of browse species, based on the proportion of each species in monthly elephant diet, as determined from our feeding trail data (**Chapter 3**), and for grass we used a standard average. We calculated the dietary input by multiplying the proportion of C₃ or C₄ in the diet in each

month with the nutrient values corresponding with their season, after which we summed both browse and grass values to reach the total.

3. Results

3.1 Isotope results

Mean $\delta^{15}\text{N}$ values did not show a clear seasonal pattern, while mean $\delta^{13}\text{C}$ values were highest during the months January-April (Table 1), coinciding with the arrival of both grasses and crops which both have higher $\delta^{13}\text{C}$ values than browse (Table 2). During these months, the s.d. of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ increased, indicating individual variation in dietary responses to seasonal changes to changes in vegetation quality (Table 2).

Table 1. Mean and standard deviation (s.d.) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values, mean and standard deviation (s.d.) of percentage of nitrogen of elephant faeces and number of faecal samples (n) collected in the eastern panhandle of the Okavango Delta October 2015-September 2016. Seasons are divided into Late Dry (LD), Early Wet (EW), Late Wet (LW) and Early Dry (ED).

	Mean	s.d.	Mean	s.d.	Mean %	s.d. %	n	
Month	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	Nitrogen	Nitrogen		Season
October	5.15	0.57	-25.48	0.78	1.06	0.20	10	LD
November	4.76	0.63	-24.89	1.44	1.11	0.14	11	EW
December	4.83	0.95	-24.52	1.84	1.35	0.25	10	EW
January	5.41	1.25	-23.52	2.40	1.58	0.45	10	EW
February	5.48	1.43	-21.40	3.14	1.13	0.34	8	LW

Table 1. Continued

	Mean	s.d.	Mean	s.d.	Mean %	s.d. %	n	
Month	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	Nitrogen	Nitrogen		Season
March	NA	NA	NA	NA	NA	NA	0	LW
April	5.08	1.88	-23.65	2.16	1.28	0.32	8	LW
May	NA	NA	NA	NA	NA	NA	0	ED
June	5.67	0.59	-26.63	0.54	1.57	0.29	10	ED
July	4.79	0.47	-26.42	0.42	1.28	0.22	10	ED
August	4.14	0.36	-25.39	1.08	0.88	0.20	10	LD
September	3.98	0.46	-25.61	0.82	0.86	0.12	10	LD

Table 2. Mean and standard deviation (s.d.) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values, mean and standard deviation (s.d.) of percentage of nitrogen of different vegetation types in elephant diet and number of vegetation samples (n) collected in the eastern panhandle of the Okavango Delta October 2015-September 2016. Seasons are divided into Late Dry (LD), Early Wet (EW), Late Wet (LW) and Early Dry (ED). See appendix I for species details.

Season	Type	Mean $\delta^{15}\text{N}$	s.d. $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	s.d. $\delta^{13}\text{C}$	Mean % Nitrogen	Mean % Carbon	s.d. Nitrogen	s.d. Carbon	n
LD	C4 grass	2.38	2.42	-14.36	0.91	0.71	43.15	0.51	1.73	5
LD	Browse	3.97	1.47	-27.00	0.74	2.57	45.93	0.87	2.09	13
EW	C4 grass	3.56	2.37	-14.33	0.51	1.28	43.01	0.55	2.19	11
EW	C3 grass	2.68	0.04	-27.17	0.06	0.55	42.50	0.04	0.06	1
EW	Browse	3.59	1.24	-27.14	0.91	2.66	46.05	1.12	2.74	13
LW	C4 grass	3.50	2.49	-13.64	0.80	0.93	42.57	0.26	2.08	6
LW	Browse	5.28	1.35	-27.43	1.18	2.38	46.68	0.74	2.28	13
LW	C4 crop	6.39	0.16	-12.79	0.67	1.72	39.56	0.31	3.06	2

Table 2. Continued.

Season	Type	Mean $\delta^{15}\text{N}$	s.d. $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	s.d. $\delta^{13}\text{C}$	Mean % Nitrogen	Mean % Carbon	s.d. Nitrogen	s.d. Carbon	n
LW	C3 crop	6.23	2.84	-25.37	0.47	3.20	38.91	0.57	5.04	3
ED	C4 grass	3.75	1.20	-14.17	0.83	0.72	43.48	0.34	2.20	6
ED	Browse	5.30	1.23	-27.74	0.97	1.85	45.65	0.41	2.37	13

3.2 Linear two-source mixing model

The results of the linear two-source mixing model indicated that the percentage of grass varied between 10% in June to 47% in February, while browse remained the majority of the diet in all months, ranging from 52% in February to 88 and 90% in June and July, respectively (Figure 2).

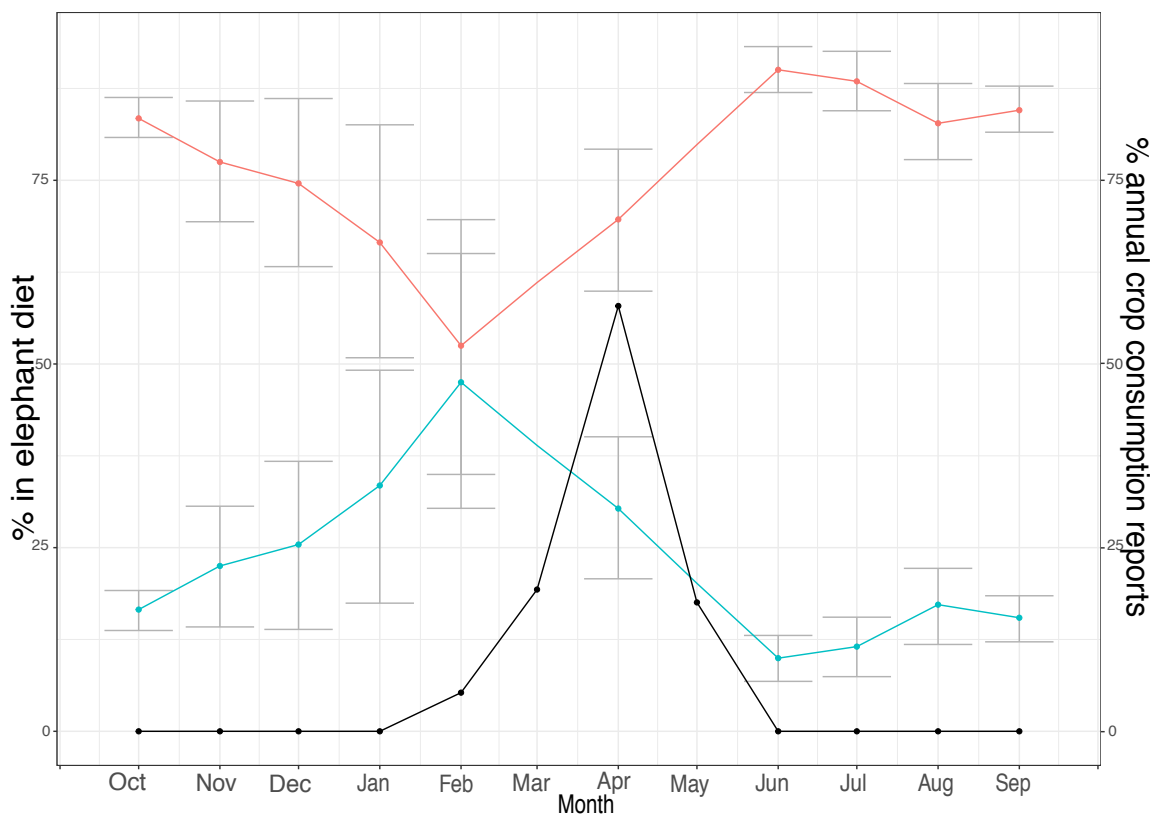


Figure 2. Percentage of C_3 (red line) and C_4 (blue line) vegetation in elephant faeces per month, and percentage of reports of crop raid incidents (black line). Error bars represent s.d. of calculated percentages of elephant faecal samples (n=8-11 per month, total of 98 samples).

3.3 Bayesian tracer mixing model

The results of our initial Bayesian tracer mixing models in which we did not distinguish between C_3 crop types indicated high correlation between browse and C_3 crops (**Supplementary information Figures C.2 and C.3**). This resulted in unrealistic overestimations of C_3 crop in elephant diet in the Late Dry and Early Dry seasons (**Supplementary information Figures C.1**). Even when we separated C_3 crop types, the estimated dietary proportions deviated from what to be expected based on plots of the raw data variance per season (Figure 3). According to the models, crop consumption mainly took place in the Late Dry and in the Early Dry seasons (Table 3), while faecal data points were clearly more drawn towards crop consumption in the Late Wet season (Figure 3). This is also the only season with available crops for elephants and farmers reported crop consumption. The model for the Early Dry season has the lowest DIC values of all models; however, the amount of browse, grass and crops predicted to be present in elephant diets in these months is highly unlikely (Table 3). The pairwise correlation plots indicate the reasons for these unrealistic results, as the models were highly likely to confuse browse and *Arachis hypogaea* C_3 crops (groundnuts) due to their overlapping probability distributions and positive correlation (Figure 4). Gelman diagnostics indicated that the number of variables that did not converge and have a Gelman diagnostic over 1.1 (**Supplementary information Table C.1** and Table 3).

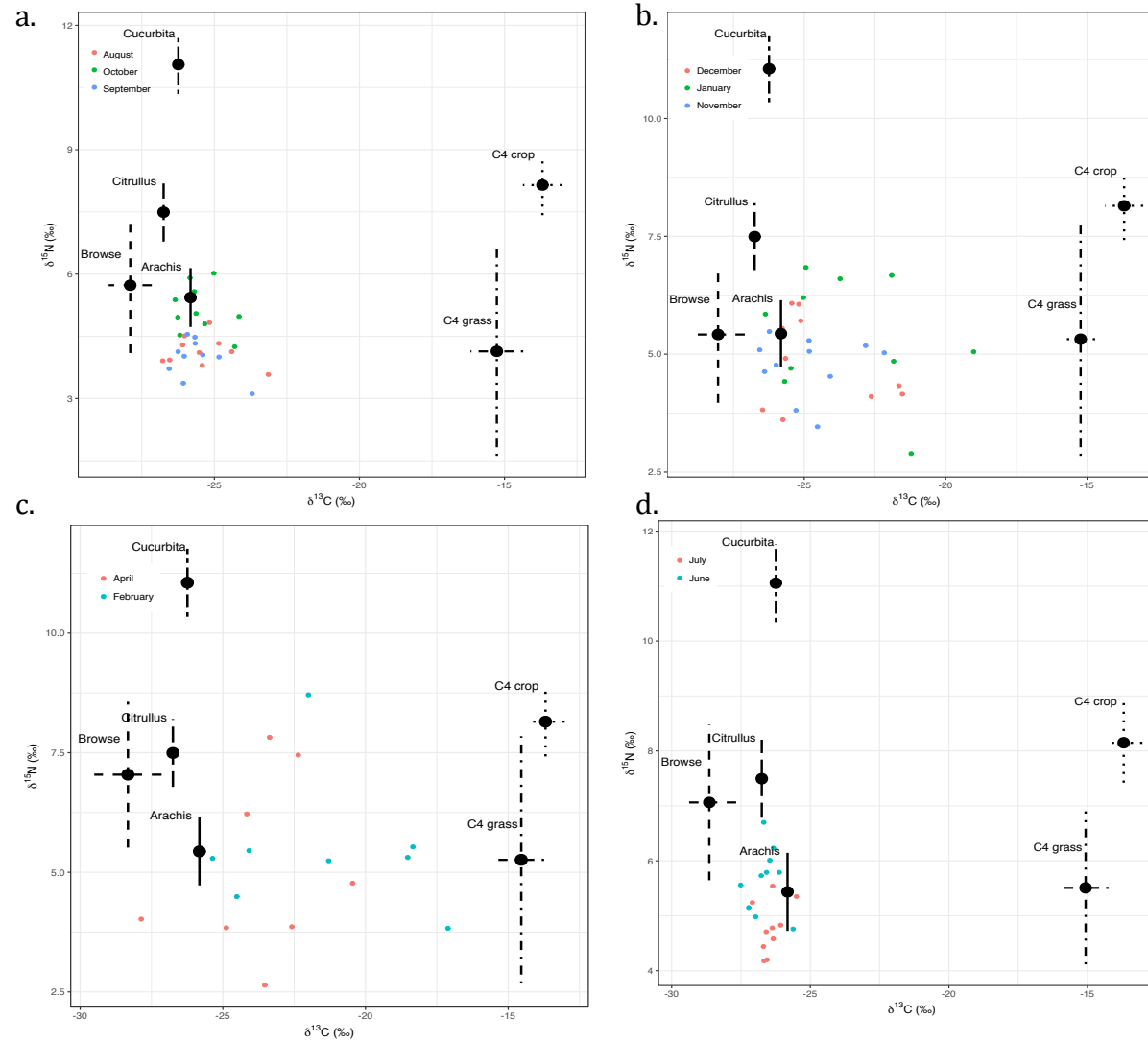


Figure 3. Raw data plots of average and s.d. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of Browse, C4 grass, and C3 and C4 crops; and faeces $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope value, per season, a= Late Dry, b=Early Wet, c=Late Wet and d=Early Dry.

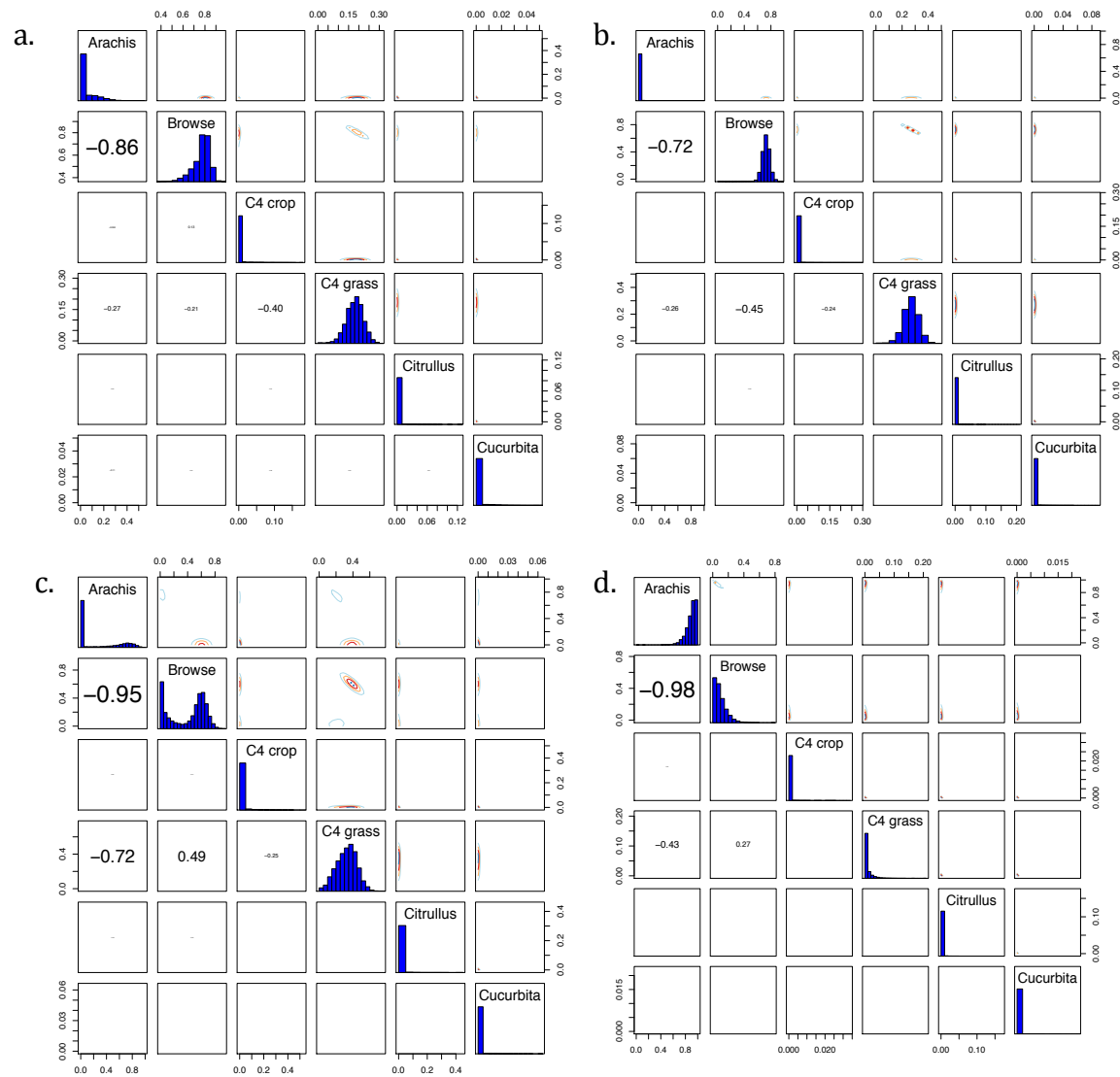


Figure 4. Pairwise correlation plots of Browse, C4 grass, and C3 and C4 crops model results, per season, a= Late Dry, b=Early Wet, c=Late Wet and d=Early Dry.

Table 3. Estimated percentages of vegetation species in elephant diet as estimated via the Bayesian tracer mixing models.

Month	Season	Gelman	DIC	Non-crop	C4 grass	C4 crops	C3 crop	C3 crop	C3 crop
		diagnostics		C3 in %	in %	in %	<i>Arachis</i>	<i>Citrullus</i>	<i>Cucurbita</i>
		(>1.1)		(browse)			<i>hypogaea</i> in %	<i>lanatus</i> in %	<i>sp.</i> in %
August	Late Dry	21	81.41	77.1 ±7.5	17.9 ±4.3	0.3 ±1.5	4.4 ±7.9	0.1 ±0.7	0.1 ±0.4
September	Late Dry	21	81.41	80.9 ±5.7	16.5 ±4.3	0.2 ±1.1	2.3 ±4.8	0.0 ±0.4	0.0 ±0.2
October	Late Dry	21	81.41	62.4 ±24.3	16.3 ±7.0	0.9 ±3.8	19.3 ±29.9	0.5 ±3.3	0.5 ±2.0
November	Early Wet	11	92.95	75.2 ±8.3	23.5 ±5.9	0.1 ±1.2	1.1 ±7.8	0.0 ±0.5	0.0 ±0.3
December	Early Wet	11	92.95	72.0 ±7.9	26.7 ±5.9	0.2 ±1.4	1.0 ±7.3	0.0 ±0.5	0.0 ±0.3
January	Early Wet	11	92.95	61.8 ±8.0	36.6 ±6.3	0.3 ±2.3	1.1 ±7.5	0.1 ±1.0	0.1 ±0.5
February	Late Wet	0	77.56	31.5 ±20.2	46.2 ±12.4	1.0 ±4.3	21.0 ±27.2	0.3 ±1.9	0.0 ±0.4
April	Late Wet	0	77.56	40.7 ±26.0	32.4 ±11.9	0.7 ±2.8	25.9 ±33.2	0.2 ±1.9	0.0 ±0.3
June	Early Dry	0	36.95	17.8 ±12.3	0.8 ±1.4	0.0 ±0.2	81.3 ±12.9	0.1 ±0.7	0.0 ±0.2
July	Early Dry	0	36.95	9.5 ±7.7	0.8 ±1.4	0.0 ±0.1	89.6 ±8.3	0.0 ±0.4	0.0 ±0.1

3.4 Dietary changes and crop consumption

The proportion of browse versus grass in elephant faeces was significantly associated with the intensity of elephant crop consumption (GLM; $\chi^2=819.91$, d.f.=2, $p<0.0001$), with an increase of the proportion of browsing in elephant diet during crop consumption (Figure 3). The proportion of browse in elephant diet also had a significant positive association with nitrogen concentration of both C_3 ($\chi^2=727.25$, d.f.=1, $p<0.0001$) and C_4 ($\chi^2=692.21$, d.f.=1, $p<0.05$).

3.5 Dietary content calculations

From June to December elephant diet was dominated by C_4 forage, therefore dietary calculations for these months closely resembled the nutritious qualities of browse (Table 4). From January to April, grass quality increased due to its lower fibre content and higher nutrient levels (**Chapter 3**). During this period, both the grass quantity and total fibre content of the elephants' diet increased, but the level of many of the nutrients analysed, decreased.

Table 4. Percentage of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), Neutral Detergent Fibre (NDF), Acid Detergent Fibre (ADF) and mg/g tannins in elephant diets each month.

Month	N	P	K	Ca	Mg	Na	NDF	ADF	Tannin
October	2.45	0.18	1.19	1.08	0.23	0.01	53.98	34.75	24.73
November	2.68	0.18	1.48	0.63	0.70	0.04	57.23	35.79	20.50
December	2.63	0.18	1.49	0.61	0.68	0.05	57.76	35.85	19.76
January	2.50	0.17	1.52	0.57	0.63	0.06	59.22	36.02	17.73
February	2.02	0.12	1.40	0.71	0.22	0.02	62.07	36.81	19.41
March	2.20	0.12	1.33	0.78	0.23	0.02	60.26	36.17	22.24
April	2.38	0.13	1.27	0.84	0.24	0.02	58.45	35.54	25.07
May	1.55	0.10	1.00	1.45	0.28	0.01	54.02	34.95	17.71
June	1.66	0.10	0.91	1.61	0.30	0.01	51.31	33.83	19.96
July	1.65	0.10	0.92	1.59	0.30	0.01	51.73	34.01	19.62
August	2.43	0.18	1.19	1.07	0.22	0.02	54.15	34.80	24.55
September	2.47	0.18	1.19	1.09	0.23	0.01	53.70	34.67	25.04

Table 5. Minimum and average requirements of nutrients in elephant diets, from Pretorius et al. 2012.

Nutrient	% N	% P	% K	% Ca	% Mg	% Na	% ADF
Minimum requirement	1.3	0.15	0.5	0.4	0.1	0.1	30
Average	2.1	0.2	0.7	0.6	0.3	0.2	48

Comparing the dietary content (Table 4) with elephant dietary requirements (Table 5) indicated that, with the exception of phosphorus (P) and sodium (Na), the micronutrient levels sampled were sufficiently high throughout the year. Sodium levels from vegetation were continuously below their required minimum, while phosphorus concentrations were below levels required by elephants during the months of February to July (Figure 5).

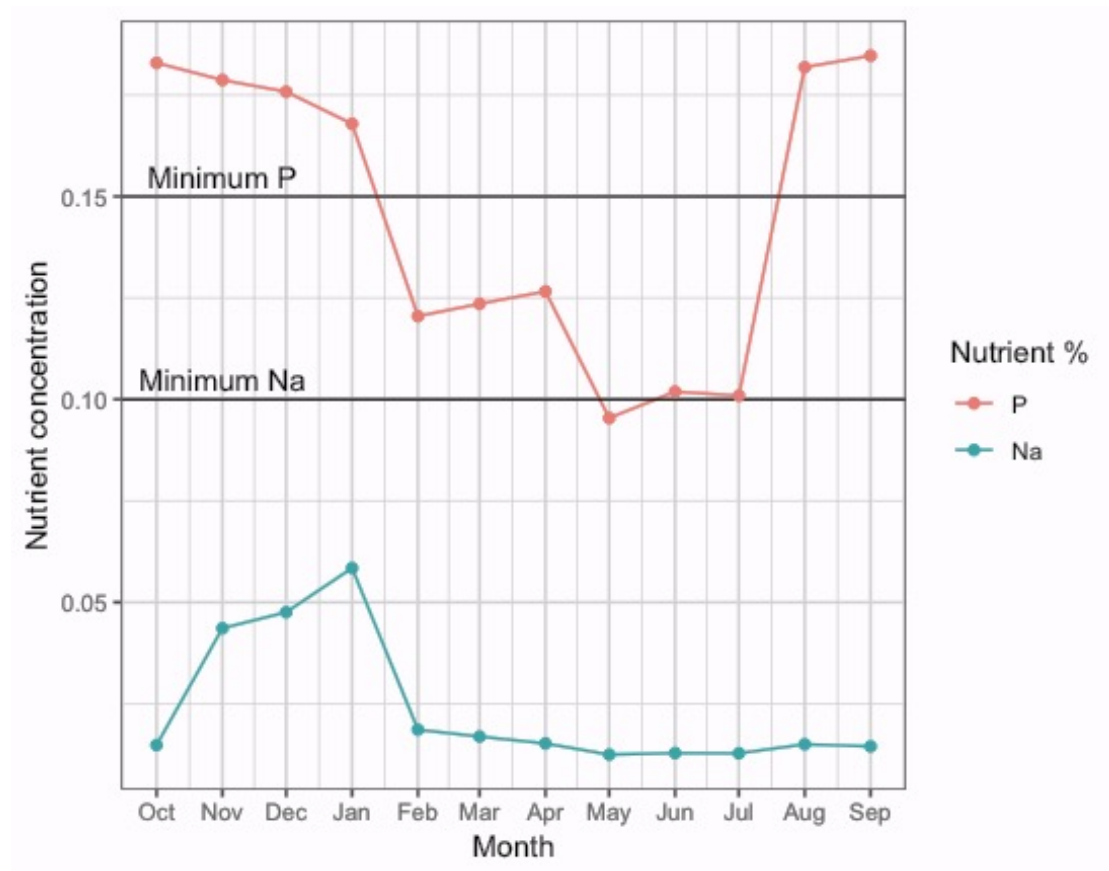


Figure 5. Changes in phosphorus and sodium availability throughout the year as calculated from faecal samples (diet composition) and plant samples (forage quality parameters), and the minimum requirements in elephant diet, revealing dietary deficiencies.

4. Discussion

Our elephant faeces isotopes linear mixing model indicated that browsing dominated elephant diet in the Okavango Delta throughout the year. However, grass intake significantly increased in the Early Wet season, probably peaking in February, although this could be one month later since we have no faecal data for March. In February, browse and grass intake was almost equal, after which grass consumption declined considerably to its lowest levels in June and July. This decline in grass consumption may relate to the increase in fibre and decrease in nutrient concentrations in the Early Dry season (**Chapter 3**). The April peak in crop consumption, as indicated by farmer reports, coincided with the beginning of the harvest season. This peak occurred 1-2 months after the peak in grass consumption, suggesting that crop consumption did not occur during the ‘window of opportunity’ when elephants switch from grazing to browsing. Nevertheless, GLM results demonstrated that crop consumption intensity is significantly associated with changes in the proportion of browsing and grazing in the diet. The proportion of browse versus grass in elephant diet was also positively associated with the nitrogen concentrations (i.e. protein content) of browse and grass, indicating that the quality of natural forage and seasonal changes play a role in determining diet, and that crop consumption may be, in part, a response to declining vegetation quality.

We decided to maintain the analyses of elephant diet with the linear model, rather than the more advanced Bayesian two-source mixing models, due to issues with convergence, a strong correlation between forage sources, and because model outcomes were very sensitive to prior selection. We considered that the linear mixing model that only took the $\delta^{13}\text{C}$ into account, better discriminated between browse and grass sources. Unfortunately this meant it was not possible to estimate the percentage of crop species

in the elephants' diet. However, crops likely play an important role in diet and nutrient intake of individual elephants, but we expect only a small percentage of individuals (<5%) to be involved with crop consumption; thus, linear model results are likely to be reliable proxy for changes in the amount of grazing and browsing. Nevertheless, future extensions of this study with more crop samples may enhance the resolving power of a Bayesian mixing model to differentiate between forage sources.

Phosphorus and sodium deficiencies are wide spread in (sub-) tropical regions (McDonald et al., 2011, McDowell 2003, O'Halloran et al., 2010). Both of these elements play important roles in many bodily functions, e.g. the development and growth of animals, fertility and reproduction (McDonald et al., 2011). In our study area, dietary content calculations revealed that from February to July, elephant diets are deficient in phosphorus, while sodium intake appeared to be below requirements for the entire year. However, the actual nutrient requirements of elephants in the wild have not yet been determined accurately, and neither has the amount of sodium and phosphorus obtained from sources other than plant material by elephants yet been determined. Still, other regions indicate average phosphorus levels that were approximately double of the levels in our elephant diet (Rode et al., 2006). Furthermore, there is sufficient evidence that salt craving (or sodium craving) occurs in elephants and influences their behaviour (Holdø et al., 2002; Rode et al., 2006; Pretorius et al., 2012). Likewise, debarking of trees by elephants is thought to be motivated by the relatively high concentrations of phosphorus in bark (Ihwagi et al., 2011). Elevated levels of phosphorus can also be found in soil licks (Klaus et al., 1998) and in the vegetation on termite mounds (Grant & Scholes, 2006). Phosphorus deficiencies are further intensified if there is an increase in the ratio between calcium and phosphorus, as can occur in the dry season (McNaughton, 1990). The diets of elephants in the study area appeared to be especially high in calcium

and potassium compared to minimum and average requirements for elephants (Pretorius et al., 2012). Consuming crops could be a strategy to reduce a phosphorus deficiency, since crops contain significantly higher levels of phosphorus compared to both grass and browse (Chapter 2).

5. Conclusion

As nutrient deficiencies in phosphorus coincided with the crop consumption season, we consider our results an indication that phosphorus –and potentially sodium- deficiencies, play an important role in elephant dietary choices and could lead to crop consuming behaviour. Therefore, we see scope for using this information to develop mitigation measures by supplying elephants with these nutrient sources (Zhang & Wang, 2003), both to reduce this deficiency and to attract elephants away from agricultural fields and mitigate elephant crop consumption.

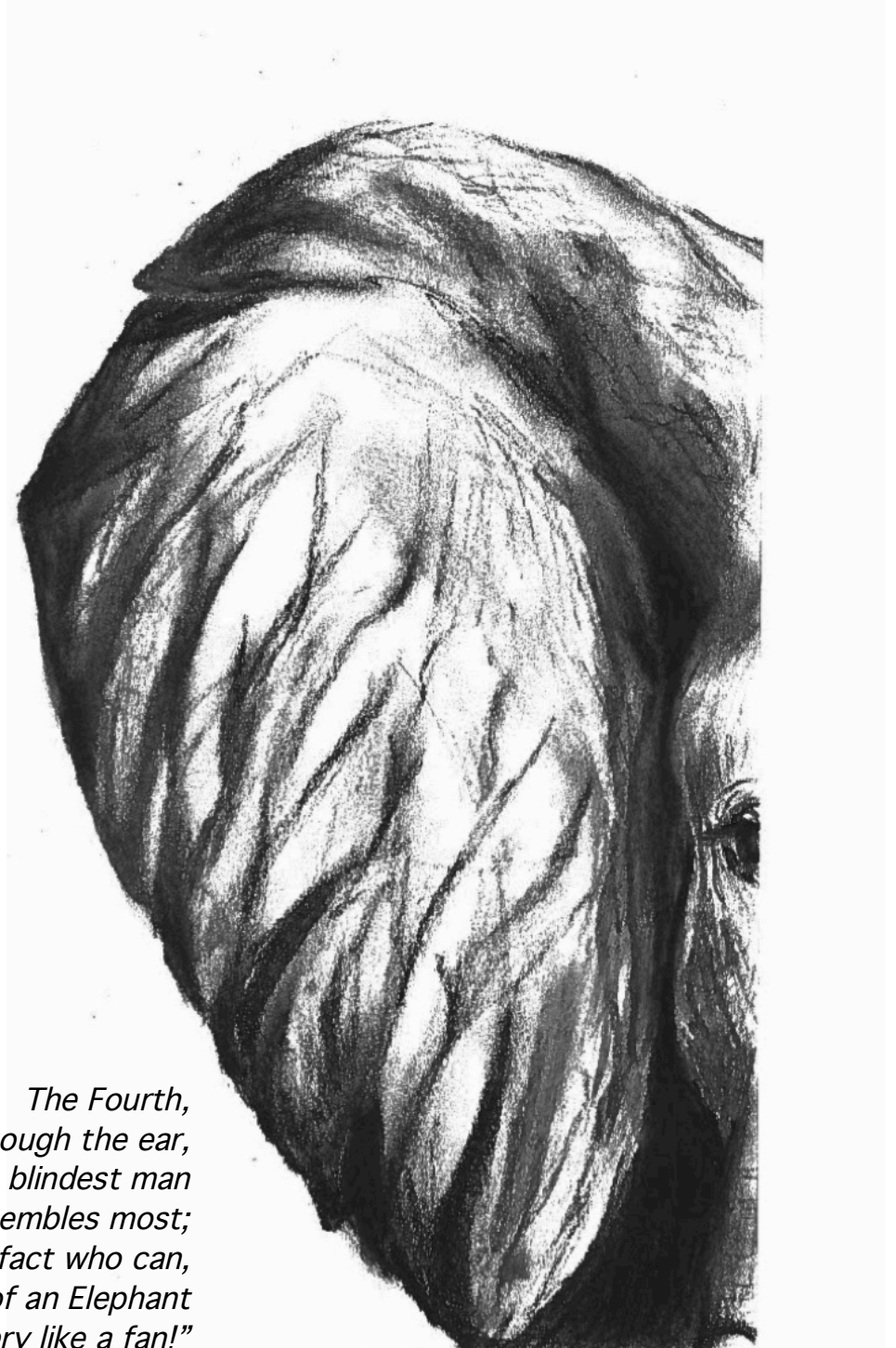
6. Acknowledgements

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5

Mitigation decisions



*The Fourth,
who chanced to touch the ear,
Said: "E'en the blindest man
Can tell what this resembles most;
Deny the fact who can,
This marvel of an Elephant
Is very like a fan!"*

Chapter 5. To mitigate or not? That is the farmer's question.

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Abstract

To improve coexistence between elephants and farmers, governments and non-governmental organisations (NGOs) aim to support farmers in using methods to mitigate elephant crop consumption. However, these interventions are unsustainable or ineffective when farmers are not consulted or there is a lack of awareness of the role of power and social relationships in shaping these interventions. We used Ethnographic Decision Models to understand reasons behind farmers' mitigation measure decisions, and how the government and NGOs enable or impede the empowerment of farmers to mitigate elephant crop consumption. Farmers' decisions on whether or not to adopt a mitigation measure were based on monetary income, belief in effectiveness, belief in danger, manpower, severity of issues with elephants, the weather, knowledge about the method and the availability of material. Governmental departments and NGOs enabled farmers to mitigate elephant crop consumption by providing opportunities for cash income, and providing materials and knowledge. Yet, there was disparity between the materials farmers received and methods they wished to adopt. One-off inputs of materials did not result in a sustainable use of mitigation methods. We see an opportunity for governmental departments or NGOs to stimulate logistics to increase availability of mitigation materials and facilitate community sharing of mitigation ideas, especially regarding elephant conscious farming, as only a few farmers used these techniques.

Key-words

Ethnographic decision model, behavioural control, political ecology, human-elephant co-existence, crop consumption

1. Introduction

The future of wildlife critically depends on the success of their coexistence with humans (Dickman, 2010; St John et al., 2010). Large, wide ranging species, like elephants (*Loxodonta africana* and *Elephas maximus*) in particular, must be able to coexist with humans to thrive outside of protected areas (O'Connell-Rodwell et al., 2000; Hoare & Toit, 2010; Bouché et al., 2011). Coexistence between humans and wildlife implies competition over space and food resources, which can imperil the livelihoods of subsistence farmers, by affecting labour and income, damaging property, and lowering safety and food security. These challenges can ultimately reduce the support people have for wildlife and threaten conservation efforts (Redpath et al. 2015). In the case of elephants, their consumption or damaging of cultivated crops can severely affect farmers' livelihoods (Mackenzie & Ahabyona, 2012) and put elephants at risk of being killed in retaliation (Tchamba, 1996). Elephants are a priority species in conservation and considered vulnerable (*Loxodonta africana*) or even endangered (*Elephas maximus*) according to the IUCN red list (Blanc, 2008). Therefore, non-governmental and government organisations have sought farmer-elephant coexistence, mainly by encouraging farmers to adopt methods to deter elephants from agricultural lands (Parker et al., 2007; Fernando, 2008; Hoare, 2012). By doing so, these organisations aim to change farmers' behaviour and stimulate farmers to participate in actively scaring elephants away, the construction of fences or changing what, where or when they farm (Sitati et al., 2005; Songhurst, McCulloch, et al., 2015).

Policy instruments that aim to protect biodiversity and wildlife by changing people's behaviour are often ineffective or even counterproductive (Malawska et al., 2014). In some cases, conservationists have been criticised for promoting policies that are based on conventional wisdom, prejudices, or assumptions rather than on scientific evidence

(Simsik, 2002; Pullin & Knight, 2005). There is further criticism that conservation organisations often fail to collaborate (Pullin & Knight 2005), and that scientists fail to identify appropriate interventions or communicate with people in local communities and policy makers (Pullin & Knight, 2001, 2005; Cook et al., 2010; Hall & Fleishman, 2010). This is particularly the case with conservation interventions related to ‘human-wildlife conflicts’—a misleading term as the issues referred to are often better described as conflict between humans, either regarding wildlife or for other underlying complex social, power and historical reasons (Madden 2004; Madden & McQuinn 2014; Naughton-Treves & Treves 2005). Elephant crop consumption is a common example of this complex issue (Naughton-Treves & Treves, 2005). There is a large body of literature testing different passive and active measures to deter elephants from agricultural fields (Fernando, 2008; Hoare, 2012), and collaborations between organisations do exist (Parker et al., 2007). Yet, despite decades of innovative research and even lengthier experience with traditional methods and the existence of many promising mitigation measures, farmers do not seem to adopt methods that are deemed successful by researchers and conservationists in northern Botswana (Sitati & Walpole, 2006; Graham & Ochieng, 2008; Noga et al., 2015).

The challenge to adequately support farmers in deterring elephants from fields can be related to conservationist being insufficiently aware of the political factors that surround mitigation interventions. This de-politicisation of conservation can be the result of a failure to acknowledge social and power relationships between conservationists and subjects of conservation efforts (Büscher 2010; Redpath et al. 2015), i.e. in this case farmers experiencing elephant crop consumption. The failure to reduce the negative effects of human-elephant coexistence, has in some cases led governments and NGOs to opt to separate agricultural and elephant roaming areas with expensive and sometimes

‘politically charged’ electric fences (Evans & Adams, 2016). When imposed on farmers, these depositions of boundaries on communal land, together with historical displacements of peoples, contribute to the exclusion of communities that live with elephants from the discourse and decision-making around living with elephants (Sullivan 2006; Evans & Adams 2016). Because of this, living with elephants can not only kindle sentiments of fear and uncertainty for communities, but could also lead to frustration with outsiders (DeMotts & Hoon, 2012). Therefore, in some cases killings of elephants by farmers could not only be considered an expression of retaliation (Ogra, 2008), but potentially also as a form of protest and resistance against governmental or non-governmental conservation organisations appropriating power and land from local communities (Mariki et al., 2015). Similarly, Naughton-Treves & Treves (2005) found that farmers’ reports on issues with wildlife are not only based on actual accounts, but may also reflect their perceived, lower social status compared to the government, conservation authorities and researchers. The question of who ‘owns’ elephants and consequently of whom should bear the responsibilities of the costs of living with them remains central within this discourse (DeMotts & Hoon, 2012). Government and NGOs support can be aimed as a tool to empower small-holder farmers in their livelihood and safety, but if not carefully developed and implemented it can instead become a tool to symbolically reinforce ownership of elephants by those distributing support, thus disempowering farmers (Ogra & Badola, 2008; Ogra, 2008; DeMotts & Hoon, 2012; Evans & Adams, 2016). On the other hand, communities can also deliberately frame ownership of elephants as belonging to the government (e.g. ‘the government’s cattle’) in order to enforce their support in reducing the costs of living with elephants (O’Connell-Rodwell et al., 2000).

An answer to this could be the use of integrated policy assessment tools or agent-based models that take farmer decision making into account (Milner-Gulland et al., 2006; Malawska et al., 2014). By understanding the reasoning behind farmers' decisions, we can understand how social and power relationships either facilitate or inhibit farmers from successfully protecting crops against elephants. Farmers choosing not to adopt a elephant deterrent method that is advised or even provided by governmental departments and NGOs, can in part be the result of inadequate involvement and consultation of farmers or farmers feeling disrespected (Noga et al., 2015, 2017). This study is an effort to understand the decisions farmers make on how to deter elephants from consuming crops. This is part of a larger study by the NGO Ecoexist, which tries to find ways to support human-elephant coexistence in northern Botswana. They aim to reduce issues arising from elephants and humans sharing space, water and food, by studying their root causes and facilitating improvements in cropping and mitigation techniques and assisting in collaborations with governmental organisations (www.ecoexistproject.org). These aims are in line with the movement of 'bridging NGOs' that strive to empower local people by increasing their involvement in nature conservation and taking their voices into account (Shen & Tan, 2012; KimDung et al., 2016; Charleston et al., 2017). In this it is important to acknowledge that the role of neither humans nor elephants can be reduced to that of a victim, as both are actors with needs and wishes, and both have the power and agency to shape their co-existence and conflicts (Barua, 2014b; Evans & Adams, 2018). Therefore in this study we aim not to simplify the social and cultural complexity of small-holder farmers involved in conservation interventions (Evans & Adams, 2016), but rather focus on farmers' agency and their power and knowledge to make decisions about how to deter elephants from fields, and how they are facilitated and limited in this empowerment.

In general, it seems accepted that successful demonstration of the effectiveness of elephant deterrent methods, or the failure to do so, will result in farmers respectively implementing or refusing to implement mitigation measurements (Graham & Ochieng, 2008; Gunaryadi et al., 2017). Although experiencing the effectiveness of methods can increase willingness to invest in a method (Graham & Ochieng, 2008), considering an unwillingness to adopt a new method as solely the result of a lack of demonstrated success is a simplistic view of farmers' decision-making (Dickman, 2010; St John et al., 2010). Successful demonstrations of farm-based elephant deterrents do not guarantee uptake by farmers (Sitati & Walpole, 2006). Instead, the mismatch of intended conservation goals and outcome of conservation interventions can be the result of perceiving farmers' decisions as solely and merely rationally economic decisions (Malawska et al. 2014; Milner-Gulland 2012; St John et al. 2010). The decision not to use an innovative mitigation method can be linked to inadequate involvement and consultation of local farmers in the implementation of interventions, limited resources available and ambiguities in project implementation (Noga et al. 2015; Noga et al. 2017). Farmers base their decisions on many factors, and conservationists must look at these factors underlying performed behaviours (Fishbein & Ajzen 2010; Gladwin, 1983; Gladwin, 1989b).

Therefore, there is a need to review the assumption that farmers' mitigation decisions are grounded on demonstrated effectiveness of the methods. Existing decision-making theory can illuminate the rationale of local farmers and the resources available to them - both in materials and power (Dickman 2010; St John et al. 2010; Sitati & Walpole 2006; Noga et al. 2015; Gunaryadi et al. 2017; Madden & McQuinn 2014; Gladwin 1983). Decision-making tools are valuable when aiming to understand issues farmers have with conservation of wildlife (Davies et al., 2013). Within farmer decision-making

research, hierarchical ethnographic decision models (or EDMs) have proven to be an insightful and effective tool to study the uptake and non-uptake of farming techniques (Gladwin, 1983; Darnhofer et al. 1997; Darnhofer et al. 2005; Ryan & Bernard 2006; Bernard 2006). By using ethnographic data, these models let farmers identify the reasons for their decisions themselves, while the hierarchical element of the models takes into account that in real-life decisions, decision criteria have hierarchical levels of importance (Gladwin, 1983; Ryan & Bernard, 2006). These models go beyond analysing behavioural intentions, and aim to identify the causal relationships between actual behaviour and criteria, allowing us to predict farmer behaviour (Gladwin, 1989a; Ryan & Bernard 2006; Bernard 2006). The result of this method is a hierarchical decision tree, with each node a criterion farmers take into consideration, while different routes on the tree end up with different choice results (Gladwin 1989b). Previous studies have for example revealed factors influencing the adoption of organic farming methods (Fairweather, 1999; Locke, 2006; Bravo-Monroy et al., 2016) or conservation agriculture methods (Bell et al., 2018).

To gain insight into decisions individuals make, we also need to put them in their historical and current political and power contexts (Gupta, 2013). It is particularly important when analysing issues surrounding the co-existence of humans and wildlife, as social factors such as imbalanced power relationships are crucial in defining and transforming these issues (Redpath et al., 2004; Madden & McQuinn, 2014). Therefore, we argue that a political ecology framework is needed (Robbins 2004; Miller et al. 2014). The use of this framework has previously revealed how power struggles between different groups of people over access and use of natural resources are linked to biodiversity degradation (Simsik, 2002), and that women bear a disproportionate amount of the ‘hidden costs’ of living with wildlife, such as psychological impact,

workload and financial burden (Ogra, 2008). We particularly focus on how perceived and actual behavioural control influences farmers' successful uptake of mitigation methods, and how different external actors enhance or restrict farmers in this (Fishbein & Ajzen 2010). Perceived behavioural control is one of the three behaviour predictors in the theory of planned behaviour framework, together with personal attitudes and perceived norms (Fishbein & Ajzen 2010). Personal attitudes represent individual attitudes and beliefs about a potential behaviour, while perceived norms are the beliefs about the norms and expectations of others regarding this behaviour. The decision to do or not do something is based on these attitudes and perceived behavioural control, of which the latter reflects the power attributed to self-efficacy, like skills and material resources, and the freedom to choose to do or not do something (Ajzen & Fishbein 1980; Ajzen 2010; Vallerand et al. 1992). Therefore, we use the tool of ethnographic decision models to create farmers' decision hierarchical decision trees and use a political ecology approach to identify the role and power of different stakeholders in supporting or restricting farmers in the uptake of mitigation methods.

2. Methods

2.1 Case-study: implementation of elephant mitigation methods in northern Botswana

2.1.1 Study site

An ideal study system to use ethnographic decision models to predict the use of elephant deterrent methods is the northern panhandle of the Okavango Delta, in Botswana. This area is known for its high number of elephants and complicated human-elephant dynamics, while most farmers depend on their agricultural crops for subsistence. This makes mitigation methods deterring elephants from agricultural fields a priority in both agricultural and conservation initiatives (Jackson et al., 2008; Noga et al., 2015; Songhurst, Chase, et al., 2015).

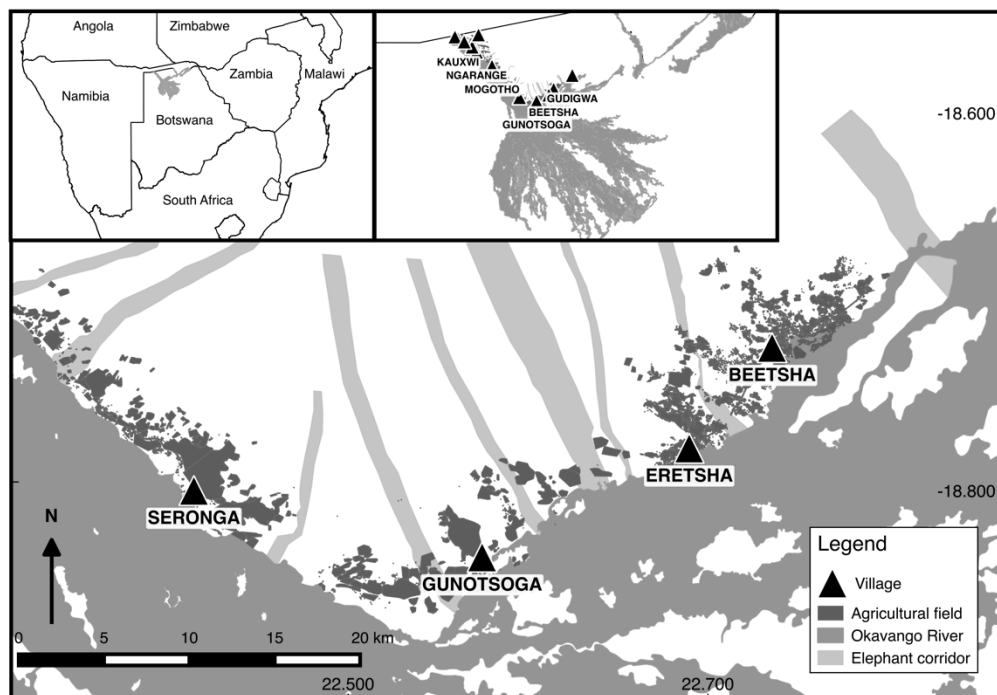


Figure 1. Map of the four villages of the northern panhandle of the Okavango Delta included in this study: Beetsha, Eretsha, Gunotsoga and Seronga

Here, both the Botswana government and non-governmental organisations have a history of involvement with farmers' agricultural methods and have provided them with mitigation interventions, although the cultural appropriateness and effectiveness of some of these measures and policies can be taken into question (Jackson et al., 2008; Cassidy et al., 2011; Shinn, 2016; Noga et al., 2017).

Botswana is home to 37% of the total African elephant population, which makes its elephant population the largest of all nations, with on average 1.28 elephants per km² (Chase et al., 2016). While poaching appears to be increasing, currently less than seven per cent of the elephant population are carcasses, which is relatively low compared to other countries (Chase et al., 2016). Of the elephants in this area, over 80 per cent roam outside of protected areas, where they have a protected status (Thouless et al., 2016).

The northern-panhandle of the Okavango Delta in northern Botswana is an area of just over 8,000 km² where around 18,000 elephants (Songhurst, Chase, et al., 2015) and 16,000 people co-exist (CSO, 2011). The soil in the area mainly consists of nutrient poor Kalahari sands (Dougill & Thomas, 2004), nevertheless most inhabitants of the area are mainly dependent on collecting natural resources such as fishing, livestock and crop production mainly for their subsistence (Cassidy et al., 2011; Motsholapheko et al., 2011). Only a small proportion of farmers sell their harvest for cash income, and short-term labour-intensive public works (*Ipelegeng*) are popular for temporary cash income, especially among young people (Motsholapheko et al., 2011; Gupta, 2013). The Okavango River with its annual flood, together with the annual rainfall periods in the region, play important roles in agriculture. Homesteads and agricultural fields are concentrated around the stretch of the river and floodplains, and most farmers depend on rainfall for irrigation, also called dry land farming, or *molapo* farming, on the edge of the floodplains (Motsholapheko et al., 2011). The river and its floods are also vital in

elephant feeding ecology, movements and social behaviour, and elephants show daily and annually reoccurring movements patterns towards and away from the river (Jackson et al., 2008). During those movements they make use of heavily used elephant corridors that often pass through the same habitat as farmers inhabit and plough (Songhurst et al. 2015).

We focus our study on four of the 14 villages along the Okavango River, Beetsha, Eretsha, Gunotsoga and Seronga, the latter the largest and most central village of the eastern panhandle (Figure 1). The people living in these villages are from four main ethnic groups. The HaMbukushu who are traditionally agro-pastoralists, the BaYei who were fisherman and the BaSarwa who consist of hunter-gatherers (Demotts et al., 2009), and the BaKgalagadi who were mainly hunter-gatherers and sometimes part-time agro-pastoralists (Hitchcock et al., 2011). People from all four ethnic groups inhabit Seronga, while most people living in Beetsha are HaMbukushu, and some are BaKgalagadi or BaSarwa. In between Seronga and Beetsha lie the village of Eretsha with both people from HaMbukushu and BaYei origin, and the village of Gunotsoga with mainly BaYei people (Noga et al., 2017). Poverty, unemployment and illiteracy are prevalent in the area (Noga et al., 2015; Statistics Botswana, 2016b, 2018).

2.1.2 Political context of elephant mitigation methods in Botswana

Tensions between agricultural livelihoods and elephant conservation have been building up on a local and governmental scale, and it is necessary to understand the history of disempowerment of local communities in order to understand current circumstances. While there are signs of San hunter-gatherers already inhabiting the area over 100,000 years ago, the other three of the mentioned ethnic groups immigrated into the area within the last few centuries, mainly motivated by expansions of Kingdoms and

escaping slave traders and colonial and civil wars (Demotts et al., 2009). British colonial and post-colonial rule dismantled the local ruling system and they locally ruled by assigning village leaders Dikgosi (singular: Kgosi) and collective meetings (Kgotle), that sorted issues like the use of natural resources (Demotts et al., 2009). During this time, protected areas were created by colonial rule, and peoples forcefully removed from their land; negatively impacting their livelihoods by restricting the use of land, wildlife resources and other natural resources (Mbaiwa, 2005). Consequently, agriculture and cattle herding became the main strategies to sustain local livelihoods, while tourism and diamond mining became the focus of the national economy (Demotts et al., 2009; DeMotts & Hoon, 2012). This resulted into clashes between the livelihood strategies of communities of livestock herding and agriculture on the one hand and wildlife based tourism on the other (Magole & Magole, 2009). While wildlife tourism is important to post-independent Botswana government (Natural Resources and People, 2007), the government also provides extensive support to local communities with subsidies and training (Ministry of Agriculture Botswana, 2008; Ministry of Agriculture Botswana, 2008; Gupta, 2013). Land Boards appointed by the government are responsible to manage and allocate land to public organisations or to individuals (free of charge) for residential or agricultural purposes (Magole & Magole, 2009). Nevertheless, the appropriation of land in the past and lack of involvement of rural communities in current decision-making continue to cause disagreements about land-ownership and natural resource use (Kgomotso & Swatuk, 2006; Demotts et al., 2009; Magole & Magole, 2009; DeMotts & Hoon, 2012). Recently, the Land Boards in collaboration with local people and the NGO Ecoexist, are including elephant mitigation strategies in their land-use planning by allocating elephant corridors, areas heavily used by elephants when they cross agricultural fields to the river. Besides the placement of road signs, no

future agricultural fields will be allocated in these corridors and farmers of current fields can voluntarily opt to relocate to other areas (Songhurst, McCulloch, et al., 2015).

The Botswana government is a welfare state with national policies aimed to eliminate poverty, and extensive logistics set in place to facilitate promoting poverty relief (Seleka et al., 2007; Magombeyi & Odhiambo, 2017; Seleka & Lekobane, 2017). For over 50 years, the state has provided food support to the very poor or vulnerable, to primary school children, providing full livelihood support for orphans and healthcare to the terminally ill, and financial support to people of old-age and veterans from the World War II (Seleka et al., 2007; Seleka & Lekobane, 2017). Despite a reduction in poverty, reaching the envisioned programme coverage and the inclusion of all vulnerable groups remains challenging (Seleka et al., 2007; Magombeyi & Odhiambo, 2017). Moreover, the provision of food in-kind support could reduce the incentive to invest in agriculture, since the two can directly compete (Seleka & Lekobane, 2017). The government also provides *Ipelegeng*, a source of temporary employment, an opportunity especially seized by youths (Gupta, 2013). With regards to agriculture, the Botswana government started an Accelerated Rainfed Arable Program in 1983, later replaced by the Integrated Support Programme for Arable Agriculture Development (ISPAAD) in 2008. The latter aims to offer subsistence farmers free arable land plots, water sources, seeds, fertilizer, access to credit, diesel, pesticides, and financial support for the farmers' labours costs for ploughing, planting and harrowing, which farmers can also use to borrow subsidized tools from the government (Ministry of Agriculture Botswana, 2008; Ministry of Agriculture Botswana, 2008).

To put the extent of this government support in perspective: over half (55%) of the people in northern Botswana claim to be solely depended on government support for

their income, while over 70 percent of households receive agricultural inputs through government support systems (72.4%) and directly receive food support from the government (71.1%) (Gupta, 2013). Yet, so far ISPAAD has not had the desired effect of alleviating poverty of vulnerable groups nor has it increased food security to its desired extent (UNDP-UNEP, 2013). To support farmers with crop losses to elephants specifically, there is currently a compensation scheme in practise, although it appears challenged by flaws in the reporting, payment, gender-biases, incorrect information and its focus on measurable costs (Jackson et al., 2008; DeMotts & Hoon, 2012; Das et al., 2014). The government also provides subsidies for cluster farming and electric fences to protect fields (Ministry of Agriculture Botswana, 2008). The Department of Wildlife and National Parks (DWNP) furthermore provides advise on which mitigation methods to use (Gupta, 2013), and delivers material assistance and training in the use of innovative mitigation methods (Noga et al., 2017). An example of this is a collaboration between the World Bank and the DWNP in 2009, where the World Bank provided a grant of several million dollars to the DWNP to distribute beehives and chilli fences among farmers (World Bank, 2009), though with limited uptake success, especially in the case of beehives (Ministry of Environment Wildlife and Tourism & Department of Wildlife and National Parks Botswana, 2016; Noga et al., 2017). The project made use of extension workers that distributed the material and training to Village Project Committees (VPCs) who in their turn were responsible to train other farmers (Noga et al., 2017). However, there have been issues with the low levels of uptake, and lack of ownership and commitment of the farmers towards mitigation methods (Noga et al., 2015, 2017; Ministry of Environment Wildlife and Tourism & Department of Wildlife and National Parks Botswana, 2016). Besides, the extension workers struggled to adapt their support to the local context, both practically and culturally, and to provide enough

material and convince farmers of the effectiveness of the methods, resulting in farmers feeling disrespected (Noga et al., 2017). Finally, in their evaluation of the project, the government suggested the need for a full supply chain as materials to construct chilli fences were not easily available in the area (Ministry of Environment Wildlife and Tourism & Department of Wildlife and National Parks Botswana, 2016).

2.2 Data collection

2.2.1 Construction of ethnographic decision models

We conducted interviews and focus group discussions from January-April 2017, in the villages of Beetsha, Eretsha, Gunotsoga and Seronga of the eastern panhandle of the Okavango Delta, Botswana. Because agricultural crops start to grow in January, and mature around April-May when most farmers harvest them (Gerhardt-Weber, 2011; DeMotts & Hoon, 2012), most farmers were attending to their fields during the research period. Therefore, we visited them in their fields or at their homesteads before or after going into the field. At the time we conducted the fieldwork, a prolonged dry season took place.

After receiving approval from the Dikgosi of each of the villages, we held a focus group discussion in each village with ca. six farmers, in which we encouraged a dialogue around mitigation methods, their effectiveness and farmers negative and positive experiences with living with elephants (**Supplementary information D2 and D3**).

Subsequently in each village we held five in-depth open interviews regarding the use of mitigation methods. We purposely selected respondents for the initial interviews from a database of people farming in the study site, including both farmers who had experienced elephant crop consumption and farmers who had not, constructed by the

Ecoexist team between 2008-2016. As this was the most accurate and extensive representation of farmers' distribution available to us, we used this database to select our sample to construct and test our EDMs. We chose a selection approach to make sure that for each mitigation measure we included farmers who did and did not use the method (Gladwin, 1989a).

We aimed to record all methods adopted by farmers in the area, and all potential reasons they adopted or did not adopt the methods. Therefore, we did not pre-emptively decide which mitigation methods we would include in the study, yet probed to make sure farmers included all passive, active, innovative and elephant conscious farming methods they applied. During the individual interviews we started by asking which methods the farmer used, followed by how these methods worked and why they used them, after which we systematically went through all the other mitigation measures mentioned by other farmers to check whether the farmer indeed did not employ them, and asked the reason for this non-adoption. Of each of the mentioned mitigation methods, we created pictogram cards that described the method, if possible representing its local use, e.g. a chilli fence constructed with cloths and a sign of chillies. For the remainder of the interviews and discussions we used the pictograms to describe mitigation methods to farmers, to avoid misunderstandings due to different levels of illiteracy, in particular in the focus group discussions. Beforehand, a research assistant from Eretsha was trained in interview techniques such as probing and biases, and interviews and focus group discussion questions were translated and piloted in Setswana. Interviews were held in English when appropriate, or translated from Setswana, Mbukushu or Siyei depending on the culture and language of the respondent. Questions asked during the interviews and focus group discussion can be found in **Supplementary information D2**.

After we conducted the initial interviews, for each of the types of mitigation measure we ordered all reasons to adopt or not adopt the method given by the respondents. There are three types of criteria that occur within EDMs, i.e. elimination criteria, motivation criteria and constraints. We used these reasons to create dichotomous questions that formed each of the nodes in the decision model. When appropriate, we grouped similar reasons while retaining the language of the original answers, for example ‘borrow from family member’ when different family members were mentioned by different respondents (Gladwin, 1989a). We then sorted the hierarchical order of importance of these reasons, since some conditions were mentioned by most farmers, while others by only a subset of them. If backtracking a respondent’s answers on the decision tree made the respondent ended up with a different decision than they actually made, or ended up with the correct choice, yet reached this point in the decision tree without including all of their conditions given, this was considered an ‘error’ (Gladwin, 1989a). We continued examining the position of the adoption conditions until in at least 85% of the cases we correctly predicted the mitigation choice of our respondents along their route of reasoning. We piloted each of the draft decision trees in English and Setswana, to make sure the order of questions was logical and correct.

2.2.2 Testing ethnographic decision models

In total we tested 16 decision models, each on 81 farmers of which 64.9% were female. From the database of farmers, we selected a stratified random sample for each of the villages, initially a sample of 20 farmers per village (Bernard 2006). In each of the four villages, the NGO Ecoexist employs a community member to assist and train farmers and report the issues farmers face with elephants back to Ecoexist. Since these staff members knew most of the farmers in their village, we collaborated together with them

and the Kgosi of each of the villages to verify the location of our respondents. As our aim was to interview ca. 20 respondents for each of the villages, depending on the number of non-responses per village, we randomly selected another ca. 10 farmers from the database per village. In total our non-response was 52 out of 133 farmers, of which seven were deceased, 15 moved to a different village/town, eight were not present upon three consecutive visits, and we were not able to locate three respondents. We excluded 14 of the selected respondents because they had not recently ploughed (either that year or the previous year), and five respondents because a family member with whom they shared their field/mitigation methods was already interviewed, or they themselves were already interviewed during the construction of the decision models. For two of the decision trees regarding elephant conscious farming we had two or three extra non-responses as we were still developing these EDMs in the first few interviews, so they were used for the construction not the testing of the models.

During the test-phase of the EDM, we did not ask or visually check which mitigation measure the respondent deployed until the end of the interview, to avoid the ability of bias in our questions. After we followed the constructed EDM, we would verify if the result we expected correctly predicted the mitigation decisions of the farmer. We successfully predicted the decision when the decision tree questions showed the mitigation measure that the farmer confirmed they applied in their field. If after following the tree the respondent arrived at an “incorrect” mitigation method, this is considered to be an error. For clarity, we also marked the point at which a question resulted in the respondent starting to follow an incorrect path along the decision tree with an error. Therefore, the sum of errors at a final point of the tree can be traced back to the previous nodes where errors started to occur in the answers. After conducting all

the interviews, we calculated success rates of our predictions in percentages, and by making use of Klecka's tau. This is a measure predicting power of our model compared to a prediction of mitigation measure merely by chance (Ryan & Bernard, 2006).

Ethnographic decision models are considered to accurately represent farmers' decisions criteria if the models correctly predict decisions for at least 85% of the farmers (Gladwin, 1989a).

We divide the mitigation methods farmers mentioned into four classes: passive methods (e.g. fences), actively scarring elephants away (e.g. sound), innovative methods (e.g. chilli pepper and beehives), and the adaptation of agricultural decisions farmers make in order to reduce the likelihood of elephants entering the fields (Parker et al., 2007; Hockings & Humle, 2009). There is an increasing interest in methods that address the issue of crop consumption more sustainably, by adapting land-use planning and make agricultural choices that are more 'elephant sensitive' (Parker et al., 2007; Gunaryadi et al., 2017), which we group under 'elephant conscious farming' (Hockings & Humle, 2009). Examples of these are buffer regions around fields or dry vegetation (Sitati et al., 2005), cleared vegetation (Osborn & Parker 2002), the use of alternative or buffer-crops (Gross et al., 2016, 2017). The timing of planting could also play a role in elephant crop consumption in this area (Jackson et al., 2008), and ploughing early could avoid this by subsequently harvesting before the elephants arrive. Finally, choosing crop types that are less attractive to elephants to consume could reduce crop raid risk (Gross et al., 2016). Beyond individual farmer's decisions, this also includes larger scale land use planning, such as to set aside specific regions or corridors for elephants to roam (Jachowski et al., 2013; Songhurst, McCulloch, et al., 2015; Adams et al., 2016). Active guarding is reported to be more effective to deter elephant from fields than merely passive methods (Sitati & Walpole, 2006). Most farmers employ different mitigation

methods simultaneously, combining both passive and active measures (Hoare, 2012).

While accessing electric fencing currently requires clustering of fields and sharing fences in order to obtain government support, the other decision models we create are for individual decisions regarding use of mitigation methods.

3. Results

3.1 Mitigation measure uptake criteria

In the initial interviews and focus group discussions, farmers informed us on 16 different passive, active, innovative and elephant conscious farming elephant crop consumption mitigation measures they applied. Passive methods included traditional fencing in the form of wire fences and bush fences, the application of tin cans and plastic on these fences, or the use of electric fences and trenches. Active methods included using a torch, shouting, drumming or clapping and the use of fire, dogs and a watch hut to guard at night. Innovative measures included beehive fences, chilli pepper fences and chilli pepper burning, while elephant conscious farming included adapting the location of the field, the type of crop or composition of crops in the field, and ploughing early. The decision criteria that farmers used to explain their (non-) adoption of mitigation measures can be divided into elimination, motivation and constraint criteria. The difference between the three types of criteria depends on the hierarchical order of the elements in the decision tree. For example, if lack of availability of (elements of) a method quickly eliminates the farmer from the tree during the first stage of the tree, it is categorized as elimination criterion. Instead, if the provision of the material itself is the reason for applying a method, it is considered a motivation criterion. Finally, a criterion becomes a constraint if only in the final stages of the tree farmers mention this criterion as a reason to not adopt the method. These differences may sound trivial, but when constructing an EDM this is crucial, since interchanging an elimination criterion and a constraint could mean overlooking the ‘real’ reason a farmer does or does not use a method.

Table 1. Elimination, motivation and constraint criteria of farmers' decisions to use or not use certain mitigation methods.

Criteria	Elimination	Motivation	Constraint
Monetary income	Bush fence	Wire fence, torch, chilli fence	Tin cans (wire/string)
Belief in effectiveness	Dog, beehive, plastic	Watch hut, crop type and crop composition, location	
Belief in danger	Shouting, drumming and clapping, fire, torch		Crop type (crop raid risk early maturing crop species)
Manpower	Trenches, bush fence		
Severity of issues with elephants			Chilli fence and chilli burning, tin cans
Knowledge on method	Trenches, beehives, electric fences, chilli fence and burning		

Table 1. Continued

Criteria	Elimination	Motivation	Constraint
Availability of material	Early ploughing (ox and mould), dog	Beehive, chilli fence, chilli burning, electric fence, tin cans	Tin cans, torch (torch and batteries), chilli fence and burning (chilli), crop type (not planted crops not for sale)
Weather	Early ploughing		

3.1.1 Passive mitigation methods

Although traditional fences in the form of bush and wire fences were widely applied in the study area, these were generally not considered to be effective at deterring elephants from entering fields. Bush fences are constructed by cutting down spiny bushes and trees such as *Acacia* spp., transporting these to the field with manpower or the help of donkeys or cattle, and stacking these around the field. Wire fences consist of one or multiple wires stretched around the field, supported by poles or cut tree trunks. Bush fences were mainly constructed to keep smaller animals like goats and porcupines out of the fields, while wire fences were targeted at cattle and elephants. Therefore, bush fences were usually only employed if small animals were considered a pest and the wire fence as insufficient to deal with this. Therefore, the need to prevent small

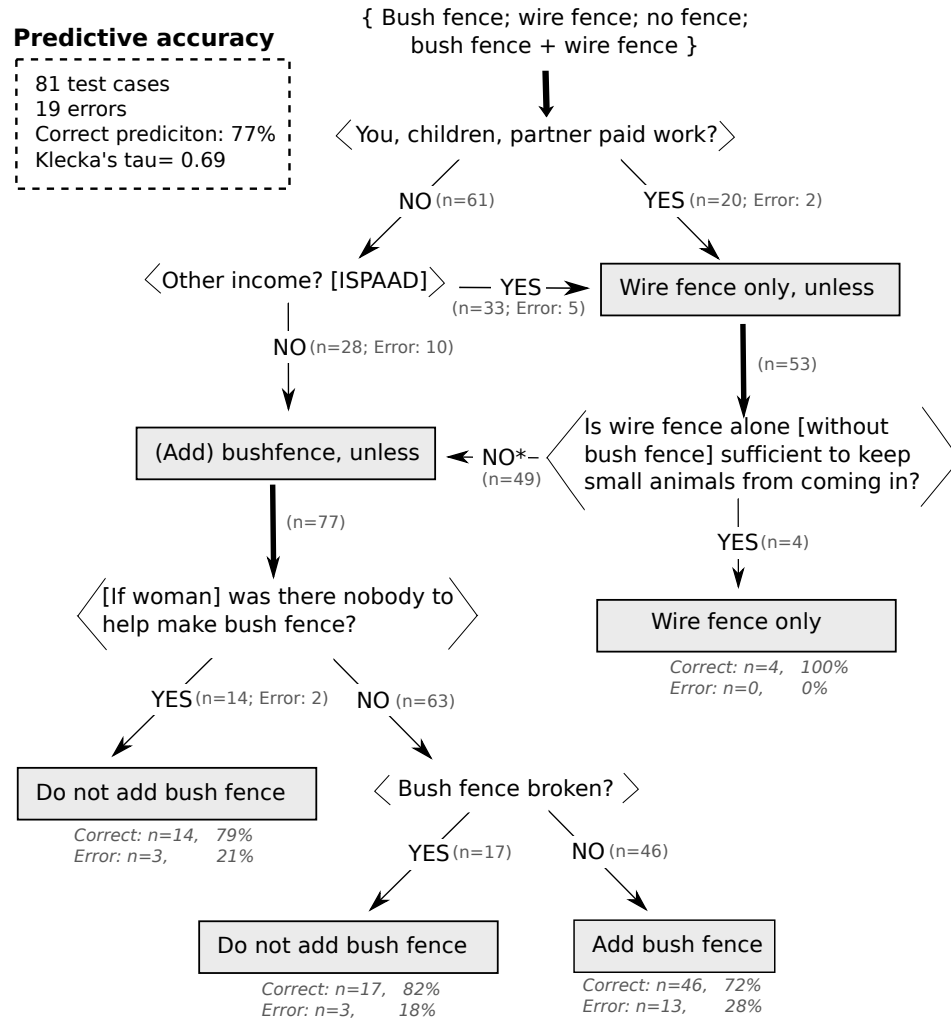
mammals from entering the field is a motivation criterion for bush fences. Income was simultaneously an elimination criterion for bush fences, and a motivation criterion for wire fencing. Regarding bush fences, farmers face the constraints of lack of manpower and fence breakage by elephants.

During the construction phase of the EDMs, several farmers mentioned that they received tin cans from the NGO Ecoexist, while during the test phase this was mentioned by none of the farmers, and all alternative sources were collection from dustbins. Some farmers mentioned that they could not gather tin cans from dustbins as this was considered socially undesirable behaviour. Because collecting tin cans requires effort, the construction phase and test phase of this model show us that farmers apply tin cans only when they consider elephant crop consumption to be a severe issue. We did check with those farmers, who did not have alternative tin can sources if they considered elephant crop consumption not to be an issue, but this was only in two of the 40 cases and therefore we consider the decision tree correct as it is. One farmer in the test phase did not use tin cans but mentioned that instead he uses metal sheets tied to his fences to scare elephants off.

The elimination criterion for electric fences was whether or not a farmer had heard about the use of electric fences, while the motivation criterion was whether the farmer received material. When farmers considered the application of plastic as efficient against elephants, they applied plastic as a mitigation method (20 farmers). If they considered it inefficient against elephants they would still apply plastic when they considered it useful to deter birds (32 farmers).

Of the respondents, only two farmers previously tried to use trenches. Both of them could not continue the maintenance of the trenches due to lack of manpower. One

farmer mentioned that he tried it in 2015 “but it [the trench] was too shallow and elephants jumped [over] it. Someone was digging for water pipes and an elephant got killed by falling [in] the ditch, so they should dig deeper.”



* Wire fence is expected to be present, the rest of the EDM is to determine whether bush fence is also present.

Figure 2. EDM on the use of traditional fences.

3.1.2 Active mitigation measures

The lack of financial ability to buy a torch appeared the main elimination criterion for the use of torches, while farmers would use the torch if they did not consider it aggravating elephants. Yet, most farmers were unable to use torches because they were constrained by a broken torch or run-down batteries.

Most farmers eliminated the use dogs due to its ineffectiveness “elephants are big, and dogs are small”, or danger “it can kill you, it [the dog] is the elephant’s natural enemy.” Most respondents agreed that it was dangerous to use dogs to scare elephants from their fields, yet this did not stop farmers from using their dogs to protect their crops from elephants if they thought there was a (small) probability that elephants would be scared of the dog.

The adoption or non-adoption of fire, drumming and clapping and shouting appeared solely related to whether the farmer considered it dangerous to use the method, by attracting elephants and making them aggressive. One farmer explained why drumming makes elephants aggressive by stating “Makgowa [white people/foreigners] gave sweets and bread to the elephants after beating a bell, now they come after drumming”.

Finally, almost all farmers used a watch hut because they slept in their field at night to guard their fields when the crops are maturing.

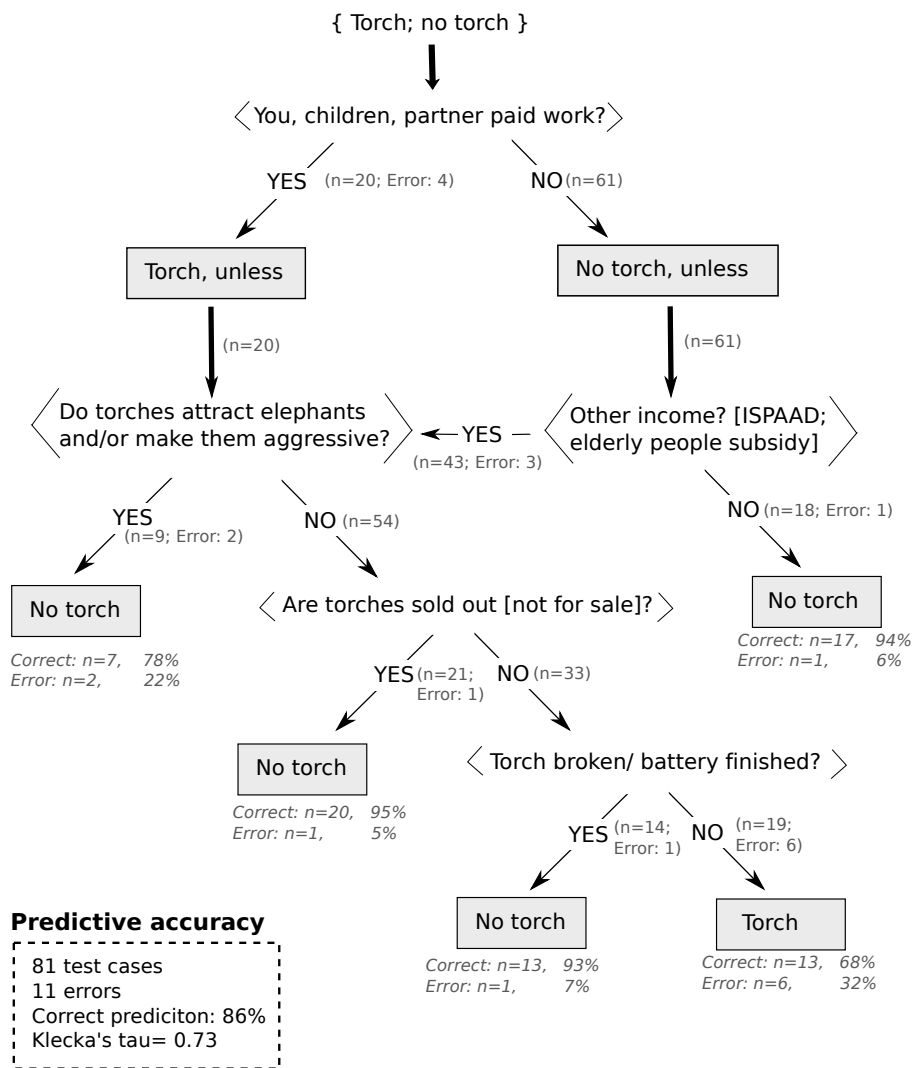


Figure 3. EDM on the use of torches.

3.1.3 Innovative mitigation measures

The provision of information and the continuous supply of material appeared crucial in the decision to use or not use chilli fences and chilli burning. Lack of chilli supplies and fences broken by elephants were important reasons not to use these methods. If the supply of chillies would not have been an issue, 15 farmers would have a chilli fence and burn chillies and 32 would burn chillies. Additionally, if elephants had not broken their fences, 19 of these latter farmers would additionally have a chilli fence. Four farmers did buy material to construct chilli fences themselves, and one created a chilli fence with traditional poles and wire made from tree materials. Only one farmer tried planting his own chilli plants, although he complained about the difficulty of watering the plants. No farmers merely used chilli fences without also burning chilli. Both methods required input of energy, but chilli fences also required input of extra materials such as poles, wire, oil and cloths. By ‘using chilli fence’ we made sure that farmers only said yes if they recently applied new chilli grease on the cloths, and old non-maintained fences were not included.

When constructing the EDM on the use of beehives, one farmer did use beehives, yet for commercial purposes and not to deter elephants. These beehives were donated by the tourism and airline company Wilderness safaris. This farmer previously also used the beehives given by the World Bank to create a beehive fence, and he planted papaya trees to attract bees to his field. However, elephants were also attracted to his field and they tore down the beehive fences and papaya trees. During the test phase, two farmers used bees for commercial purposes from the same source. One farmer was given all material from the World Bank to construct the beehive fence, but she did not construct the fence as she did not receive wire or beekeeper suits. Most farmers responded jokingly about beehive fences, distrusting the effectiveness “A bee can not work at

night, elephants are active at night, so the bee can not spot it”, “the leather [of elephants] is too hard to be stinged”, “It would be funny if an elephant would run from a small bee”, “bees are seasonal” and “I am scared of bees, they can not scare elephants because they are too big”. Or they did not consider themselves capable of using it: “Who can find bees?”, “Nobody explained this too me, I do not have the skills, how would I catch bees?”, “I have to see it [that it works] with my eyes first”. Some farmers mentioned that they went for a lesson on the use of beehives or that “the government came to bring it [material], and they proved it can work”, or that it would work because the trunk of the elephant is sensitive. However, people kept referring to the previously mentioned farmer that did apply the beehive fence by name and stated that “others used it and it did not work”, or that “on this side it does not work”, one respondent explained this lack of effectiveness was because there was not enough water for bees.

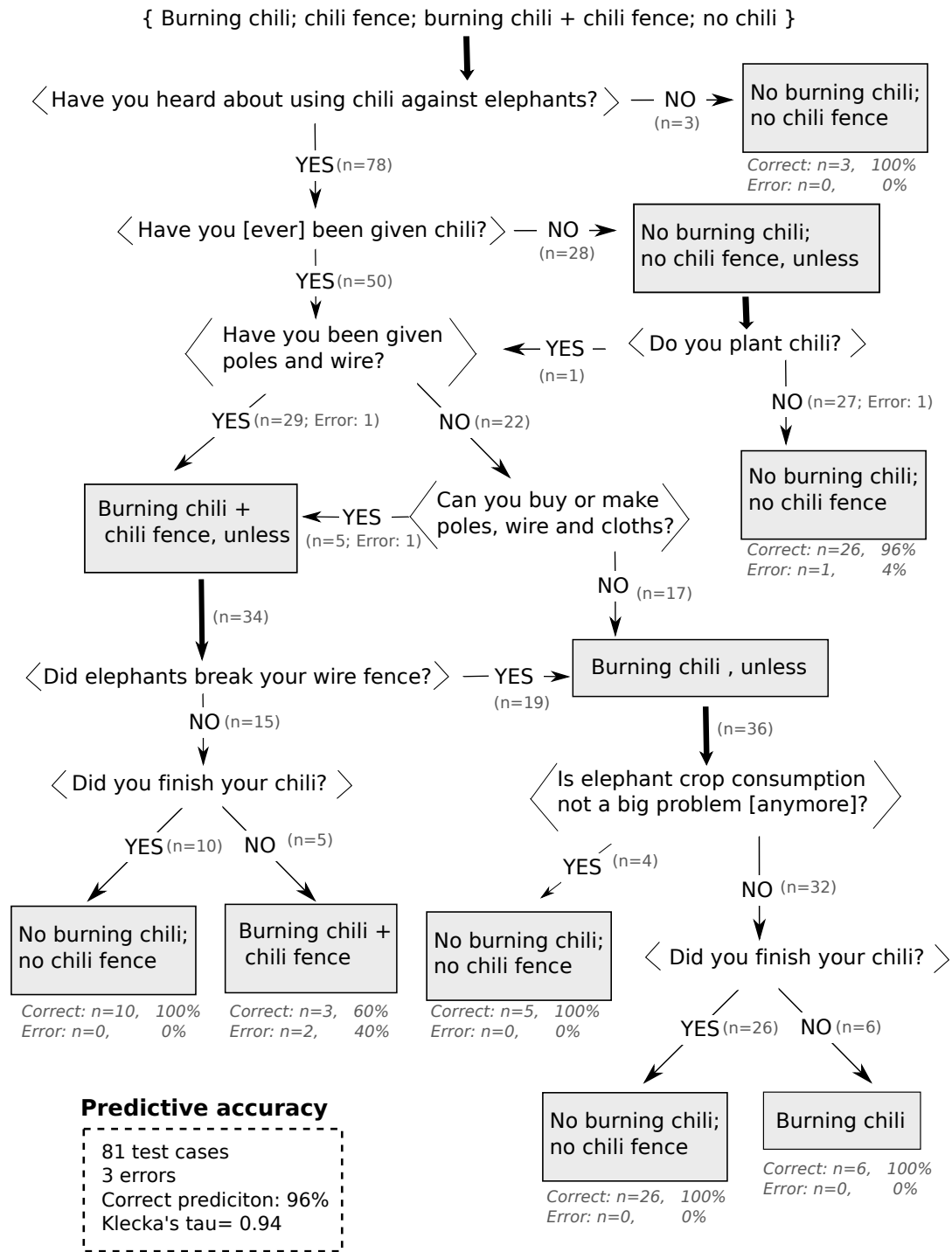


Figure 4. EDM on the use of chilli fences and burning chilli.

3.1.4 Elephant conscious farming

Most farmers that adapted the composition of their crops to mitigate crop losses to elephants, planted crops that elephants did not like near the edges of the fields, and those that elephants preferred in the middle. One farmer mentioned “I plant millet near the fence, and sorghum and watermelon in the middle of the field, so I wake up in time”, while another preferred to plant millet in the middle and watermelon near the watch hut to keep an eye on it. One of the farmers who adapted his crop type to reduce elephant impact, mentioned that he avoided planting the ‘short millet’ that farmers received for free from the government, because “elephants like that type of millet the most”.

Many farmers mentioned that their father or husband picked the location of the field, which made them unable to adapt the location. In order for farmers to adapt the location of their field, they had to be convinced that elephants use some areas more than others, and that the plots in those areas highly utilized by elephants (‘elephant corridors’) did not have better soil and vegetation conditions than those outside of them.

In general, if possible farmers would plough early. Therefore, all criteria of this EDM were based on whether or not the farmer had access to equipment early enough, and whether the rains arrived early enough.

Supplementary information D.4 contains the EDMs not displayed in this chapter.

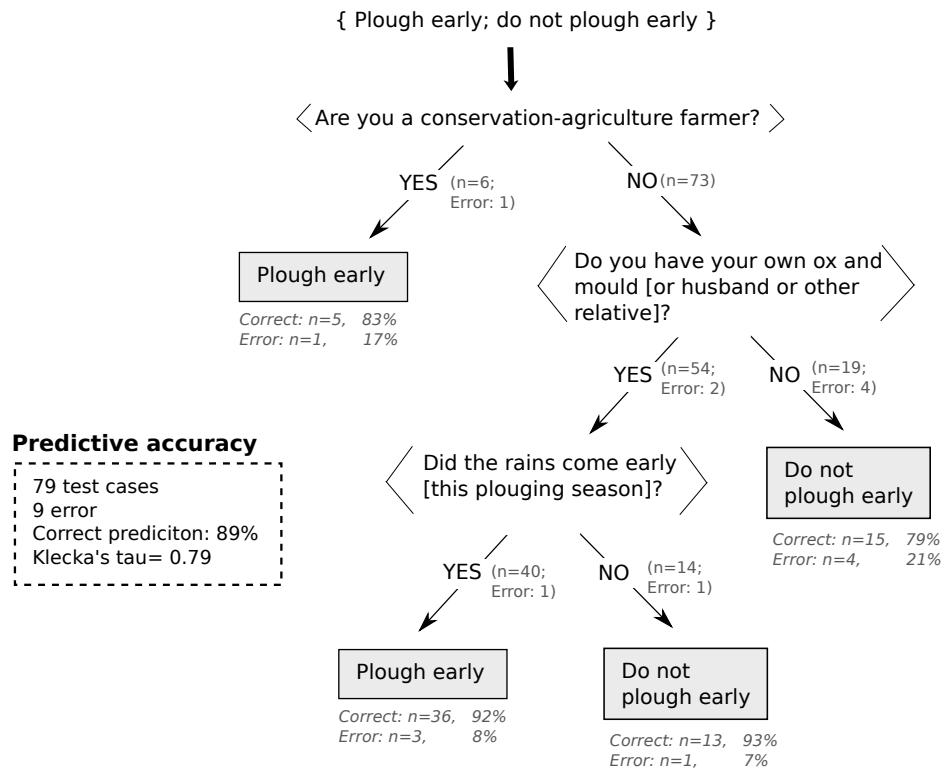
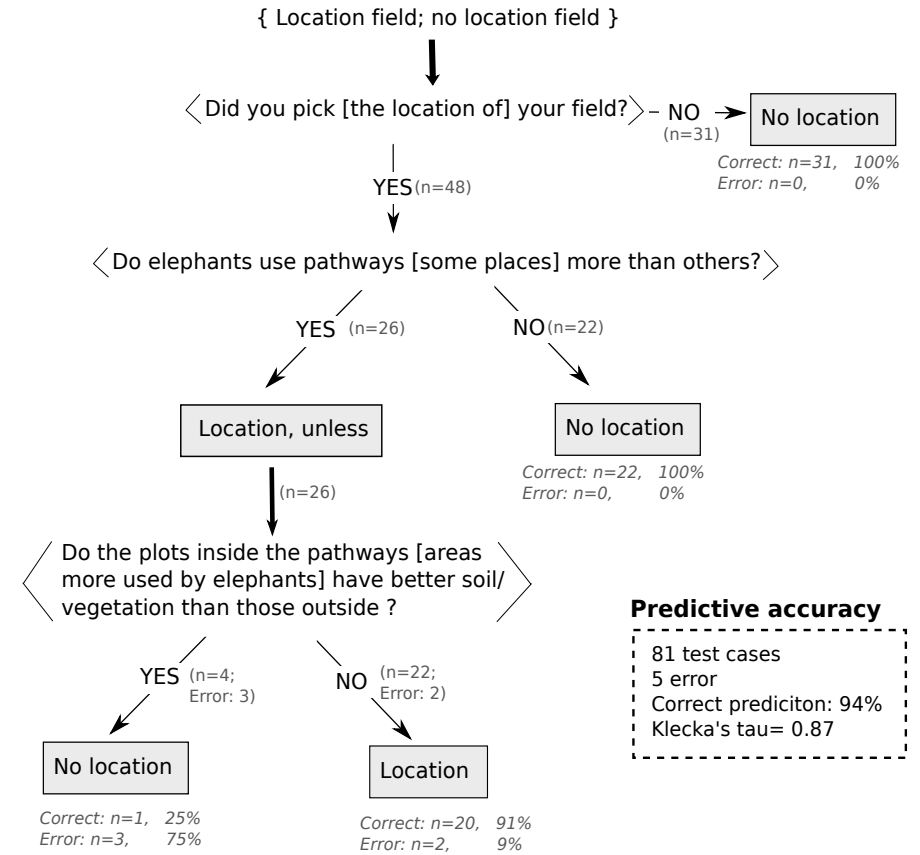
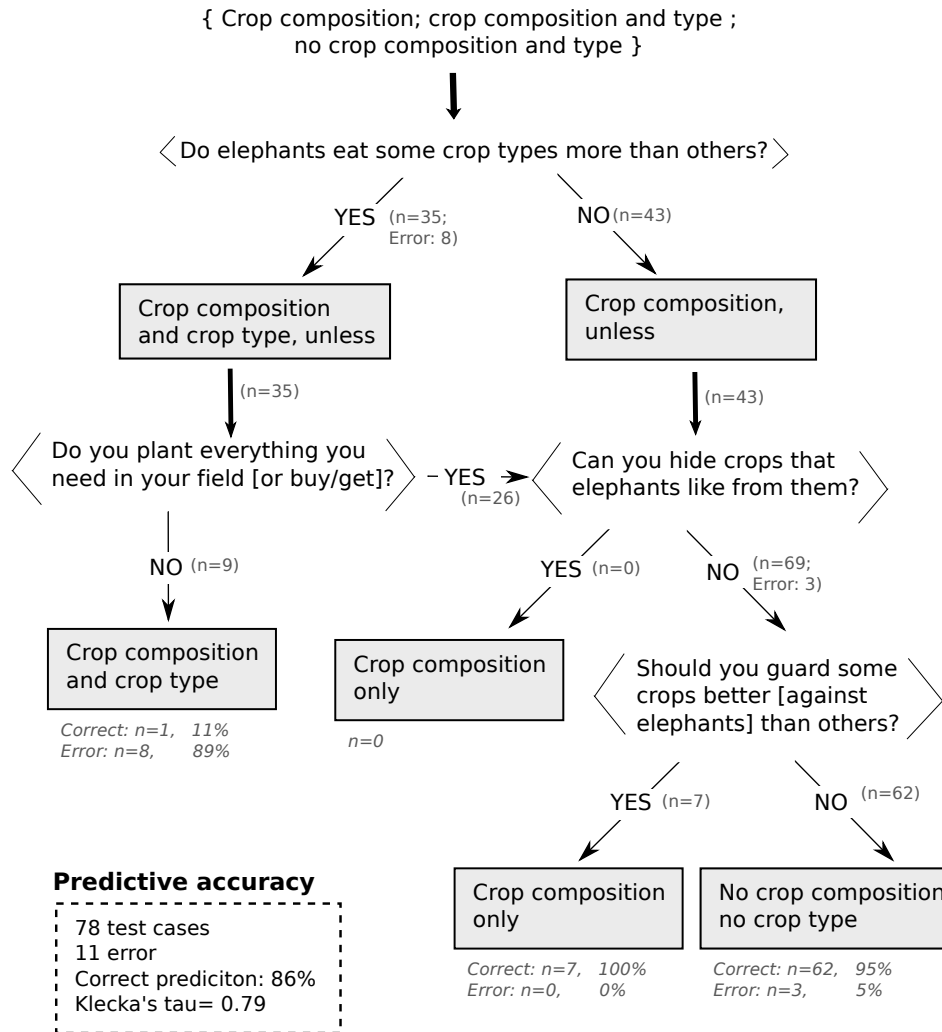


Figure 5. EDM adapting timing of ploughing.



3.2 Ethnographic decision model efficiency

3.2.1 *Passive mitigation methods*

Of our 16 decisions only two models failed to accurately predict farmers' decision criteria for at least 85% of the farmers, i.e. the models predicting the use of traditional fencing (77%) and of plastic (84%; Table 2). Most of the errors of the EDM on traditional fencing techniques occurred when we asked about 'other sources of income' such as ISPAAD. Of these errors, five respondents complained they did not receive sufficient funding from ISPAAD to construct a wire fence, while one farmer did not receive support from her working children. Vice versa, eight farmers had other sources of income that they did not consider fell under the criteria 'other source of income', e.g. previous governmental support through "applying with a form a long time ago". One respondent mentioned he received this support in 1996 as compensation for elephant damage. Two respondents inherited a wire fence from their father or husband who were killed by an elephant. One respondent used leftover material he received for a chilli fence from the World Bank project to create a wire fence.

Three errors occurred because farmers were not able to make a bush fence or did not want or need one, and two elderly female farmers managed to construct the bush fence on their own. Regarding the low predictability of the EDM on plastic use, six farmers had never heard about using plastic to deter animals, while other farmers "tried it anyway" even though they were not convinced by its usefulness. As collecting and hanging plastics requires energy, some farmers mentioned that the problems with elephants and birds was either not "a big issue" or that they were "too lazy to do it". Our EDM for tin cans had a high prediction accuracy, with only one error occurring. This farmer claimed the DWNP told him off for collecting tin cans "They said that I was

littering the environment, so I stopped collecting [tin cans]”. The EDMs on trenches and electric fences were 100% accurate, which together with the small number of farmers who adopted these strategies serves as a warning signal that we did not manage to explore all reasons to adopt or not adopt electric fences (Gladwin 1989a). While in our original sample several farmers had tried to make trenches, most farmers in the test face had not heard about the use of trenches, and none of the farmers interviewed for the test stage had enough manpower to construct trenches.

3.2.2 Active mitigation methods

The model on the use of torches scored relatively low on Klecka’s tau values, which indicates that the model criteria only predict the use of torches 73% better than would be expected by chance. Seven errors occurred because five respondents mentioned that money they earned or received was not enough to buy a torch, and two people borrowed torches from others. One error was due to a respondent not considering it necessary to use a torch, and three because although the farmers considered torches attracting and aggravating elephants, they wanted to see where the elephant came from or show to the elephant that humans were there. The predictability of the use of dogs, fire, drumming and clapping of our models was very high (93-98%). Errors occurred out of desperation, like in the case of shouting: “We try by all means, but they get aggressive each time” or because of habit “because of natural instinct, no other reason”. The model on the use of a watch hut performed with an accuracy of 95%. Of the errors, one farmer did not want to use a watch hut as his homestead was close by and he was too scared of elephants to sleep in the field. Others either had nobody to help them make a watch hut, or fire or elephants had destroyed their watch hut.

3.2.3 Innovative mitigation methods

Although the most complex of all mitigation EDMs, we were able to correctly predict the use of chilli fences and burning in 96% of the cases. Errors mainly occurred due to the lack of other materials such as cloths to make chilli fences. The constructed EDMs for the adoption of beehive fences cannot be considered accurate, as in both the construction and the test phase there were no farmers currently using beehives.

3.2.4 Elephant conscious farming

Although we managed to accurately predict whether or not farmers adapted the type of crops they used and the composition they planted their crops in, the Klecka's tau of this model was relatively low. Most errors occurred because we predicted farmers adapt their crop type and crop composition, while they had not considered doing this. Of the other errors, one farmer mentioned she places the watermelons in the middle not because of the elephants, but just because she likes them planted in the middle. Another farmer did adapt the crop composition because of elephants, but not in order to hide or protect the crop. She planted millet along the fence and sorghum in the middle of the field to make it easier to see the elephants come through the millet. Finally, one farmer planted watermelon and other crops she thought elephants prefer along her fence where she would expect elephants to enter in order to make them stay there, since "hiding does not work". When testing the EDM on adapting field location we predicted 94% of the cases correctly. Errors occurred when farmers adapted their location to elephants even though the quality of the soil was better in corridors, since the soil was still of acceptable quality where they picked it outside of the corridors, or as one farmer put it "Who would put its field in the middle of the pathways? The elephants like to experience the good vegetation there!". One farmer reported to not care about elephants,

as she just wanted to be near the water. When predicting the reasons for ploughing early, the EDM had a high predictive accuracy of 89%, but the Klecka's tau was relatively low. Most errors occurred because of the lack of manpower, or because farmers were able to borrow an ox from distant family members or plough by hand. Only one farmer reported to not believe in early ploughing as a means to reduce the likelihood to be raided by elephants "If you start early, it [elephants] will come early".

Table 2. Percentages of farmers that adopt or not adopt, for each of the mitigation measures, and the accuracy scores for the Ethnographic Decision Models predicting this (non-) adoption.

Method		Uptake	Non-uptake	Predictability (%)
		(%)	(%)	(Klecka's tau)
Traditional fence	<i>Wire fence</i>	37 (n=30)	4 (n=3)	77 (0.69)
	<i>Bush fence</i>	27 (n=22)		
	<i>Both</i>	32 (n=26)		
Tin cans		22 (n=18)	78 (n=63)	99 (0.98)
Electric fence		6 (n=5)	94 (n=76)	100 (1)
Plastic		55 (n=45)	45 (n=36)	84 (0.68)
Trenches		0	100 (n=81)	100 (1)
Torch		23 (n=19)	77 (n=62)	86 (0.73)
Dog		35 (n=28)	65 (n=53)	94 (0.88)
Fire		85 (n=69)	15 (n=12)	93 (0.85)
Drumming/capping		93 (n=75)	7 (n=6)	98 (0.95)

Shouting		85 (n=69)	15 (n=12)	93 (0.85)
Watch hut		93 (n=75)	7 (n=6)	95 (0.90)
Chilli	<i>Burning</i>	10 (n=8)	90 (n=70)	96 (0.94)
pepper	<i>Burning</i>	4 (n=3)		
	<i>and fence</i>			
Beehive fence		0	100 (81)	86 (0.98)
Adapt location		25 (n=20)	75 (n=59)	94 (0.87)
Crop	<i>Type</i>	1 (n=1)	87 (n=68)	86 (0.79)
	<i>Composition</i>	10 (n=8)		
	<i>Both</i>	1 (n=1)		
Early ploughing		58 (n=46)	42 (n=33)	89 (0.79)

4. Discussion

Our study was able to both describe farmers' mitigation decisions and successfully predict 14 of 16 of the measures we analysed with our Ethnographic Decision Models. Including this second testing phase is a strength of our study, as it is often omitted or minimalized (Fairweather, 1999; Roth & Botha, 2009; Miller et al., 2014; Bravo-Monroy et al., 2016), making it impossible to validate the predictive power of their constructed decision trees (Gladwin 1989a).

Farmers' decisions on whether or not to adopt a mitigation measure were based on monetary income, belief in effectiveness, belief in danger, manpower, severity of issues with elephants, the weather, knowledge about the method and the availability of material. Farmers appeared to adapt their mitigation efforts to patterns of severity of elephant crop consumption (Songhurst & Coulson, 2014), as the choice for methods depended on the severity of crop consumption issues farmers personally experienced. Monetary income was an important motivator for farmers to use or not use wire fence, torches or chilli fences, while many farmers did not use a bush fence if they had enough money for a wired one. The lack of money sometimes meant that farmers were not able to purchase string or wire to hang tin cans on wire fences. Belief in effectiveness appeared not a motivational criteria for any of the mitigation methods, yet it was an elimination criteria, as for some measures farmers would not choose to adopt if they were convinced a method was completely ineffective. This is reflected in the elimination question "Does X never work against elephants?". Farmers that responded with "yes" were highly likely to not adopt method X. However, almost all farmers believed it was effective to guard the field at night, which was the main motivator to have a watch hut. Traditional farm based methods such as making noise or using fire, or

the more modern torches, would only be eliminated if farmers were convinced about its danger to always attract elephants or make them aggressive. The use of torches was also restricted by the lack of torches and batteries being for sale in the study area. The EDM for the use of dogs clearly shows the difference between those methods that were eliminated based on lack of effectiveness and those due to their danger. Almost all farmers agreed it was dangerous to use dogs to guard your fields against elephants, nevertheless they would still apply this method unless they were convinced that it would never work against elephants. This could be a reflection of the desperation of farmers or the lack of better alternatives. For trench digging and bush fence construction, farmers eliminated the method if they did not have enough manpower, as these methods are labour intensive endeavours. Farmers explained non-adoption of tin cans, chilli fencing and chilli burning by stating elephants are not a severe issue to them (anymore). This suggests that farmers would apply all other methods regardless of the severity of issues with elephants, potentially due to low input requirements or multiple uses of methods, such as fences also deterring other animals. Some farmers mentioned that the lack of rain early in the wet season was a constraint for them to plough early, however we would classify this as a perceived constraint since all farmers in this study experienced the same rainfall.

Knowledge of methods was determined to be a motivator for multiple mitigation methods, especially those to be considered innovative (beehives, chilli fences) or recent developments (electric fences). Generally, farmers mentioned they heard about methods from the Department of Wildlife, the NGO Ecoexist, or their neighbours. Besides learning how to apply chilli methods to their fields, farmers mentioned they were taught not to shout at or irritate elephants, and when coming across elephants to try to avoid them. Some farmers also mentioned it was explained to them that it would be better to

plough once the early rains started, by either Ecoexist, the Department of Wildlife or the Department of Agriculture, and that they were encouraged to report crop consumption incidents at the Kgotla. A few of the interviewed farmers were part of a conservation-agriculture project by NGO Ecoexist, of which one of the elements is to provide support and logistics for farmers to plough early. Beehive material provided by the World Bank and Department of Wildlife was rarely accepted by farmers and never applied by farmers, mainly due to farmers' lack of knowledge and belief of effectiveness of the method. In general, information on mitigation measures appeared not to be homogenously distributed and large parts of the population had not heard about certain methods, especially when it comes to elephant conscious farming. However, for chilli methods, it was not the distributed knowledge, but the availability of material to farmers by the combined efforts of the Department of Wildlife and the World Bank that was decisive of farmers adopting the method, while the termination of chilli supplies formed a constraint on farmers to apply the method. The earlier mentioned conservation-agriculture farmers still received chilli peppers through Ecoexist, yet most farmers had to stop using the chilli methods due to lack of material while considering it an effective method. This exposes some of the risks of one-off or temporary involvement of external bodies in providing mitigation methods. As the provision of materials created the expectation of continuous supplies and thus a form of dependence of farmers on those suppliers, farmers were disempowered by stripping them of some of their autonomy in applying mitigation methods. Since there were no alternative sources of chilli peppers available in the area, it also reinforced a sentiment of resentment and to a certain extent feelings of entitlement in the interviews with farmers. The evaluation report of the chilli and beehive project similarly mentioned the lack of ownership of the mitigation measures by farmers, and the unwillingness of farmers to invest own

resources in maintaining the methods (Ministry of Environment Wildlife and Tourism & Department of Wildlife and National Parks Botswana, 2016). Some farmers also mentioned Ecoexist providing them with tin cans, or assisting them to apply an electric cluster fence around their fields. Finally, the government also played a restricting role as some farmers experienced a perceived constraint of not being allowed to gather tin cans, or being charged for poaching if an elephant would fall into their trench. In this way, political factors can undermine the uptake of individual mitigation methods by farmers, due to issues like political rumours. This could also be due to insecurity and distrust among different community groups such as agriculturalists and pastoralists (Graham & Ochieng, 2008) or community's suspicion of the use of fences to appropriate land (O'Connell-Rodwell et al., 2000).

Regarding elephant and human coexistence, political ecology perspectives have indicated that issues between elephants and people are not only a reflection of competition or disagreements between humans and elephants, or amongst humans, but also of materials such as alcohol, as both human and elephant alcohol consumption play an important role in driving physical conflicts in India (Barua, 2014a). The political ecology perspective also reveals the expansion of war-time ethics to the conservation discourse, by dehumanizing poachers and accepting shoot-on-sight practises as morally justifiable (Neumann, 2004). Finally, it leads to consider the complexity of the involvement of powerful actors such as government agencies and (international) NGOs in supporting farmers to live with elephants, as instead, this support can express and reinforce authority and ownership, and thus disempower farmers (Ogra & Badola, 2008; Ogra, 2008; DeMotts & Hoon, 2012; Evans & Adams, 2016). Our study confirms that temporarily interventions, especially when guided by ideas of outsiders and their

interpretations of farmers' needs, instead of farmers themselves, plays a role in disempowering farmers. Furthermore, those to whom governmental and non-governmental agencies provide elephant deterrent methods should be considered for what they are: not one homogeneous subject, but a collection of different farmers, with different methods, cultures, needs, abilities and options (Evans and Adams, 2016), which is likewise the case for elephants (Chiyo et al., 2012; Barua, 2014b; Evans & Adams, 2018). Farmers mentioned diverse wishes, beliefs and experiences with elephants, and a method highly preferred by one farmer was disregarded or unknown by another, and farmers mentioned that some methods worked well for some elephants but not for other 'types' of elephants, referring to elephant genders or to the country of their origin.

5. Conclusion

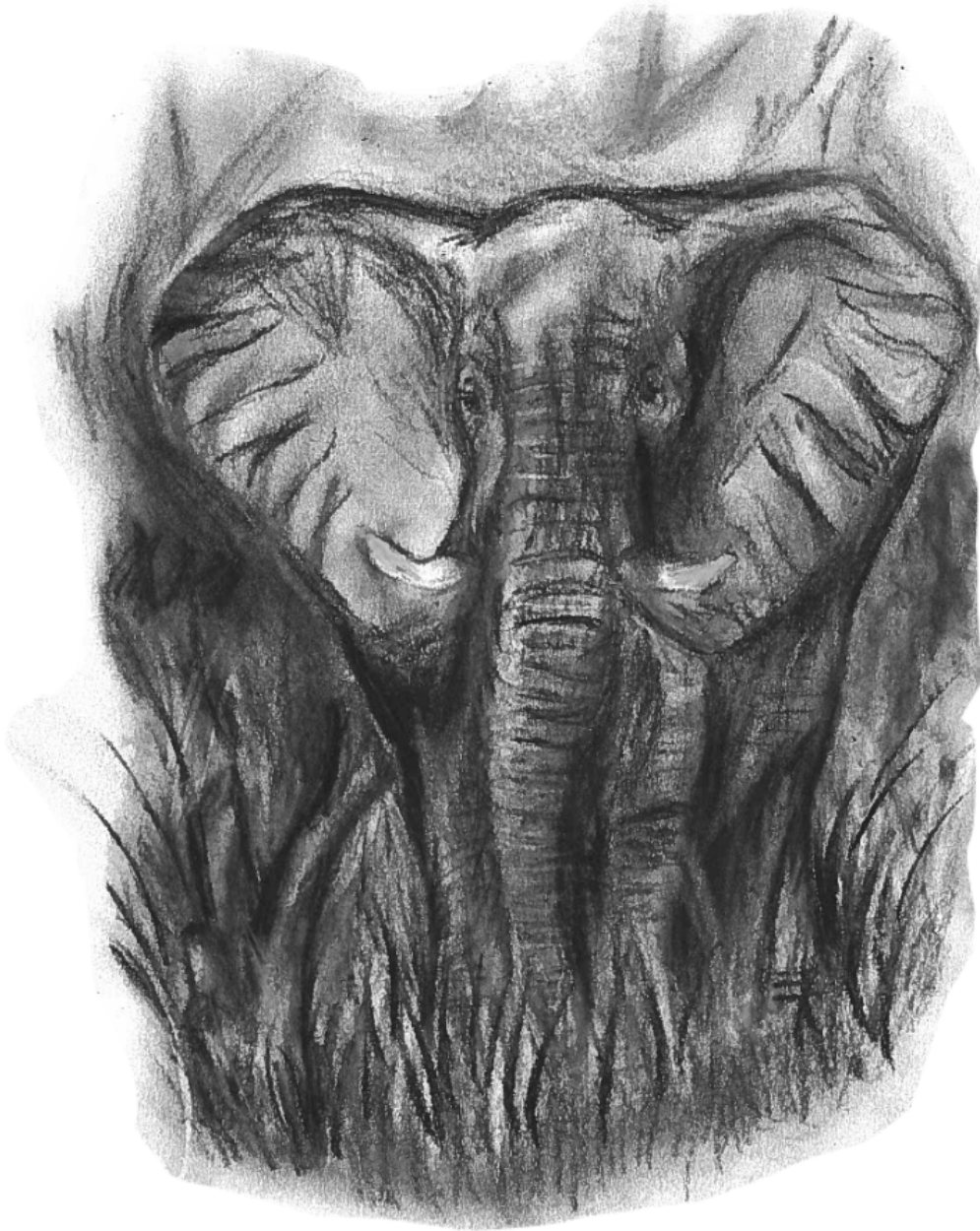
This study sought to understand farmers' choices of mitigation methods, and why interventions by (non-) government agencies to stimulate the use of certain methods have not resulted in the anticipated effects. Our Ethnographic Decision Models showed that unlike often assumed in these interventions, the adoption of mitigation method did not mainly rely on farmers' belief in the method's effectiveness. Instead, farmers often did not adopt a method because they were –or perceived to be- constrained by the weather and lack of monetary income, manpower, availability of material and knowledge. Some of these issues reflect the remoteness of the study site, which results in rare opportunities of monetary income and lack of availability of materials needed to create mitigation measures, or farm in general. The government therefore plays an important facilitating role with their provision of *Ipelegeng*, and mitigation materials in collaboration with NGOs. However, farmers' answers suggested that there was a

disparity between the materials they received and methods they wished to adopt. Moreover, farmers made it clear that one-off inputs of materials did not result in a sustainable use of mitigation methods. Some farmers indicated willingness to adopt methods like the use of chillies and flashlights, and a desire for material to be more widely available in the area. Here we see an opportunity for external bodies such as government or NGOs to stimulate the local sale of and encourage small business enterprises for material farmers indicated they needed, in particular for lighting their fields and making chill fences. This is in line with the evaluation report of the chilli and beehive project, which suggests the need for a full supply chain providing material for farmers to apply these methods (Ministry of Environment Wildlife and Tourism & Department of Wildlife and National Parks Botswana, 2016). Although there were clear signs of the distribution of knowledge on different available methods, there was heterogeneity in this distribution that caused farmers to either be miss- or uninformed. This was less the case for information on how to safely interact with elephants, as most farmers were aware of the danger of confronting elephants with methods such as dogs or fire. Considering knowledge distribution, we see an opportunity for the government or NGOs to facilitate community sharing of mitigation method ideas, especially regarding elephant conscious farming, as only a few farmers used these techniques. The use of many mitigation methods was eliminated by either their lack of effectiveness or being dangerous, or restricted by the lack of monetary income and materials. Nevertheless, although only a few farmers mentioned they used elephant conscious farming techniques, all of these farmers were positive about their experiences. Therefore, elephant conscious farming could play an important role in empowering farmers to reduce elephants consuming their crops.

6. Acknowledgements

We would like to thank the Ecoexist Project and the Howard G. Buffet Foundation and the Government of Botswana for facilitating and supporting data collection. We especially want to thank Mirkel Manyetse (Kenneth), Namu Mokgosi (Debig), Tsalano Florence Kgobero, Maipelo Molathegi and Boiteko Tlale for their contributions to the data collection. We are also thankful to the NERC Oxford DTP Environmental Research, Pembroke College Oxford and Stichting dr. Hendrik Muller's Vaderlandsch Fonds for their financial support making the research possible. Finally, we would like to thank Erin Buchholtz, E.J. Milner-Gulland and Leejiah Dorward for their input in data collection and/or writing of the manuscript.

6 | Synthesis



*And so these men of Indostan
Disputed loud and long,
Each in his own opinion
Exceeding stiff and strong,
Though each was partly in the right,
And all were in the wrong!*

Chapter 6. Synthesis

The aim of my thesis was ‘*To analyse the decisions that elephants and humans make in agricultural fields, and how these decisions influence the occurrence of elephant crop consumption.*’ I showed how elephant movement decisions and foraging decisions are influenced by the presence of crops and can lead to crop consumption. I also discovered which factors influence farmers’ decisions in mitigation methods, and how external bodies influence these choices and empower or restrict farmers in reducing elephant crop consumption. In this synthesis, I will first recap on our findings relevant to our main aim, from both the elephant and human perspectives. Following, I will bring these findings together in a conclusion in which I discuss how they contribute to the development and improvement of strategies that address the underlying causes of elephant crop consumption.

1. Elephant movement decisions

By using Bayesian hidden-Markov Models in **Chapter 2**, we could describe elephant GPS movement data into different movement states (Morales et al., 2004; Fryxell et al., 2008). By overlaying these movement states with environmental data, we could analyse how elephants change their movement type when they approach certain habitat features. We analysed how elephants responded to elephant corridors, tree groups, the Okavango River and agricultural fields.

- It was possible to divide elephant movements into two states, an exploratory state with fast, straight movements, and an encamped state portrayed by slower and more tortuous movements.

- Our results showed that in corridors exploratory movements were dominant, which underlines the importance of these corridors for elephants to pass through human inhabitant areas (Songhurst, McCulloch, et al., 2015).
- There was sexual segregation in elephant movements in agricultural fields. Males continued in exploratory movements to and from the river, while females showed a higher frequency of encamped movements at night –when most crop consumption and movements through fields occur- and during the dry season when farmers are less likely to be in fields. This could mean that female elephants deliberately target agricultural fields for foraging on crops and that male elephants consume crops on the go while passing through fields towards the river. However, it can also be that female elephants and their herds take fewer risks than male elephants and only forage in fields under the cover of darkness and in the dry season when farmers guard their fields less, which is in accordance with the predation-risk hypothesis (Chiyo et al., 2014).
- Irrespectively, this finding highlights the importance of early ploughing in order to harvest crops before the dry season commences in order to minimize the risk of elephants consuming crops.

2. Elephant foraging decisions and timings

Together, **Chapter 3 and Chapter 4** provide insights into the role of vegetation quality in determining elephant foraging decisions and crop consumption, and whether elephants need to include crops in their diet. In particular, we aimed to answer whether elephant diet contained insufficient micronutrient levels, and whether this potential deficiency could stimulate elephants to consume crops. To achieve this, we analysed the extend to which digestibility, micronutrient concentrations, and nutrient balance, make

crops an optimal alternative to browse and grass in **Chapter 3**. We focused on the role of micronutrients, as elephants are prone to be deficient in elements such as sodium, which can influence their consumption decisions (Weir, 1969; Chiyo et al., 2005; Rode et al., 2006). Besides our analyses of absolute nutrient levels, we conducted an analyses of nutritional balance, as animals do not make foraging decisions based on isolated elements, but consider foraging options as a whole (Raubenheimer & Simpson, 1993; Simpson & D. Raubenheimer, 1993; Raubenheimer, 2011). In **Chapter 4**, we calculated the monthly amount of browse and grass in elephant diet using faecal isotope levels of carbon ($\delta^{13}\text{C}$), and combined this with information on species preferences and nutritional values assessed in **Chapter 3**, to estimate the amount of nutrients elephants absorbed each month.

- Elephants preferred to select browse with high levels of phosphorus, magnesium and dry matter intake.
- Crops contained significantly higher amounts of digestible energy content, dry matter intake, nitrogen, phosphorus, potassium, calcium and magnesium, and especially distinguished themselves by their phosphorus and magnesium levels. Moreover, our analyses of nutrient balance revealed how unbalanced elephant diet was, especially in relative phosphorus levels. This suggests that in order to satisfy phosphorus requirements, elephants need to consume large amounts of vegetation, which makes crops an optimal alternative to browse and grass due to its significantly higher absolute phosphorus concentration and dry matter intake.
- **Chapter 4** supports these findings by providing quantitative support for this suggested phosphorus deficiency. These calculations affirmed our expectation of **Chapter 3** that indeed elephant diet contained insufficient amounts of phosphorus during the months crops were present and consumed by elephants.

- Together, these results indicate that phosphorus –and potentially other micronutrients like sodium - deficiencies, play an important role in elephant dietary choices and could stimulate crop-consuming behaviour.
- Supplying elephants with alternative micronutrient sources could reduce this deficiency, attract elephant away from fields and ultimately play a role in reducing elephant crop consumption.

3. Mitigation method decisions

Looking at elephant crop consumption from the human perspective, **Chapter 5** used Ethnographic Decision Models in order to understand reasons behind farmers' mitigation measure decisions, and how the government and NGOs enable or impede the empowerment of farmers to mitigate elephant crop consumption. It seems a common assumption in mitigation interventions – such as providing farmers with fencing material - that once effectiveness of a method is 'proven', farmers will want to adopt the method (Graham & Ochieng, 2008; Gunaryadi et al., 2017). However, despite involvement of the Botswana government and international organisations such as the World Bank, and millions of dollars of investments (World Bank, 2009), farmers did not appear to have gained an increase in strategies for sustainable and efficient long term mitigation. Therefore, we asked the farmers why they used the methods they do use, and why they did not use the other methods that exist.

- Besides the more easily discernible reasons of monetary income, availability of material and indeed the belief in effectiveness, the decision models we used provided us with more nuanced information than would be available from quick surveys and correlative statistical analyses.

- Other than farmers being lazy and not being willing to be proactive in mitigating elephant crop consumption (Noga et al., 2015), the models shed light on both the inventiveness and isolation of farmers. The methods individual farmers used also depended on the severities of the issues they personally experienced with elephants, which suggests that farmers adapt their mitigation efforts to patterns in severity of elephant crop consumption (Songhurst & Coulson, 2014). Farmers shared or loaned material, knowledge and money and copied mitigation methods previously provided by external bodies with material they could find in nature.
- These one-off inputs of materials by organisations did not result in a sustainable use of mitigation methods. Opportunities for cash income were limited and if farmers did manage to purchase or receive a flashlight or fencing material, the lack of logistics made it nearly impossible to maintain them. Small shops in villages generally did not provide these types of materials, and lack of public transport and tarmacked road made it a long, difficult and expensive trip to a town large enough to find materials (Ministry of Environment Wildlife and Tourism & Department of Wildlife and National Parks Botswana, 2016).
- We see an opportunity for governmental departments or NGOs to stimulate logistics to increase availability of mitigation materials.
- Some farmers were also aware of the effectiveness of elephant conscious farming methods, such as adapting the timing of ploughing and harvest and farming away from elephant corridors as discussed in **Chapter 2-4**.
- Therefore, we see potential in increasing the sharing between farmers and between farmers and researchers regarding crop consumption mitigation measures based on elephant conscious farming.

4. Conclusion

With the different chapters of my thesis, I aimed to look at elephant crop consumption holistically, by not isolating the elephants, people or environment but focussing on their interactions. I consider these chapters to work together in shedding some light at different aspects of the issue, just as any ‘solution’ to improve human-elephant coexistence needs to take different aspects into account (Hoare, 2012). Elephant crop consumption does not seem to be solved by forcing elephants out of fields or forcing farmers to use certain methods. Effectiveness of efforts of external bodies such as governments, NGOs and researchers to reduce elephant crop consumption could increase when we focus on not only deterring elephants from fields, but also attracting them to areas we do want them. **Chapter 3** and **4** indicate we could use alternative micronutrient sources to attract elephants away towards corridors that **Chapter 2** showed were important for exploratory movements through areas with human inhabitants. **Chapter 2** also showed the diversity in elephants responses, especially between males and females, which suggests that bull and breeding herd crop consumption require separate mitigation strategies, which is in line with farmers strategies in **Chapter 5**, as they describe different methods to work for different ‘sizes’ and ‘types’ of elephants. In order to empower farmers to live with elephants, external bodies could increase logistical support and facilitate the improvement of the supply-chain of materials for mitigation methods.

5. Future directions

Although my thesis contributed to out our knowledge on elephant crop consumption, there are many questions that remain unanswered. In **Chapter 2** we did not include differences in developmental stage, body size and condition (Bowler et al., 2005), nor

social interactions and internal drivers in our analyses (Getz & Saltz, 2008; Nathan et al., 2008). Such factors could play important roles in determining movement states, and including them in future studies of elephant movements can enhance our understanding of the role of agricultural fields on determining elephant behaviour. Furthermore, interpretation of movement states and their corresponding behaviours could be enhanced by linking GPS fixes to simultaneous observations of elephant behaviour on the ground. This would allow us to verify our current interpretations, and increase the possibility of understanding elephant motivations behind movement patterns.

While both **Chapter 3** and **4** suggested a phosphorus deficiency in local elephant diet and a correspondence to elephant crop consumption, this remains a hypothesis and further research is needed to understand the true extent and implications of a phosphorus deficiency. An obvious shortcoming of our study is the lack of data for certain months, and moreover a lack of repetition over years. The year we conducted our data collection the rains arrived late, which could have caused our results to be a deviation from usual dietary trends. Besides, there is a need to verify dietary requirements for wild African savanna elephants, and include alternative micronutrient sources such as saltlicks and termite mounds to give a more complete overview of nutritional values elephants consume each month. Finally, future extensions of the elephant isotope analyses with more crop samples may enhance the resolving power of a Bayesian mixing model to differentiate between forage sources, and quantify the presence of crops in elephant diet.

In a way, the results of **Chapter 5** resemble an evaluation of local issues farmers face while mitigation elephant crop consumption. The study did not include in-depth analyses of the success farmers attributed to their methods, and an extension of the focus group discussions (**Supplementary materials D.3**) could result in a

quantification of effectiveness of different methods to support farmers in co-existing with elephants. Furthermore, we did not consider that successfully deterring elephants from one farm could deflect the elephant into a neighbouring farm, nor that sharing mitigation methods (e.g. watchtowers, fencing) has been shown to be difficult in previous studies (O’Connell-Rodwell et al., 2000; Sitati & Walpole, 2006; Graham & Ochieng, 2008). However, the results of **Chapter 5** do not merely serve as an evaluation of mitigation interventions in the study site, but can have implications for mitigation interventions in general. When the goal of mitigation interventions is to empower farmers in living together with wildlife, it is essential to include this desire for empowerment in every step of the intervention. If anything, this should start with considering farmers and elephants as diverse and intellectual agents; by asking why elephants eat crops and by asking farmers how they can be supported in doing what they have been doing for longer than anyone who aims to support them, coexisting with elephants.

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Supplementary information A

A.1 Animal movement models

Animal movement models can broadly be divided into two classes: Eulerian and Lagrangian models. Eulerian models tend to be used to study animal movements at the population level, as their focus is on points in space, and the densities and fluxes of animals in that space (Turchin, 1998). These models describe the patterns of probability of occurrence of individual animals or whole populations, not taking into account details of movement itself (Smouse et al., 2010). Lagrangian models on the other hand, zoom in to the movements animals make at the individual level, and use information such as velocity and acceleration of an animal's movement path throughout a landscape (Turchin, 1998). These two approaches are not mutually exclusive and many Eulerian models are derived from Lagrangian methods of random walks, as in diffusion models, the study of home ranges (Smouse et al., 2010) or the influence of social structure and interactions on group movement patterns (Fryxell et al., 2008). Due to the current availability of high-resolution GPS data and increasing computational capacities, innovative Lagrangian approaches have been developed, which have resulted in progress in increased understanding of animal movement decisions (Nathan et al., 2008). I do not aim here to give an overview of all models available for the analyses of animal movements; I will merely position the type of model we used in the current field of random walk movement models. For more details on the different model types, their origins and application see reviews on the topics, e.g. Hebblewhite and Haydon (2010), Nathan et al. (2008), Patterson et al. (2016), Schick et al. (2008), Smouse et al. (2010) and Turchin (1998).

A.1.1 Random walk theory

In random walk theory, the movement behaviour of animals is described as moves between two subsequent stopping points in a landscape. The animal varies from the start to the end of each move on the characteristics of the move, such as distance, speed, duration, direction and turning angle. Random walk studies focus on the distance travelled and the turning angle between subsequent movements. Since speed and duration correlate with the distance travelled, turning angle is preferred over direction because it also includes the correlation of the direction of the consecutive moves (Turchin, 1998). The term ‘random’ in random walk refers to the apparent randomness when animals move around a landscape, since we lack information on the deterministic rules behind the movements. The movements of an animal may not be truly stochastic, yet for practical reasons this concept is accepted when modelling individual movements. Even though there is this (assumed) stochastic element in the animal’s decision, the movement decisions are also based on past experiences, local conditions, the conditions of the destination point and the absolute direction the animal aims to travel in (Turchin, 1998).

Random walks can be described as correlated, uncorrelated or biased random walks using information on the direction and the level of dependence of incremental step sizes (Smouse et al., 2010). Uncorrelated random walks include no direction persistence; they thus assume that each move is independent of previous and future moves. However, since paths are directional in most cases due to persistence in step orientation, correlated random walks with correlation between subsequent moves are most common (Turchin, 1998; Yackulic et al., 2011). A directional bias occurs if individuals show a specific deviance from a random walk, and drift into a particular direction (Smouse et al., 2010). These biases are often towards a fixed point such as a central point of a home range

(Yackulic et al., 2011). Biases can occur because of internal or external factors, and are either constant due to individual deviations or varying in space based on for example landscape features (Turchin, 1998).

A.1.2 Movement models based on random walks

There are many spin-offs of the idea of random walk models. Examples of this are the diffusion models. These models range from simple diffusion models that correspond to a completely random walk to generalized diffusion models that link individual movement choices to population distributions (Turchin, 1998). Often used versions of these diffusion models are Brownian motion and Ornstein-Uhlenbeck models, which incorporate the ideas of continuous time and continuous space, useful for home-range studies (Patterson et al., 2016). An alternative is to include the idea of animal's behavioural states into the diffusion models, making use of the velocity of the animal movement, but this method is rarely used (Patterson et al., 2016). A more popular method to analyse the behavioural states is to use the state-space models, which aim to study the interaction between movement data and landscape data (Jonsen et al., 2005; Forester et al., 2007; Smouse et al., 2010). These models have the advantage that they can deal with measurement error, which often occurs using lower frequency or less reliable data collection including ARGOS satellite tags, while with GPS data this error can be considered negligible. Instead of using these more complicated model types, it is also possible to make use of hidden Markov models instead when dealing with GPS data that is regularly spaced in time and observed with negligible error (Patterson et al., 2016). Hidden-Markov movement models fit models to multistate random walks, where each state is characterised by a different type of random walk (Langrock et al., 2012). This type of models was first described to analyse literature and speech, but now has

been widely applied in animal movement analyses (Jurafsky & Martin, 2000; Morales et al., 2004; Patterson et al., 2016).

A.2 Elephant movement state Stan model

```
functions{  
  // function that returns the log pdf of the wrapped-Cauchy  
  real wrappedCauchy(real phi, real rho, real mu) {  
    return(- log(2 * pi()) + log((1 - rho^2)/(1 + rho^2 - 2 * rho * cos(phi - mu))));  
  }  
  // returns exponential parameters if K==1  
  real fGammaReturn(int K, real A){  
    return(K == 1 ? A : 1.0);  
  }  
}  
  
data {  
  // base data  
  int<lower=0> N;  
  vector< upper=pi()>[N] turn;  
  vector[N] dist;  
  int<lower=1> K;  
  int missing[N];  
  
  // covariate  
  int nCovs;  
  matrix[N, nCovs + 1] X;
```

```

// out-of-sample test

int N1;

vector<upper=pi()>[N1] turnTest;

vector[N1] distTest;

int missingTest[N1];

matrix[N1, nCovs + 1] XTest;
}

parameters {

// wrapped Cauchy params

vector<lower=-pi(), upper=pi()>[K] mu;

vector<lower=0,upper=1>[K] rho;


// step parameters

real<lower=1> a_step_1;

real<lower=1,upper=3> b_step_1;

real<lower=3> b_step_2;


// switching parameters

matrix[K * (K - 1), nCovs + 1] beta;
}

transformed parameters {

matrix[K, K] Gamma_tr[N];

vector[K] B_step;


B_step[1] = b_step_1;

```

```

B_step[2] = b_step_2;

// determine switching probability matrix for each obs
// since it depends on covariates
{
matrix[K, K] Gamma[N];
matrix[K, K] Gamma1[N];

for(n in 1:N){
  int a_count;
  a_count = 1;
  for(k_from in 1:K){
    for(k in 1:K){
      if(k_from == k){
        Gamma1[n, k_from, k] = 1;
      }else{
        Gamma1[n, k_from, k] = exp(beta[a_count] * to_vector(X[n]));
        a_count = a_count + 1;
      }
    }
  }
  Gamma[n, k_from] = log(Gamma1[n, k_from] / sum(Gamma1[n, k_from]));
}
}

// trace of switching prob matrix
for(n in 1:N)
  for(k_from in 1:K)
    for(k in 1:K)

```

```

        Gamma_tr[n, k, k_from] = Gamma[n, k_from, k];
    }
}

model {
    vector[K] lp;
    vector[K] lp_p1;

    lp = rep_vector(-log(K), K);

    // forwards algorithm
    for (n in 1:N) {
        // not missing
        if(missing[n] == 0){
            for (k in 1:K){
                lp_p1[k]
                = log_sum_exp(to_vector(Gamma_tr[n, k]) + lp)
                + wrappedCauchy(turn[n], rho[k], mu[k])
                + gamma_lpdf(dist[n] | fGammaReturn(k, a_step_1), B_step[k]);
            }
        } else { // for missing just marginalise out previous state
            for (k in 1:K){
                lp_p1[k] = log_sum_exp(to_vector(Gamma_tr[n, k]) + lp);
            }
        }
        lp = lp_p1;
    }
}

```

```

target += log_sum_exp(lp);

a_step_1 ~ normal(1.5, 0.5);
B_step[1] ~ normal(2, 0.5);
B_step[2] ~ normal(3.5, 0.5);
mu ~ normal(0, 0.5);
rho[1] ~ normal(0.6, 0.1);
rho[2] ~ normal(0.1, 0.1);
for(i in 1:(K * (K - 1)))
  beta[i] ~ normal(0, 2);
}

generated quantities {

  // use Viterbi algorithm to determine optimal path
  int<lower=1,upper=K> state[N];
  real log_p_y_star;
  real lp_test_overall;
  vector[2] lp_test_element[N1];
  {
    int back_ptr[N, K];
    real best_logp[N, K];
    real best_total_logp;
    for (k in 1:K){
      if(missing[1] == 0){
        best_logp[1, K] = wrappedCauchy(turn[1], rho[k], mu[k])
          + gamma_lpdf(dist[1] | fGammaReturn(k, a_step_1), B_step[k]);

```



```

    }else{
        best_logp[1, K] = 0;
    }
}

for (t in 2:N) {
    for (k in 1:K) {
        best_logp[t, k] = negative_infinity();
        for (j in 1:K) {
            real logp;
            if(missing[t] == 0){
                logp = best_logp[t - 1, j]
                    + Gamma_tr[t, k, j] + wrappedCauchy(turn[t], rho[k], mu[k])
                    + gamma_lpdf(dist[t] | fGammaReturn(k, a_step_1), B_step[k]);
            } else{
                logp = best_logp[t - 1, j] + Gamma_tr[t, k, j];
            }

            if (logp > best_logp[t, k]) {
                back_ptr[t, k] = j;
                best_logp[t, k] = logp;
            }
        }
    }
}

log_p_y_star = max(best_logp[N]);
for (k in 1:K)

```

```

if(best_logp[N, k] == log_p_y_star)
    state[N] = k;
for (t in 1:(N - 1))
    state[N - t] = back_ptr[N - t + 1,
    state[N - t + 1]];
}

```

```

// for out-of-sample testing

```

```

{
matrix[N,K] B;
vector[K] lp_p_total;
vector[K] lp_p2;
vector[K] lp_p1a;
vector[K] lp_a;
matrix[N,K] A;
matrix[N,K] q_state;
vector[N] p_state;
matrix[N,K] p_state_all;

```

```

// test sample

```

```

vector[K] lp_test;
vector[K] lp_test_temp;

```

```

matrix[K,K] Gamma_test[N];
matrix[K,K] Gamma_1_test[N];
matrix[K,K] Gamma_tr_test[N];

```

```

for(n in 1:N1){
  int a_count;
  a_count = 1;
  for(k_from in 1:K){
    for(k in 1:K){
      if(k_from == k){
        Gamma_1_test[n, k_from, k] = 1;
      }else{
        Gamma_1_test[n, k_from, k] = exp(beta[a_count] * to_vector(XTest[n]));
        a_count = a_count + 1;
      }
    }
  }
  Gamma_test[n, k_from] = log(Gamma_1_test[n, k_from] / sum(Gamma_1_test[n,
k_from]));
}
}

```

```

for(n in 1:N1)
  for(k_from in 1:K)
    for(k in 1:K)
      Gamma_tr_test[n, k, k_from] = Gamma_test[n, k_from, k];

```

// forwards algorithm -- not Gamma_test here as it's for the sample not test

```
lp_a = rep_vector(-log(K), K);
```

```

for (n in 1:N) {
  if(missing[n] == 0){
    for (k in 1:K){
      lp_p1a[k] = log_sum_exp(to_vector(Gamma_tr[n, k]) + lp_a)
        + wrappedCauchy(turn[n], rho[k], mu[k])
        + gamma_lpdf(dist[n] | fGammaReturn(k, a_step_1), B_step[k]);
    }
  } else {
    for (k in 1:K){
      lp_p1a[k] = log_sum_exp(to_vector(Gamma_tr[n,k]) + lp_a);
    }
  }
  lp_a = lp_p1a;
  A[n] = to_row_vector(lp_a);
}

```

```

// backwards algorithm used here
// http://www.cs.columbia.edu/~mccollins/fb.pdf
// using forwards-backwards to obtain
// p(state_1(t), state_2(t) | observations(1:t))
B[N] = rep_row_vector(1, K);
lp_p_total = rep_vector(0, K);

```

```

for(n in 1:(N - 1)){
  if(missing[N - n + 1]==0){
    for(k in 1:K){

```

```

    lp_p2[k] = log_sum_exp(to_vector(Gamma_tr[n, k]) + lp_p_total)
        + wrappedCauchy(turn[N - n + 1] , rho[k], mu[k])
        + gamma_lpdf(dist[N - n + 1] | fGammaReturn(k, a_step_1), B_step[k]);
    }
} else {
    for(k in 1:K){
        lp_p2[k] = log_sum_exp(to_vector(Gamma_tr[n, k]) + lp_p_total);
    }
}
lp_p_total = lp_p2;
B[N - n] = to_row_vector(lp_p_total);
}

// estimate unnormalised state probs
for(n in 1:N){
    for(k in 1:K){
        q_state[n, k] = A[n, k] + B[n, k];
    }
}

// normalise these to find prob of state 2 (using a 2 state model)
for(n in 1:N){
    p_state[n] = exp(q_state[n, 2] - log_sum_exp(q_state[n]));
    p_state_all[n] = exp(q_state[n] - log_sum_exp(q_state[n]));
}

// out-of-sample predictive capability

```

```

// use forward algorithm to calculate  $p(Y_1, Y_2, \dots, Y_{k-1}, X_k)$ 
lp_test = to_vector(p_state_all[N]);
for (n in 1:N1) {
  if(missingTest[n] == 0){
    for (k in 1:K){
      lp_test_temp[k]
      = log_sum_exp(to_vector(Gamma_tr_test[n, k]) + lp_test)
      + wrappedCauchy(turnTest[n], rho[k], mu[k])
      + gamma_lpdf(distTest[n] | fGammaReturn(k, a_step_1), B_step[k]);
    }
  } else{
    for (k in 1:K){
      lp_test_temp[k]
      = log_sum_exp(to_vector(Gamma_tr_test[n, k]) + lp_test);
    }
  }

  lp_test = lp_test_temp;
  lp_test_element[n] = lp_test_temp;
}
// sum over  $X_k$  to marginalise
lp_test_overall = log_sum_exp(lp_test);
}
}

```

Bibliography Supplementary information A

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Supplementary information B

B.1 Functions and deficiencies of micronutrients in mammals

Nutrients in which elephants are potentially deficient are sodium (Na), phosphorus (P), nitrogen (N), potassium (K), magnesium (Mg) and calcium (Ca) (Pretorius et al., 2012). In a worldwide study of nutrient deficiencies in grazers, elements that appeared to be limiting in southern Africa were Mg, P, Na, copper (Cu), iodine (I), manganese (Mn) and selenium (Se) (McDowell et al., 1977). However, since Mn deficiencies mainly occur in poultry this element is to our knowledge not studied in relation to herbivores (McDowell, 2003). A study of the Serengeti National Park showed that in savanna grasslands, herbivores are particularly prone to deficiencies in Mg, Na and P (McNaughton, 1988).

B.1.1 Sodium

Sodium (Na) deficiencies are common in many parts of the world, especially in tropical areas in Africa. This deficiency causes lower osmotic pressure and dehydration of the body, resulting in poor growth, and a reduction in the utilization of protein and energy that is digested (McDonald et al. 2011). The occurrence of this deficiency is likely in the case of rapidly growing (young) animals that feed on forage low in Na, which is the case for most tropical forage. Other factors contributing to deficiency are the loss of sodium chloride (NaCl) due to sweating, lactating, and high levels of potassium (K), like in fertilized pastures, since K excess worsens Na deficiency (McDowell, 2003). It is unclear what exactly are the sodium requirements of elephants, yet, there is sufficient

evidence that salt craving or sodium craving occurs in elephants and influences their behaviour (Holdø et al., 2002; Rode et al., 2006). There is evidence for a naturally occurring deficiency in sodium levels in the diet of grazers, especially when lactation requires elevated sodium levels (Mcdowell et al., 1977; Jachmann & Bell, 1985). Consequently a well-known example of nutrient deficiency in elephants is sodium drive or craving, which could be leading elephants to consume crops to fulfil their sodium requirements (Sukumar, 1990; Rode et al., 2006). In general, crops have relatively high sodium concentrations compared to natural forage, which in light of expected deficiencies makes crop consumption highly attractive (Sukumar, 1990). Other known sodium sources are surface water bodies, and as elephants depend more on these water sources in the dry season, the demand to receive sodium through other sources -such as foraging- is less in this season (Weir, 1969; Pretorius et al., 2012).

Weir (1972) discovered that there is a close correlation between the level of sodium concentration of a particular water source, and the number of elephants that make use of this source. At the same time, other sodium sources, such as ‘salt licks’ were ignored in these areas with sodium rich water (Weir, 1972). Chamaillé-Jammes *et al.* (2007) however point out that this study took place in a period of low elephant population density. Therefore, they re-analysed the relationship between elephant number and sodium concentrations in waterholes over the period of Weir’s study and added new data periods until 2005. This study showed that indeed, the relationship was highly significant during Weir’s study period in the early 1960’s, yet this was not true for the subsequent periods, thus elephants did not favour the sodium rich water sources over others. Unfortunately it remains unclear what could motivate this change in water source selection (Chamaillé-Jammes et al., 2007).

Holdø et al. (2002) also re-examined the hypotheses of Weir (1972) that sodium drive in elephants determined their distributions, in addition to that, they analysed the Na content of natural forage. Their conclusion is that during the dry season elephants in the Kalahari supplement their Na intake with ‘mineral licks’, as Na concentrations in vegetation are low. This means that the Na licks appear to affect their movement and habitat use. Even though salt licks also contain above average levels of Ca and Mg, it is unlikely that salt lick use could be attributed to that (Holdø et al., 2002). This co-occurring is associated with the positive connection between the concentrations of sodium and magnesium, and in turn between magnesium and calcium (Jachmann & Bell, 1985). The use of the licks increases the amount of Ca and Mg that is secreted in faeces, which makes it unattractive to elephants deficient in these minerals. Opposite, the faeces of elephants that made use of the licks appeared to have low Na concentrations, which suggests that if these elephants are indeed deficient in Na, their gut is capable of electrolyte absorption to reduce Na loss (Holdø et al., 2002).

B.1.2 Potassium

Besides its occurrence in many studies analysing elephant nutrition, deficiencies in K levels tend to be rare in herbivores since most plants have high K contents (McDonald et al., 2011). Still this element often returns in studies of elephant nutrition, probably since it is one of the essential macro elements (Weir, 1972; Jachmann & Bell, 1985; Rode et al., 2006; Ihwagi et al., 2011; Pretorius et al., 2012). Together with sodium, chlorine and bicarbonate ions it plays important roles in osmotic regulations of the body fluids, nerve and muscle system and metabolism (McDonald et al., 2011). Even though this element occurs in bark and salt licks that are used by elephants, it is probably not the main motivator to consume them (Weir, 1969; Holdø et al., 2002; Ihwagi et al., 2011).

B.1.3 Magnesium

Deficiencies in magnesium are uncommon in animals and humans (McDowell, 2003). Nevertheless, elephants often utilized salt licks contain elevated levels of magnesium concentration (Weir, 1969; Klaus et al., 1998; Holdø et al., 2002). It is also often included in studies, without justification (Jachmann & Bell, 1985; Sukumar, 1990; Wang et al., 2007; Ihwagi et al., 2011; Pretorius et al., 2012). This has probably to do with the close association it has with calcium and phosphorus, and its essential importance in efficient metabolism of carbohydrates and lipids. Furthermore, magnesium content shows a high variability between different forage sources, so deficiencies do occur occasionally (McDonald et al., 2011).

B.1.4 Calcium

Research in Malawi has shown that deficiencies in calcium (Ca) are common among grazers, especially in the dry season (McDowell, 2003). This occurrence of deficiencies is related to the low content of calcium in natural forage (Wang et al., 2007). Calcium is the most abundant mineral element of bodies, and is important for the skeleton, teeth, living cells, tissue fluids, and the functioning of enzymes, nerves and muscles (McDonald et al., 2011). Deficiencies could cause problems to elephants with their muscles, bones, eyes, and paralysis of their trunk and throat (Wang et al., 2007). In contrast to wild grasses, cultivated crops often have high levels of calcium, and crop consumption in order to raise their calcium levels could therefore be an optimal foraging strategy for elephants (Sukumar, 1990; Von Gerhardt et al., 2014). Besides, bark of trees is also high in calcium, yet there is disagreement on the importance of the presence of calcium on stimulating tree debarking (Barnes, 1982; Ihwagi et al., 2011). Calcium also often occurs in the sodium rich soil and water consumed by elephants, yet it seems unlikely that calcium plays an important role in the existence of these

behaviours (Weir, 1969, 1972). Finally, calcium is one of the nutrients that are present in the salt licks (Weir, 1969; Holdø et al., 2002).

B.1.5 Phosphorus

Deficiencies in phosphorus (P) are widespread, since most soils worldwide are deficient in this element, especially in (sub-) tropical regions (McDonald et al., 2011, McDowell 2003, O'Halloran et al., 2010). Phosphorus has more known functions than any of the major minerals (McDonald et al., 2011). Phosphorus plays an important part in the development of cells and tissues (Ihwagi et al., 2011), energy metabolism and is in close association with calcium in bone, while a deficiency has direct impacts on fertility and reproduction (McDonald et al., 2011). Debarking of trees by elephants could be motivated by the relatively high concentrations of phosphorus in bark (Ihwagi et al., 2011). Elevated levels of phosphorus can also be found in soil licks (Klaus et al., 1998) and in vegetation on termite mounds (Grant & Scholes, 2006).

B.1.6 Nitrogen

Nitrogen can be used to measure crude protein of vegetation, since protein consists of nitrogen, together with other organic compounds such as carbon, hydrogen and oxygen (McDonald et al., 2011). Nitrogen is considered to be among the most limiting of all nutrients for in the vegetation and for herbivores in Africa (O'Halloran et al., 2010; Codron et al., 2011). In modelling forage selection by elephants, Pretorius et al. (2012) observed that during the wet season elephants tend to maximize their nitrogen intake (Pretorius et al., 2012).

B.1.7 Iodine

Another widespread deficiency is in the element iodine (I), which occurs especially in areas where the soil has been depleted, and rain and wind are inadequate to provide

enough I from its oceanic source. Of the micronutrients, iodine is particularly important for metabolism and overall general health (McDowell, 2003). Although iodine not often is included in elephant foraging studies, Milewski (2000) argues that elephants are prone to iodine deficiency, since they will require high amounts of iodine, and their food sources are deficient in the element. This iodine craving could drive them to artificial bore water (Milewski, 2000).

B.1.8 Other micronutrients

Besides these essential major elements, there are also essential micro or trace elements: iron (Fe), iodine (I), manganese (Mn), zinc (Zn) and cobalt (Co). These minerals can be very important to the metabolism of the body, but need to be present in smaller quantities than major elements (McDonald et al. 2011). To put this in perspective; on average the body nutrients are made up of 46% Ca, 29% of P, 25% of K, S, Na, Cl and Mg, while the trace elements together contribute to less than 0.3% of the body nutrients (McDowell, 2003). Minerals are held in the central reserve in the body, usually the blood plasma or bones in the case of Ca, and interchange the minerals by secretion into other compartments (McDonald et al. 2011, McDowell, 2003).

B.2 Nutritional Geometry

Nutritional Geometry methods, in particular Right-angle Mixture Triangles (RMTs) plot the ideal nutrient balance for animals, and the nutrient balance of different food sources available to them, in order to analyse how animals can reach their nutritional requirements by combining the food sources (Raubenheimer & Simpson, 1993, 1999; Simpson et al., 2004). RMTs are three dimensional spaces plotted on a two dimensional surface, showing the percentages in which different components are present in a composition, demonstrating nutrient balances and ideal compositions (figure B.1; Raubenheimer, 2011).

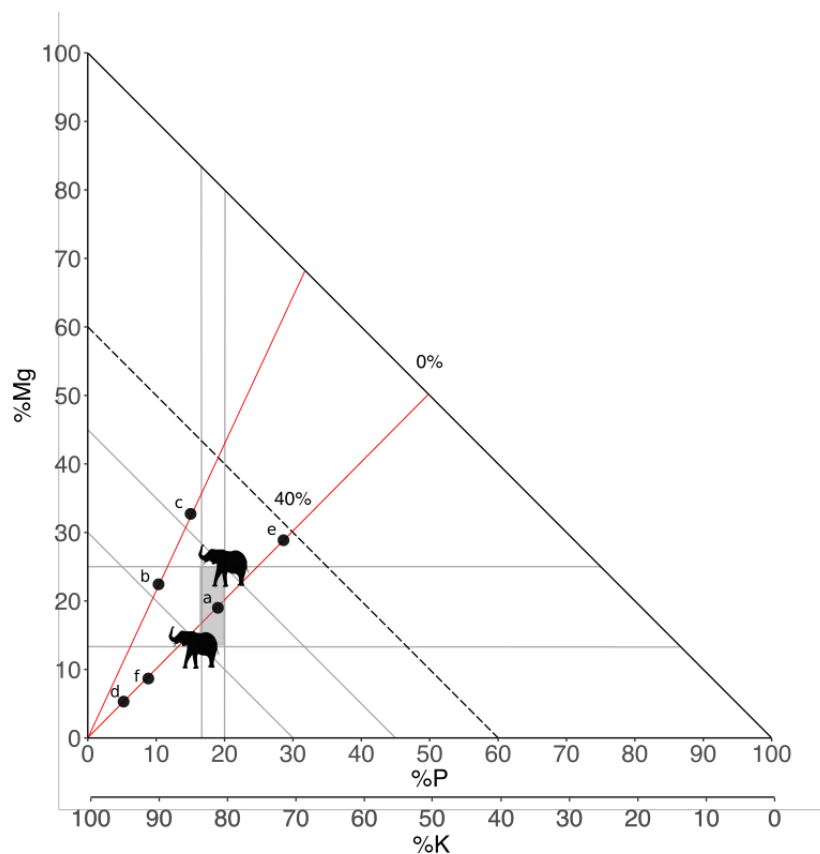


Figure B.1 Right-Angle Mixture Triangle.

RMTs do not reflect actual nutritional requirements, but demonstrates how balanced the food items are in their micronutrient composition, and how the elephant could combine food items to achieve the balanced diet the elephant requires. In figure 3.1, the X-axis

represents phosphorus (P) %, the Y-axis magnesium (Mg) % and the diagonal Z-axis potassium (K) %. The grey square between the two elephant icons indicates the nutrient space. The position of the elephants is based on the mean and lower limits of the required dietary balance of Mg:P:K for elephants. The third axes starts at the base of the triangle, reaching 40% at the dotted line. For each element the two grey lines derived from the elephant indicate the nutrient space in which that individual element is balanced. We plotted 6 hypothetical food items, with food *a* in the nutrient space of the required Mg:P:K balance. Food item *b* has the correct Mg:K balance, but falls short on the percentage of P (10%), while item *c* shows a deficiency in both P (15%) and K (53%), and a higher density of Mg than required by the elephant (32%). Food item *d* has an excessively high K-percentage of 90% while it is deficient in both P and Mg. Combinations of food items can be complementary if they are aligned on the red lines from the origin of the plot through the required dietary points, but fall on opposite sides of the intake target, as food items *d* and *e*, or are substitutable if they fall on the same side of the intake target, which is the case for *d* and *f*, which both could complement *e* (Raubenheimer, 2011).

B.3 Study site vegetation types

Table B.1 Study area divided into main vegetation categories defined by tree, shrub and grass species occurring in the categories.

Area	Vegetation category	Trees and shrubs	Grasses and plants
Floodplain	Floodplain grassland and	Jackal berry (<i>Diospyros mespiliformis</i>), water berry	Swamp savanna grass (<i>Miscanthus</i>
	Riverine woodland	(<i>Syzygium</i> spp.), sausage tree (<i>Kigelia africana</i>), leadwood (<i>Combretum imberbe</i>), large fever-berry (<i>Croton megalobotrys</i>), marula (<i>Sclerocarya birrea</i>), large-fruited bushwillow (<i>Combretum zeyheri</i>), red star apple (<i>Diospyros lycioides</i>), magic guarri (<i>Euclea divinorum</i>), brown ivory (<i>Acacia</i> <i>erubescens</i>), knobbly combretum (<i>Combretum</i> <i>mossambicense</i>), white bauhinia (<i>Bauhinia</i> <i>petersiana</i>), kalahari currant (<i>Commiphora rhus</i>), rough leaved raisin (<i>Grewia flavescens</i>), shepard's tree (<i>Boscia albitrunca</i>), russet bushwillow (<i>Combretum hereroense</i>), sickle-leaved albizia	<i>Junceus</i>), mat sedge (<i>Schoenoplectus</i> <i>corymbosus</i>), African bristlegrass (<i>Setaria sphacelata</i>), drop seed (<i>Sporobolus fimbriatus</i>), couch grass (<i>Cynodon dactylon</i>), phuka (<i>Urochloa</i> <i>brachyuran/trichopus</i>), false signal grass (<i>Brachiaria deflexa</i>), torpedograss (<i>Panicum repens</i>)

		(<i>Albizia harveyi</i>), confetti tree (<i>Gynmosporia senegalensis</i>), sourplum spp. (<i>Ximenia americana</i> , <i>caffra</i>), raintree (<i>Philenoptera violacea</i>), buffalo thorn (<i>Ziziphus mucronata</i>), peeling bark (<i>Ochna pulchra</i>)	
Dry bush	Silver terminalia sandveld	Silver terminalia (<i>Terminalia sericea</i>), sand camwood (<i>Baphia massaiensis</i>), mopane, acacia species, rain tree (<i>Philenoptera violacea</i>), white bauhinia (<i>Bauhinia petersiana</i>), kalahari current (<i>Commiphora rhus</i>), rough leaved raisin (<i>Grewia flavescens</i>), shepard's tree (<i>Boscia albitrunca</i>), marula (<i>Sclerocarya birrea</i>), large-fruited bushwillow (<i>Combretum zeyheri</i>), russet bushwillow (<i>Combretum hereroense</i>), confetti tree (<i>Gynmosporia senegalensis</i>), sickle bush (<i>Dichrostachys cinerea</i>), raintree (<i>Philenoptera violacea</i>), Camel thorn (<i>Acacia</i>	<i>For all dry bush categories:</i> Couch grass (<i>Cynodon dactylon</i>), phuka (<i>Urochloa brachyuran/trichopus</i>), false signal grass (<i>Brachiaria deflexa</i>), torpedograss (<i>Panicum repens</i>), silky bushman grass (<i>Stipagrostis uniplumis</i>), lovegrasses (<i>Eragrostis porosa</i>, <i>Eragrostis rotifer</i>, <i>Eragrostis lehmaniana</i>)

		erioloba), knobthorn (<i>Acacia nigrescens</i>), peeling bark (<i>Ochna pulchra</i>)	
	Mopane woodland	Mopane (<i>Colophospermum mopane</i>), sand camwood (<i>Baphia massaiensis</i>)	
	Mixed mopane woodland	Mopane (<i>Colophospermum mopane</i>)*	
	Acacia woodland	Camel thorn (<i>Acacia erioloba</i>), knobthorn (<i>Acacia nigrescens</i>), flame thorn (<i>Senegalia ataxacantha</i>), buffalo thorn (<i>Ziziphus mucronata</i>)*	
	False mopane, Zambezi teak and wild syringa woodland	False mopane (<i>Guibourtia coleosperma</i>), Zambezi teak (<i>Baikiaea plurijuga</i>), wild syringa (<i>Burkea africana</i>), peeling bark (<i>Ochna pulchra</i>), sand camwood (<i>Baphia massaiensis</i>)	
Agricultural fields	Crops		Millet (<i>Pennisetum glaucum</i> / Eleusine coracana), sorghum (<i>Sorghum vulgare</i>) and maize (<i>Zea mays</i>), beans (<i>Vigna</i>

aconitifolia/ Phaseolus vulgaris),
groundnuts (Arachis hypogaea),
watermelon (Citrullus lanatus),
pumpkin (Cucurbita spp.)

* This category additionally includes the species of category 'Silver terminalia sandveld' in limited amounts.

B.4 Table B.2 Browse species on focal list

Code	Common name	Latin name	Sestswana name
SCW	Sandcamwood	<i>Baphia massaiensis</i>	/
SB	Sickle bush	<i>Dichrostachys cinerea</i>	Moselesele
RT	Rain tree	<i>Philenoptera violacea</i>	Mopororo
CaT	Camel thorn	<i>Acacia erioloba</i>	Mogotho
Mop	Mopane	<i>Colophospermum mopane</i>	Mophane
SP	Sour plum spp.	<i>Ximenia americana, caffra</i>	Moretologana, Morokolo
ST	Silver terminalia	<i>Terminalia sericea</i>	Mogonono
RSA	Red star apple	<i>Diospyros lycioides</i>	
ConfT	Confetti tree	<i>Gynmosporia senegalensis</i>	Mothone
LW	Leadwood	<i>Combretum imberbe</i>	Motswere
RLR	Rough leaved raisin	<i>Grewia flavescens</i>	Mokgompatha
WB	White bauhinia	<i>Bauhinia petersiana</i> <i>(urbaniana)</i>	Motshantsha
KT	Knobthorn	<i>Acacia nigrescens</i>	Mokaba
LFBerry	Large fever berry	<i>Croton megalobotrys</i>	Motsebi
Mag	Magic guarri	<i>Euclea divinorum</i>	Mothakola
ZT	Zambezi teak	<i>Baikiaea plurijuga</i>	
WS	Wild Syringa	<i>Burkea africana</i>	Mosheshe
FM	False Mopane	<i>Guibourtia coleosperma</i>	
OP	Peeling bark	<i>Ochna pulchra</i>	Monyelenyele
KC	Kalahari currant	<i>Rhus tenuinervis</i>	Morupaphiri

BuffT	Buffalo thorn	<i>Ziziphus mucronata</i>	Mokgalo
FT	Flame thorn	<i>Senegalia ataxacantha</i>	Moloto
ShepT	Shepard tree	<i>Boscia albitrunca</i>	Motopi
BrIv	Brown ivory	<i>Berchemia discolor</i>	Motsintsila
Kcomb	Knobbly creeper	<i>Combretum mossambicensis</i>	Motsheketsane

B.5 Data collection classification categorizations

Table B.3 Description of plant elephant impact types included in the study.

Impact type code	Description	Range of damage %
No damage	No sign of elephant impact	0
Lv	Leaves: Only leaf stripping	0-10
Tw,lv	Twigs, leaves: Only twigs (usually <5 cm circumference) and leaves removed	10-30
Br	Branches: Branches are broken and/or bark stripped in most cases branches are >5cm circumference	10-50
Deb	Debarking: The bark is stripped from the main stem	10-50 (unless ringed and dead than 100%)
MS	Main stem broken: The main stem of the tree is broken or removed.	50-100 (100 if tree dead)
R	Root damage/uprooting: The elephants have dug up the roots, and/or have removed or debarked them	10-100 (100 if completely uprooted and tree dead)

Table B.4 Description of Forage Quality Index (FQI) types included in the study.

FQI code	Description	Range of FQI%
No	There is nothing on the tree	0
Old	There are old leaves on the tree	25-100, OR <10
Bud	There are leaves or flower buds on the tree, and some are starting to open	0-25, OR <10
New	The buds have opened and there are new leaves on the tree	25-100, OR <10
Fruit	There are fruits growing on the tree (fresh fruits, not seeds)	25-50, OR <10
Flower	There are flowers on the tree	25-50, OR <10

B.6 Supplementary results Chapter 3 Tables

Table B.5 GLM with binomial error structure of the proportion of plots in which a species is eaten in which it is found in each season (d.f.=97) simplified with a backward selection procedure (Type II test).

Explanatory variable	Estimate	Standard error	z-value	p
Early Dry (intercept)	-2.60958	0.42082	-6.201	<0.0001
Early Wet	0.50343	0.19256	2.614	<0.01
Late Dry	0.47674	0.18138	2.628	<0.01
Late Wet	-0.50209	0.21566	-2.328	<0.05
% P	5.52599	1.08332	5.101	<0.0001
% K	-0.39674	0.15871	-2.500	<0.05
% Mg	0.34204	0.16203	2.111	<0.05
Dry Matter Intake	0.5604	0.1579	3.551	<0.001

Table B.6 Test results of comparing fibre measurements between vegetation types.

Explanatory variable	Df	Test	F/Chi-Square	p
NDF	2	One-Way ANOVA	109.6	<0.0001
ADF	2	One-Way ANOVA	40.39	<0.0001

Digestible Energy	2	One-Way	41.52	<0.0001
		ANOVA		
Dry Matter Intake	2	Kruskall Wallis	156.52	<0.0001
N	2	One-Way	72.98	<0.0001
		ANOVA		
P	2	One-Way	38.89	<0.0001
		ANOVA		
K	2	Kruskall-Wallis	26.516	<0.0001
Ca	2	Kruskall-Wallis	42.511	<0.0001
Mg	2	Kruskall-Wallis	23.783	<0.0001
Na	2	Kruskall-Wallis	1.8489	0.4877
Tannin	2	Kruskal-Wallis	96.288	<0.0001

B.7 Supplementary results Chapter 3 Figures

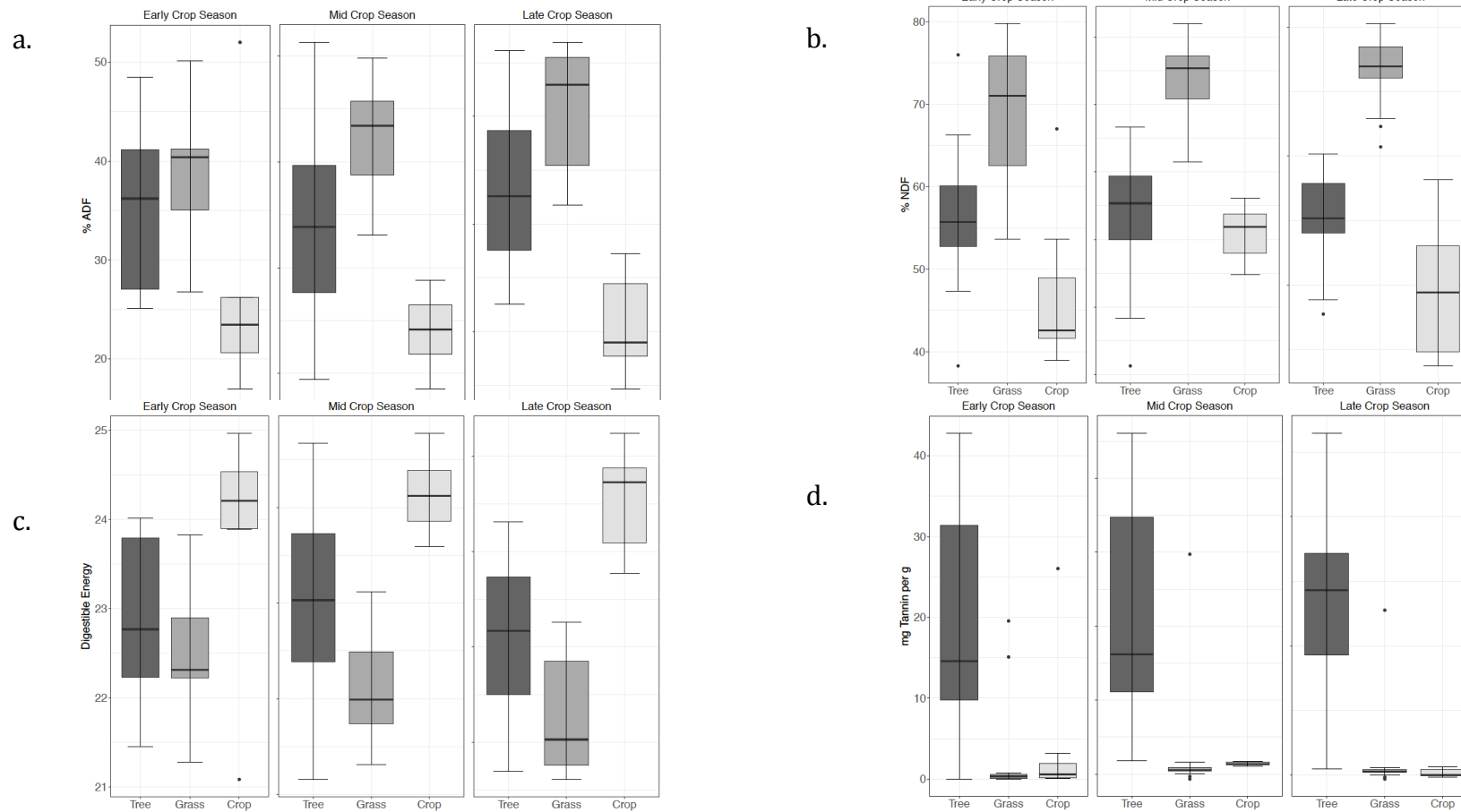


Figure B.2 Boxplots comparing the differences in the vegetation characteristics a. ADF, b. NDF, c. Digestible Energy and d. Tannin between trees, grasses and crops, and their changes over the crop season.

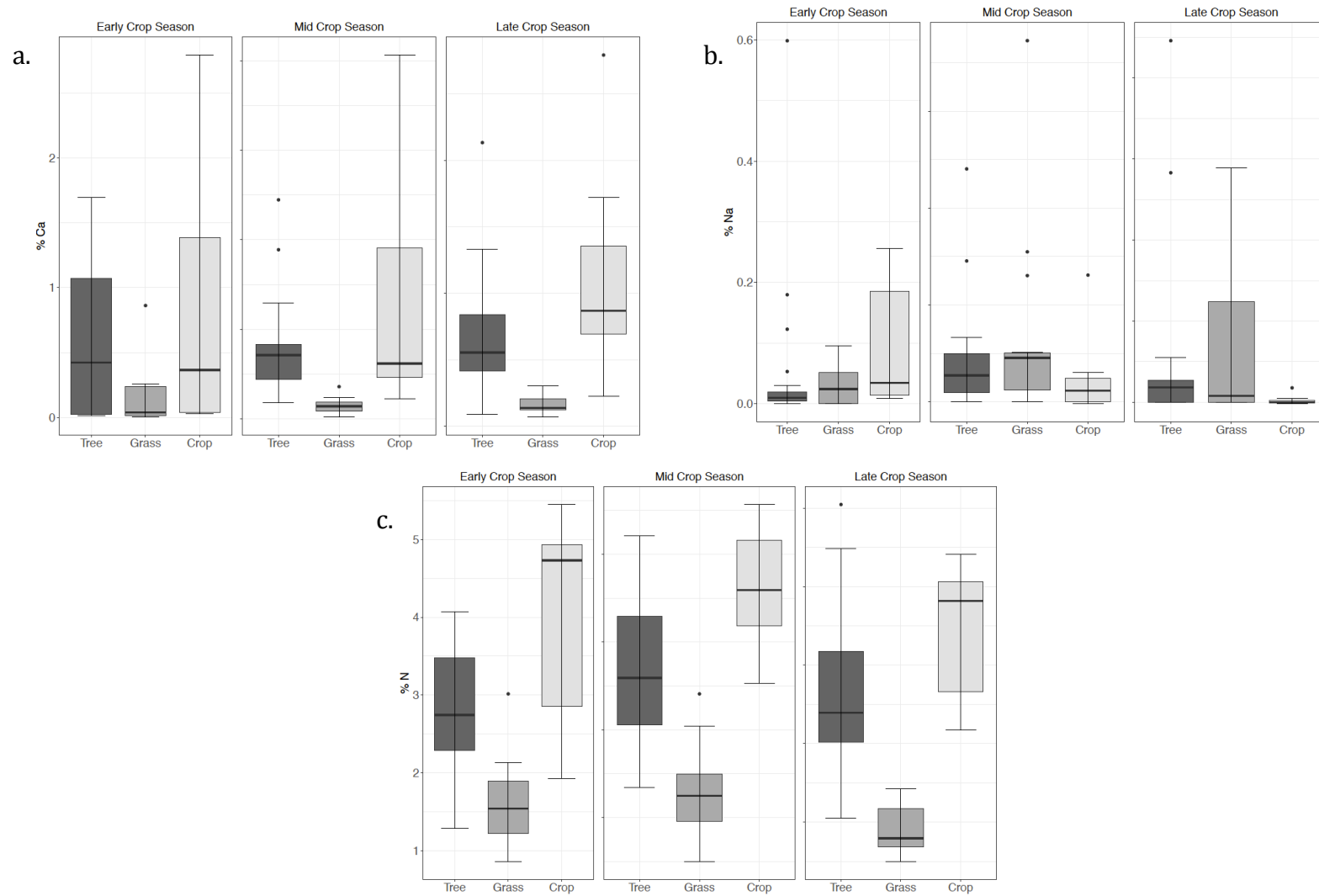


Figure B.3 Boxplots comparing the differences in the vegetation characteristics a. calcium (Ca), b. sodium (Na), c. nitrogen (N) between trees, grasses and crops, and their changes over the crop season.

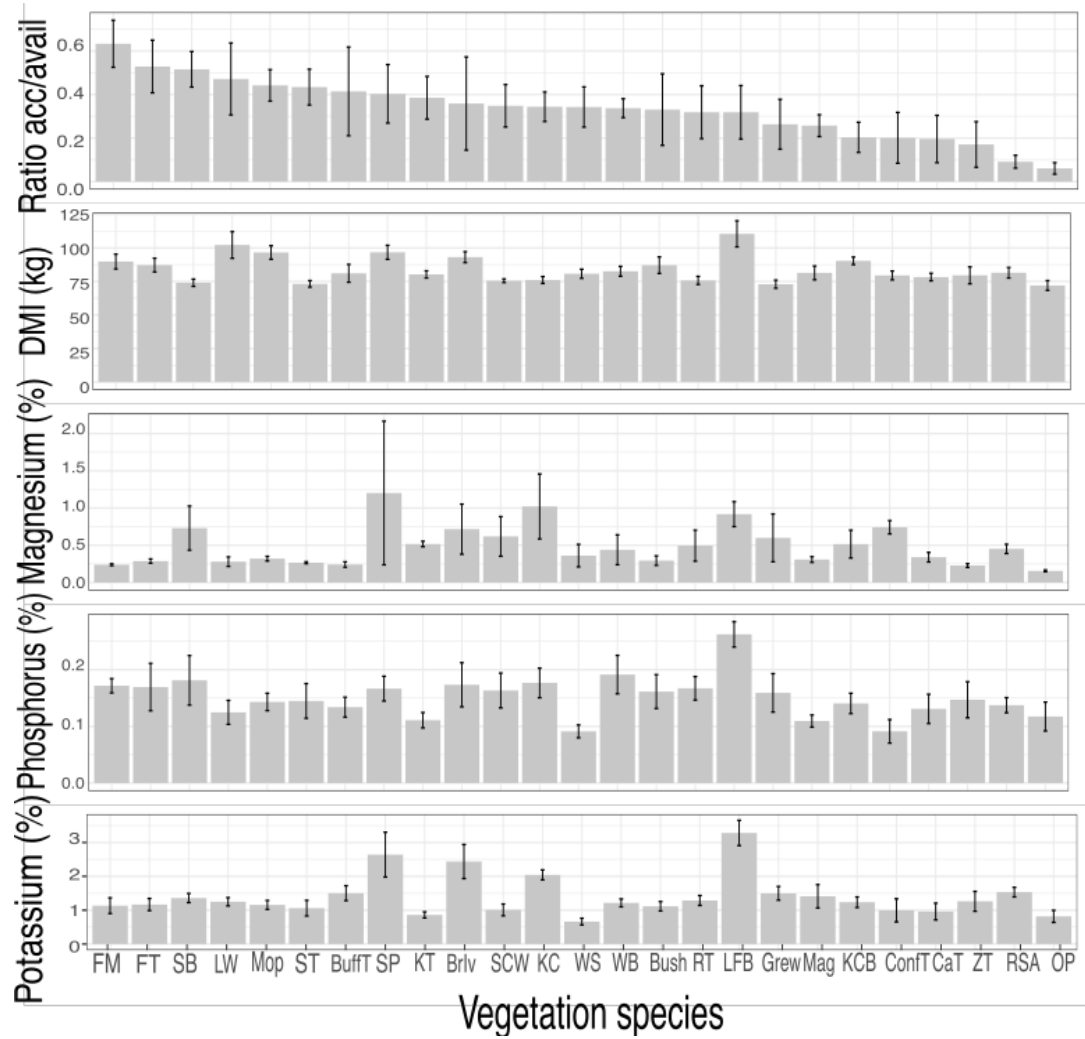


Figure B.4 Plots of elephant dietary choices and their vegetation characteristics, sorted in order of acceptance/availability ratio.

B.8 Supplementary results Chapter 3 PCA results

vegetation type comparisons and tree preference groups

B.8.1 PCA results comparing vegetation types

B.8.1.1 Early Crop season

Table B.7 PCA results comparing the vegetation characteristics of the three vegetation types tree, grass, crops early crop season.

	Comp. 1	Comp. 2	Comp. 3
Eigenvalue	5.799	1.131	0.825
Percentage of Variance explained	52.7%	16.9%	10.3%
Cum. Percentage of Variance explained	52.7%	69.7%	80.0%

	%NDF	%ADF	Tannin	%N	%P	%K	%Ca	%Mg
Comp. 1	-0.356	-0.377		0.355	0.350	0.327		0.228
Comp. 2	0.248		-0.224	-0.125		0.260	-0.535	0.525
Comp. 3	0.220	-0.102	-0.834	-0.124			0.322	-0.206

	%Na	DE	DMI
Comp. 1	0.202	0.378	0.359
Comp. 2	0.421		-0.231
Comp. 3	-0.143		-0.143

B.8.1.2 Mid Crop season

Table B.8 PCA results comparing the vegetation characteristics of the three vegetation types tree, grass, crops, mid crop season.

	Comp. 1			Comp. 2			Comp. 3		
Eigenvalue	5.365			1.998			1.214		
Percentage of Variance explained	48.8%			18.2 %			11.0 %		
Cum. Percentage of Variance explained	48.8%			66.9%			78.0 %		
	%NDF	%ADF	Tannin	%N	%P	%K	%Ca	%Mg	
Comp. 1	-0.360	-0.404		0.340	0.232	0.278	0.298	0.293	
Comp. 2	0.279		-0.598		0.518	0.424			
Comp. 3	-0.257	-0.160			0.117		-0.577	-0.594	
	%Na	DE	DMI						
Comp. 1	-0.104	0.405	0.332						
Comp. 2	0.209		-0.254						
Comp. 3	0.240	0.158	-0.348						

B.8.1.3 Late Crop season

Table B.9 PCA results comparing the vegetation characteristics of the three vegetation types tree, grass, crops late crop season.

	Comp. 1	Comp. 2	Comp. 3
Eigenvalue	5.925	1.598	0.833
Percentage of Variance explained	53.9%	14.5%	9.5%
Cum. Percentage of Variance explained	53.9%	68.4%	78.0%

	%NDF	%ADF	Tannin	%N	%P	%K	%Ca	%Mg
Comp. 1	-0.372	-0.377		0.316	0.326	0.187	0.316	0.301
Comp. 2	0.205		-0.674	-0.283	0.188	0.580		0.133
Comp. 3	-0.158		0.184	-0.124	-0.297		0.221	0.241

	%Na	DE	DMI
Comp. 1	-0.118	0.377	0.363
Comp. 2	0.158		
Comp. 3	0.849		

B.8.2 PCA results trees and preference groups

B.8.2.1 Late Dry season

The PCA of the tree characteristics across the year shows a different pattern than the PCAs comparing the three vegetation types. The first component exists out of all the characteristics except for calcium, with the fibre characteristics (NDF, ADF, DE and DMI) playing an

important role. This component however only explains 40% of the variance and the other components all contain similar elements. Judging from the PCA biplots there is large scatter and overlap between the three preference groups in the late dry season (Table B.10, Figure B.5).

Table B.10 PCA results on the vegetation characteristics of the three elephant dietary preference groups: preferred, intermediate and avoided in Late Dry season.

	Comp. 1	Comp. 2	Comp. 3
Eigenvalue	4.263	2.230	1.420
Percentage of Variance explained	38.8%	20.3%	12.9%
Cum. Percentage of Variance explained	38.8%	59.0%	71.2%

	%NDF	%ADF	Tannin	%N	%P	%K	%Ca	%Mg
Comp. 1	-0.428	-0.398	-0.178	0.343	0.283	0.166		0.141
Comp. 2	-0.109	-0.180	-0.113	-0.363	-0.439		0.522	0.406
Comp. 3	0.297	-0.371	0.177		-0.250	-0.639		-0.420

	%Na	DE	DMI
Comp. 1	-0.220	0.399	0.427
Comp. 2	0.368	0.180	0.109
Comp. 3	-0.186	0.369	-0.288

B.8.2.2 Early Wet season

There are very small differences between the PCA of the late dry and the early wet season, with the components containing the same elements, yet the first component explains marginally more than that of the late dry season. The scatter plot however shows a different pattern than that of the late dry season, with a more concentrated low preference group positioned towards fibre and tannin (Table B.11, Figure B.5).

Table B.11 PCA results on the vegetation characteristics of the three elephant dietary preference groups: preferred, intermediate and avoided in Early Wet season.

	Comp. 1	Comp. 2	Comp. 3
Eigenvalue	4.263	2.230	1.420
Percentage of Variance explained	42.8%	20.3%	11.2%
Cum. Percentage of Variance explained	42.8%	63.1%	74.4%

	%NDF	%ADF	Tannin	%N	%P	%K	%Ca	%Mg
Comp. 1	-0.418	-0.398	-0.178	0.343	0.283	0.166		0.141
Comp. 2	-0.109	-0.180	-0.113	-0.363	-0.439		-0.522	0.406
Comp. 3		-0.371	0.177		-0.250	-0.639		-0.420

	%Na	DE	DMI
Comp. 1	-0.220	0.399	0.427
Comp. 2	0.368	0.180	0.109
Comp. 3	-0.186	0.369	

B.8.2.3 Late Wet season

Again, there is very limited difference with the PCA component information compared to the previous season, the early wet and late wet appear to have the same variance explanations.

On the PCA biplot the low preference group appears to be concentrated even more, again around tannin and ADF and NDF (Table B.12, Figure B.5).

Table B.12 PCA results on the vegetation characteristics of the three elephant dietary preference groups: preferred, intermediate and avoided in Late Wet season.

	Comp. 1	Comp. 2	Comp. 3
Eigenvalue	4.263	2.230	1.420
Percentage of Variance explained	42.9%	17.3%	11.9%
Cum. Percentage of Variance explained	42.9%	60.2%	60.2%

	%NDF	%ADF	Tannin	%N	%P	%K	%Ca	%Mg
Comp. 1	-0.418	-0.398	-0.178	0.343	0.283	0.166		0.141
Comp. 2	-0.109	-0.180	-0.113	-0.363	-0.439		0.522	0.406
Comp. 3		-0.371	0.177		-0.250	-0.639		-0.420

	%Na	DE	DMI
Comp. 1	-0.220	0.399	0.427
Comp. 2	0.368	0.180	0.109
Comp. 3	-0.186	0.369	

B.8.2.4 Early Dry season

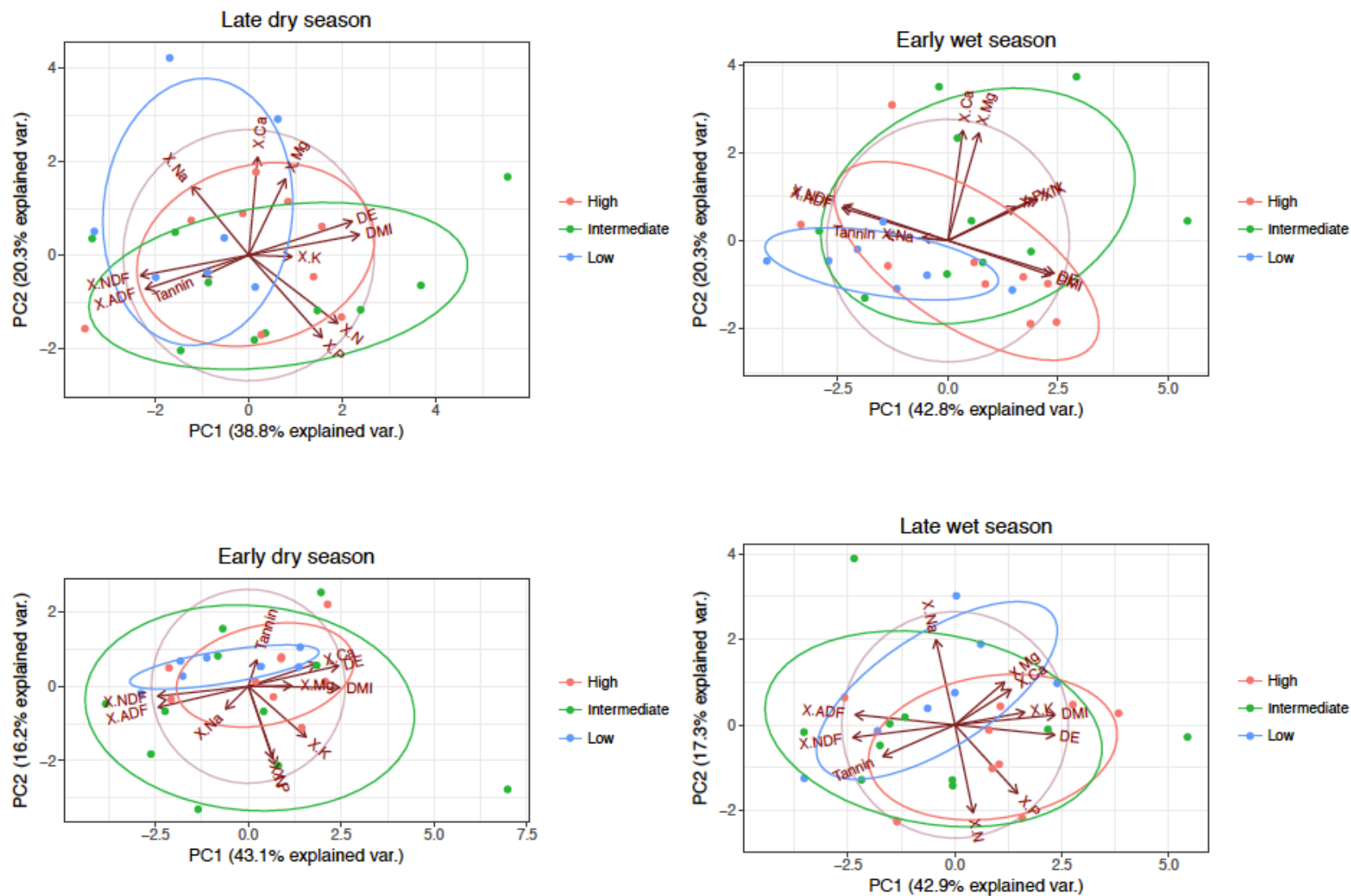
During the early dry season there are again not many differences with the PCA component information compared to the previous season, however it is different from the late dry season when looking at the explaining of variance. The low preference group becomes less clustered and goes again to the more scattered pattern as in the late dry season biplot (Table B.13, Figure B.5).

Table B.13 PCA results on the vegetation characteristics of the three elephant dietary preference groups: preferred, intermediate and avoided in Early Dry season.

	Comp. 1	Comp. 2	Comp. 3
Eigenvalue	4.263	2.230	1.420
Percentage of Variance explained	43.1%	16.1%	13.7%
Cum. Percentage of Variance explained	43.1%	59.3%	73.0%

	%NDF	%ADF	Tannin	%N	%P	%K	%Ca	%Mg
Comp. 1	-0.418	-0.398	-0.178	0.343	0.283	0.166		0.141
Comp. 2	-0.109	-0.190	-0.113	-0.363	-0.439		-0.522	0.406
Comp. 3		-0.371	0.177		-0.250	-0.639		-0.420

	%Na	DE	DMI
Comp. 1	-0.220	0.399	0.427
Comp. 2	0.368	0.180	0.109
Comp. 3	-0.186	0.369	



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Supplementary information C

C 1. Bayesian two-source mixing model results C3 crops grouped

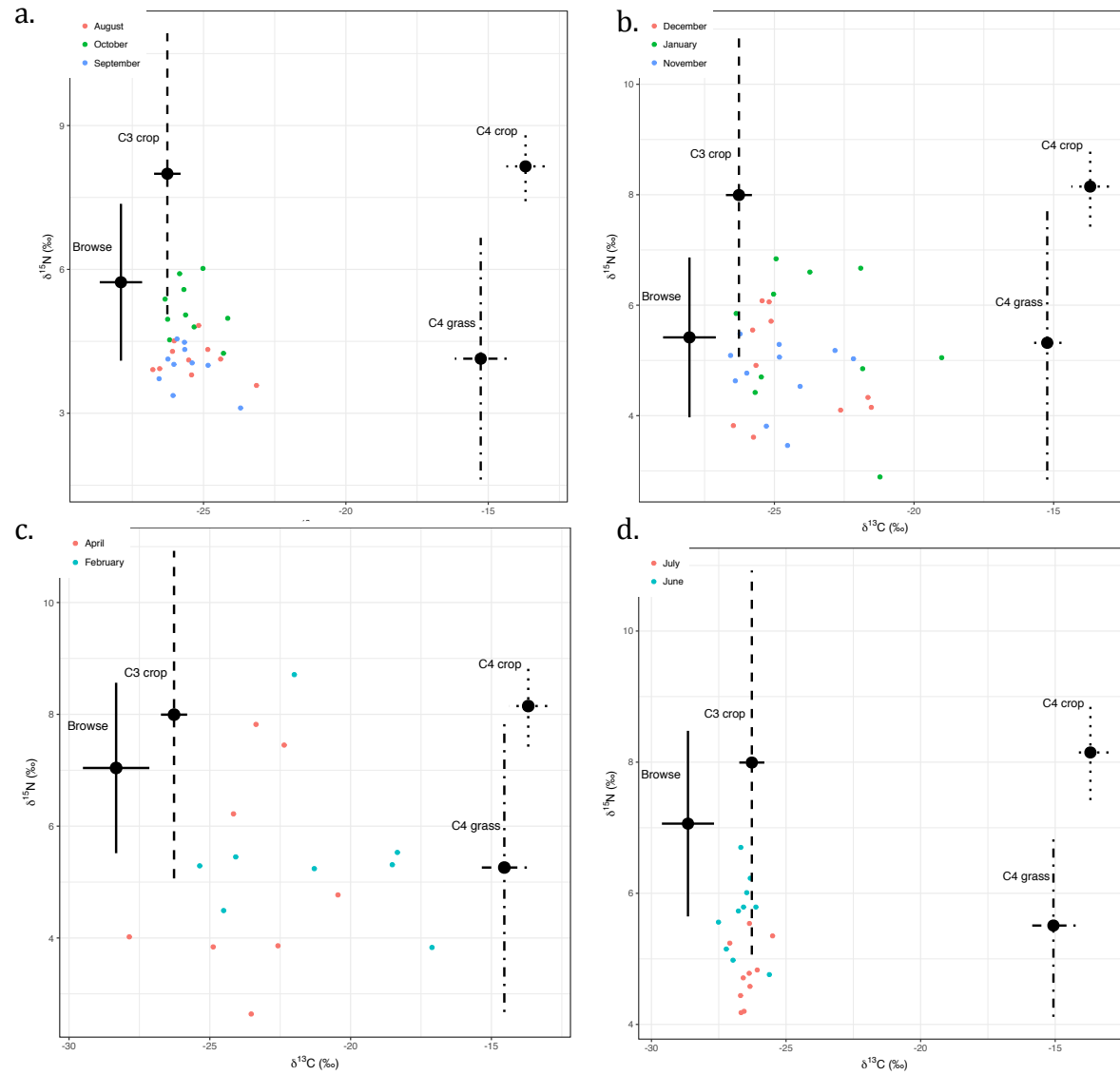


Figure C.1 Raw data plots of average and s.d. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of browse, C4 grass, and C3 and C4 crops; and faeces $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope value, per season: a=Late Dry, b=Early Wet, c=Late Wet and d=Early Dry.

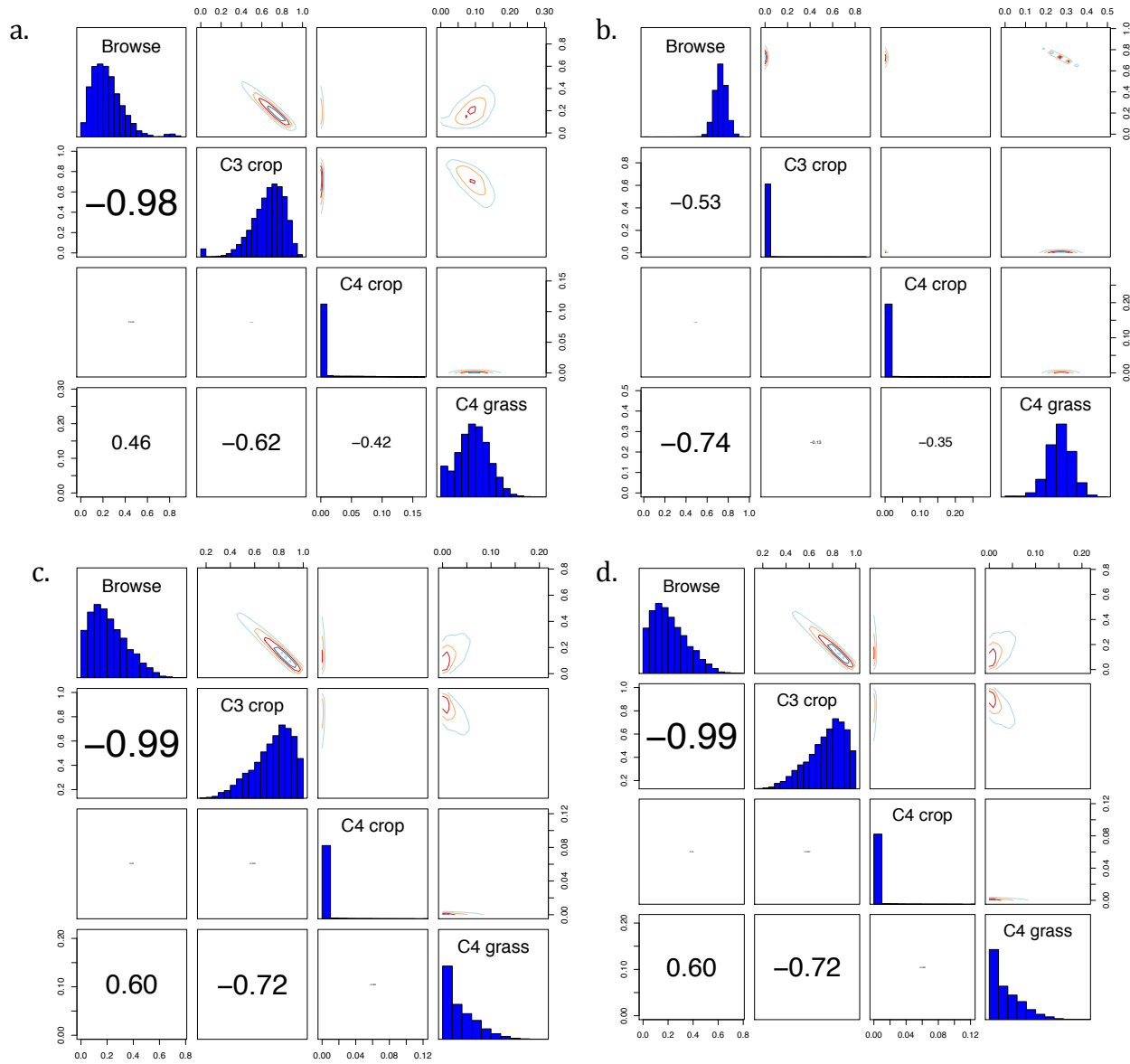


Figure C.2 Pairwise correlation plots of Browse, C4 grass, and C3 and C4 crops model results, per season, with a= Late Dry, b=Early Wet, c=Late Wet and d=Early Dry.

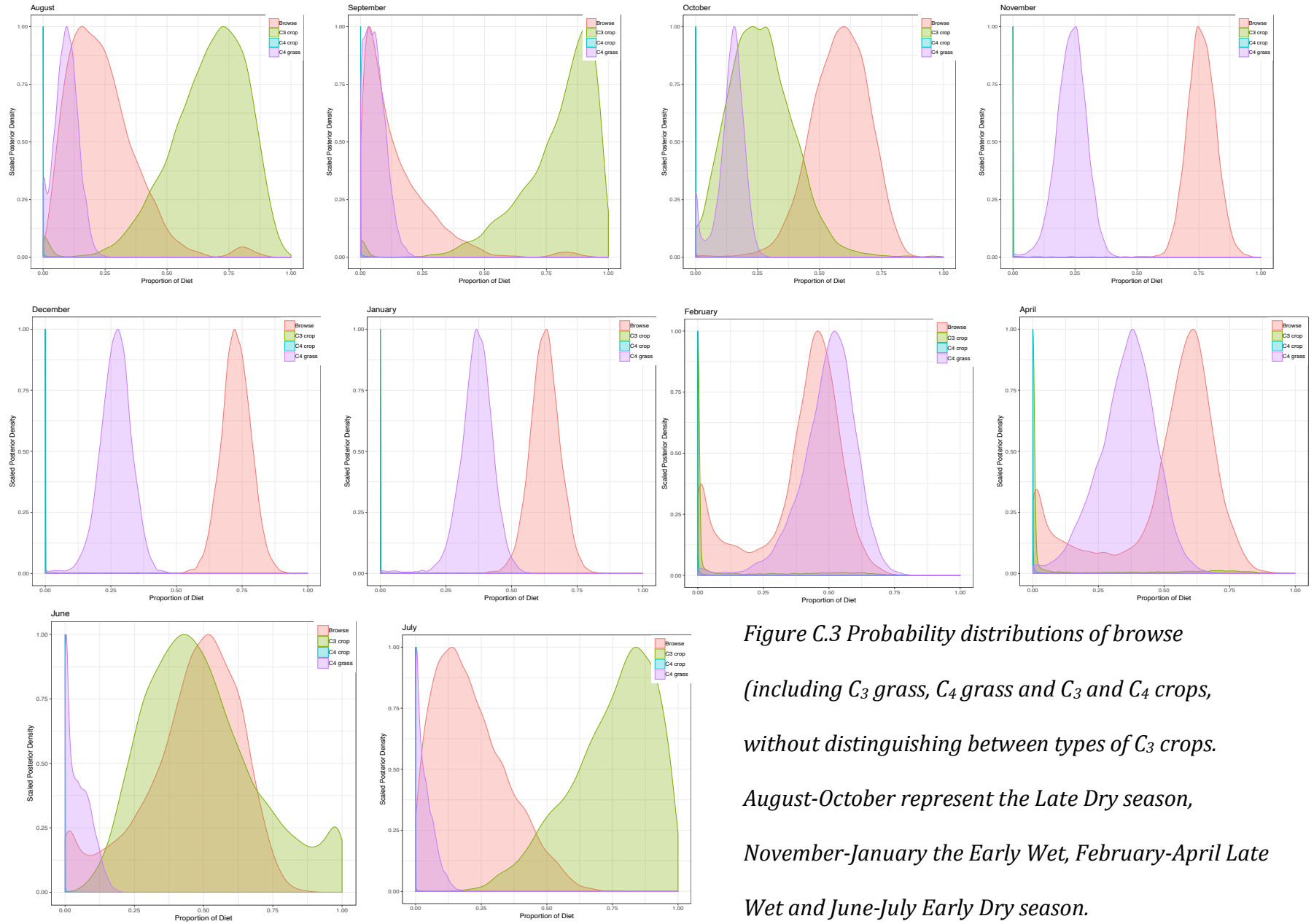


Figure C.3 Probability distributions of browse

(including C_3 grass, C_4 grass and C_3 and C_4 crops, without distinguishing between types of C_3 crops.

August-October represent the Late Dry season,

November-January the Early Wet, February-April Late

Wet and June-July Early Dry season.

Table C.1. Estimated percentages of vegetation species in elephant diet as estimated via the Bayesian tracer mixing models.

Month	Season	Gelman diagnostics (>1.1)	DIC	Non-crop C3 in % (browse)	C4 grass in %	C4 crops in %	C3 crop in %
August	Late Dry	4	36.50	23.9 ±14.0	9.3 ±4.6	0.6 ±2.0	66.2 ±16.6
September	Late Dry	4	36.50	14.5 ±14.3	5.9 ±4.1	0.4 ±1.4	79.2 ±17.0
October	Late Dry	4	36.50	58.1 ±11.5	14.3 ±5.3	1.1 ±3.6	26.4 ±13.1
November	Early Wet	0	94.92	75.8 ±7.1	23.5 ±5.9	0.2 ±1.6	0.5 ±5.2
December	Early Wet	0	94.92	72.5 ±6.5	26.8 ±6.0	0.3 ±1.8	0.4 ±4.2
January	Early Wet	0	94.92	62.6 ±6.3	36.6 ±6.5	0.4 ±2.9	0.4 ±3.9
February	Late Wet	0	78.44	38.9 ±16.7	49.6 ±10.9	0.9 ±4.4	10.6 ±20.6
April	Late Wet	0	78.44	50.3 ±21.2	35.7 ±10.8	0.6 ±2.8	13.4 ±25.7
June	Early Dry	0	33.35	45.4 ±17.7	4.9 ±4.3	0.2 ±1.0	49.5 ±20.4
July	Early Dry	0	33.35	21.4 ±13.8	3.6 ±3.4	0.1 ±0.6	74.9 ±16.1

Supplementary information D

D 1. Political Ecology and Decision-making

D 1.1 Political ecology framework

Understanding decision-making has always been a part of political ecology, especially when the focus is on risks and hazards, and where decisions to buffer and mitigate are critical (Turner & Robbins 2008; Robbins 2004; Robbins et al. 2015). In the analysis of decision-making, the focus in political ecology lies on the involvement and exclusion of groups of people in decision-making processes and how these reflect, alter or reinforce relations of power (Robbins, 2012; Sovacool, 2018). Descriptive political ecology research has given crucial insights in the often negative interactions between farmers and conservation and interventions of NGOs (Massé, 2016). These seemingly local factors affecting farmers' decision-making can be influenced by larger scale regional, national, or even international factors and political powers that define the social, political, and economic setting of the questions (Turner & Robbins, 2008; Massé, 2016).

Within conservation science, a political ecology framework has shown that biodiversity degradation can be related to the failure to address the power struggles between different groups of people over access and use of natural resources in conservation interventions (Simsik, 2002). For example, feminist political ecological research has uncovered that when humans co-exist and compete with wildlife over resources, women bear a disproportionate amount of the 'hidden costs', like psychological impact, workload and financial burden (Ogra, 2008). Effective implementation of interventions therefore depends on taking these power relationships into account and strengthening

the relationships between those involved (Madden & McQuinn, 2014). Those conducting research within the realms of human-wildlife co-existence are also required to be aware of this, as farmers' reports on issues with wildlife are not only based on actual accounts, but reflect their perceived social status compared to government and conservation authorities and in particular the researchers themselves (Naughton-Treves & Treves, 2005). Finally, conservationists are warned against simplification of the social and cultural complexity of those groups of people (e.g. small-holder farmers) involved in conservation interventions (Evans & Adams, 2016).

Political ecology has also given us insights specific to elephant crop consumption and other sources of physical and material issues and conflict between elephants and farmers (Ogra & Badola, 2008; Ogra, 2008; DeMotts & Hoon, 2012; Evans & Adams, 2016). These situations are not only a reflection of competition or disagreements between humans and elephants, or amongst humans, but also of materials such as alcohol, as both human and elephant alcohol consumption play an important role in driving physical conflicts in India (Barua, 2014a). The political ecology perspective also reveals the expansion of war-time ethics to the conservation discourse, by dehumanizing poachers and accepting shoot-on-sight practises as morally justifiable (Neumann, 2004). It also leads to consider the complexity of the involvement of powerful actors such as government agencies and (international) NGOs in supporting farmers to live with elephants, as instead, this support can express and reinforce authority and ownership, and thus disempower farmers (Ogra & Badola, 2008; Ogra, 2008; DeMotts & Hoon, 2012; Evans & Adams, 2016). Furthermore, those to whom (non-) governmental agencies provide elephant deterrent methods should be considered for what they are: not one homogeneous subject, but a collection of different types and scales of farmers, with different cultures, needs, abilities and options (Evans and

Adams, 2016), which is likewise the case for elephants (Chiyo et al., 2012; Barua, 2014b; Evans & Adams, 2018).

D 1.2 Farmer decision-making theory

The literature on farm management decision-making (FMDM) is vast. A subgroup focuses on how farmers actually make decisions (Kim & Cameron, 2013). Factors mentioned range from internal aspects, such as farmers' attitudes and characteristics, to external factors like environmental and economic factors, government policies, farmers' preferred information sources, the role of this information and information systems (Kim & Cameron, 2013). These factors can be grouped as agricultural and environmental regulation, economic factors, physical conditions, social factors and personal/psychological factors (Malawska et al., 2014).

To better understand farmer's decision-making concerning conservation initiatives, the theory of planned behaviour is an appropriate conceptual framework (Beedell & Rehman, 1999; St John et al., 2010; Milner-Gulland, 2012; Noga et al., 2015). The theory distinguishes three behaviour predictors: personal attitudes, perceived norms and perceived behavioural control (Fishbein & Ajzen 2010). Personal attitudes represent individual attitudes and beliefs about the potential behaviour, while perceived norms are beliefs about the norms and expectations of others regarding this behaviour. Finally, the decision to do or not do something is determined by perceived behavioural control, which is based on the power attribute to self-efficacy, like skills and material resources, and the freedom to choose to do or not do something (Ajzen & Fishbein 1980; Ajzen 2010; Vallerand et al. 1992). The first two elements are based on behavioural and normative beliefs and could be grouped as 'attitudes', which for decades have been assumed to influence decisions (Ajzen & Fishbein 1980). The more favourable we

perceive these attitudes to be, the stronger our intention to perform a particular behaviour (Ajzen & Fishbein 1980). The third factor is not an attitude, but it describes the perceived restrictions and enhancements of the behaviour, and the person's perspective of the degree that they are capable to perform a behaviour and have control over it (Fishbein & Ajzen 2010; Ajzen & Fishbein 1980). All three of these factors together determine the readiness and intention of a person to perform a type of behaviour. Nevertheless, it is still possible that the intended behaviour does not occur, due to the actual behavioural control measures like the lack of skills and abilities or presence of environmental constraints (Fishbein & Ajzen 2010).

Although these three predictors are expected to influence decisions to different extents, conservation science tends to focus on attitudes, therefore studies including perceived behavioural control are limited (St John et al., 2010). Perceived behavioural control can be measured by asking direct questions regarding the informant's ability to perform a behaviour or indirectly about the beliefs they have regarding specific factors that influence their ability to conduct the behaviour (Ajzen, 2002). In order to understand why farmers apply or do not apply mitigation measures, and ultimately how conservationists can effectively assist them co-existing with elephants, we need to understand farmers' reasoning behind their responses to these conservation interventions, and in particular about their perceived behavioural control. On a regional or landscape level agent-based models seem promising in achieving this (Milner-Gulland et al., 2006; Malawska et al., 2014). Yet, we argue that we need to start by focussing on ethical reasoning –reasons defined by the respondent themselves- and not emic reasons –as defined by the researcher (Gladwin 1989). This will allow farmers to identify those factors considered crucial in their decision making themselves, and avoid us focussing on factors that are not important, or even overlook unobvious factors

(Pattanayak et al., 2002). Ethnographic decision models allow us to identify these ethic decision criteria, and identify farmer types with different overall strategies (Gladwin, 1983; Darnhofer et al., 2005).

D 1.3 (Non-) adoption of crop consumption mitigation methods by farmers

While we lack insight on farmers' reasoning behind (non-) adoption of elephant deterrents, we know from research on other mammal species that farmers prefer to implement methods that are effective, sustainable, locally appropriate, cost-effective, easily manipulated to adapt and with minimal labour input (Hsiao et al., 2013).

According to farmers, the methods that match most of these criteria when it comes to bush pigs and baboons are paid guards, guard dogs, wire fences, lights and alarms.

Factors that reduce the sustainability of methods and the likelihood of uptake are costs, weather, labour, termite damage and theft (Hsiao et al., 2013). Other research on wild boar deterrents showed the importance of distance of the field to roads, the size of the field, topographical features, conducting non-farm activities, and the gender of the farmer to influence deterrent choices (Hua et al., 2016).

Most of our knowledge on farmers' reasoning behind the adoption or non-adoption of mitigation methods to deter elephants is based on anecdotes on individuals' investments to adopt methods on own initiative, or sporadic farmers' opinions mentioned in the evaluation of mitigation intervention experiments (Sitati & Walpole 2006; Sitati et al. 2005; Connell-Rodwell et al. 2000). Examples of these are one farmer who privately bought a trip alarm after experiments (O'Connell-Rodwell et al., 2000), the evaluation that farmers with large farms choose to have fewer guards and rely more on physical barriers (Sitati et al., 2005), and that farmers increase their field size because of the

success of chilli fence and early warning systems (Sitati & Walpole, 2006). Some studies do include more in-depth and systematic reviews of farmers' perspectives on innovative methods such as beehives (Noga et al. 2015; Noga et al. 2017) and chilli-fences (Wiafe & Sam, 2014; Noga et al., 2015, 2017). In Ghana, information distribution on the construction and effectiveness of chilli fences increased the uptake of the method, while costs involved in construction and maintenance of the fence prevented farmers from adopting this strategy (Wiafe & Sam, 2014). Contrary to expectation, in northern Botswana the uptake of innovative mitigation methods with chilli or beehive fences did not directly reflect farmers' attitudes, income and risk aversion (Noga et al., 2015). However, for Botswana farmers, risk aversion could play a minimal role in agricultural decisions in general, due to the intense support of the government providing a social safety net that reduces individual investment costs and risks (Gupta, 2013). Instead, non-adoption appeared to be related to inadequate involvement and consultation of local farmers in the implementation of interventions, limited resources available and ambiguities regarding project implementation (Noga et al. 2015; Noga et al. 2017). Despite these valuable insights in farmers motives behind the adoption of innovative measures, there is a countermovement away from innovative mitigation methods, that aims to reconsider the importance of (traditional) farm-based methods that are easy and low-cost to implement (Osborn & Parker, 2003; Graham & Ochieng, 2008; Noga et al., 2017). Of both these farm-based and innovative methods, it seems that farmers decide not to maintain deterrent methods if they experience labour constraints related to the fear of the indirect cost to their material (e.g. burglary) and human capital (e.g. health, education; Noga et al. 2017; Osborn & Parker 2002).

D.2.1 Full Oral Information Giving and Consent

Seeking Process

Hello, my name is Susanne Vogel. I'm doing some research and I wondered if you'd be interested in being involved. I'm currently a PhD at the University of Oxford in Zoology and I work together with the NGO Ecoexist. My research is on elephant crop consumption. Can I tell you more about the study? *[Await confirmation]*

In my study, I want to investigate how adult farmers try to mitigate elephant crop consumption. We selected you to ask you some questions randomly from a list of all the farmers of this village. If you choose to be a part of this project, here is what will happen:

- I will have a conversation with you where I will ask a whole range of questions about how you make decisions about your farm, how you are affected by crop consumption of elephants, and how you try to mitigate crop consumption.
- The answers you give will form the basis of my PhD thesis. The personal information you will share with me will not be passed to any third party. After we have conducted the interview I will remove any information that may be used to identify you so that afterwards not me or anybody else will be able to find out that you gave these answers. After we have finished interviewing farmers in every village I will give the anonymous results back to Ecoexist and we will make sure that you will hear what the results of the study are.
- This research is anonymous, which means that in any publications, your name will not be used. Killing an elephant when it is not threatening yourself or possessions (crops etc.) is illegal. Therefore, when I am told about incidents of killing of elephants and the police asks me about this, I may need to tell them, so

if you are concerned about this, please do not tell me about illegal activities of you or others.

- Taking part is completely voluntary and we can stop any time you like without giving a reason and without any negative consequences.
- With your permission, I would like to make an audio recording of our discussion to make sure I'm getting an accurate record of your thoughts. Alternatively, I can take notes in my notebook. Which would you prefer? I may want to re-contact you to clarify information you gave me in your interview. In that case, I will ask you if you have time to answer some more questions.
- If you agree to take part in this project, the research will be written up as part of my thesis.
- On successful submission of the thesis, it will be deposited both in print and online in the University archives, to facilitate its use in future research.
- The research may also be published in academic journals.
- If you have any complaints or concerns please feel free to contact me in the first instance. My mobile is 0026773388767. You can also reach me at Susanne.Vogel@zoo.ox.ac.uk.
- This research project has been reviewed and approved by an Oxford University ethics committee. If, after contacting me with any concern, you remain unhappy and wish to make a formal complaint, please contact the ethics committee. Their email is ethics@socsci.ox.ac.uk. I will also give you their postal address and this project's ethics reference number. If you do not know how to email, please request xxx (Eco officer of the current village) and they will be able to email for you.
- Do you have any questions?

- If at any time you have a question, or you do not understand my question, please let me know.

[Oral consent seeking stage, after participant has had sufficient time to think about whether s/he wants to take part]

- Do you give your permission for me to interview you? Do you give me permission to audio record you?
- Are you over 18? Are you happy to take part?
- Ok, thanks, in which case let's start.

D.2.2 Interview scheme of EDM testing phase

A. Traditional fences (bush fence: BF, wire fence: WF)		Yes	No
1.	Do you, your children or your partner have paid work?	3	2
2.	Do you have another source of income [e.g. ISPAAD]?	3	BF
3.	Is wire fence alone [so without bushfence] sufficient to keep small animals from coming into your field?	WF	4
4.	Was there nobody to help you make the bush fence?	WF	5
5.	Is your bushfence broken [by elephants]?	WF	WF +BF
6.	Do you use bushfence against elephants eating crops? Do you use wire fence against elephants eating crops? Why/Why not?		
B. Tin cans (TC)		Yes	No
1.	Is there a bottle store or bar nearby?	4	2
2.	Did Ecoexist give you tin cans?	4	3
3.	Can you collect tin cans in town [like from dustbins]?	4	No TC
4.	Is cropraidding not a big problem anymore [solved]?	No TC	5
5.	Do you have no wire to put tin cans on [or string, or tree rope]?	No TC	TC
6.	Do you use tin cans against elephants eating crops? Why/Why not?		
C. Plastic (P)		Yes	No
1.	Does plastic <u>never</u> work against elephants [entering]?	2	P
2.	Does plastic help against other animals [birds]?	P	No P
3.	Do you use plastic against elephants eating crops? Why/Why not?		

D. Torch (To)		Yes	No
1.	Do you, your children or your partner have paid work?	3	2
2.	Do you have another source of income [e.g. ISPAAD, elderly people income]?	3	No To
3.	Do torches attract elephants and/or make them aggressive?	No To	4
4.	Are torches sold out/ not for sale?	No To	5
5.	Is your torch broken or are your batteries finished?	No TC	TC
6.	Do you use a torch against elephants eating crops? Why/Why not?		

E. Chillies (Burning chilli: BC, Chilli fence: CF)		Yes	No
1.	Have you heard about using chillies?	2	No BC, No CF
2.	Have you (ever) been given chillies?	4	3
3.	Do you plant chillies?	4	No BC, No CF
4.	Have you been given poles and wire?	6	5
5.	Can you buy or make poles, wire and cloths?	6	7
6.	Did elephants break your chilli fence?	7	9
7.	Is crop raiding not a big problem anymore?	No BC, No CF	8
8.	Did you finish your chilli?	No BC, No CF	BC
9.	Did you finish your chilli?	No BC, No CF	BC, CF
10.	Do you use a chilli fence against elephants eating crops? Do you use burning chilli against elephants eating crops? Why/Why not?		

F. Beehive fence (BH)		Yes	No
1.	Have you heard about using beehives against elephants	2	No BH

	entering the field?		
2.	Can beehives [sometimes] help against elephant crop raiding?	3	No BH
3.	Have you been given material for beehives?	4	No BH
4.	Can you not find bees?	No BH	5
5.	Do you use a beehive fence against elephants eating crops? Why/Why not?		

G. Electric fence (EF)		Yes	No
1.	Have you heard about using an electric fence against elephants entering the field?	2	No EF
2.	Have you been given material for an electric fence?	EF	No EF
3.	Do you use an electric fence against elephants eating crops? Why/Why not?		

H. Trench (TR)		Yes	No
1.	Have you heard about using a trench against elephants entering the field?	2	No TR
2.	Do you have more than seven people working on your field?	3	No TR
3.	Do you have digging tools?	4	No TR
4.	Are you worried about animals falling in trenches [elephant or farm animals]?	No TR	TR
5.	Do you use a trench against elephants eating crops? Why/Why not?		

I. Shouting (S)		Yes	No
1.	Does shouting <u>always</u> attract elephants or make them	No SH	SH

	aggressive in the field?		
2.	Do you use shouting against elephants eating crops? Why/Why not?		
J. Drumming/clapping (DR)		Yes	No
1.	Does drumming/clapping <u>always</u> attract elephants or make them aggressive in the field?	No DR	DR
2.	Do you use drumming or clapping against elephants eating crops? Why/Why not?		
K. Fire (F)		Yes	No
1.	Does fire <u>always</u> attract elephants or make them aggressive in the field?	No F	F
2.	Do you use fire against elephants eating crops? Why/Why not?		
L. Watch hut (WH)		Yes	No
1.	Do you guard your field at night when the crops are maturing?	WH	No WH
2.	Do you use a watch hut against elephants eating crops? Why/Why not?		
M. Dogs (Do)		Yes	No
1.	Do you have a dog or dogs?	2	No Do
2.	Do elephants <u>never</u> run away from dogs?	No Do	Do
3.	Do you use dogs against elephants eating crops? Why/Why not?		

N. Location (Loca)		Yes	No
1.	Did you pick [the location of] your field?	2	No Loca
2.	At the time of picking the plot, did elephants use pathways [some places] more than others [or are they everywhere the same amount]?	3	No Loca
3.	Do the plots inside the pathways [areas more used by elephants] have better soil or better vegetation than those outside?	No Loca	Loca
4.	Did you take elephants into consideration when picking your field? Why/Why not?		
O. Crop type (Crop) and crop composition (Comp)		Yes	No
1.	Do elephants eat some crop types more than others?	2	3
2.	Do you plant everything that you need in our field [or can you buy/get things you need somewhere else]?	3	Crop + Comp
3.	Can you hide crops that elephants like from them?	No Crop + Comp	4
4.	Should you guard some crops better against elephants than others?	No Crop + Comp	No Crop + No Comp
4.	Do you think about elephants when you decide which crops to plant? Do you think about elephants when you decide where to plant which crops? Why/Why not?		

P. Timing (Early)		Yes	No
1.	Are you a conservation agriculture farmer [from Ecoexist]?	Early	2
2.	Do you [or your husband or other relative] have your own ox and mould?	3	No Early
3.	Did the rains come early [this ploughing season]?	Early	No Early
4.	Did you plough early this ploughing season [before Christmas]? Why/Why not?		

D.3 Summary of Focus Group Discussions

In January 2017 we conducted four focus group discussions (FGD), in the Kgotla (community meeting area) of the villages Eretsha, Gunotsoga, Beethsa and Seronga. We invited farmers informally through snowball sampling. Formal discussion took place after lunch and for approximately one hour, during which we provided two rounds of drinks and a variety of cookies. The farmers, main researcher, the local Ecoexist community officer (Eco) of the village and a translator from Eretsha who was trained in interview techniques were present during the meeting. Focus group discussions started with general dialogue about the crops the farmers planted, the time of planting of the crops, the role of the government in providing information, material and financial support, and the role of private organisations (NGOs) in providing information, material and financial support. These private organisations usually meant Ecoexist or the World Bank. Finally, we spoke about the help farmers received from both government and these private organisations. After this we played a 'living with elephants game' developed by the main researcher, based on decision modelling techniques described by Redpath et al., 2004. After discussing the full oral information giving and consent seeking process (supplementary information A.1) we explained the rules of the 'living with elephants game'. During the game, we asked farmers about their experiences of living with elephants in relation to the following categories: family, materials, environment and money. After the farmers mapped out all the impacts of elephants on these aspects of their lives, we asked them to rate the severity of each of the recorded impacts by placing numbered cards around the mind maps, after coming to a mutual agreement on this score. During the second phase we asked farmers to go over all methods available to reduce the impact of elephants on their life, and rate how effective each of these methods was in solving the impacts of elephants in the different

categories, when applicable. We finished the meeting by specifically discussing positive aspects of living with elephants, as these generally did not appear during the game. Conversations were in language most farmers felt comfortable with, usually Setswana. We aimed to disturb the conversation as little as possible, therefore only intervened in the game or conversation if there was a misunderstanding of procedures or translation.

D.3.1 Eretsha

*Present: Four female farmers (ages 66, 43, 36, 24) and one male farmer (age 55),
Susanne Vogel, Mikel (Kenneth) Manyetse and Namu (Debig) Mokgosi.*

D.3.1.1 Agricultural decisions and support

Farmers prefer to plant millet, there are different seed varieties they use and sometimes they keep seeds in their save box to save them for next time. Pumpkin and maize were also preferred species; they are best ploughed at the start of the early rainfall, and grow well in termite mounds. Other species they planted were cowpeas, groundnut, Jogo-beans, sweet reed, sorghum and watermelon.

Farmers start ploughing in early December and apply nutrients and natural fertilizers to their fields. The government gave them advise to: remove weeds, plough on time, use early seeds as they are good for early harvest, to grow on lines ('row planting'), and encourages them to different crop types and use crop rotation schemes. The government also provided farmers with materials: seeds like millet, beans, sorghum, maize, they also received a tractor to share however they can not use it because there are too many tree stumps in the field and it is too difficult to remove them all. Previously, farmers have been given chilli and beehive fences from the government, but there were no bees. The government also provided financial support is farmers applied row planting, of 800

pula per hectare. The Botswana marketing board sometimes comes to buy crops after harvest. Private organisations provided advise to dig basins, plant in rows/lines, take leaves and manure and spread it across the fields to avoid water to evaporate. They also motivate farmers to plant earlier. They have not received material, because they are not conservation agriculture farmers. Some of them are given electric fences or a normal fence, and others were given hoes. The government helped with elephants by providing chilli through the Department of Wildlife and National Parks (DWNP) in 2012.

However, the trial ended and there was not enough monitoring, they expected elephants to continue to raid, as it was difficult to grow enough chilli. If the elephants destroy your crops, the government will come and compensate, but not enough. Private organisations help with living with elephants by motivating to do cultural fairs, where they were asked to come up with topics, for example a drama about conflicts between humans and elephants or making drawings. People that take part get money and afterwards they get information and learn about how elephants act, behave and how to deal with them. For example, what to do when you come across an elephant and how you notice it charges.

D.3.1.2 Results ‘Living with elephants’ game

Category	Impact of living with elephants	Score
Family	Can not enter field or work in the field	5
	Disturbance of movements, can not go to the toilet	4
	Children can not go to school	5
	Disturbance of herding	3
	Comprise safety: when in danger they kill or injure people	5

	Disturbance of fetching water	4
	Hunger	5
	Disturbance of playing children	2
Material	Destroying of watch huts	4
	Destroying of tools (axes, hoes)	5
	Destroying of bush fence and wire fence	5
	Messing up the road (dung, dirty)	1
	Falling down of trees on the road, can not pass	3
	Destroying of water ditches	5
Environment	Taking all acacia thorns, that farmers need for bush fences	5
	Distorting the shape of the environment (badly)	5
	Digging holes in nature and the road	4
	Reducing shade by destroying trees	3
	Destroying natural resources, like trees (Marula trees)	5
	Eat fruits that people also eat	4
Money	Can not sell wild fruits	4
	Disturb local fisher men, can not sell fish	5
	Need to buy need equipment (box to collect tools, shoes)	5
	Local crafts men can not use wood: elephants disturb the collection and destroy trees	5
	Need to buy new fence as elephants destroys	5
	Can not sell crops because the elephant eats	5
	Destroys grass to make a roof on houses	5

D.3.1.3 Effectiveness of mitigation methods

Method	Score	Reason
Bush fence	2	Can keep elephants out if it is thick
Beehive fence	1	Not sure it works, no proof
Electric fence	5	Sure it works
Wire fence	2	Works
Chilli fence	3	Sometimes works
Tin cans	4	They make good sound
Plastic	1	Elephants can touch it and still enter
Watch huts	3	It is good to stay and guard
Dogs	4	It sometimes helps, they can warn for danger
Burning chilli	4	According to the condition it can work, if there is no wind or rain it does not work
Torches	4	Are good to scare elephants

D.3.1.4 Closing comments and positive experiences

Elephants keep them from ploughing all the way up into the woods. Elephants are easy to see, but sometimes it is difficult in the dark. Elephants bring tourists to the area.

Elephants are pruners of the wild; they keep the environment alive, like the mopane trees. Their tracks can take you to the river if you are lost. Elephants are big and seen from a distance, if elephants were lions there would be no more people, elephants are better than lions.

D.3.2 Gunotsoga

Present: Three female farmers and two male farmers (ages: 52, 79, 61, 47, 64), Susanne Vogel, Mikel (Kenneth) Manyetse and Boiteko Tlale. Gunotsoga is the village in which Ecoexist supports some conservation agriculture farmers, two of the farmers in our focus group belonged to this project.

D.3.2.1 Agricultural decisions and support

Farmers prefer to plough cowpeas, beans, millet, maize, groundnuts, sorghum, watermelon, pumpkin, sweet reeds and Jogo-beans. One farmer expresses the importance of these crops: “We live with that to survive, it is our food, you can also sell them and take your children to school”. The government advised the farmers to plough early at the first rainfall, the government motivates them not to plough fields in the paths of elephants, and they teach and explain about early seeds. They also provide farmers with materials such as wheel barrels, rakes, digging tools, ropes, poles, wire fences, lamp poles and watering cans. The government provides financial support when farmers plough in rows; they pay per hectare. Private organisations train farmers to dig basins in rows and teach them skills, for example on how to use chilli. Conservation agriculture farmers are taught how to grow crops in basins and use a small space for farming. They also receive materials like chilli, hoes, digging tools and buckets. They do not receive any financial support from private organisations. The government supports farmers in living with elephants by providing compensation, but elephants destroy lots, and the compensation is less than before and only a little amount. Private organisations support farmers in living with elephants by providing them with information explaining on how to use chilli to chase elephants away. One farmer who was not a conservation agriculture farmer mentioned that she heard about this from

conservation agriculture farmers. They also received information to stay at the field after ploughing and guard. Finally, they received material support of chillies, and people in Kacherachera (cattle post) and Xakao.

D.3.2.2 Results ‘Living with elephants’ game

Category	Impact of living with elephants	Score
Family	Kill people, safety	5
	Loose crops, hunger	5
	Cannot go to the cattle post to protect the cattle from being killed by lions and milking the cows	5
	Stops children from going to school	4
	Stops people from gathering firewood	3
	Stops people from fetching water	5
Material	Break/looses tools (axes, hoes)	5
	Destructs cars	4
	Break trees on the path to the fields	3
	Destroy watch hut	
	Destroy bush fence	4
	Destroy kraals and kill cattle	5
	Break poles of fences	5
Environment	Finish traditional medicines for the future of children	4
	Cannot make traditional mats (they finish the papyrus)	5
	Finished reeds so there is nothing to make a yard fence	5

	Finished grasses for the roofing of houses	5
	Contaminate water (by urinating and dung)	5
	Finish jackalberry (breaking down trees)	5
	Finish waterlilly (traditional food, now they need a license to harvest because of conservation)	5
	Finish phuka (type of short grass), which is the natural vegetation (natural vegetables)	5
Money	No money for education (school fees, uniform)	5
	Less compensation from the government than they could have from selling the crops	5
	They need to buy material for maintenance (elephants break the fence)	5
	Loss of crops is no money for clothes	5

D 3.2.3 Effectiveness of mitigation methods

Method	Score Crops	Score Cattle
Bush fence	1	
Beehive fence	1	
Electric fence	5	
Wire fence	1	
Chilli fence	1	
Tin cans	4	
Plastic	1	

Watch huts	5	
Trenches	1	
Gun	5	
Dogs	2	2
Burning chilli	5	
Torches	5	5
Shouting	4	
Fire	4	
Drumming	3	

D.3.2.4 Closing comments and positive experiences

Elephants are a source of income, it creates jobs for people in the community, it brings tourists. Okavango community trust employed some people; it is voluntary though and has only a few benefits. The importance is for the government, they bring the tourists, and the only purpose of elephants is for the government.

D.3.3 Beetscha

Present: Three female farmers and three male farmers (ages: 34, 23, 25, 36, 29, 50),

Susanne Vogel, Mikel (Kenneth) Manyetse and Maipelo Molathegi.

D.3.3.1 Agricultural decisions and support

Farmers like to plant millet, sorghum, maize, watermelon, pumpkin, Jogo-beans, groundnuts, cowpeas, sweet reeds. Farmers choose to plant maize, cowpeas and beans because you can sell them to the government, per 1 kg you receive 700 Pula. Millet

grows quick to maturity and beans are important for soup and porridge. Some of these crops need more rain than others.

The government gives farmers information about early seeds, which grow quickly. They also advise farmers to plant in rows, and make space between crops. The government motivates to dig own boreholes inside of the field to catch water, and motivates to have your own strong wire fence. They provide farmers with materials such as seeds for beans, cowpeas, sorghum, millet and maize, and fertilizer. They receive money from the government for row-planting, they give more money per hectare, so if you have a big field you will gain more money. Private organisations have provided farmers with information as well. The World Bank has thought farmers through the wildlife department [DWNP], and given poles, chilli and fences. The wildlife department teaches some people in their town and they then teach others. The government has not given the farmers any teaching about elephants, no materials and no compensation. Private organisations have thought farmers on how to use chilli, how to train dogs to chase elephants, and motivate to try and find electricity wires. They have provided farmers with wheel barrel, spades, fences, water cans, and chilli materials.

D.3.3.2 Results ‘Living with elephants’ game

Category	Impact of living with elephants	Score
Family	Cannot sleep well, stress	4
	Cannot gather firewood	5
	Hunger	5
	Cannot go to cattle post	3
	Attacks, safety	5

	Cannot go to field	5
Material	Break cars	5
	Break axes, hoes	4
	Destroy the house	5
	Destroy the fence poles	5
	Dig holes in road	4
Environment	Destroy materials for traditional medicine	4
	Can not make bushfence	5
	Makes water dirty and contaminated	5
	No wild fruits to eat (Jackalberry, Mokwa)	5
	Kill all the grasses, nothing left to fetch the house	5
	No shade (trees are collapsed)	3
	Take all the good tree species (trees go extinct)	4
	Take the water lilies (food)	2
Money	No money left for education	5
	No money for clothes	5
	Spend money on mitigation and assistance	5
	Loose crops = loose money	4

D.3.3.3 Effectiveness of mitigation methods

Method	Score Firewood	Score Can not sleep well	Score Attack, safety	Score Hunger
Bush fence				
Beehive fence				1
Electric fence		5	5	5
Wire fence			1	
Chilli fence		2	2	3
Tin cans		2	4	
Plastic				
Watch huts		4	2	5
Trenches		5	5	5
Gun	5	5	5	5
Dogs	2	2	2	2
Burning chilli		4	3	3
Torches	4	4	4	4
Shouting	4	4	4	
Fire				
Drumming		4	4	

D.3.3.4 Closing comments and positive experiences

Farmers were positive about elephants as an attraction of tourism, and a source of income by generating into jobs. They also mentioned that elephants decorate the environment and built the Okavango Community Trust and Ecoexist, however they mentioned that people that did not work there did not have a benefit. Elephants are important because an elephant can plant a tree that was not there by dropping dung from an other place, and elephants do a lot in a community, they bring herbs and grasses. Finally, they were positive about the meat of elephants. Famers also complained that in Namibia people can sell ivory for their poor families and eat elephant meat, while “in Botswana we have nothing: we own them, but we can not sell one elephant”.

D.3.4 Seronga

Present: Three female farmers and one male farmer (ages: 68, 76, 48, 39), Susanne Vogel, Mikel (Kenneth) Manyetse and Tsalano Florence Kgobero.

D.3.4.1 Agricultural decisions and support

Farmers preferred to plant maize, sorghum, millet, cowpeas, beans, groundnuts, Jogo-beans, sweet reed, watermelon and pumpkin. The farmers have grown up with these crops, they eat them every year, time and again, they contain nutrients, protein, fat. The government provided farmers with information on how to grown crops in rows (row-planting), to not depend on the government, they should provide from the farm, plough their own fields and the shop prices will go down. The agricultural department have given them forms to fill in, if you are lucky you win, some don't even know about

these forms. Things you can get with these forms are a mould, cattle, rake, wire fence, seeds, tractor (in Shakawe). Regarding financing, the government gives money if you do row-ploughing, 400 Pula per hectare. When asked about information they received from private organisations, farmers answered that the World Bank trained them to use chillies, 38 people were there, they talked about using chilli fences, there were lots of ideas, others thought about how to use dogs, or bees: this was a separate category, you choose what you wanted to do. The World Bank gives tools, technique etc. but the department of wildlife was in charge. The government also came to explain about elephants, they came to the Kgotla and explained the behaviour of elephants and how to behave around them, and what elephants like and not like. When you have damage by elephants they measure the distance and give you a little compensation. Other people got wire fence, but they do not have it.

D.3.4.2 Results 'Living with elephants' game

Category	Impact of living with elephants	Score
Family	Kill, injury, safety (orphans)	5
	Cannot go to cattle post	4
	Cannot go to clinic	5
	Lack of education, no money for uniform etc.	5
	Cannot share with extended family	3
	No future improvements	3
	One farmer raided affects many people (they sell to Beetsha)	5
	Loose crops: hunger	5
Material	Break and throw away hoes, rake, mould	5

	Destroy fence bush/wire/poles	5
	Oush down hut and eat all water melon, pumpkin and millet (the whole harvest)	5
	They make ditches in their road	3
	They destroy the watch hut at the field (there is no place to sleep)	5
Environment	Digs waterlilly and kill it (the farmers like to eat them with river potatoes and depend on it for food in the drought season)	5
	No trees: soil erosion, wind erosion that destroy the houses	5
	Makes water dirty (not suitable for drinking anymore)	5
	Kills grasses that they use to fetch the houses	5
	Destroy and break down all the trees: fruit trees, traditional medicine	5
Money	Loose money from employing people to plough	5
	No money for repairing bush fences	5
	Government sometimes don't pay compensations, sometimes elephants take the roots of the crops and then there is no proof of crop raiding	5
	Loose money because of raiding (beans 1kg=700 Pula, watermelon)	5
	No money to employ people to plough for you again next season	5

D.3.4.3 Effectiveness of mitigation methods

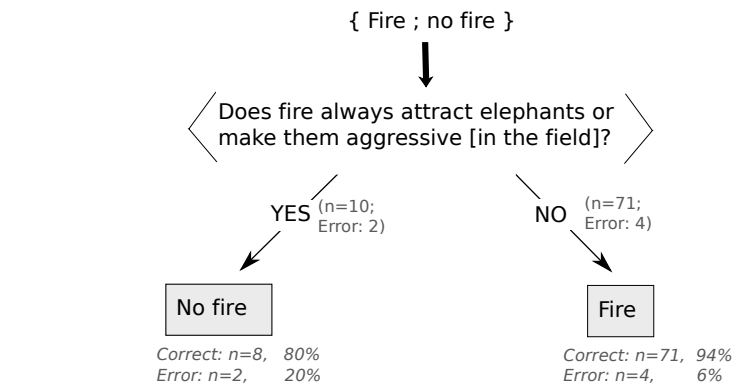
Method	Score Crop loss/ hunger	Score Kill, safety	Score Go to cattle post/ clinic	Score Lack of education, cannot share with extended family, 1 farmer raided many affected, no future improvement
Bush fence	1			
Beehive fence	1			
Electric fence	5			
Wire fence	1			
Chilli fence	2			2
Tin cans	2			
Plastic	1			
Watch huts	3			
Trenches	4			
Gun	5	5	5	
Dogs	1	1	1	
Burning chilli	4			
Torches	1	1	5	
Shouting	4	1	1	
Fire	3			
Drumming	4	1	1	

D 3.4.4 Closing comments and positive experiences

Elephants create jobs for their children (they give as an example the two Ecoexist employees present at the meeting). They also have ivory and bring tourists (clients) to watch the elephants. They are important because the farmers' children can learn from them, they just don't want them around their fields. They also want the electric fence. One lady has a chilli plot that is farmed by a farmers committee, near the boat station [in Seronga], but they want the chilli in their own plot.

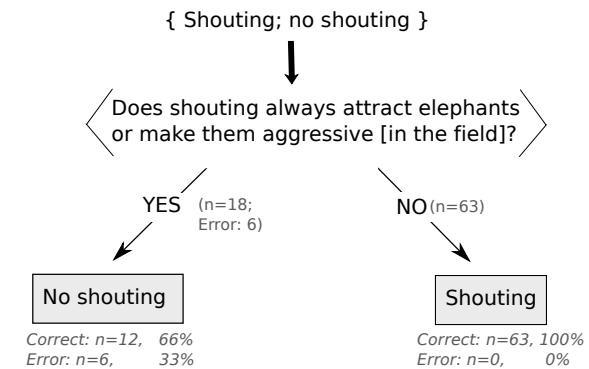
D.4 Supplementary EDM results Chapter 5

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Predictive accuracy

81 test cases
6 error
Correct prediction: 93%
Klecka's tau= 0.85



Predictive accuracy

81 test cases
6 error
Correct prediction: 93%
Klecka's tau= 0.85

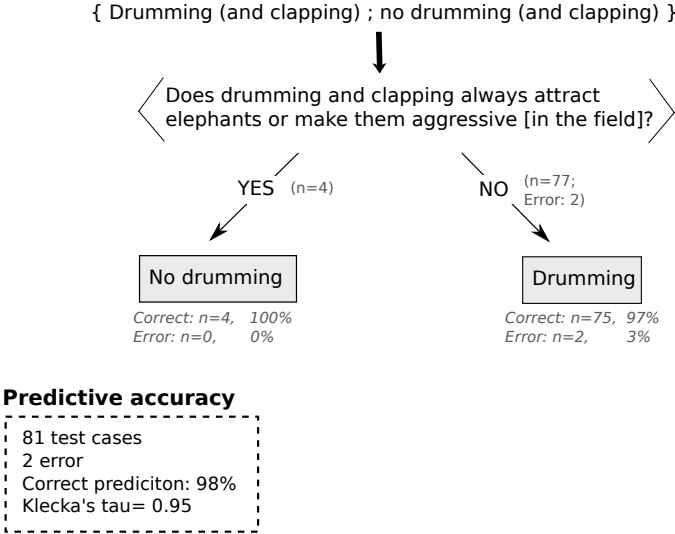


Figure D.3 EDM on the use drumming and/or clapping.

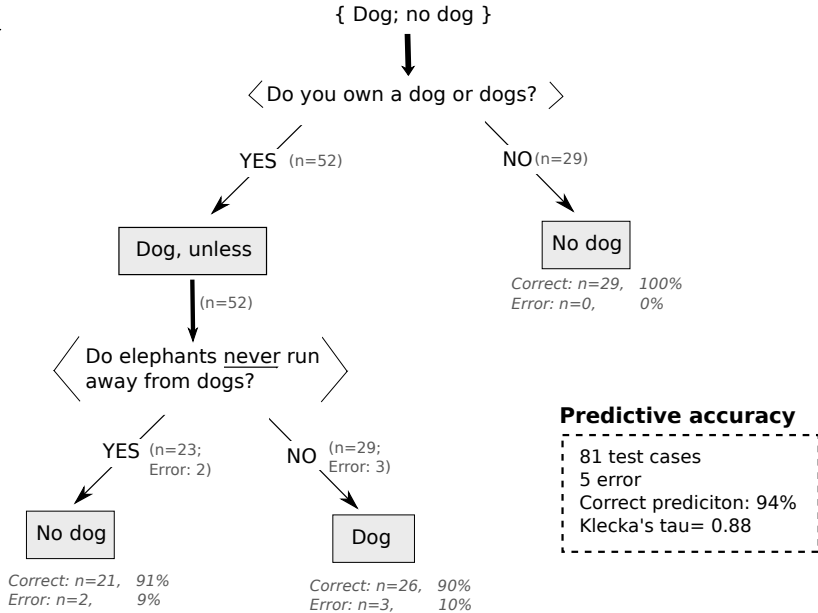
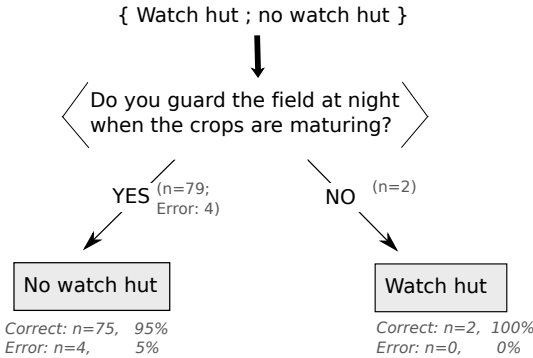


Figure D.4 EDM on the use of guard dogs.



Predictive accuracy

81 test cases
4 error
Correct prediction: 95%
Klecka's tau= 0.90

Figure D.5 EDM on the use of a watch hut.

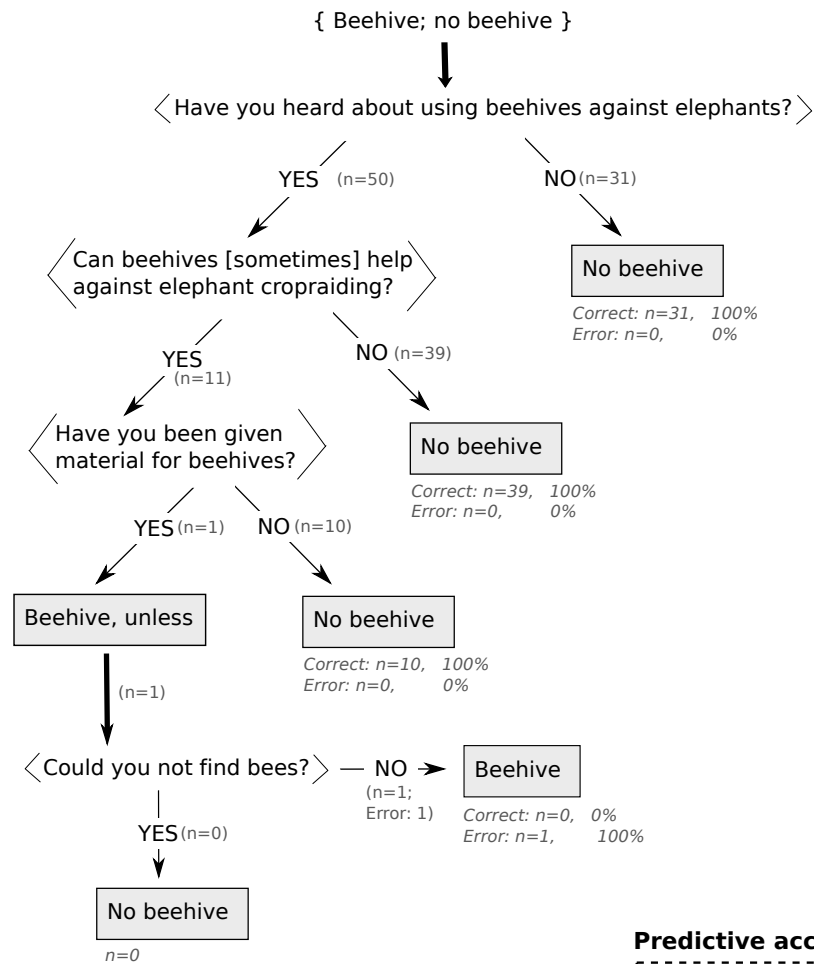


Figure D.6 EDM on the use of beehives.

Predictive accuracy

81 test cases
1 error
Correct prediction: 86%
Klecka's tau= 0.98

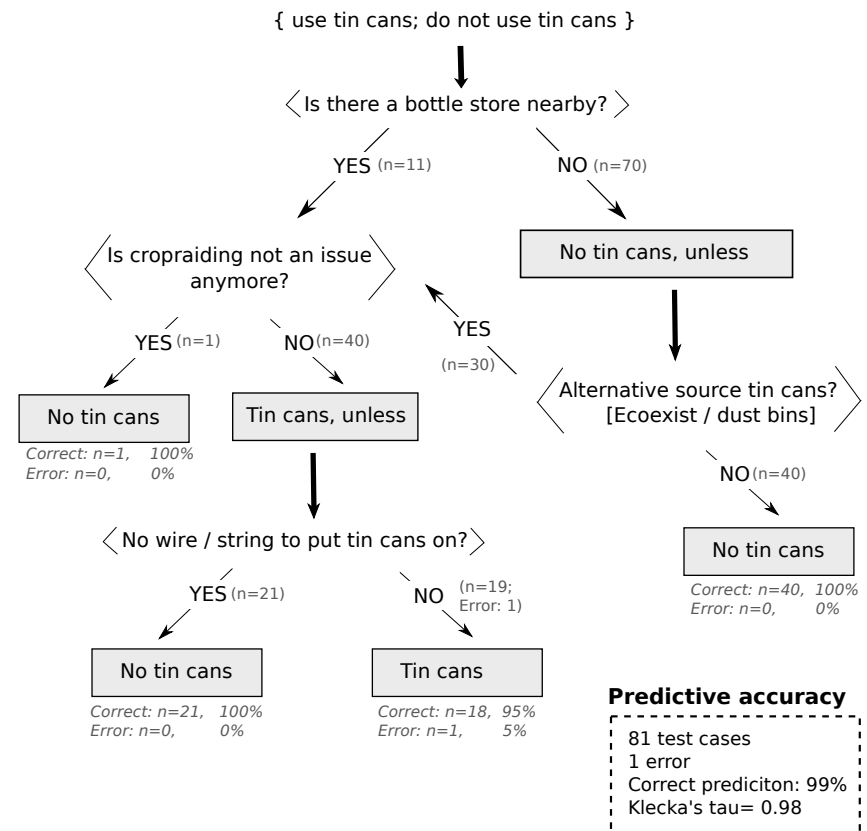


Figure D.7 EDM on the use of tin cans on fences.

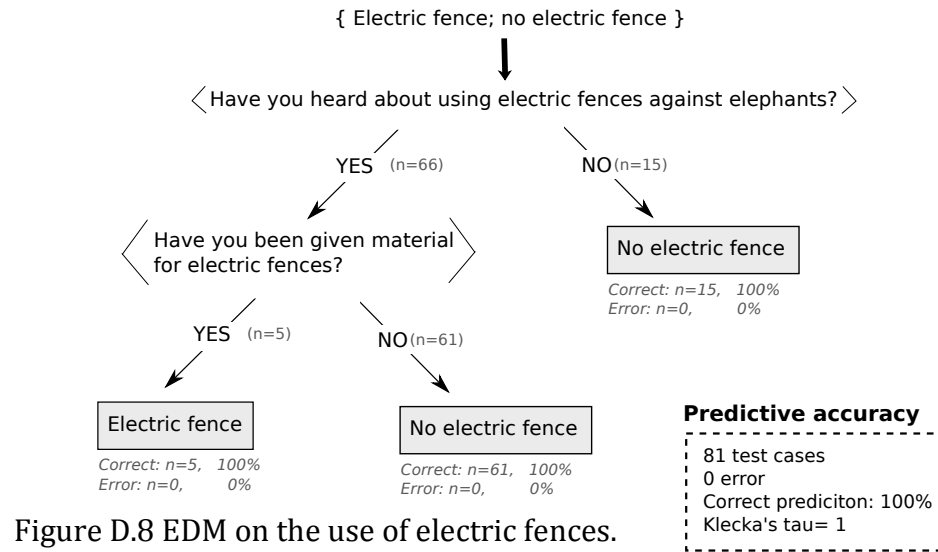


Figure D.8 EDM on the use of electric fences.

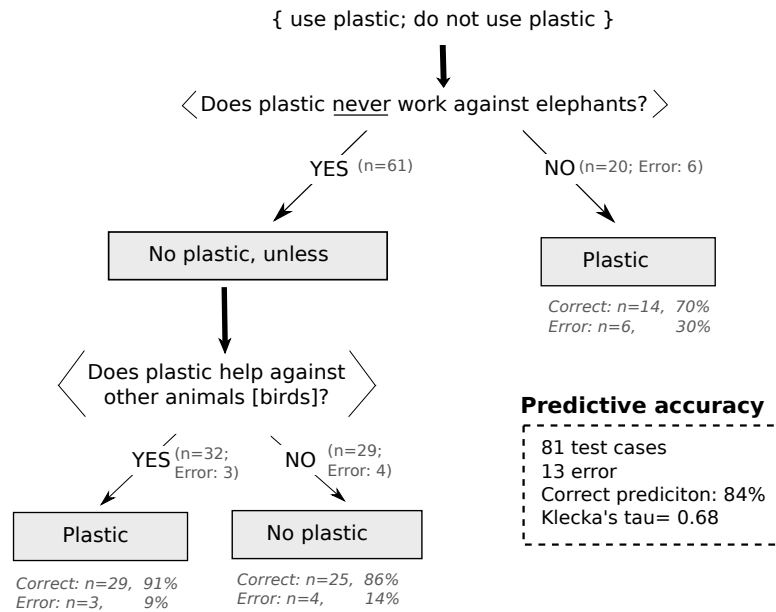


Figure D.9 EDM on the use of plastic on fences.

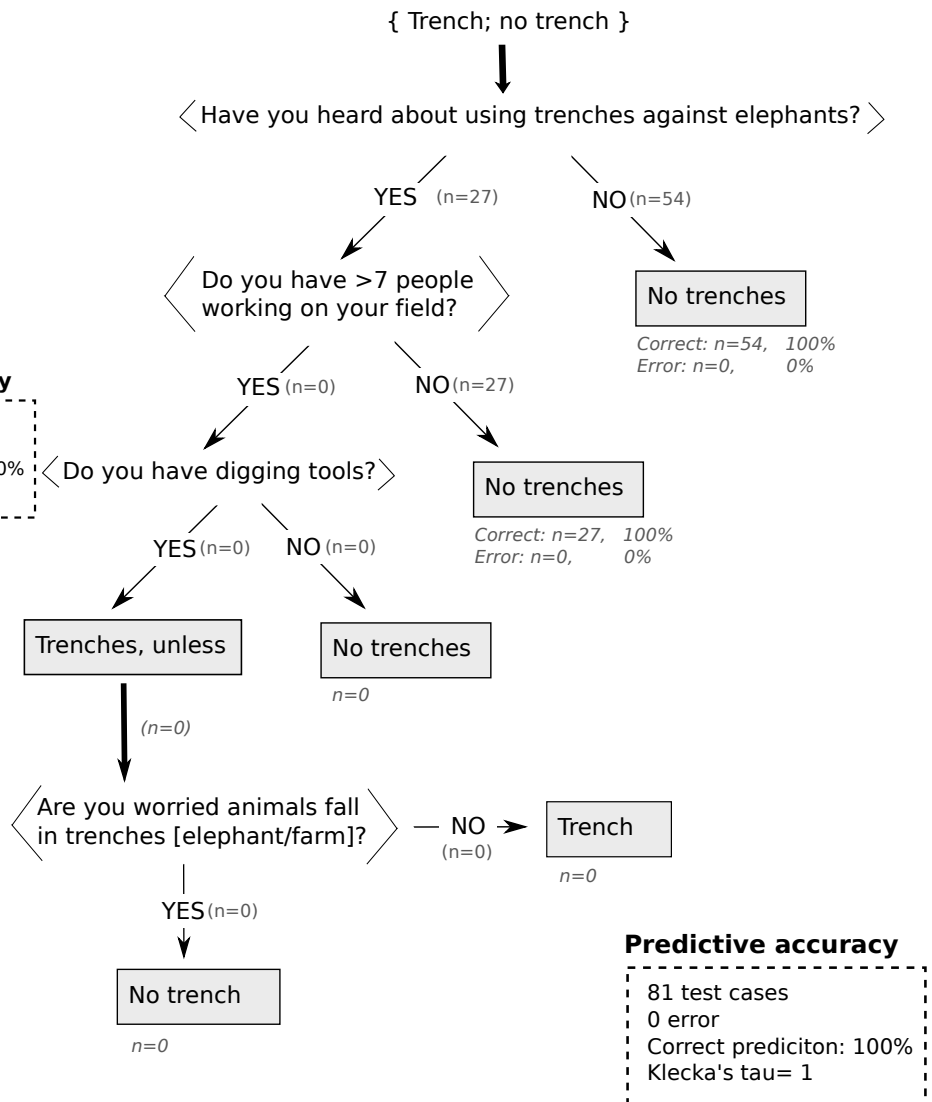


Figure D.10 EDM on the use of trenches.

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The blind men and the elephant

John Godfrey Saxe, 1872

I.

It was six men of Indostan
To learning much inclined,
Who went to see the Elephant
(Though all of them were blind),
That each by observation
Might satisfy his mind.

II.

The *First* approached the Elephant,
And happening to fall
Against his broad and sturdy side,
At once began to bawl:
"God bless me!—but the Elephant
Is very like a wall!"

III.

The *Second*, feeling of the tusk,
Cried: "Ho!—what have we here
So very round and smooth and sharp?
To me 't is mighty clear

This wonder of an Elephant

Is very like a spear!"

IV.

The *Third* approached the animal,

And happening to take

The squirming trunk within his hands,

Thus boldly up and spake:

"I see," quoth he, "the Elephant

Is very like a snake!"

V.

The *Fourth* reached out his eager hand,

And felt about the knee.

"What most this wondrous beast is like

Is mighty plain," quoth he;

"'T is clear enough the Elephant

Is very like a tree!"

VI.

The *Fifth*, who chanced to touch the ear,

Said: "E'en the blindest man

Can tell what this resembles most;

Deny the fact who can,

This marvel of an Elephant
Is very like a fan!"

VII.

The *Sixth* no sooner had begun
About the beast to grope,
Than, seizing on the swinging tail
That fell within his scope,
"I see," quoth he, "the Elephant
Is very like a rope!"

VIII.

And so these men of Indostan
Disputed loud and long,
Each in his own opinion
Exceeding stiff and strong,
Though each was partly in the right,
And all were in the wrong!

MORAL.

So, oft in theologic wars
The disputants, I ween,
Rail on in utter ignorance
Of what each other mean,

And prate about an Elephant

Not one of them has seen!