Seasonal effects on the ecology and sociality of male African elephants (*Loxodonta africana*) in the Okavango Delta, Botswana



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Abstract

Large mammals often migrate to survive seasonal changes. However, in an ever-changing world with increasing limitations put on movement of animals by humans, important resources are becoming more limited. It is therefore imperative that we fully understand the requirements of such animals if we are going to successfully conserve them into the future. African elephants, the largest land mammal, are facing an uncertain future due to recent increased poaching and conflict with humans. Seventy percent of the remaining African elephant population resides outside of protected area for part or all of their time.

The Okavango Delta in Botswana has a unique ecology; unlike other areas of Africa it does not have a distinct dry and wet season, as it is flooded annually. This system therefore presents a unique scenario for the African elephant, and an ideal opportunity to see how this affects the social and ecological systems of elephants. The annual flood fragments habitats for a plethora of mammalian species, resulting in limitations of food resources. Data were collected on elephants in the western Okavango Delta to assess the affects of season on the ecology of male elephants, specifically the numbers of male elephants utilising the area, their social groupings, their food selection and physical condition. The data I collected to answer these questions included daily elephant sightings, behavioural focal data and road transect surveys.

My study showed that seasonality played a pivotal role in the ecology and sociality of male elephants in the Okavango Delta. I found that the numbers of male elephants utilising the study area were not affected by an increase in the flood. However, the social groupings of male elephants were influenced by the seasons, with a higher number of lone male elephants sighted in the flood season compared to the rainy season. Season also affected their food selection, with male elephants feeding on a greater diversity of species in the flood season, when resources were limited. The flood also affected their group structure in that they tended to be more widely spaced.

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Declaration

I declare that the work contained in this thesis was carried out in agreement with the regulations of the University of Bristol.

The data sets from 2004 to mid March 2008 were collected by Dr Kate Evans and other members of Elephants for Africa and have been included in these analyses. Mr Simon Buckingham prepared the study area maps with the assistance of Mr Joseph Molekoa, Mr Thapelo Sebetlela, and Dr Kate Evans, and Helen Whiteside carried out the Generalised Linear Model(s) in R Version 10.2.1. With the exceptions that are indicated by special references in the text, I declare that the work in this dissertation is my own and no part of the dissertation has been submitted for any other academic award. The views expressed in this dissertation are solely my own and do not represent those of the University of Bristol.

Mphoeng Ofithile

March 2012

Dedication

This thesis is dedicated to my mother, grandmothers and my family and in the memory of Seba, an elephant that was released from captivity and killed by a farmer. He paid the price of the competition for space that threatens their existence, as do hundreds of elephants, which are killed each year. It is the reality of impending danger that elephants are facing as they increase their range into historical ranges now occupied by humans.

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Abbreviations

O	=	Degrees Centigrade		
CKGR	=	Central Kalahari Game Reserve		
DWNP	=	Department of Wildlife and National Parks		
EBS	=	Elephant Back Safaris		
EfA	=	Elephants for Africa		
GPS	=	Global Positioning Syfstem		
GLM	=	Generalised Linear Model		
km	=	Kilometres		
BE	=	Boma Ecosystem		
KTP	=	Kgalagadi Transfrontier Park		
SE	=	Serengeti Ecosystem		
MEWT	=	Ministry of Environment, Wildlife and Tourism		
m	=	Metres		
mm	=	Millimetres		
MNP	=	Makgadikgadi National Park		
Ν	=	Sample size		
NP	=	National Park		
Ρ	=	Probability		
WMA NG26	=	Wildlife Management Area Ngamiland 26		
Yr	=	Year		
X ²	=	Chi-square test statistics		

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Chapter 1

Introduction

1.1. Seasonal movements of mammals

Mammals have adapted to inhabit almost every ecosystem and survive in climatic conditions from the extreme cold, for example polar bears (*Ursus maritimus*), to the hottest regions, for instance gemsbok (*Oryx gazelle*). Throughout this range of habitats they are faced with dynamic changes that occur on a daily, yearly or more permanent basis. Consequently they need to adjust morphologically, physiologically and behaviourally to maximise their fitness in any habitat (Ramenofsky and Wingfield 2007). There are many examples of these sorts of adaptations. An extreme morphological adaptation to the cold is shown by the arctic fox (*Alopex lagopus*) and snowshoe hare (*Lepus americanus*), which grow a thick fur protecting them from the bitter cold (Randall *et al.* 1997; Lister 2004). The Arctic fox also has a physiological adaptation to reduce heat loss; it has a counter-current arrangement of the arterial and venous blood supply, which means cooled blood leaving the leg is warmed by blood entering. This helps the Arctic fox retain heat in the core of the body while simultaneously maintaining a supply of nutrients and oxygen to the peripheral parts (Randall *et al.* 1997).

Physiological changes include hibernation, a state of torpor where certain organisms become inactive to avoid periods of unfavourable conditions. Small mammals hibernate in burrows to escape extreme cold and undergo physiological changes. Burrows are a thermal refuge (Schwimmer and Haim 2009) and these strategies enable small mammals to survive the low temperatures, as they cannot migrate to other areas.

In extreme heat, small mammals also release the hormone vasopressin from the pituitary gland to the blood stream as a response to water shortage. Vasopressin causes the contraction of the arterioles in the glomeruli, resulting in an increase in re-absorption of water (Schwimmer and Haim 2009). Golden spiny mice (*Acomys russatus*) show the most extreme adaptation as they are able to elevate urine concentrations and decrease the urine volume (Schwimmer and Haim 2009). Migration is a behavioural adaptation to predictable seasonal changes of the environment (Lister 2004; Ramenofsky and Wingfield 2007; Robinson *et al.* 2009) and is driven by resource availability. Therefore migratory species can exploit the temporarily abundant food resources and escape harsh environmental conditions prevalent at other times (Robinson *et al.* 2009). It is generally large terrestrial mammals that migrate as they can walk long distances (Lister 2004; Schwimmer and Haim 2009). However some bat species have been found to make long latitudinal migrations between their summer and the winter ranges (McGuire *et al.* 2012). Seasonal variation is influenced by weather conditions, such as unreliable rainfall, and the distribution of food and water resources. Therefore an animal's use of certain areas changes in conjunction with landscape cues that pinpoints the availability of vegetation, shelter, or those prey species favoured by particular predators. This utilisation often fluctuates seasonally and changes at different life stages (Paquet and Darimont 2010).

In temperate mountainous areas, for instance, snow covers food resources in winter, resulting in a shortage of food and driving migration of mammals to lower altitudes (Ramanzin et al. 2007; Bee et al. 2010; Sánchez-Prieto et al. 2010). In fact the availability of food resources and free water sources are key factors driving mammal movements throughout the world's various ecosystems. In Fiordland National Park in New Zealand, red deer (Cervus elaphus scoticus) vary their diets with season; woody dicotyledonous plants are consumed more in winter, whereas grasses and herbaceous dicotyledons are consumed less in winter as snow cover limits accessibility. Therefore feeding patterns are superimposed by seasonal variation of plant species and the altitude, and therefore snow. Red deer move into lower areas in winter to avoid snow, foraging in higher altitudes in summer (Bee et al. 2010). In south-western Spain, movements of red deer are also influenced by changes in grazing resources, although here the hardest season is the summer. This is when the herbaceous vegetation dries up, forcing the red deer to congregate in a few seasonal patches that remain green. Coincidently, the rutting season also starts when food sources are scarce and rutting males defend the seasonal patches of grasses, to mate with females when they move into the green patches (Sánchez-Prieto et al. 2010).

Similarly, seasonal migration of European roe deer (*Capreolus capreolus*) in the Alpine region of north-eastern Italy is a common strategy to avoid deep snow and variability in climate conditions. Roe deer migrate between the high elevation summer ranges and the low elevation winter ranges, moving into lower areas in April (spring) to feed on re-sprouting fresh vegetation (Ramanzin *et al.* 2007). The deep winter snow limits food availability as most food resources will be covered under ice and snow.

Animals also need to move to patchy and ephemeral resources in savannah environments (Fennessy 2009), where they are often restricted to permanent water sources in the dry season. With the onset of the rainy season, animals are able to expand their range, as rainy season forage quality meets their nutritional requirements and there is an increase in water availability. Forage nutritional quality varies over seasons, as the grasses are low in nutrients during the dry season. In the Tarangire National Park, a dry season range for migratory ungulates in northern Tanzania, a spectrum of species, including the African elephant (Loxodonta africana), Cape buffalo (Syncerus caffer), impala (Aepyceros melampus), giraffe (Giraffa camelopardalis), Grant's gazelle (Gazella granti) and eland (Tragelaphus oryx) disperse over large areas in the rainy season (Voeten et al. 2009). Spatial aggregations of herds of forest buffalo (Syncerus caffer nanus) in Dzanga-Ndoki National Park, Central African Republic vary with habitat type and seasons. The food resources in the rainy season are abundant and evenly distributed and forest buffalo herds are less aggregated than in the dry season (Melletti et al. 2010), when they tend to form large herds.

The movements of giraffe in the Namib Desert are not influenced by surface water availability but by changes in preferred plants species (Fennessy 2009). Giraffe in Niger were observed to feed on tiger bush, a type of shrubby vegetation, in the Fandou region during the rainy season and moved into cultivated areas during the dry season (Pendu and Ciofolo 1999).

Phenology of trees also has a localised effect on mammalian movements as certain deciduous plants flower and bear fruits at different times of the year. In the Okavango Delta most trees regenerate new leaves and flowers in spring. Many mammal species will become specialised feeders at this time, moving from tree to

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tree to make the most of this temporary resource. The trees attract species such as kudu (*Tragelaphus strepsiceros*) and giraffe (*pers. obs.*). The fan palm (*Hyphaene petersiana*) fruits in July and August in the Okavango Delta and the male elephants move from tree to tree and island to island to shake down these fruits (Evans 2006; Evans and Harris 2012; *pers. obs.*).

Water is another resource that triggers migration, either the lack of it or overabundance. Zebra (*Equus burchelli*) and blue wildebeest (*Connachaetes taurinus*) movements between rainy and dry season habitats in east Africa are influenced by water availability (Voeten *et al.* 2009). In Northern Botswana, zebra were observed to spend the dry season in the Okavango Delta and migrate into the grasslands of the Makgadikgadi National Park (MNP) in the rainy season (Bartlam-Brooks *et al.* 2011). A large zebra migration also occurs between the rainy season grazing areas of Mababe-Savuti depressions and dry season grazing on the Kwando-Linyanti and Chobe floodplains of Botswana (Fynn and Bonyongo 2010). Low rainfall regions, such as the MNP, experience low leaching of soil nutrients and form key rainy season range for large herbivores, as grasses are nutrient-rich (Fynn and Bonyongo 2010).

Black wildebeest (*Connochaetes gnou*) that are endemic to southern Africa previously migrated seasonally from the more arid south-western parts of South Africa to the eastern highlands of the Free State and Lesotho. Historically, black wildebeest roamed throughout the grasslands of South Africa. However, due to the erection of fences in the late 1800s that blocked migration routes, only an estimated 17,000 black wildebeest remain (Bothma *et al.* 2002).

In contrast, too much water can encourage the movement of animals out of areas. Whilst the seasonal movements of blue wildebeest in the Serengeti are connected with the availability of green grasses with their high protein content (Holdo *et al.* 2009), animals move out of the Mara-Serengeti ecosystem in the rainy season due to water-logging (Ogutu *et al.* 2008). Evans (2006) and Ramberg *et al.* (2006) also identified annual flooding in the Okavango Delta as a major factor limiting habitat availability and therefore influencing animal distribution.

Feeding specialisation coupled with water requirement of species may trigger seasonal movements, whilst rainfall and seasonal changes possibly influence the directions of movements. Zebra, tsessebe (*Damaliscus lunatus*), hartebeest (*Alcelaphus buselaphus*) and waterbuck (*Kobus ellipsiprymnus*) are grazers and strongly water-dependent. The giraffe is exclusively a browser and impala are mixed feeders (Ogutu *et al.* 2008). Most water-dependent species such as elephant and Cape buffalo walk long distances between rainy and dry season ranges. Browsing ungulates are less water-dependent than grazers, as they are able to obtain moisture from evergreen trees and shrubs, but are forced to travel to water sources if few leaves are left in the dry season (Owen-Smith *et al.* 2010).

Reproduction opportunities also influence migration. The timing and synchrony of birth are important for the reproductive success of mammals inhabiting seasonally variable environments (Ogutu *et al.* 2010). The animals need to time birth of their young with periods of abundant food resources to ensure survival. Black wildebeest are seasonal reproducers, giving birth in the rainy season (Bothma *et al.* 2002), whilst elephant and Cape buffalo give birth throughout the year, although there is a peak in births in the rainy season (Bothma *et al.* 2002; du Toit 2002a, b). Warthog (*Phacochoerus africanus*) and tsessebe also have a peak in the birth of offspring in the rainy season.

Predation risks may play a role in the movements of ungulates. For example, the grazers in the Mara-Serengeti ecosystem migrate into cattle ranch areas during the late rainy season to feed on highly rejuvenated and nutritious grasses in the ranches. Additionally, there is decreased predation risk that has been attributed to increased visibility of predators in open plains (Ogutu *et al.* 2008). As competition for food resources and water increases between zebra, blue wildebeest and the domestic stock in the late dry season, the zebra and blue wildebeest are forced to migrate into areas of tall grasses in the Mara-Serengeti, where they are more vulnerable to predation (Ogutu *et al.* 2008).

Seasonal movements of predators are closely linked to seasonal movements of their prey. Spotted hyaenas (*Crocuta crocuta*) in Etosha National Park, Namibia increased their territory size in the rainy season when prey species scatter because they mainly feed on migratory species such as springbok (*Antidorcas marsupialis*), blue wildebeest, zebra and gemsbok. In the dry season there is a high concentration of migratory mammals in Etosha (Trinkel *et al.* 2004) around the limited water holes. Water is not limited in the rainy season, and so at the beginning of the rainy season migratory herbivores disperse, causing a prey decline in the hyaena territories.

Recently, anthropogenic activities are also having a profound effect on animal movements (Ramenofsky and Wingfield 2007). In the Namib Desert, bull giraffe were observed to feed in an area with considerable forage availability but females were never observed foraging there because of its proximity to human settlements, which posed a danger to their young.

Mammals are also facing new challenges due to climate changes affecting habitat (Ramenofsky and Wingfield 2007): many species are losing key habitat resources as a result of frequent droughts, dramatic changes in rainfall patterns and habitat fragmentation. So seasonal movements are an important adaptation in helping ensure the survival of mammalian species. However, the options to migrate to seasonal resources and/or out of unsuitable habitat are becoming more limited. With 25% of the world's mammals at risk of extinction (IUCN Red List), the impact of climate change could have dire consequences for many mammals.

The seasonal movement of mammals, for whatever reason, prevents the overuse of feeding resources (Bothma *et al.* 2002). Isolation of conservation areas such as the Kgalagadi Transfrontier Park (KTP) and Central Kalahari Game Reserve (CKGR) by veterinary fences and human settlement has blighted the conservation of the Kgalagadi Ecosystem because there is no connectivity between high quality rainy season grazing in the saline grasslands of Schwelle and the MNP and dry season grazing of the CKGR (Fynn and Bonyongo 2010). The Okavango Delta used to provide dry season grazing and water to migratory mammals but more recently large ungulate populations have declined dramatically due to fences fragmenting key seasonal resources (Spinage and Matlhare 1992; Fynn and Bonyongo 2010).

The northern Botswana elephant population undertakes long distance movements across five countries: Angola, Botswana, Namibia, Zambia and Zimbabwe (Chase and Griffin 2009). The Okavango, Linyanti and Zambezi rivers provide perrenial water for these elephants. The elephants from northern Botswana seasonally move into southeast Angola and the elephants of the Caprivi Strip, Namibia seasonally migrate into northern Botswana in the rainy season (Chase and Griffin 2009). However, veterinary fences are limiting these movements and having a negative impact on the long distance seasonal movements that elephants undertake in this area (Chase and Griffin 2009).

1.2. Elephants

Understanding the seasonal movements, adaptations habitat and requirements of African elephants is particularly important for their conservation. The total population of African elephants declined from an estimated 1.3 million in 1979 to 609,000 in 1989 (Douglas-Hamilton 1989), mostly due to poaching for their tusks. Blanc et al. (2007) estimated that the population has declined further, despite the end of the ivory trade in 1989, to 472,269 elephants. Southern Africa holds by far the largest number of elephants, with approximately 321,000; this is nearly twice the population of east Africa, the next most populous region with about 166,500 elephants. Over three-quarters of the regional elephant population in southern Africa are in Botswana and Zimbabwe; however, recent evidence from aerial censuses suggests that southern Africa has lost a substantial proportion of their population due to poaching in recent times (Wasser et al. 2008).

An estimated 200,000 to 400,000 elephants lived in Botswana at the beginning of the 19th century (Campbell 1990). During the next 80 years uncontrolled commercial hunting for ivory exterminated elephants from southern Botswana and reduced their population to mere remnants in the far north (Campbell 1990). Since then, numbers have recovered, and today the majority of the elephants are to be found in northern Botswana (*c* 150,000: Blanc *et al.* 2007; Fynn and Bonyongo 2010). Botswana's population is integrated with the Hwange/Matetsi complex in Zimbabwe (Dublin 1989) and crosses other international borders into Angola, Namibia, South Africa, Zambia and Zimbabwe (Craig 1996; Blanc *et al.* 2003; Chase and Griffin 2009).

Female elephants live in breeding herds that are controlled by a matriach, generally the oldest cow in the herd, with all the herd members being closely related. However, on rare occassions unrelated breeding herds fuse, raising the possibility that some herds consist of unrelated females (Charif *et al.* 2005). Bull society is a loose fission-fusion system, with season not affecting average male group size

(Evans 2006; Chase and Griffin 2009). Males, post-independence, spend time alone, in association with other males in temporary male groups and sometimes join female herds for a short period (Charif *et al.* 2005). As the young male elephants mature they engage in contests with other young males to establish their rank in the male hierachy. In their late twenties male elephants begin to spend a proportion of their time each year in a hormonal and behavioural condition called musth (Poole 1984; Charif *et al.* 2005). Adult bulls mostly visit breeding herds when cows are in oestrus (Bothma *et al.* 2002).

Elephants are mixed feeders, but in times of plenty (rainy season) the majority of their diet consists of grasses, with herbaceous species, shrubs, tree leaves and woody material comprising the rest (Laws *et al.* 1975; Evans 2006). As non-ruminants, elephants feed by plucking large bundles of vegetation, resulting in a diet of high fibre, particularly in the non-rainy season (Laws *et al.* 1975). Fruits may also constitute a large proportion of an elephant's diet. Older male elephants in the Okavango Delta vigorously shake fan palms to feed on the nuts (Evans 2006; Evans and Harris 2012). Similar feeding behaviour was also observed in the Savuti in northern Botswana, where elephants shake camel thorn trees (*Acacia erioloba*) to feed on the seed pods (Barnes 2001) and the shaking of camel thorn by male elephants has also been observed in the MNP (*pers. obs.*).

There is large seasonal fluctuation in the types of food utilised by elephants, with more browse being taken in the non-rainy season (Laws *et al.* 1975). Evans (2006) observed that male elephants in the Okavango Delta fed mainly on browse in the flood season, grasses and herbaceous layer in the rainy season, and a diverse diet in the non-rainy season (Evans 2006). Male elephants bulk feed, spending more time foraging on one plant before moving on to another tree than females to maintain their large body size (Stokke and du Toit 2000). An adult male elephant can weigh 5500 to 6000 kg, whereas females weigh 2500 to 2800 kg (Owen-Smith 1988). Female elephants feed by defoliating trees; sub-adult males displayed the same behaviour and both sub-adult males and females were more selective in their feeding preferences in Chobe National Park (Stokke and du Toit 2000). However, this was not the case in the Okavango Delta, where social grouping rather than age affected sub-adult male habitat selection and male elephants were more selective of their habitats than females (Evans and Harris 2012). Unlike females and sub-adult

males, large male elephants appeared to be better able to tolerate variation in their diets (Stokke and du Toit 2000).

Desert elephants in the Namib Desert are constantly on the move during the rainy season when there are good food resources, whereas in the dry season movements of male elephants are restricted by lack of food resources (Leggett 2009). Due to good food availability, the males could gain weight and maintain musth during the rainy season (Smit *et al.* 2007; Leggett 2009), whereas more male elephants in the Okavango Delta exhibited musth more frequently during the flood season when resources are more limited (Evans 2006).

The whole of the Okavango Delta consists of nutrient-poor Kalahari sands (Ramberg *et al.* 2010). Floodplains accumulate phosphorus, the most limiting factor in the Okavango Delta (Ramberg *et al.* 2010). Although vegetation and water are abundant in the Okavango Delta, elephants forage over large areas (Evans 2006; Ramberg *et al.* 2006) because of the nutrient limitations imposed by floodwater covering the floodplains, thereby limiting resource availability.

1.3. The study area

In Botswana, National Parks and Game Reserves cover over 17% of the land area, and a further 21% is administered as Wildlife Management Areas (WMAs) (Wheelwright *et al.* 1996). The western Okavango Delta, Botswana, in southern Africa (Figure 1.1) started to be recolonised by male elephants in the late 1980s (P. Holbrow *pers. comm.*) and females in the early 2000s (K.E. Evans *pers. comm.*). The Okavango Delta is utilised by an estimated 20,000 to 30,000 elephants (Meldensohn and el Obeid 2004). My study was based in WMA Ngamiland 26 (WMA NG26) that covers an area of ~1853 km². The study area was 215 km² centred on the research camp at S19.40420, E22.56162 (decimal degrees).

The Delta is made up of large wetlands that cover an alluvial fan 150 km in length (Milzow *et al.* 2010a). The wetland area is between 2,000 km² and 12,000 km² dependent upon the inflow of water from Okavango River, local rainfall and the rate of evapotranspiration (Milzow *et al.* 2010b). The Okavango River starts in the highlands of Angola, with a subtropical humid climate, and an annual rainfall of about 1300 mm/year (Mendelsohn *et al.* 2010; Milzow *et al.* 2010a). This river runs through

southern Angola and the Namibian Caprivi Strip before it reaches the Okavango Delta in north-western Botswana, where there is a semi-arid climate and an annual rainfall of about 450 mm/year (Mendelsohn *et al.* 2010; Milzow *et al.* 2010a).

Distinct dry and rainy seasons in the headwater of the river result in marked seasonality of the river discharge, with annual flood peaks between 400 m³/s and 900 m³/s, and a base flow of 150 m³/s. Okavango wetlands loose approximately 94% of the discharge through evapotranspiration. Another 3% filtrates into regional ground water and 3% goes into the Boteti River (Milzow *et al.* 2010a).

In 2010, the Boteti River flowed for the first time since 1989 (M. Ives and P. Wolski *pers. comm.*). Contributing factors to the resurgence of the Boteti River are thought to be high floods received in 2010, higher than average rainfall and tectonic movements in the region. As a consequence, male elephants are re-establishing their old home ranges in the Boteti Sub District. With male elephants moving into these areas, breeding herds and other species of mammal are likely to follow. Male elephants may move into these areas due to the restriction that the seasonal floodwaters impose on elephants in the Okavango Delta, as floods reduce forage availability. Alternatively, with water available in the Boteti area, elephants are able to increase their range as water is no longer a limiting factor. Increases in range often lead to an overlap with human settlements, and hence there is an increase in conflict between humans and elephants.

In the Okavango Delta, the secondary floodplains are low-lying areas adjacent to the rivers that are flooded for several months a year (Lindholm *et al.* 2007). The extent of the annual floods in the Okavango Delta reduces the dry land available, causing extensive movements of many of the larger mammals (Medelsohn and el Obeid 2004). Dense grasses on the primary floodplains are an important food source for large mammals, and so the availability of primary floodplains controls the population size of many species of large herbivores (Milzow *et al.* 2010b). However, primary floodplains are flooded most of the time, resulting in limited accessibility to most mammals, which is coupled with the danger posed by crocodiles. The drying out of the secondary floodplains gives rise to regenerating vegetation that attracts a range of mammals (Lindholm *et al.* 2007) for the dry season grazing. The habitat types in the study area are summarised in Tables 1.2 and Figure 1.2.

1.4 Seasons in the Okavango Delta

The three main seasons in the Okavango Delta are the rainy season (November to March), the flood season (April to September), and the dry season (October, sometimes into November) (Evans 2006; Evans & Harris 2008; Evans and Harris 2012). Defining the seasons by month worked well between 2002 to 2007. However, subsequent years were characterised by floodwaters arriving early and permanent water available throughout the year; early rains were also experienced in 2009 (Figure 1.3). As the Okavango Delta is experiencing a 'wet phase' the following seasons for the years 2008 to 2011 were recognised: rainy, flood (including any late rains) and non-flood/non-rainy (Table 1.1).

The flood level in the study was mostly influenced by the amount of the floodwater from the Angolan catchment area, where most of the water comes from. Additionally the amount of rain received in the Okavango Delta influenced the flood levels. The amount of water in different areas of the Okavango Delta is affected by shifts in water as a result of tectonic plate movement and silting of channels (Mendelsohn *et al.* 2010).

Different measures were used to determine the arrival of floodwater: (i) the rise of the water in the floodplains surrounding the research camp, determined by water level gauges in Seba Lagoon and Abu Bridge, and (ii) the influx of flocks of birds following the floodwaters; as the water slowly filled the floodplains the birds wait in anticipation to prey on crustaceans, fish and on the insects forced upwards by the approaching water. The end of the floods were based on two features: (i) whether it was easy to drive most routes around the study area and the water was starting to disappear quickly, and (ii) the influx of flocks of birds to feed on the exposed zooplankton and fish in the drying floodplains. However, there was no absolute measure to determine when the floodplains were completely exposed. The start of the rainy season was determined by the onset of the first substantial rainfall (>5 mm) that was followed by more rains (>5 mm) over different days that month and into the following month.

Table 1.1: Classification of months in different years into rainy season (R), flood season (F) and the dry season (D). The dry season in later years is referred to as non-flood/non-rainy-season (NFNR); however dry seasons and non-flood non-rainy season were excluded from the analysis because of limited data. From 2008 onwards the floodwater started to arrive earlier in the year as highlighted in the table.

Months	2004	2005	2006	2007	2008	2009	2010	2011
January	R	R	R	R	R	R	R	R
February	R	R	R	R	R	R	R	R
March	R	R	R	R	F	F	F	F
April	F	F	F	F	F	F	F	F
Мау	F	F	F	F	F	F	F	F
June	F	F	F	F	F	F	F	F
July	F	F	F	F	F	F	F	F
August	F	F	F	F	F	F	F	F
September	F	F	F	F	F	F	F	F
October	D	D	D	D	NFNR	R	NFNR	NFNR
November	R	R	R	R	R	R	R	R
December	R	R	R	R	R	R	R	R



Figure 1.1 Maps showing the study area in relation to southern Africa (a) and the location of the EfA camp in WMA NG26 of the Okavango Delta (b)

Table 1.2: Codes used for habitat classification in the study area (Evans 2006).

Habitat code	Habitat description
1.1	Muddy soil, dark green grasses, often water - primary floodplain communities
1.2	Sandy soil lightened grasses, sometimes water - secondary floodplain communities
1.3	Grassland, spiky sporobolus, Sporobolus spicatus communities
2.1	African mangosteen, <i>Garcinia livingstonei</i> and fig trees, <i>Ficus sycomorus</i> - closed riverine woodlands
2.2	Wild date palms, <i>Phoenix reclinata</i> , water berry, <i>Syzygium cordatum,</i> termite mounds
3.1	Knobthorn, Acacia nigrescens and fever berry, Croton megalobotrys
3.2	Real fan palm, <i>Hyphaene petersiana</i> , fever berry, palm woodland and palm
3.3	Leadwood, Combretum imberbe, fever berry, woodland
4.1	Umbrella thorn, Acacia tortilis, savanna woodland
4.2	Camel thorn, Acacia erioloba, woodland
4.3	Silver terminalia, <i>Terminalia sericea</i> , common bush willow, <i>Combretum collinum</i> , savanna woodland and scrub savanna
4.4	Mopane, <i>Colophospermum mopane</i> , woodland and pyrophytic scrub savanna
4.5	Fever berry, and <i>Grewia</i> species i.e. brandy bush, <i>G. flava</i> sand paper raisin, <i>G. flavescens</i> etc.



Figure 1.2: Photos of the five main habitats found in the study area: (a) floodplain habitat; (b) mopane woodlands (*Colophospermum mopane*) - note coppiced mopane shrubs; (c) other woodland; (d) silver cluster leaf terminalia (*Terminalia sericea*); and (e) island vegetation habitat.

1.5 Rationale for the project

We know relatively little about the behaviour of male elephants, and this limits our ability to conserve and manage them, both *in situ* and *ex situ*. Male elephants are more exploratory than females, and are the first to re-colonise old parts of their range and populate new areas (Stickel 1954). Thus the exploratory nature and high risk strategies of male elephants increases the chances of conflict with humans, and male elephants are generally the main crop raiders, both in Africa and Asia (Sukumar 1989; Sukumar 1990; Hoare 1999; Graham *et al.* 2010; Davies *et al.* 2011; Workeneh 2011).

Crop raiding in Botswana is an economic issue affecting food security. The lives of subsistence farmers can be negatively affected by crop raiding elephants, which are often shot by Problem Animal Control. In 2005, the Department of Wildlife and National Parks (DWNP) in the North West District of Botswana paid out P17,494 in compensation for 119 reported cases of elephant damage. In 2006 from April to June the total compensation to the farmers in North West District was P25,831: a total of 102 cases were reported (Sola 2006). These amounts were in compensation for crop damage, destruction of fences and water storage tanks in farms. So whist incident numbers appear to have dropped, the amount of damage has increased. To date there have been few incidences of loss of human life to elephants in northern Botswana (Sola 2006).

Understanding the seasonal patterns of habitat utilisation will help mitigate human elephant conflict by predicting the movements of male elephants into areas of human settlement. Batswana are mostly subsistence farmers, relying on summer rainfall to plant their crops. However, elephants also increase their home range during the rainy season (Mosojane 2004; Evans 2006; Jackson *et al.* 2008; Loarie *et al.* 2009), increasing conflict in farming areas as there is an overlap in the harvest and elephant seasonal movements. A better understanding of the social groupings of male elephants may also help with conflict mitigation. For instance, when are male elephants spending more time with female elephants? This is important to know because they are less likely to move into human settlements as female elephant movements are restricted by the need to protect calves, and so they generally avoid areas with humans (Mosojane 2004; Jackson *et al.* 2008).

This information can also be used for better management of small fragmented populations that are prone to extinction due to encroachment, restriction on seasonal movements by human settlements and agricultural practices. My study also addressed the national research priorities of the DWNP, as they need to develop novel ways to manage elephant populations that are increasing their range. Also, increases in seasonal floods in the Okavango Delta means that elephants, especially males, are expanding their range into areas occupied by human settlements and therefore crop fields and cattle ranches. Thus there are applied benefits to this study.

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1.6 Aims of the project

The aims of the study were to:

- Assess the effect of season on the number of male elephants that utilise the study area.
- Assess the affect of season on male elephant social groupings.
- Assess whether food selection by elephants is influenced by season.
- Assess how season affects the physical condition of male elephants
- 1.7 Hypotheses
- H1: Season does not affect the number of male elephants utilising the study area.
- H2: Male elephant social groupings are not affected by season.
- H3: Food selection of male elephants is not affected by season.
- H4: The physical condition of male elephants is not affected by season.

Chapter 2

Seasonal effects on elephants

2.1 Introduction

The Okavango Delta was an ideal area to examine the habitat and social requirements of male elephants. There is limited information on male elephants' seasonal needs and feeding patterns, even though changing seasonality has a greater impact on male than female elephants, in part because male elephants go through a transitional stage at adolescence when they leave their natal herds. So during this period changes in seasonal patterns put them at greater risks due to their lack of knowledge of the surrounding area. The Okavango Delta is unique in that it receives annual floods and I wanted to know what impact the associated loss of habitat has on the ability of male elephants are also high, so elephants are relatively mobile, foraging over larger areas (Laws *et al.* 1975). Floodwaters reduce the resources available to elephants in the Okavango Delta and hence influence their movements, habitat selection and sociality (Evans 2006; Evans and Harris 2012).

2.2 Methods

2.2.1 Elephant sightings

The majority of the data used in analyses were collected over 57 months, from January 2007 to September 2011. Six set routes between 12.8 km and 22.6 km long were driven to locate elephants; these routes covered all the habitats in the study area (Figure 2.1). Routes were driven in the morning (06:00 to 12:00) or afternoon (16:00 to 19:00). Whether each route was driven clockwise or anticlockwise was recorded and routes and direction selected randomly. Although routes were chosen randomly it was at times not possible to drive a transect because of tourists safari activities. However I ensured that each route was driven at least once every month. Data were also collected opportunistically from random routes. Before leaving camp, the start time and odometer reading on the vehicle were recorded. Every time an elephant or elephant group were sighted, their social grouping (Table 2.1), the GPS coordinates, number of individuals, and the sex and

an age estimate of each individual (Table 2.2) were noted. Elephant groups with a collared released elephant(s) or sightings of a lone released elephant from the Abu Camp captive herd were excluded from all the analyses. This was to avoid bias as it was not known whether groupings were influenced by the presence of a released elephant.

Social codes	Social group
1	One male elephant alone
2	2-5 males only
3	6 or more males
4	Female herd with one or more young males <20 years
5	Mixed herd: female herd with one or more males ≥21 years. All males <20 years old were presumed to be part of the herd

 Table 2.1: Social codes used to record elephant sightings (from Evans 2006).

Sex was determined by body size, with males tending to be bigger and taller than females (Lee & Moss 1986), the shape of the forehead (females are mostly square in profile while males tend to be rounded), tusks (males have more tapered tusks), the pelvic areas (females are bigger than males and mostly round), and external genitalia. Infants and juvenile elephants were hard to sex because most of these features were not obvious (Evans 2006), so other features were used, such as genital morphology when visible. After the age of five sexing of elephants gets easier as most features will be pronounced and easier to see. However, sexing infants and juvenile elephants is difficult, as mother elephants are protective and the female herds in the area were more nervous than lone males or bull groups (Evans 2006; Evans & Harris 2012).

Age was estimated by body size, thickness of the tusks and the size of the hind footprints. When elephant(s) were sighted crossing the road, the length of their hind footprint was measured using a 5m measuring tape (Webco Tools, D.I.Y. Power Tape, Johannesburg, South Africa), taking measurements of at least three prints from the same foot and averaging them to estimate age (Figure 2.2 and Table 2.2).

Male elephants were also aged from the head shape: with age the tusk base thickens, so that older males have hourglass-shaped foreheads (Figure 2.3).

Table 2.2: Age classification of male elephants; based on Lee and Moss (1986) and Western *et al.* (1983).

Class	Foot length (cm)	Height (cm)	Age (years)	Description
Class 1	36 – ?	204 -228	10-15	Male head more noticeable; tusk circumference and shoulder height greater than females of the same age
Class 2	? - 41.9	229 -243	16-20	At about 17 years males reach same height as largest adult female over 40 years
Class 3	42 - 45.9	244 -275	21-25	Taller than most females; but most still slender and narrow in the head compared to older males
Class 4	46- 49.9	276 -296	26-35	Head shape had changed to an hour-glass shape, which gets broader as they move through the age group; height increases steadily
Class 5	50-53.9	>297	≥36	Very big, tower over largest female by three feet or more at shoulder, neck thick, tusk circumference at lip strikingly greater than younger males and all females

Elephants were individually recognised from the natural markings on their ears (Figure 2.4) and other distinctive features such as lumps on their ears, forehead or body, few or no hairs on the tail, and whether the elephant had no tail, half a tail, a kinked tail or other distinctive features. Photographs were taken of the ears and other distinctive features to assist with identification, downloaded at camp, and compared to the elephant identification files. If an elephant had not previously been recorded, a new identification file was opened.



Figure 2.1: Maps showing the set research routes driven from the research camp (green triangle): route (a) was 22.6 km, (b) 18.0 km, (c) 17.9 km, (d) 18.5 km, (e) 12.8 km and (f) was 18.2 km. Note some routes intercept because of the restrictions imposed by the Okavango Delta floodwater and so a bridge or main crossing points had to be used. For example routes a, b, e, and f all utilise the bridge to cross the river channel.

I defined musth with the following prominent features; dribbling of urine, green penis sheath, odour and aggressive behaviour (Poole 1996; Ganswindt *et al.* 05). Additionally the swelling of temporal glands and extent of secretions (Table 2.3 and Figures 2.5 & 2.6) were used.



Figure: 2.2: Author measuring the hind foot length of an elephant.

Physical condition was assessed on a scale of 1-5, with 1 being emaciated and 5 being fat (Table 2.4 and Figure 2.7). At times elephants were given an intermediate body condition score of 2.5 or 3.5; on averaging physical conditions by seasons the averages were rounded to the nearest whole number. Generalised Linear Model(s) were run on continuous data or ordinate data with lots of categories so to account for this a Poisson Model was fitted. Elephant(s) with a physical condition 1 were never sighted during the study period and so this value was omitted from analyses (Figure 2.7). After initial testing of the full model with main fixed effects of age, season and musth, the minimal model accepted had the main fixed effect age with a Poisson error and log link function. The other terms included in the original full model were dropped due to insignificance.



Figure 2.3: Photos of heads of male elephants of different age groups: (a) 10-15 years, (b) 16- years, (c) 21-25 years, (d) 26-35 years and (e) \geq 36 years old. Note the development of the hourglass shape as male elephants mature.



Figure 2.4: Examples of identification photographs for male elephants: (a) B144 (Robin Hood), (b) B571 (Earl Grey), (c) B47 (William Wallace) and (d) B549 (Plato).


Figure 2.5: Photographs illustrating some examples of temporal gland swellings in the male elephant B47 (William Wallace): (a) and (b) swelling 0, (c) swelling 2 and (d) swelling 3.



Figure 2.6: Photographs illustrating some examples of how I evaluated the secretions of temporal glands: (a) 1tn, (b) 1to, (c) 2tn, (d) 2to, (e) 3tn, (f) 3mo, (g) 4wn, and (h) 4wo, where the number codes the length of the secretion (Table 2.3), the first letter indicates whether the secretion was thin (t), medium (m) or wide (w), and the second letter denotes whether it was new (n) or old (o).

Table 2.3: Assessment of temporal gland secretions (TGS) length. The width (thin, medium and wide) and whether the secretion was new or old were also noted (Evans 06).

Code	Length of TGS – description
1	From gland to eye
2	From gland to top of upper jaw
3	From gland to corner of the mouth
4	From gland to bottom of lower jaw

 Table 2.4: Assessment of physical condition of male elephants.

Code	Physical condition description
1	Extremely thin: ribs visible, shoulder blades and backbone protruding and a sunken stomach
2	Very thin: shoulder blades, pelvic bone and backbone protrude
3	Thin: shoulder blades, pelvic bone and backbone are visible
4	Good: slight sinking in front of pelvic bone
5	Fat: no sign of shoulder blade or pelvic bones or backbone protruding and fat hangs from the body

2.2.2 Focal data

On sighting a breeding herd, mixed herd, lone male or a group of males, a focal male was selected at random and observed for 30 minutes, with activities recorded every five minutes (Table 2.5). A stopwatch (Oregon Scientific 100 Lap Memory) was used to time these intervals and binoculars (Nikon, *Action* 8x40 8.2, Tokyo, Japan) used for observation of activities, depending on visibility and distance. Any interesting behaviours or activities that occurred between the five-minute intervals were also recorded. The vehicle was repositioned if the focal male moved out of sight. One "no-visual" was allowed per half hour focal, where a "no visual" was when a focal animal disappeared into an area where it could not be seen when the beeper went on the stopwatch.

Distance to the focal animal varied with type of habitat (Figure 1.2), but I always kept far enough away not to disturb the animal(s). Focals were abandoned if the animals were disturbed. The different habitats that an elephant utilised in the 30-minute focals were recorded using the codes in Table 2.5. Whether the focal elephant was in musth, injured, its age, the distance in metres from its nearest neighbour and the age, sex and identification (where possible) were recorded. The food species male elephants fed on were recorded, with the trees identified to species level but were grouped as non-grass for the chi-square analysis. The grasses, sedges and herbaceous layers were grouped together and collectively referred to as grasses.



Figure 2.7: Photos showing examples of the physical conditions scores of male elephants: (a) 2, (b) 3, (c) 4 and (d) 5.

In addition, a monthly survey of the numbers of elephants and other mammals utilising the area was started in January 2004 and continued until September 2011, and so covered a period of 93 months. Whilst the aim was to do monthly road surveys, this was not always possible due to lack of access to a vehicle and road conditions, and so there are some gaps in the data, with only 45 road surveys available for analyses. These surveys were part of our research permit requirements, but I only used the elephant data from these surveys in my thesis. It was a set route of 44.4 km (Figure 2.8) and the time and odometer reading on the vehicle was recorded at the start and finish of each survey. The direction the survey was carried out was alternated.

When an elephant was sighted, where possible the elephant(s) were aged, sexed and their social status recorded as in Section 2.2.1, and photographed for later identification. Elephants sighted on the monthly mammal road survey were used to supplement the elephant sighting data but focal data were not collected during these surveys.

Activity codes	Activity
1	Sleeping
2	Eating
3	Drinking
4	Social
4.1	Greeting
4.2	Sparring
4.3	Play
4.4	Push from behind
4.5	Display
4.6	Head on back
5	Bathing/dusting
6	Walking
7	Walking and eating
8	Standing
9	Vocalising (focal animal)
9.1	Vocalisation another elephant in view
9.2	Vocalising unseen elephant
10	Running

Table 2.5: Codes used for recording activity of focal elephants (Evans 2006).

As I was part of a research group and others will use the data I collected, I collected all behaviours of interest to the group. However I only analysed feeding behaviour (Table 2.5).

2.2.3 Statistical analysis

Data were analysed using SPSS 16, 2007, SPSS 18-PASW, statistics, Chicago, United States of America, Minitab 15 and R version 10.2.1.

The data to test for seasonal differences in the numbers of male elephant (hypothesis 1) were not normally distributed and could not meet assumptions of parametric tests when log transformed, so a nonparametric Mann-Whitney U test was used. Separate tests were run on the rainy and flood season of both pre and post 2008 to find out if the increase of floodwater post 2008 had an impact on male elephant numbers.

For hypotheses 2 (male elephant social groupings are not affected by season) and 3 (food selection of male elephants is not affected by season), chi-square cross tab contingency tests were used to assess the seasonal influence on male elephants' social groupings and the seasonal impact on their food selection.

For hypothesis 4 (the physical condition of male elephants is not affected by season), a Generalised Linear Model (GLM) was used to assess the impact of season, age group and musth on the body condition of male elephants.

For proportional data, such as the ratio of young to old males, the proportion of time spent feeding and the proportion of \geq 26yr males in musth, data were square-root transformed and tested for normality with Anderson-Darling tests. ANOVAs were used to see if season and year affected the proportion of old (\geq 26yr) to young (\leq 25yr) males that were sighted, and the proportion of \geq 26yr males in musth. Data on proportional feeding times, number of male elephants and the distances between male elephants were not normally distributed even after log transformation, and so a Mann-Whitney *U*-test or Kruskal-Wallis test were used.

Two seasons, the flood and rainy season, were compared for all hypotheses: the dry and non-flood non-rainy seasons were excluded, as the sample sizes were too small. The results were considered significant at α 0.05 and throughout the thesis 2-tailed significances were used. The underlying assumptions were met for all tests (Zar 1984). Sample sizes are shown in Table 2.6. and the error bars on graphs were standard error (SE) unless specified otherwise.



Figure 2.8: Map of the monthly mammal road survey route, covering 44.4 km. Image from Google Earth.

Sample size	Rainy	Flood	Total
Physical condition scores	271	270	541
Mammal road surveys	14	19	33
Male social groups	543	971	1514
Distances to nearest neighbour	63	69	132
Focal data	126	143	269
Feeding focal data	81	111	192

Table 2.6: Summary of data collected.

2.3 Results

2.3.1 Seasonal changes in numbers

From 2008 onwards the influx of water into the Okavango Delta from the Angolan catchment area increased. This, as well as the increase in rainfall levels in the Okavango Delta, swelled flood levels in the research area. In addition there was substantial late rainfall extending into March and April (Figure 1.3). The wet years in the Okavango Delta are usually in cycles of 10-15 years (M. Ives and P. Wolki *pers. comm.*), and higher floods and more permanent water occurred in the study area from 2008 indicating a wet cycle. Consequently, I analysed my data in two phases as pre-2008 and 2008 onwards to see if the increase in floodwaters had an effect on the distribution of male elephants, forcing them into smaller areas.

There was no significant difference in male elephant median group size sighted on the monthly road surveys in the flood and the rainy seasons or pre and post 2008 (Figure 2.9; pre-2008, (U =0.45, N_{RAINY} =9, N_{FLOOD} =3 P=1.00) and post 208 U=0.119, N_{RAINY} =14, N_{FLOOD} =19 P=0.67).





Figure 2.9: The median number of male elephants in the pre-2008, dry phase, and post 2008 wet phase, $N_{RAINY}=9$, $N_{FLOOD}=3$ and post 2008, $N_{RAINY}=14$, $N_{FLOOD}=19$).

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Numbers of musth males in relation to non-musth males were compared to see when musth was occurring in the Okavango Delta and proportions of the adult males coming into musth. As musth sightings were uncommon, data were analysed bi-monthly. Only males ≥26 years were used, as this is the age most male elephant begin to exhibit musth (Poole 1986). Each two-month period was treated independently, with only the first sightings in each two months used to determine if a male was in musth for that two-month period. Musth males were sighted throughout the year, and formed only a small proportion of the mature males utilising the area (Figure 2.10).

2.3.2 Seasonal changes in social groupings

The data used in analysing the seasonal changes in social groupings was from males ≥ 21 years, because males ≤ 20 years may not be independent from their herd, and so female herds without males ≥ 21 years with them were excluded from the analysis. The social groupings of male elephants were affected by season (χ^2 =41.16, *d.f.*=3. *P*=0.001), with the number of lone male sightings higher in the flood season compared to the rainy season (Figure 2.11).

Male elephant group ratios (ratio of males ≥ 26 years old to males ≤ 25 years old) were also analysed to see if elephants of specific ages had a preference to be in the area at certain times of the year. There were more ≤ 25 year old males seen throughout years and seasons (Figure 2.12). The proportion of older to younger males was affected by year, with a larger proportion of younger males seen in later years ($F_{1,4} = 2.65$, P=0.044). Season did not affect the proportion of young to old male elephants ($F_{1,1} = 0.49$, P=0.488).



Females

- Non-musth males (≥26yr)
- a Musth males (≥26yr)

Figure 2.10: The percentage of \geq 26yrs male elephants in musth, \geq 26yrs male elephants not in musth and female elephants bimonthly in the years 2007-2011. Musth males \geq 26yr, *N*=84, not musth male \geq 26yr, *N*=569, and female *N*=2807



Figure 2.11: Male social groupings in the rainy and flood seasons. Rainy season lone male elephants N=296, 2-5 males, N=165, 6 or more males, N=28, and mixed herds, N=54. Flood N=627, N=205, N=12, and N=127 respectively.

2.3.3 Seasonal changes in feeding behaviour

The first identified food species that a male elephant fed on during each half hour focal (Section 2.2.2) was used for analysis. This avoids pseudo-replication, since the first species that a focal animal takes may influence the next species it feeds on. The first focal sample per season each year was used for the known male elephants to avoid over presentation of their activity patterns. Food selection of male elephants was influenced by season ($\chi^{2=}15.03$, *P*=0.001, Figure 2.13), with a higher diversity eaten in the flood season.



Months of the year

Figure 2.12: Number of older males (\geq 26 years - grey) in relation to the number of younger male elephants (\leq 25 years - black). The first *N* value in each year represents males \geq 26 and second is males \leq 25 years in (a) 2007, *N*=165, 354, (b) 2008, *N*=235, 478, (c) 2009, *N*=430,107, (d) 2010, *N*=793, 214 and (e) 2011, *N*=72, 438.

I expected male elephants to spend more time foraging in the flood season as food is limited and with low nutritional value. I also expected that males would be further away from their nearest neighbour during the flood season compared to the rainy season due to competition for food. However, I found that the proportion of time male elephants spent feeding was not affected by season (U=16570, P=0.4900), although male elephants spread out more in the flood season, with nearest neighbour distances being larger in the flood season compared to the rainy season (U=3701.5, N_{RAINY} =63, N_{FLOOD} =69, P=0.0263: Figure 2.14).





Figure 2.14: The median \pm SE distance to nearest neighbour (m) in the rainy and the flood seasons.

2.3.4 Seasonal changes in body condition

The body condition scores of known male elephants were averaged seasonally to avoid over representation and bias. Variation of body condition in relation to age group, season and musth was investigated to see which factor(s) contribute to body condition. The body condition of male elephants was significantly affected by age of male elephants (GLM = 6.085, *d.f.*= 1, *P*=0.014), with younger males being in poorer condition (Figure 2.15).



Figure 2.15: The mean \pm SE physical condition scores for males \leq 25 years and \geq 26 years in the rainy and flood seasons.

2.4 Discussion

Although the seasonal floodwater in the study area changed tremendously over the study period I show that the numbers of male elephants utilising the study area throughout the seasons in pre-2008, the dryer phase, and after 2008, the wetter phase, were not significantly different, although on average more male elephants were recorded in the flood season. However, data on the number of male elephants utilising the study area (sighted on monthly road surveys) need to be treated with caution as sample sizes were small (Figure 2.9).

The tendency for more male elephants to be sighted during the flood season may be attributed to the floodwater forcing elephants onto the remaining dry land (which I was able to access and drive on), thereby restricting their movements. The Okavango Delta is an important dry season resource for migratory mammals (Fynn and Bonyongo 2010), including elephants, so the floodwater remaining into the traditionally dry months could explain higher averages of male elephants sighted in the flood season.

In the rainy season the average number of male elephants was lower because they disperse to the wet season range, for example the MNP. This supports short grasses that are nutritious because the area receives low rainfall and so there is less leaching of soil nutrients (Fynn and Bonyongo 2010). Dispersal of elephants in the rainy season results in an increase of crop raiding, with escalations in March and April when crops ripen. Consequently an overlap of harvesting time with the periods when elephants disperse in the rainy season leads to an increase of conflict between humans and elephants (Mosojane 2004), as occurs in the Boteti district near the MNP.

Another factor that may affect the level of crop-raiding is the recent increase of elephants in the Chobe district, which may be pushing elephants into the Boteti district. Whilst elephants are generally blamed for crop damage, other perpetrators include livestock such as cattle, sheep and donkeys (Brooks and Maude 2010).

Whilst I did not use the dry season data in my analyses due to small sample size, I think it is interesting to note that during the dry season the increased

floodwaters experienced by the Okavango Delta in recent years has meant more areas of the Okavango Delta have water available for longer. Therefore water limitation is not restricting animal movements as much. During the dry season the grasses that the Okavango Delta floodplains provide sustain migratory animals, including elephants.

In the Okavango Delta, season plays a pivotal role in the sociality of male elephants. I found that season has an impact on the social grouping of male elephants, with the number of lone male sightings being higher in the flood compared to the rainy season. The floodwater restricted feeding resources as the floodplains, with nutritious grasses underwater, so male elephants may be solitary to reduce competition for limited resources.

A lot more of the independent male elephants \geq 21 years were joining females in the flood season in the study area. This is possibly because of restrictions by floodwater forcing habitat overlap of independent males and female herds. Additionally, the male elephants in the study area were not forming large groups in either the rainy and flood seasons, possibly due to the difficulty of sourcing feeding resources. Chase and Griffin (2009) reported no changes in male elephant group size between the dry and rainy seasons in northern Botswana: this may reflect differences in the quality of population dynamics data gathered from the ground versus aerial data. The male group ratios show that there were more young males compared to older males utilising the study area (Figure 2.12). In Amboseli, Kenya, fewer than 40% of male elephants reach the age of their first musth (Lee *et al.* 2011). Male mammals, particularly adolescent males, are generally higher risk takers (Laviola & Adriani 1998; Spear 2000), exploring new areas and competing for mates. However the disparity I found between the number of younger and older males may also be associated with the recent changes in the ecology of the study area.

When the long-term study started in 2002 the region was a bull area (Evans 2006), whereas in recent times more female herds are sighted (*pers. obs.*). This increase in the number of females in the study area may be attributed to higher floodwater, as water restrictions no longer limit the elephants, especially the females, from utilising the western Okavango Delta.

Sightings of young males are higher in the flood season, compared to changes in the number of older males, and this may be related to more female herds seen in the flood season and the young males recorded are with them. It may also be because few male elephants reach adulthood as predation of young male elephants by lion and spotted hyaena occur in the Delta (Joubert 2006; G. Atkinson *pers. comm.*). The dispersal nature of the male elephants from the natal herds make them vulnerable to predation, especially because they lose the protection they had when they were still part of the natal herd. In addition old males are trophy hunted in some parts of Botswana under licence.

Since only a few male elephants survive to reach adulthood, we would expect to see fewer. Lee *et al.* (2011) discovered the average life expectancy of a male elephant after birth to be 24 years, with deaths attributed to illness, accidents, predation, drought and human caused mortality. Therefore losses due to human causes probably reflect risk-taking behaviour by male elephants throughout their lives. Risky behaviours place male elephants in close proximity with humans, increasing conflict between humans and elephants as in the MNP. Simultaneously male elephants are involved in competitive contests with each other, which also has a risk of injury and/or death. This risk-taking behaviour means that male elephants are also generally responsible for most of the crop raiding in Africa and Asia (Sukumar 1989; Sukumar 1990; Mosojane 2004; Jackson *et al.* 2008). So a lot of male elephants are killed by farmers protecting crops or by the Problem Animal Control unit of DWNP in Botswana.

Season also influences their feeding ecology, with male elephants in the Okavango Delta feeding on a diverse range of vegetation in the flood season, whereas in the rainy season they fed mainly on grasses. Flood season caused a limitation of preferred food species so the elephants were forced to feed on sub-optimal food resources, whereas in the rainy season they tended to feed on the preferred food resources. Similar feeding behaviour has also been recorded in bats species, whereby they feed on sub-optimal food sources in period of scarcity (Lewanzik *et al.* 2012; G. Jones *pers. comm.*). At La Selva Biological Station, Costa Rica, it was discovered that frugivorous short-tailed bats (*Carollia perspicillata*) needed to visit a diversity of feeding sites and travel longer distances when fruits densities were lower in rainy season (Lewanzik *et al.* 2012). Evans (2006) observed

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the same trends on the feeding behaviour of male elephants and Pretorius *et al.* (2012) believed that seasonal changes in nutrient availability triggered changes in the foraging strategy by elephants to maintain their metabolic requirements. Additionally elephants increase feeding efforts in the dry season (Pretorius *et al.* 2012). I observed a similar trend on focal male elephants feeding on a diverse range of species in the flood season comparative to the rainy season (Figure 2.13).

Median distance between nearest neighbours within male elephant groups was also larger in the flood season. The may be due to a limitation of food resources and so increased competition. During the rainy season they are able to feed in closer proximity because there is an abundance of food resources in the rainy season (Evans 2006) and so less intra-specific competition.

I found that older male elephants' are generally in better body condition than the younger males. This makes sense as adolescent male elephant's energy costs are higher than older male elephants due to a growth spurt at this time (Lee *et al.* 2011). Additionally young male elephants invest some energy into learning about the area and where food resources are, as well as getting to know new individuals (Evans & Harris 2008). Older male elephants know where to find the food resources in different seasons through the knowledge they have gained through experience: young males may learn by following the older males (Evans & Harris 2008). Older male elephants have the ability to feed on prime resources like the fan palm nuts (Evans 2006) by utilising their body size, as these trees need vigorous shaking to release the nuts. Camel thorn trees in MNP are shaken by older male elephants to feed on the fruits (*pers. obs.*) Even though young male elephants may also feed on fan palm nuts they invest a lot of energy following older male elephants and at times wait for the older males to move to another tree so they can feed on the leftovers.

Poor body condition of male elephants' \leq 25 years old may be a contributing factor to many not reaching maturity. Poor condition leads to susceptibility to diseases, increases mortality rates during drought and increases the risk of predation, as two thirds of elephants killed by lions in Savute were young male elephants (Joubert 2006). Fewer male elephants \geq 26 in this study may be an indication that few of the younger male elephants' \leq 25 in poor condition are able to reach maturity. Growth costs diminish with age but competitive costs increase. To be

a successful, a male elephant needs to be a large male to compete and so it is important for mature males to maintain good size and body condition.

The presence of musth males in the study area is not linked to the number of females or season. This has changed since Evan's study (2006), where more musth male elephants were observed in the flood season. It also differs from Amboseli, where there is seasonal variation in reproductive activity in male elephants (Eltringham 1982; Ganswindt *et al.* 2005): males often time their musth cycle to ensure that they are not in musth simultaneously with their close associates (Eltringham 1982; Ganswindt *et al.* 2005; Lee *et al.* 2011). Although more individual males were seen in musth in the rainy season in Amboseli, some individual males were seen in musth throughout the year, with higher numbers in January to July than it was from August to mid-January (Poole *et al.* 2011). In both the Okavango Delta and Amboseli the seasonal patterns were similar across the years.

Musth did not impact on the body condition of male elephants. I expected musth to impact on the body condition as less time is spent feeding and musth male elephants roam over long distances in search of oestrous females (Poole *et al.* 2011). In Amboseli (Poole *et al.* 2011) found that males that were in musth for longer periods lost more body condition in comparison to males with short musth episodes. The male elephants in the Okavango Delta roam over long distances, which may explain the disparity in results and musth sightings, were sporadic. Rutting male takin (*Badorcas taxicolor*) in captivity put weight on in spring and lost body condition in summer during the breeding period. This makes sense because the energetic demands of ungulates increase in the breeding season as male fights to access females are common (Guan *et al.* 2012). I would expect male elephants to be in musth for longer periods after the rainy season when they have bulked up on the grasses. Musth in male elephants, as rutting in ungulates, may ensure that females are able to mate with strong and resilient males.

Additionally must duration increases with age until a male elephant is approximately 50 years of age, after which it starts to decline. Males of 26-35 years tend to come into must for approximately two weeks and for several times a year rather than one long period as seen in older individuals. Must in male elephants >35 years occurs once a year for 4-8 weeks, and for 46-50 year-old elephants for more than eight weeks (Poole *et al.* 2011).

Hunting may be impacting negatively on male elephants as it is generally males >35 years that are killed for trophy hunting; these are the males with longer musth periods. By taking out the dominant individuals it is likely that competition will increase amongst the less dominant to take their place. In addition this active selection by hunters of larger males means that females may mate with less-strong individuals.

Professional hunting is still taking place in some areas of Botswana. A recent aerial survey by Chase (2011) in the Okavango Delta showed a dramatic reduction of animal species. As a consequence the Botswana Government is reviewing their hunting policy and considering stopping hunting completely (Gaothobogwe 2011). Whilst the campaign to switch from hunting to photographic safaris is strongly supported by some safari operators, some wildlife conservationists argue that hunting quotas empower and develop local communities in Botswana. Even if hunting is banned in Botswana, hunting persists in Angola, Namibia, Zambia and Zimbabwe, which form part of the range of elephants of northern Botswana. The management of elephants in this region needs an integrated approach as these elephants do not respond to borders: the Kavango Zambezi Transfrontier Park (KAZA) between the five countries will play an integral part in the future management of the elephants of northern Botswana (Hanks & Cronwright 2006).

In the next chapter I will relate my findings to elephant conservation and the issues discussed in the introduction.

Chapter 3

3.1 Foreword

In this final chapter I reflect on my findings and how they can be applied to the conservation issues currently facing African elephants, in particular how my findings increase our knowledge on the seasonal movement of mammals, its applicability to human-wildlife conflict and the management of elephants, and the importance of the Okavango Delta for large mammals.

The over exploitation of the African elephant in the past two centuries has caused serious range reduction, local extinction and large scale population declines (Bouche *et al.* 2011). In many range countries elephants are now struggling to survive. With their requirement for large areas to meet their ecological needs, African elephants are in competition with humans, with 70% of the remaining population living outside protected areas (Blanc *et al.* 2007). So understanding the seasonal effects on male and female elephants will enable us to make better management decisions in the future and help predict movements in response to climate change.

3.2 The importance of the Okavango Delta as a resource for elephants

The Okavango Delta is an important dry season resource for elephants and other mammals, providing grazing for the migratory mammals that move between the Okavango Delta and the MNP (Fynn and Bonyongo 2010). However, resource availability in the non-rainy season in the Okavango Delta is limited by floodwaters, and the increasing levels of the flood in recent times has affected large mammal species, especially elephants.

The buffalo fence on the edge of the Okavango Delta was erected to stop the transmission of foot-and-mouth disease between buffalo and cattle, but it is stopping animals from reaching dry season resources in the Okavango Delta and rainy season resources in the MNP, and may be contributing to the decrease in large mammal numbers in northern Botswana (Chase 2011).

The Okavango Delta itself is far from a stable ecosystem, with seasonal and other temporal changes due to raising floodwaters, rains and occasional drought. This has had an effect on the elephants in the western Okavango Delta, which has changed from a predominantly bull area to an area suitable for female herds. The seasonal changes also affects the male elephants groupings, with the floods forcing them into small areas of dry land and increasing competition for food, resulting in more lone males being seen and, when they are in a social group, they are more spread out.

3.3 Botswana

Whilst the Okavango Delta is often described as an independent entity for wildlife, we are now realising that we must conserve elephants and other wildlife on a meta-population scale for northern Botswana and beyond to incorporate their social and ecological requirements throughout the seasons. Botswana's conservation areas, and in fact many of Africa's conservation areas, were designated without considering the seasonal requirements of mammals. These protected areas are often suitable for either the rainy season or dry season range of the migratory animals and do not support the annual needs of animals, rendering them dysfunctional (Fynn and Bonyongo 2010). This has unfortunately led to the drastic reduction of animal populations in Botswana, with veterinary fences being put up from the 1950s furthering the fragmentation of populations (Keene-Young 1999; Mbaiwa & Mbaiwa 2006). Immediate economic benefits in developing countries are often put before sustainable income that healthy wildlife populations can offer, and agricultural development in many countries is being driven by the needs to meet European Union requirements. This has detrimental effects on the conservation of migratory mammals (Mbaiwa & Mbaiwa 2006).

The KAZA between Angola, Botswana, Namibia, Zambia and Zimbabwe will encourage migratory mammals to re-establish their migratory routes, as it is opening up a vast area for wildlife. This will reduce pressure on some conservation areas such as the Chobe National Park that is currently supporting a lot of elephants and other mammalian species.

Environmental changes are influencing animal movements in the Okavango Delta. The current wet phase in the Okavango Delta will be here for the next 10-15 years and during this period there will be a big shift in elephant movements, which we are already seeing, with large numbers of male elephants being sighted in the MNP (Chase 2011). So the Botswana Elephant Management Plan needs to be flexible to incorporate changes in the dynamic ecosystems of the country and plan for the associated changes. Understanding the social and ecological requirements of elephants in Botswana will assist the government to meet these requirements.

3.4 Seasonal movements of mammals

Human population increase throughout the world, which reached 7 billion in 1 (United Nations 2011), is resulting in loss of habitat for wildlife and increased human wildlife conflict. Ecosystem management needs to take into consideration seasonal movements of mammals, which are influenced by resource availability, reproduction opportunities, predation risks and anthropogenic activities. Some conservation areas are not encompassing the rainy and dry season range of migratory mammals: reconnecting conservation areas through corridors for migratory mammals helps in the long-term conservation of viable populations of mammalian species. For the ecosystems that can be restored, resources need to be channelled to ensure the reestablishment of migratory routes. The Kruger National Park in South Africa, Kgalagadi Ecosystem in Botswana and Etosha National Park in Namibia are dysfunctional because of the lack of connectivity between rainy and dry season resources, whereas the Serengeti Ecosystem in Tanzania and Boma Ecosystem in Sudan are functional conservation areas supporting large populations of ungulates. Although the Serengeti Ecosystem is currently fully functional, it may experience major declines in the ungulate populations with the planned road that will transverse the ecosystem, cutting the Serengeti in two (McVeigh 2011). Roads may reduce resource quantity and quality whilst proximity to the roads may present an unacceptable risk to the elephants and other animals (Blake 2008; Bouche *et al.* 2011).

In most of their range the remaining elephants are now isolated in a few protected areas surrounded by agriculture. The spatial constriction bound by increasing human activities results in conflict between humans and elephants (Bouche *et al.* 2011). However, these areas will change over time as the climate changes and then the elephants are likely to move into human habited areas and the conflict will increase, with humans likely to be the victors.

The removal of fences or identification of migratory corridors will help in the conservation of the Kgalagadi Ecosystem of Botswana: this needs swift implementation. Although the politicians are major decision makers vested with the powers to implement the advice from scientific communities, they are mainly focusing on short-term political benefits. However, internationally Botswana is working with neighbouring countries to develop Transfrontier Peace Parks to better manage large populations and enable them to restore ancient migration routes.

It is not only fences that act as barriers: roads are a similar barrier to movements and can directly cause deaths. For instance, deaths on the Trans-Canada highway frequently included black bear, coyote (*Canis latrans*), wolf (*Canis lupus*), moose (*Alces alces*), big horn sheep (*Ovis canadensis*), deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) (Clevenger *et al.* 2001). Therefore development in conservation areas, with barriers to movements such as fences and major roads, is detrimental to conservation. It isolates populations, leading to possible inbreeding, susceptibility to diseases and inability to escape adverse conditions. In addition to habitat fragmentation, roads cause disorientation of the animals from the noise pollution produced by traffic.

3.5 Importance of this work to conservation and application to elephant conservation and management

The management of elephants and understanding the behaviour of male elephants helps in the management of conflict between humans and elephants, as male elephants are responsible for most crop raiding (Mosojane 2004; Jackson *et al.* 2008). If we improve our knowledge of male elephants ecological and social requirements, we will be better equipped to manage them *in situ* and *ex situ* and help improve mitigation techniques.

Elephants are an umbrella species as they need large areas, and so if we understand the requirements of elephants and conserve them we can conserve other mammals that utilise the same area, including many other migratory species.

3.6 Conflict

The conflict between elephants and humans is increasing in Botswana and throughout Africa because elephants are spreading back into historical ranges now occupied by humans, and humans are encroaching into wildlife areas. The Botswana government needs to develop novel ways to manage this conflict, and my study adds to the body of science helping understand male elephants and their management. Knowing more about seasonal requirements of male elephants, which are the main crop raiders, may assist with predicting crop-raiding and used as an early warning system for farmers to help prevent damage occurring (Mosojane 2004; Jackson *et al.* 2008). Much the same has been seen with gray wolf (*Canis lupus*) predation, which is influenced by seasonal variations that change prey vulnerability (Metz *et al.* 2). Predation events with gray wolves are opportunistic, and the same may occur with elephants. More data are needed on the feeding preferences and nutritional requirements of male elephants to understand seasonal patterns of resource exploitation and availability.

Social networks also provide a new approach to understanding male elephant society, and have been particularly useful for unraveling the social structure in fission-fusion animal societies (James *et al.* 2009). Understanding the social structure of male elephants will be key to developing new management techniques. So, for instance, knowing when male elephants join herds will help in mitigation of conflicts between human and elephants and advance our ability to understand elephant movement patterns. Throughout this study I have reported to the DWNP on a quarterly basis to assist with their understanding of male elephants and how they

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utilise the Okavango Delta in particular. These reports have highlighted the changes in the social ecology of elephants in the area and when male elephants move out of the Delta, possibly into human-habituated areas. Furthering our understanding of male elephant seasonal movements, behaviour and sociality will enhance our ability to mitigate problems and manage elephant populations more effectively.

3.7 Future research

I believe that there is still some way to go to understand the social network of male elephants, particularly those inhabiting larger more open areas such as those found in Botswana, where their social groupings may be more representative of elephant behaviour before populations became fragmented. Conservation in the past has often just focused on numbers, but their social and ecological requirements are equally important if we are to have sustainable populations. Thus Caribbean flamingos (Phoenicopterus ruber ruber) will only breed if their social grouping is above a certain size (Stevens 1991). This has led to the use of mirrors in captive flocks to stimulate breeding. Using social networks to understand the social behaviour of marine mammals (e.g. Lusseau 2007; Connor et al. 2011) has been instrumental in advancing their conservation and management, and provides a good example of what could be achieved for elephants. On leaving their natal herds, male elephants have a choice of association with other male elephants and the areas of foraging are unconstrained by family decisions (Lee et al. 2011). With this independence, male elephants start to roam over large areas to explore the available food resources and to bulk up to maximise access to reproductive females and reduce the risks of competition and mortality (Lee et al. 2011). Young male elephants spend more time with females in comparison to older males. Hunters often wrongly assume that males do not have a role to play in elephant society, particularly after they pass their reproductive peak, and so they believe that the loss of older males will not be detrimental to elephant ecology (Lee et al. 2011). However, older male elephants play an important role in mentoring the young male elephants, a role similar to matriarchs in breeding herds (Evans 2006; Evans & Harris 2008).

After independence male elephants will develop particular preference for "bull areas" (Lee *et al.* 2011). These are distinct from areas favoured by females and mixed herds (Lee *et al.* 2011). In Botswana, the MNP is a typical example of a bull area; in

recent years there has been an influx of male elephants, which are forming larger groups than in the Okavango Delta. However, this is also leading to a large number of reported incidents of human-wildlife conflict. A study needs to be commissioned on human elephant conflict in the Boteti region. In particular, the animals that are responsible for most of the damage need to be identified to determine if there are repeat, "crop raiders" or if this is a random and opportunistic event. Work also needs to be undertaken with the communities in those areas to mitigate the conflict. Finally, due to increasing interaction between wildlife and livestock, more studies are needed on the potential transfer of zoonosis between livestock and wildlife. These developments will help us move towards human-wildlife coexistence.

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