2019

African Savannah Elephant Group Size and Behavior in the Makgadikgadi Pans National Park, Botswana

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May 20th, 2019

A thesis submitted to the faculty of the Environmental Studies Program in partial fulfillment of the graduation requirements for the Degree of Bachelor of Arts with honors in Environmental Studies

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ABSTRACT

African savannah elephants (*Loxodonta africana)*, the largest elephant species, influence the structure of the environment they inhabit. Elephants exhibit complex patterns of social behavior between individuals within a population. Many behavioral studies focus on interactions among individuals within a population rather than broader trends related to group size. My study seeks to understand how male African savannah elephant group size is influenced by seasonality, age, physical condition and distance to permanent water resources. I examined the interaction of these variables in two ways: (1) a literature review of elephant behavior and conservation, and (2) an analysis of male behavior using data collected by the non-profit Elephants for Africa (EfA) in the western Makgadikgadi Pans National Park, Botswana. I used ArcGIS to extract distance from water for each observation and R to conduct parametric and non-parametric tests to evaluate the relationship between season, age, physical condition, and distance to permanent water sources. Major findings of this study include the greater independence ($p = 0.001$) and physical conditions of older males, as well as increased proportions of older males in the dry season, and better physical conditions in the wet season due to seasonal resource availability. These results are consistent with other studies that find young males to be more sociable and dependent on quality resources. My findings provide insight into the patterns of age, physical condition and resource availability related to seasonality which are useful in developing management strategies around water and forage across seasons to mitigate human-wildlife conflict.

ACKNOWLEDGEMENTS

I would like to extend a huge thank you to everyone who supported me throughout this research. This includes, but is not limited to, my faculty advisor Dr. Philip Nyhus who has pushed me to produce my best work and learn what it means to conduct this kind of research. I would also like to thank Dr. Kate Evans for advising throughout the process and being an invaluable source of knowledge on elephants in Botswana that was vital to the interpretation of these data. Many thanks go Elephants for Africa (EfA) for allowing me access to their historical data, a special thanks to all the EfA team members who collected the data over the years. These data were collected by EfA with permission of the Ministry of Environment, Natural Resources, Conservation & Tourism, Botswana under permit number EWT8/36/4XXXII(35). Thank you to Dr. Manuel Gimond for providing unlimited support in navigating ArcGIS and R as well as interpretation of statistics. I also owe a huge thank you to my funding sources, the Colby College Environmental Studies F. Russel Cole Fellowship, Davis Connects, and Round River Conservation Studies who provided me with a summer internship opportunity in Botswana that lead to the connection with EfA.

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CHAPTER I: INTRODUCTION

Overview

The largest of the world's elephant species, African savannah elephants (*Loxodonta africana*), and forest elephants (*Loxodonta cyclotis*) have recorded populations ranging from Egypt to South Africa (Jetz et al. 2012). African savannah elephant habitat consists of grasslands, woodlands and forests where they are both browsers and grazers (Chiyo et al. 2005). Weighing approximately six tons, male elephants have a significant impact on their environment through soil compaction, foraging, and boring behavior (Haynes 2012). How elephants move across the landscape is important to understanding the spatial and temporal impacts they have on the wildlife and humans that share their environment.

The social structure of elephant communities influences how individuals interact with each other, and thus how they interact with their environment. Many studies on African savannah elephant behavior use complex social analysis to determine levels of association between individuals as a means to understand broader trends in the social structure of elephant populations (Wittemyer et al. 2005, Pitfield 2017). The socio-ecological structure of elephants is complex, made up of varying levels of interaction and association between related and unrelated individuals (Wittemyer et al. 2005).

Social interactions among male elephant populations are also influenced by both seasonality and individual factors such as sex and age. Several studies conclude that adolescent males are the most sociable age group, typically seeking association with older males, who have the greatest number of individual associations in the population (Evans and Harris 2008, Chiyo et al. 2011). Sociality of females on the other hand is highly determined by relatedness of individuals within a group. The functions of female groups such as calf defense, parenting assistance, and shared ecological knowledge are most beneficial when these groups consist of related individuals (Archie et al. 2006, Archie and Chiyo 2012).

With one of the largest remaining populations of African savannah elephants, Botswana is home to an estimated 134,000 individuals (Thouless et al. 2016). The majority of the populations in Botswana (70-80%) lives outside the borders of protected

areas (Thouless et al. 2016). As populations of African savannah elephants grow, it becomes increasingly important to understand their behavior, social interactions and movements within and outside the protected areas of Southern Africa. Metapopulation theory suggests this expansion may be necessary for maintaining smaller satellite populations through migration (van Aarde and Jackson 2007); however, expanding populations have cascading effects on the natural environment and on the humans that inhabit it.

Areas of high elephant density are typically subject to crop raiding, property destruction, and suppression of natural vegetation (Skarpe et al. 2004, Sankaran et al. 2008). Local management practices have typically dealt with alleviating the symptoms of such conflict rather than targeting the causes of increased elephant densities in areas like the Okavango Delta, Botswana (van Aarde and Jackson 2007). Hypotheses for increased population densities include higher density of vegetation and artificial water holes (Chamaillé-Jammes et al. 2007) or a change in surface water availability due to climate change (Chamaillé-Jammes et al. 2008). Another is that fluctuations in the population are natural, and even adaptive for creating more resilient ecosystems (Skarpe et al. 2004, van Aarde and Jackson 2007).

In this thesis I sought to explore factors affecting elephant behavior in central Botswana. I first conducted a literature review to better understand environmental and individual factors that influence elephant behavior. The factors identified in this review guided my exploration of drivers of male elephant social structure. In Chapter II, I use behavioral data collected by Elephants for Africa (EfA), a non-profit NGO based in Botswana, to examine the effects of age, physical condition, and seasonality on group size of males in the Makgadikgadi Pans National Park (MPNP).

Land Use in Botswana

Botswana contains six protected areas (game reserves and national parks), many of which are connected by wildlife management areas (Fig. 1). One noticeable gap in these protected areas is that between the Central Kalahari Game Reserve (CKGR) and the MPNP, an area dominated by pastoral and residential land uses. African wildlife has faced great loss in connectivity across the continent, in large part due to livestock grazing

and human population growth (Schüßler et al. 2018). A better understanding of how elephants use these areas on both a seasonal and daily time frame can help to inform policies that promote connectivity and to mitigate human-wildlife conflict.

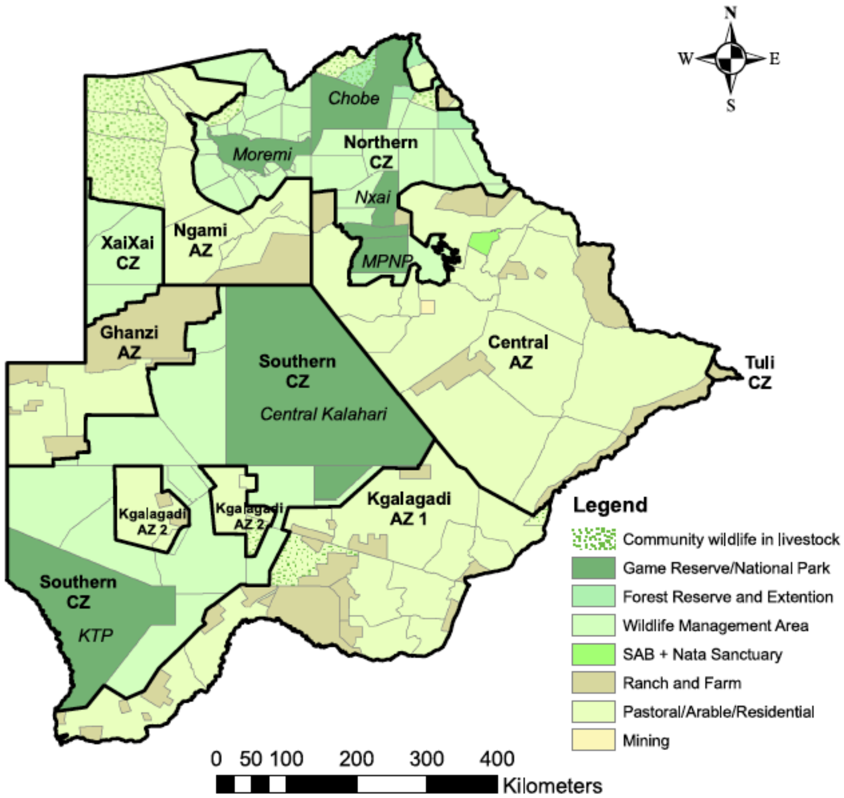

Figure 1. Map of land use and protected areas in Botswana (Winterbach et al. 2015).

Loss of habitat connectivity can affect seasonal movement and migration patterns of African savannah elephants. While African savannah elephants are not a migratory species, individuals may migrate opportunistically over annual time scales as a result of excessive population density, insufficient forage abundance (Purdon et al. 2018), or low availability of water resources (Galanti et al. 2006, Tshipa et al. 2017). On shorter time scales, elephants may move between “home sectors,” often located inside protected areas, each connected by travel corridors (Douglas-Hamilton et al. 2005). Understanding how elephants use these corridors is complicated by the presence of natural and artificial barriers.

Factors Affecting Elephant Movement

Using the search terms, “African elephant”, “behavior”, and “movement” in the Scopus database, I found 23 papers about elephant movement and behavior. I recorded the factors affecting elephant behavior in each paper. Many papers discussed more than one topic. Water availability and distribution was the most common factor mentioned in 52.2% of papers, followed by forage availability mentioned in 39.1% and risk related to mortality and predation mentioned in 30.4% of papers. Six of the nine papers on forage also mentioned water availability as a key connection to spatial and seasonal factors that influence the small- and large-scale movements of elephants. This is likely a result of the seasonal component of both water and forage abundance, particularly on arid landscapes such as that found in Botswana.

Water Distribution and Availability

Botswana has two clearly distinct seasons. In the wet season (months with >10 cm precipitation), typically November or December to April or May, water is widely available in ephemeral waterholes. During the dry season only perennial sources of water are available (Pitfield 2017). These seasonal shifts in water availability can lead to changes in elephant behavior, which occur at the end of the dry season, just before the first rains, and at the end of the wet season (Birkett et al. 2012). Permanent sources of water are typically visited more often by elephants during the dry season (Wittemyer et al. 2008) leading to smaller dry season ranges compared to wet season ranges (Galanti et al. 2006). These seasonal patterns in space use are linked to the average speed at which individuals and groups travel, typically traveling greater distances in the dry season and faster and more randomly in the wet season to access more widespread water resources (Cushman et al. 2005, Loarie et al. 2009, Birkett et al. 2012). This change in movement speed and distance in the wet season can be taxing on vulnerable individuals, particularly juveniles that face higher risk of predation with long distances traveled to water in the dry season (Loveridge et al. 2006). Elephant movement is more randomized in the wet season when water resources are dispersed. In the dry season when water resources are restricted, advanced spatial memory allows elephants to move in a highly directional manner towards permanent water sources (Polansky et al. 2015). Naturally permanent

water sources like rivers can act as important functional corridors between protected areas (Van de Perre et al. 2014). Artificial water sources like boreholes pumped year-round by humans can also alter elephant movement by allowing for larger dry season ranges and contributing to the development of partial migration in some populations (Loarie et al. 2009, Tshipa et al. 2017). Seasonal fluctuations in water availability also increases the potential impact of artificial water sources. For example, creating artificial waterholes in remote areas could be a strategy to draw elephant populations away from human settlements (Tshipa et al. 2017). The effects of water availability on individual elephants within a population may depend on a variety of factors, including age, sex, and present physical condition. For example, older males are typically the least affected by harsh, low water conditions during the dry season compared to females or younger males (Evans 2006).

Forage Abundance

The influence of forage abundance on seasonal elephant movement patterns cannot be entirely separated from the effects of water distribution and availability. There are a few important differences in how elephant diets change between age, location, and season. The body size of adult females allows them to consume more woody material than newly weaned juveniles (Woolley et al. 2011). Juveniles are dependent on forage quality, making them more susceptible to seasonal shortages than adult females (Woolley et al. 2009). Similarly, older male elephants can endure prolonged periods of low forage abundance compared to females and younger males (Evans 2006). Elephant populations residing in habitats with different vegetation distributions do not consume significantly different diets based on local abundance, but rather they select forage based on nutritional needs, specifically protein content (Codron et al. 2006). Seasonal changes in forage availability in the same location during the wet season generally results in higher quality diets than the dry season, when high protein grasses are less available (Woolley et al. 2009). Variability in forage by season can also influence group size. Chiyo et al. (2014) found that males form larger groups in areas of higher primary production (forage availability). This is likely a result of decreased competition for resources providing the

opportunity for social interactions without the negative impacts of overcrowding when resources are limited.

Mortality and Predation Risk

Where, how long, and in what group size elephants spend their time can also be influenced by the risk of mortality and predation in different landscapes. Elephants typically spend the majority of their time in core areas located inside protected areas; however, the major range of many elephants is located outside of protected areas (Douglas-Hamilton et al. 2005). Human-induced mortality risk can drive elephants to move faster outside of protected areas compared to inside (Douglas-Hamilton et al. 2005, Galanti et al. 2006). Risk may also affect the rate of movement on a daily cycle, where elephants remain in protected areas during the day, and venture outside of protected areas at night, when the risk of human encounter is reduced (Galanti et al. 2006, Hemson et al. 2009).

Perceived risk by elephant populations can also fluctuate seasonally based on the level of vegetation available for camouflage. Chiyo et al. (2014) found that males form larger groups for safety in areas of low primary production outside of protected areas. This is potentially a result of increased anthropogenic mortality in these areas, particularly in the dry season when there is little vegetation to conceal their presence on human landscapes (Chiyo et al. 2014).

Sociality and Group Composition

Elephant herds tend to follow set patterns in composition of age, sex and sexual receptivity. These group demographics and behaviors may also experience seasonal fluctuations. Among female elephant social groups, one of the strongest predictors of group fusion is relatedness of older females, meaning related individuals and groups of females tend to associate more with each other than unrelated ones (Archie et al. 2006). While in these tight knit groups, individuals may keep track of other individuals in their herd through chemical identifiers in their urine (Bates et al. 2008). The formation of social bonds among related adult females becomes adaptive through group defense of

calves, parental assistance, resource defense, and shared social and ecological knowledge (Archie et al. 2006).

Groupings of juvenile and adult male elephants function much differently than that of females. Older males typically have a greater number of social associations than younger ones, reflecting clear leadership roles in older males across elephant societies as a whole (Chiyo et al. 2011). Evidence suggests that other individuals, such as adolescent males, recognize this knowledge held by old males. Adolescent males are the most social group of bull elephants, often associating with an older male from whom they can gain social and ecological knowledge (Evans and Harris 2008). All of these interactions fit into complex, four-tier social systems within elephant populations. The first tier consisting of individual interactions, the second, family groups of two-three individuals, the third, a combination of multiple familial groups, and the fourth, an even broader connection through association of third tier groupings (Wittemyer et al. 2005). In some areas, including the MPNP, bull elephants function as temporary residents. This can occur particularly in the dry season, when there are more old adult males present compared to the wet season (Pitfield 2017).

Human-Wildlife Conflict and Poaching

Elephant behavior can also be used to evaluate risk and potential solutions to human-elephant conflict. Human settlement alongside protected wildlife areas has resulted in significant crop and livestock damage. In the crop lands in the northern panhandle of the Okavango Delta, 78% of crop damage was attributed to wildlife, specifically elephants (Campbell 2004). Jackson et al. (2008) found that crop raiding alone contributed to an 11% decrease in income for farming families. This study also examined how conflict such as crop raiding can vary depending on seasons around the Okavango Delta. The authors found that crop raiding by elephants was greatest during the transition from the dry to the wet season as elephant herds began to move away from concentrated water sources.

Poaching

Poaching can also alter elephant behavior. Through the selection of adult males with large tusks, poaching has the potential to reduce the adaptive value of social relationships when fewer knowledge-holding males are available for adolescents to bond with (Archie and Chiyo 2012). Such selection can also result in inbreeding, particularly in small populations, that increases the loss of genetic diversity (Archie and Chiyo 2012).

Crop Raiding

Many studies across Africa and Asia have focused on both spatial and temporal patterns of crop raiding by elephants. Studies typically agree on the seasonal pattern of increased incidence of crop raiding during the wet season, when crops mature (Galanti et al. 2006, Chen et al. 2016). Social factors also influence the likelihood of crop raiding by specific individuals. For example, Sitati et al. (2003), in a study of Asian elephants (*Elephus maximus*), reveals a correlation between the area under cultivation and crop-raiding events by both male and family groups. Male crop raiding was also correlated with the proximity to towns, meaning family groups are more cautious around human settlements (Sitati et al. 2005). A study in China exploring spatial determinants of crop raiding found the highest correlation between distance to protected areas and settlement density to incidents of crop raiding (Chen et al. 2016).

Fencing and Mitigation

Fencing around protected areas has been a popular human-wildlife conflict mitigation strategy used in Botswana in recent years; however, fencing is often not successful because it is permeable to wildlife populations. Elephant movements in particular are minimally affected by even electrified fences. Elephants can easily knock down fences opening passages for other wildlife (Ferguson and Hanks 2010, Kesch et al. 2014a). Elephants can become habituated to using the fence gaps they create and have been observed returning to these areas even after the removal of fences (Dupuis-Desormeaux et al. 2018). Fence crossings by both elephants and lions is more common in the dry season, particularly when fences block access to a major water source. For example, fencing along the Boteti River in central Botswana separated the MPNP from

the river in some spots, leading to frequent occurrences of wildlife crossing the fence to access this perennial water source (Kesch et al. 2014b).

In some areas, fencing blocks elephant movement more effectively, including blocking movement to wider wet season territories. Where this is the case, elephants still attempt to break through, and therefore threaten the sustainability of fences (Ferguson and Hanks 2010). When elephants are retained in relatively small areas during the wet season, they are forced to visit the same areas for forage more than usual, creating an unnaturally high level of herbivory on vegetation in these areas (Loarie et al. 2009).

Summary

Seasonality is an important driver of elephant behavior and movement across landscapes. In Botswana, seasonality changes habitat and affects the availability of important resources such as forage and water. Fluctuations in these resources drives elephants to change the way they interact with the landscape and with each other. These shifts in behavior mean that elephants take on very different roles in the ecosystem during different seasons. Negative interactions with humans and the barriers that they erect challenge elephant behavior and ultimately alter it, leading to a dynamic interaction between elephants, humans, and the landscape they share.

CHAPTER II: FACTORS AFFECTING GROUP SIZE

Introduction

African savannah elephants are highly social creatures, relying heavily on familial ties and connections between individuals to survive (Archie et al. 2006; Chiyo et al. 2011). Elephant behavior and movement are influenced by land use, physical barriers, and seasonal fluctuations, such as rainfall events that alter the availability of surface water (Douglas-Hamilton et al. 2005, Chamaillé-Jammes et al. 2007, Loarie et al. 2009, Birkett et al. 2012). Elephants possess excellent spatial memory allowing them to develop advanced understanding of their surrounding landscapes, reflected in highly directional movements toward desired locations (Polansky et al. 2015). Social standing of individuals can also influence patterns of behavior, where more dominant individuals tend to move more consistently than subordinate ones, and younger males seek out groups containing older males in order to learn from older individuals (Evans 2006, Evans and Harris 2008, Wittemyer et al. 2008).

Male elephants are often concentrated in bull areas, places with a higher proportion of males than females, where short-term associations between individuals occur. The Makgadikgadi Pans National Park (MPNP) in Botswana is an important bull area for surrounding populations, where young males learn from older ones (Pitfield 2017). Bull areas are important social resources for elephant populations because of the learning opportunities they provide. Males leave their herds at adolescence, roaming between natal and bull areas (Archie and Chiyo 2012). Adolescent males from 10 to 20 years of age are typically the most sociable age group, favoring groups with males greater than 36 years old (Evans and Harris 2008).

Most studies surrounding elephant sociality focus on the associations of individuals within the broader social network (Evans and Harris 2008, Pitfield 2017). My study seeks to understand the variables affecting individual group size of males in bull areas, specifically that of the MPNP. Anecdotal evidence suggests the demography of male populations in the area has been changing in recent years (Kate Evans, personal communication, March 2019). Analyzing how age and physical condition influence group size is vital to understanding the social dynamics of this population. As elephant populations in the protected areas of Botswana increase and expand into surrounding

human settlements, group size dynamics may influence patterns of conflict. Understanding how factors such as age, physical condition, and seasonality create fluctuations in habitat and social structures is important to the impact of this changing population on the landscape.

For this study, I used behavioral data collected in the western MPNP by Elephants for Africa, a non-profit NGO. I hypothesized that (1) there is lower observed physical condition, larger observed group size, and higher observed proportion of old individuals in the dry season, (2) there is a negative relationship between observed age and physical condition and observed group size, and (3) elephants observed in older age classes are observed farther from permanent water sources than young elephants.

Methods

Study Location

The focus area of this study was the western MPNP (Fig. 2). This reserve borders the perennial water source of the Boteti River that supplies water to humans and wildlife in this area year-round. This section of the park is bordered by pastoral land to the west and wildlife management areas and the Nxai Pan National Park to the north. Several safari companies operate tours in this area of the park, known for its immense migrations of ungulates that take advantage of the Boteti River and artificial waterholes. The MPNP is an important environmental resource for elephants as well. This area is classified as a bull area. The population is dominated by males and appears to have an important social context where younger males are creating their network and may be picking up knowledge from these older individuals (Pitfield 2017).

Data Collection

From 2012 to 2018 Elephants for Africa collected behavioral elephant data by vehicle through four-hour research sessions where established routes were chosen at random. Observations were also conducted at the Boteti River. Only elephant groups that arrived at the river together were recorded in order to diminish error of short-term associations with large groups of individuals. Group size, habitat, GPS location, group leader and individual age, sex, physical condition and must status were noted. Age is

classified into 5- or 10-year increments (1-4yrs, 5-9yrs, 10-15yrs, 16-20yrs, 21-25yrs, 26-35yrs, 36+yrs). Physical condition was evaluated based on 5 categories (Table 1). Data used in my analysis included observations from 2012 to 2018, with 4,658 elephant observations.

Table 1. Physical condition classification by Elephants for Africa (Moss and Poole 1983).

Code	Physical condition
1	Emaciated: Very, very thin
2	Very thin. Shoulder blades, pelvic bone visible
3	Thin. Shoulder blades, pelvic bone and backbone 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

Data Selection

I used ArcGIS (ESRI 2018) to extract data on proximity of elephants to two permanent water sources, the Boteti River and an artificial water hole inside MPNP (Fig. 2). I used R (R 3.5.2 2018) to select data on age class, physical condition, and group size among males. Males were the focus of this analysis because the MPNP is a bull area where the population is dominated by males.

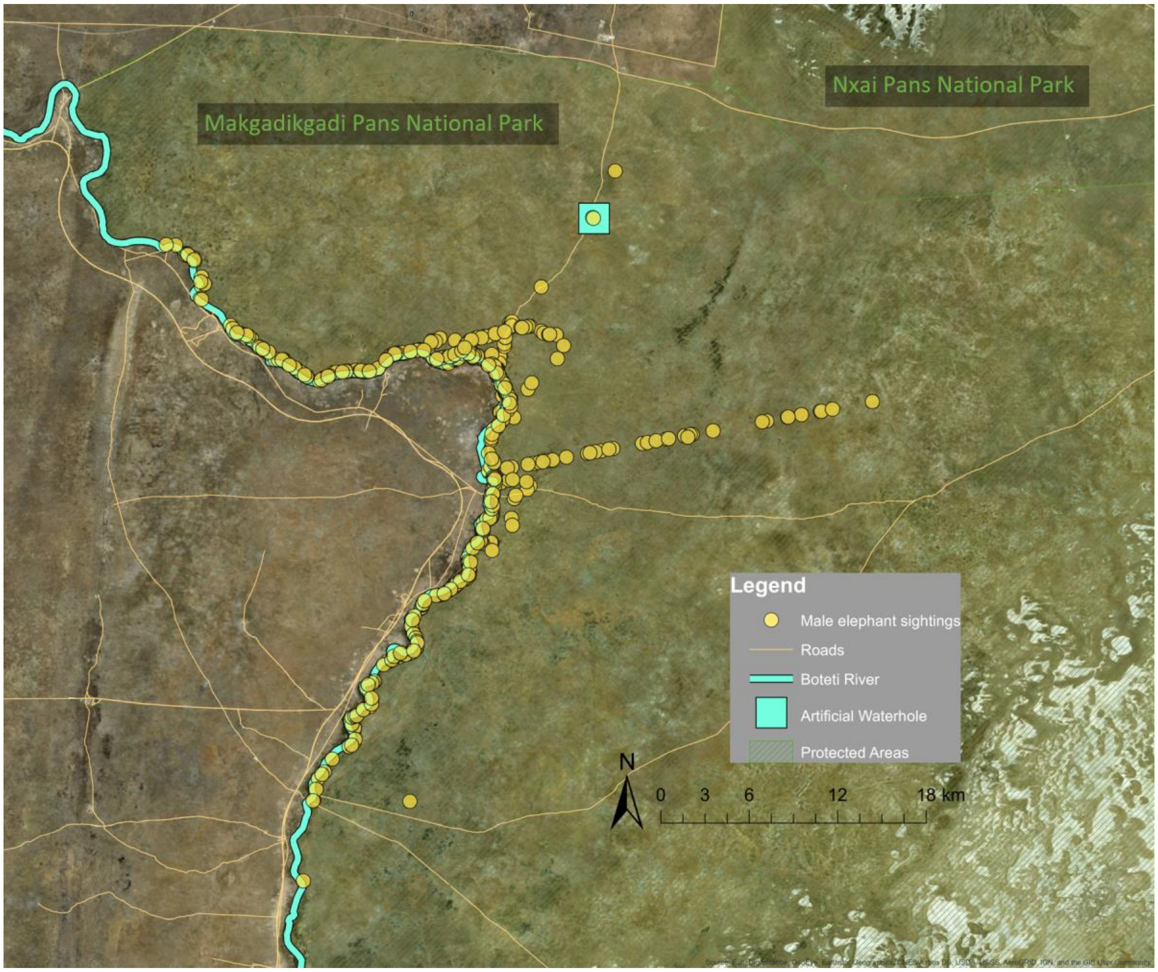

Figure 2. Map of study area portraying western MPNP, elephant observations, the Boteti River and artificial waterhole.

Statistical Analysis

I classified dry and wet season dates based on the methods of Pitfield (2017) using rainfall data from the Botswana Department of Wildlife and National Parks (DWNP) where the wet season is defined as months with >10cm precipitation and the dry season is defined as months with precipitation <10cm. Each measure of individual group size, age and physical condition was compared to these classified seasons. I explored Box Cox power transformations to normalize the observed group size between seasons. T-tests were used to test the difference between transformed mean observed group sizes between seasons.

I grouped age into young (≤25yrs) and old (>25yrs) in order to explore how differing levels of knowledge and vulnerability influence physical condition and distance from water. The 1-4-year-old age group was excluded from analysis since there was only

one observation throughout the study period. Physical condition was grouped into three categories, low (2-2.5), intermediate (3-3.5), and high (4-4.5), to increase sample size within each group. Observations with physical condition < 2 and > 5 were not recorded and thus not included in this analysis. I compared the relationship between age, grouped into young and old, and physical condition, grouped by low, intermediate, and high, by conducting exploratory analysis of age and physical condition proportions by season and the proportion of physical conditions among observations of young and old elephants.

A Jonckheere-Terpstra test was implemented to analyze the ordinal relationship between age class and observed group size. An ANOVA test was implemented to assess if the observed physical condition can explain some of the variability in the observed log transformed group size. A post-hoc Tukey HSD test was then implemented to compare pairwise differences between physical conditions. These same tests were used to compare physical condition and observed log transformed group size within each season.

I examined the relationship between the observed distance to permanent water sources and age class of observed individuals. By plotting the mean observed distance to water for each observed age class I qualitatively explained the relationship between these variables. I compared the observed transformed mean distance to water between observed age groups of young (≤25yrs) and old (>25yrs) individuals by implementing a t-test.

Results

Seasonality

Observed male group size was significantly larger during the dry season with a transformed mean observed group size of 2.41 ± 1.03 (n = 895) compared to the wet season transformed mean observed group size of 2.11 ± 1.03 (n = 620) (t = 3.436, df = 1321.7, p < 0.001). Comparing observed dry and wet season proportions of each age class reveals a greater observed proportion of older age classes, 26-35 years (0.151) and 36 + years (0.0350), in the dry season compared to the wet season (0.121 and 0.0176). This comparison also showed that there were greater observed proportions of 16-20 year-old males in the wet season (0.378) relative to the dry season (0.322), suggesting that the distribution of observed age classes was more spread in the dry season (Fig. 3).

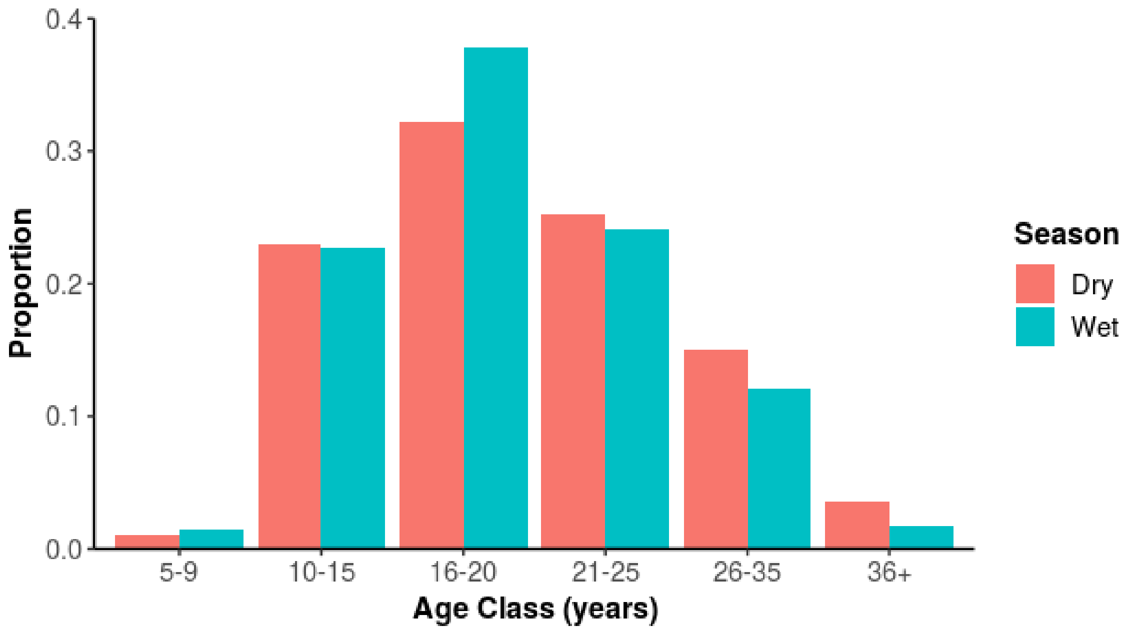

Figure 3. Observed proportion of age classes in the wet and dry season. There is a greater observed proportion of individuals from the 16-20 year-old class in the west season and greater observed proportions of 26-35 year-olds and 36+ year-olds in the dry season.

A smaller observed proportion of elephants exhibited a low physical condition scoring in the wet season (0.0190) compared to the dry season (0.114), and a larger observed proportion of elephants were recorded with a high physical condition scoring in the wet season (0.369) compared to the dry season (0.241). Overall, the population may be observed in better physical condition in the wet season (Fig. 4).

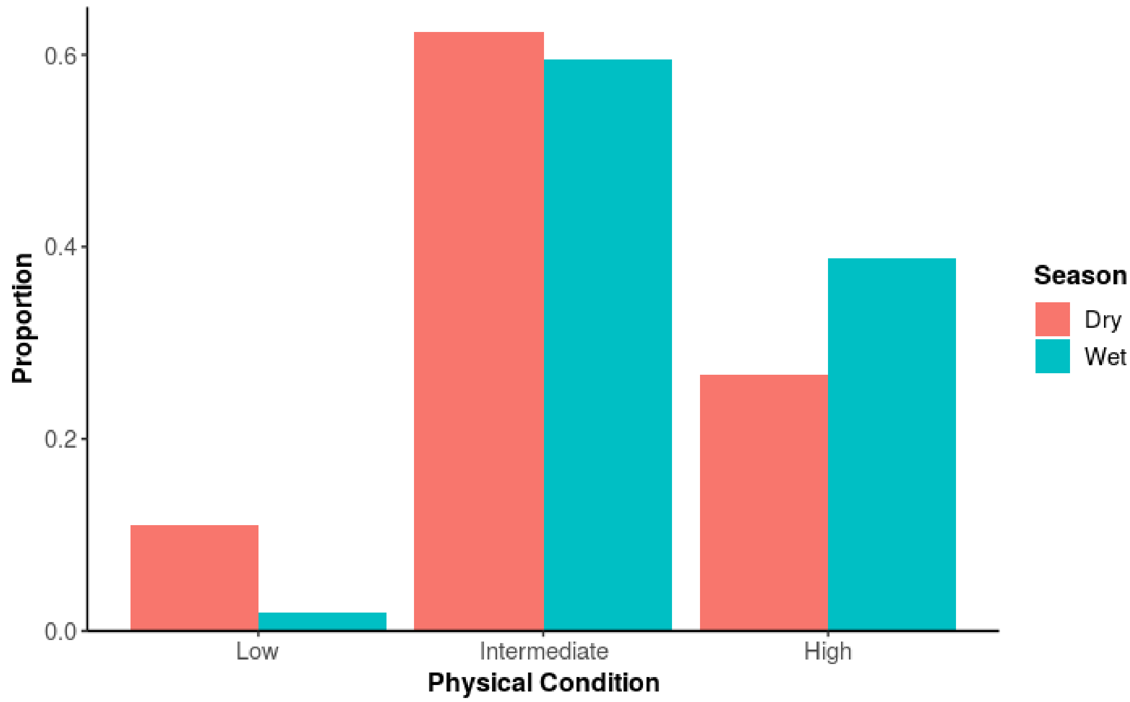

Figure 4. Observed proportion of grouped physical condition by season. There is a smaller observed proportion of individuals with low physical condition and larger observed proportion of individuals with high physical condition in the wet season.

Individual Characteristics

Both observed age and observed physical condition of the population changed between the dry and wet season. There is a larger observed proportion of individuals with intermediate physical condition among ≤ 25 year-olds (0.646) relative to >25 year-olds (0.464) and a larger observed proportion individuals with high physical condition among >25 yr olds (0.474) relative to ≤ 25 year-olds (0.283). Old males tend to be observed in better physical condition than young males (Fig. 5).

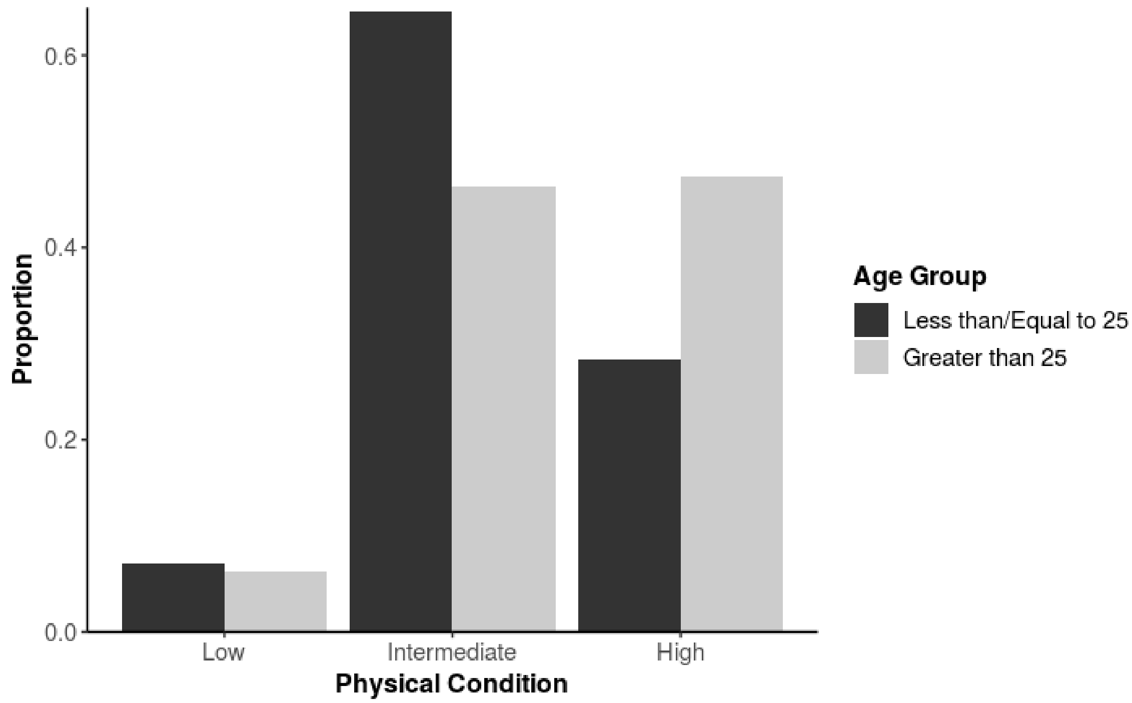

Figure 5. Observed proportion of low, intermediate, and high physical condition by age group. There is a larger proportions of individuals with high physical condition among >25 year-olds.

A Jonckheere-Terpstra test (JT) suggests a significant inverse relationship between observed group size and observed age (JT = 3020600, p = 0.001) (Fig. 6). Individuals of all age classes were observed alone.

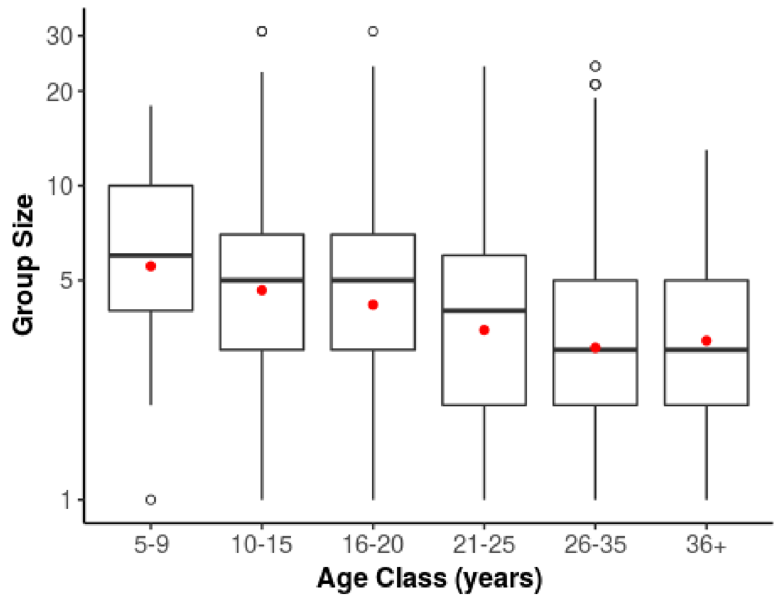

Figure 6. Spread of observed group size on a log transformed y-axis by age class. Red points represent log transformed means by age class. Increasing observed age class resulted in a trend of decreasing observed group size (JT = 3020600, $p = 0.001$).

On average, observed males of intermediate physical condition were observed in significantly larger groups (5.43 ± 0.06, $n = 2590$) compared to individuals of low (4.46 ± 0.21, $n = 312$) and high (4.77 ± 0.12, $n = 1334$) physical condition ($p < 0.001$ and $p < 0.001$). There was no significant difference between mean observed group sizes of individuals observed with low and high physical conditions ($p = 0.930$) (Fig. 7).

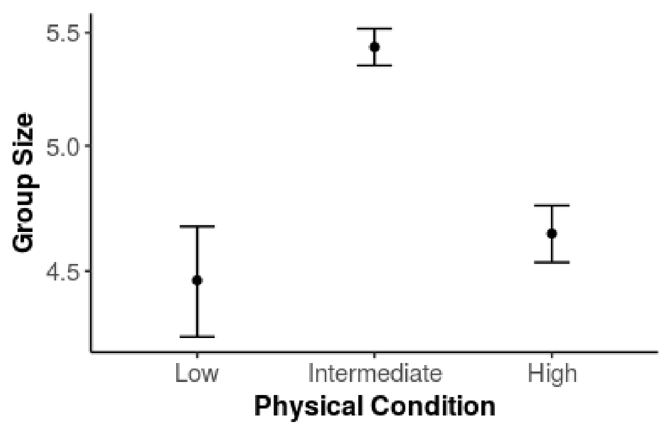

Figure 7. Mean observed group size on log transformed y-axis by observed physical condition. Individuals with low and high observed physical conditions have significantly lower mean observed group sizes than individuals with intermediate physical condition ($p < 0.001$ and $p < 0.001$).

Individuals with low observed physical condition were in significantly larger observed groups in the wet season (6.68 ± 1.01, n = 31) compared to the dry season (4.22 ± 0.02, n = 281) (t = -2.9534, df = 36.42, p = 0.0055). Individuals with intermediate physical condition were observed in significantly larger groups in the wet season (6.05 ± 0.16, n = 997) compared to the dry season (5.05 ± 0.09, n = 1593) as well (t = -2.9761, df = 1883.1, p = 0.0029). There is a significant inverse relationship between observed physical condition and observed group size in the wet season (JT = 269030, p = 0.002), but not in the dry season (JT = 774290, p = 0.842) (Fig. 8).

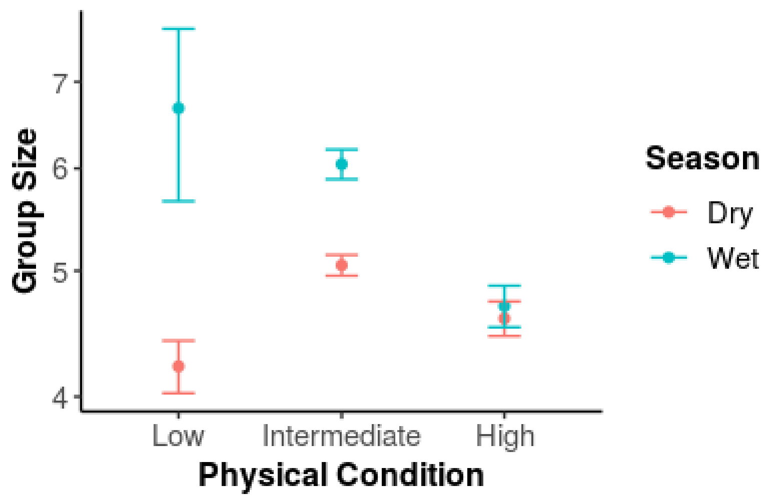

Figure 8. Mean observed group size on a log transformed y-axis by grouped by observed physical condition divided by dry (red points) and wet (blue point) seasons. There is a significant inverse relationship between observed group size and observed physical condition in the wet season (JT = 269030, p = 0.002). Significant differences in mean group size observed between seasons among individuals with low and intermediate physical conditions (t = -2.9534, df = 36.42, p = 0.0055 and t = -2.9761, df = 1883.1, p = 0.0029).

Distance to Water

There appears to be a U-shaped relationship between age class and distance to water. The youngest and oldest age classes were observed to be, on average, further from permanent water sources than intermediate age classes (Fig. 9).

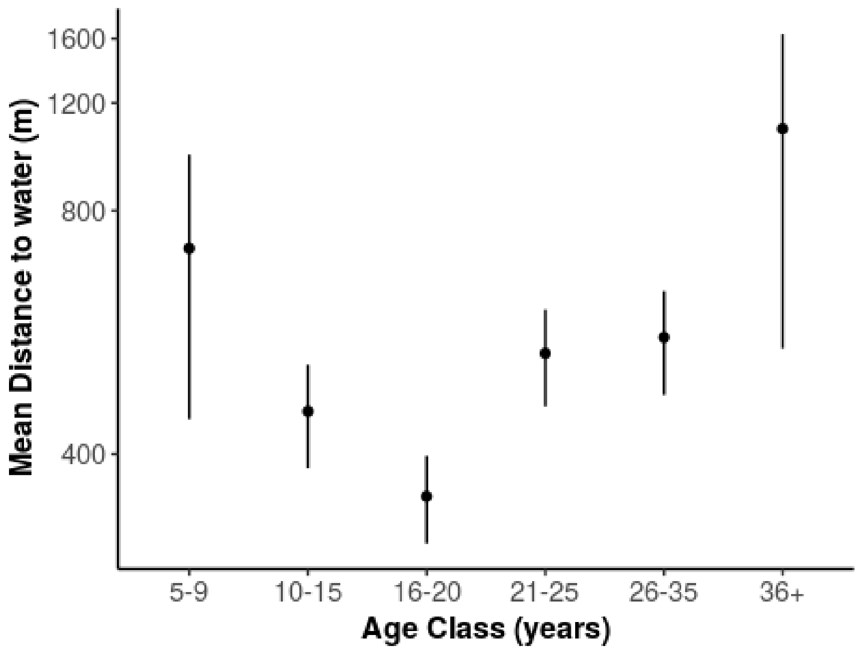

Figure 9. Mean of observed distance to water on a Box Cox transformed y-axis by age class. Old (>25yrs) individuals are found on average at distances significantly further from permanent water sources than young (≤25yrs) individuals ($t = -4.3426$, $df = 1032.6$, $p < 0.001$).

When evaluating the mean observed distance from permanent water between old (>25 years) and young (≤25 years) individuals using a t-test with Welch's correction, old elephants were observed at significantly greater distances from water than young individuals ($t = -4.3426$, $df = 1032.6$, $p < 0.001$).

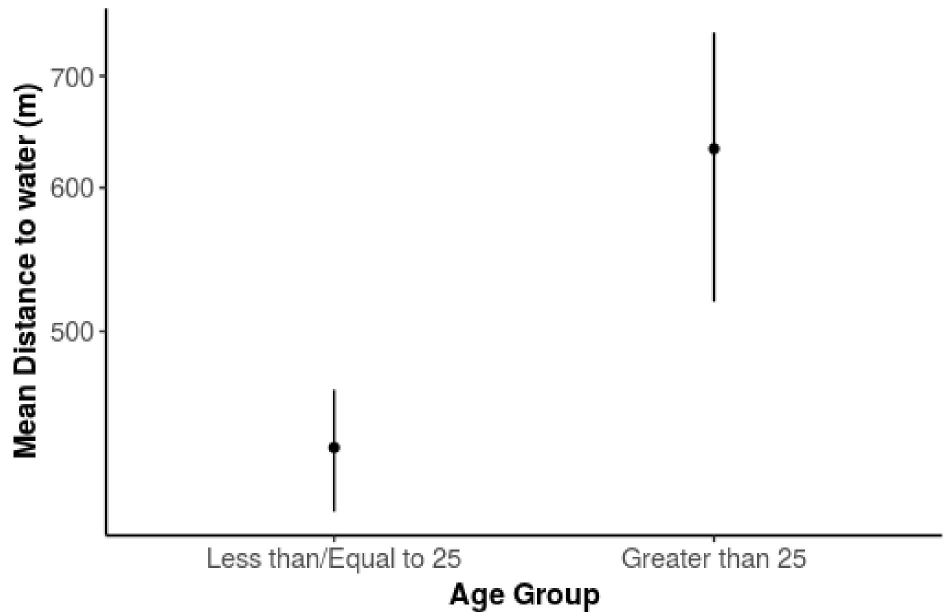

Figure 10. Mean observed distance from water on a Box Cox transformed y-axis by young and old age classes. Males greater than 25 years old are observed at significantly greater distances from water than males less than or equal to 25 years old ($t = -4.3426$, $df = 1032.6$, $p < 0.001$).

Discussion

The results of this study suggest relationships between elephant age, physical condition, seasonality and distance to water. Comparing age and physical condition individually reveals a relationship that influences their interaction with seasonality, group size and distance to water. Connecting the results from each piece of this analysis provides a greater understanding of the interactions by approaching them from several different angles.

Seasonality and Habitat

Surface water availability and forage abundance are two factors related to

seasonality that may contribute to patterns of groups size, age, and physical condition observed in this study. Both of these environmental variables are linked to the increased rainfall that defines the wet season in the MPNP (Pitfield 2017). An increase in normalized difference vegetation index (NDVI), a measure of vegetation cover, is associated with seasonal patterns in rainfall during the wet season in Botswana (Cerling et al. 2006, Chiyo et al. 2014). Regardless of season, elephant population density is typically positively related to NDVI and the density of artificial waterholes (Chamaillé-Jammes et al. 2007). The observation of larger observed group size in the dry season compared to the wet season in this study is consistent with my hypothesis and could be linked to both surface water and forage abundance. Decreased availability of surface water (through temporary waterholes) during the dry season means that individual elephants cover greater distances to reach water (Birkett et al. 2012). This could lead to larger groups around permanent water sources in the dry season compared to the wet season when the population is more dispersed. Similarly, reduced vegetation during the dry season contributes to higher predation risk, particularly for younger elephants (Loveridge et al. 2006), which could explain the higher group size during the dry season as a protective measure.

The broader distribution of age classes in the dry season is highlighted by larger proportions of intermediate aged individuals in the wet season and larger proportions of older individuals in the dry season. This is consistent with my hypothesis that older males make up a larger portion of the population in the dry season relative to the wet season.

Smaller proportions of individuals with low physical condition and larger proportions of individuals with high physical condition in the wet season is likely a function of the environmental conditions. Given the environmental variables of forage abundance and surface water availability, this is unsurprising as nutrient intake is increased (Bartlam-Brooks et al. 2011) and exertion required to reach forage and water is reduced during the wet season (Birkett et al. 2012).

The higher physical condition of old males is consistent with the findings of Pitfield (2017). This result, along with my finding that a larger proportion of old individuals were observed in the dry season, would predict higher physical conditions in the dry season as a result of population composition. Despite the trend that old males

have better physical condition, and old males make up a greater proportion of the population in the dry season, there overall is still a trend of higher physical condition in the wet season. This suggests that higher physical condition in the wet season is a result of environmental factors as I predicted rather than changes in the age composition of the population.

Individual Characteristics

My results suggest that as elephant age class increases, observed group size tends to decrease. This could be explained in part by the previous result that old males tend to have higher physical condition. This is supported by both the results of this study (Fig. 5) as well as Pitfield (2017). A more robust physical condition, and simply physical size, may mean that old bulls rely less on the protection of larger groups, particularly in areas of high predation risk. Another factor may be the role of old bulls in the social structure of an elephant population, and more specifically an elephant group. Within an elephant population it is hypothesized that older bulls are typically the leader as well as models for younger males. Evans and Harris (2008) find that young males are much more likely to be associated with groups that include an old bull. This does not necessarily mean that the old males must be found in the same large groups as young males. It is possible that young males prioritize group size over the presence of old males, meaning they would choose association with a larger group before association with an individual old male. Old bulls do not require this kind of social interaction. Because old males have spatial knowledge, they do not require large groups to find resources. This could explain a tendency of old males to remain in smaller groups, or be solitary, more often than younger males.

The differences in mean observed group size between individuals with low, intermediate, and high physical conditions reflect relatively small variation in overall elephant group size. This suggests that physical condition may have little effect on the group size in which individuals are observed.

Seasonal observations of group size by physical condition reveal that individuals with low and intermediate physical conditions are observed in larger group sizes in the wet season. This results in different relationships between physical condition and group

size between seasons. My results suggest that in the wet season, as physical condition improves, group size tends to decrease consistent with my hypothesis. Smaller group sizes for individuals with high physical condition in the wet season may be a result of old males tending to have higher physical conditions (Fig. 5) and old males tending to be found in smaller groups than young males (Fig. 6). The difference in group size among individuals with low and intermediate physical condition between seasons may be a result of forage abundance. A greater availability of food in the wet season means that individuals with low physical condition would be able to choose larger groups without having to compete for limited resources. Smaller group size in the dry season may be due to individuals of low physical condition choosing solitary or smaller groups to minimize exertion required for competition (Purdon et al. 2018). The observational nature of this data set is an important limitation for consideration. Multiple periods of data collection in this small geographic area along the western boarder of the MPNP means there are bound to be multiple observations of the same individual in this data set. This means that all results from this data set must be interpreted on an observational basis and not on an individual elephant basis. Another possible bias at play is observer bias for the classification of physical condition. This would be a useful variable to explore in future analysis in order to determine the degree of observer bias between individuals and between seasons or time of day.

Distance to Water

The relationship between observed age class and observed distance to water is not consistent with my hypothesis that older elephants would be observed at greater distances as there is a clear U-shaped relationship between these variables (Fig. 9). The notably low observed distance from water for observations among the 16-20 year old age class is not a function of sample size. Given the distribution of age classes observed in an earlier section, the 16-20 year old class was the most common across both the dry and wet seasons (Fig. 3). One possible explanation for this observation could be that the 16-20 year old time frame is typically when males leave their natal groups, and become more solitary. This could mean that they are under greater stress, and thus require a closer

proximity of resources such as water. This is a relationship worth exploring further, perhaps within season or across different times of the day.

The observation that older males > 25 years old can be observed at significantly greater distances from permanent water sources than younger males ≤ 25 years old is representative of multiple factors already explored in this analysis. Older males tend have higher physical condition scoring and are typically observed in smaller groups. Each of these characteristics may contribute to older males being observed further from permanent water sources. Better physical condition might mean old males can go longer without water or food, and smaller groups provide the ability to move quicker across the landscape. These results are consistent with Pitfield (2017) which describes the ability of older males to last longer than younger ones without water. This could have implications for wildlife conflict mitigation strategies that use isolated waterholes to draw elephants away from human settlements where they may cause conflict (Tshipa et al. 2017). The findings from my study that old males tend to have better physical condition, potentially linked to their higher frequency of observation further from permanent water, suggests that the artificial waterhole strategy might not actually be as useful in preventing crop raiding by male elephants, the most common instigators (Stevens 2018).

Conclusion

The results of this study support the conclusion that seasonality plays an important role in the behavior and group dynamics of elephant populations. Dry season conditions support larger group sizes and higher proportions of males in the population, while wet season conditions lead to higher physical condition among individuals in the population and an inverse relationship between physical condition and group size. Age also plays an important part in these dynamics, where older individuals have higher physical condition, choose smaller groups, and are observed at greater distances from water than young males. All of these findings are important considerations, particularly in the context of mitigating human-wildlife conflict, where season and age of elephants influence the incidence of conflict events. The results of this study should not be applied to all elephant populations, but only those that constitute bull areas in arid habitats similar to the MPNP. Understanding the ways that season and age interact with each other, as

well as physical condition and water resources is useful in determining the best mitigation practices involving environmental resources for different times of year. Future studies examining the ways in which the relationship between age and distance to water changes between seasons would also be useful in assessing conservation practices related to human-wildlife conflict around resource availability.

PERSONAL COMMUNICATIONS

Dr. Kate E. Evans. Personal Communication. March 2019.

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APPENDIX

R codes conducted in Rstudio Cloud:

```
#### START OF SCRIPT ####

# Install and load libraries
library(readxl)
library(batman)
library(dplyr)
library(lubridate)
library(stringr)
library(bimixt)
library(manipulate)
library(scales)

# Load excel sheet and make data frame
alldata <- read_excel("./Data_frames/alldata_1_28.xlsx",
                      sheet ="alldata")

# Delete unneeded columns, edit data types, edit columns

alldata2 <- alldata %>%
  mutate(Elephant_ID = if_else(Elephant_ID == "-", NA_character_,
Elephant_ID),
         Date = Date.y,
         Season = case_when(Date >= "2012-04-01 00:00:00" &
                            Date < "2012-01-01 00:00:00" ~ "D",
                             Date >= "2013-02-01 00:00:00" &
                            Date < "2013-12-01 00:00:00" ~ "D",
                             Date >= "2014-05-01 00:00:00" &
                            Date < "2014-12-01 00:00:00" ~ "D",
                             Date >= "2015-05-01 00:00:00" &
                            Date < "2016-02-01 00:00:00" ~ "D",
                             Date >= "2016-05-01 00:00:00" &
                            Date < "2016-12-01 00:00:00" ~ "D",
                             Date >= "2017-04-01 00:00:00" &
                            Date < "2017-12-01 00:00:00" ~ "D",
                             Date >= "2018-04-01 00:00:00" &
                            Date < "2019-02-01 00:00:00" ~ "D",
                             TRUE ~ "W"),
         Season = type.convert(Season),
         Physical_Condition_ID =
type.convert(Physical_Condition_ID),
         Time = ymd_hms(Time),
         Age_Range_ID = as.factor(Age_Range_ID),
         Activity_ID = as.factor(Activity_ID),
         Social_ID = as.factor(Social_ID),
         Habitat_ID = as.factor(Habitat_ID),
         Indv_Sex = as.factor(Indv_Sex),
         str_replace_all(Distance_To_Observer, "m", ""),
```

```
         Distance_To_Observer = as.numeric(Distance_To_Observer),
         Number_Of_Elephants = as.numeric(Number_Of_Elephants),
         In_musth = to_logical(In_musth),
         Year = year(Date),
         Month = month(Date, label = TRUE)) %>%
  select(Elephant_Sighting_ID, ID_Elephant_Visual, Elephant_ID,
           Time, Age_Range_ID, In_musth, Physical_Condition_ID,
           Event_ID, Date, Season, Latitude, Longitude,
           Activity_ID, Social_ID, Habitat_ID,
           Musth_Male_Present, Indv_Sex, Distance_To_Observer,
           Number_Of_Elephants)

# Testing group size by season ----
group_se <- alldata2 %>%
  mutate(Elephant_Sighting_ID = as.factor(Elephant_Sighting_ID))
%>%
  count(Season, Elephant_Sighting_ID, name = "GS") %>%
  mutate(BC_GS = BC(GS, 0.05))

# distribution of GS by season
ggplot(group_se, aes(x = BC_GS)) + geom_histogram() +
  facet_wrap(~ Season)

ggplot(group_se, aes(sample = BC_GS)) + geom_qq(distribution =
qnorm) +
  geom_qq_line(line.p = c(0.25, 0.75), col = "blue") +
ylab("BC(GS, 0.1)") +
  facet_wrap(~ Season, nrow = 1) + ylab("BC(GS, 0.05)")

# Wilcoxon test on un-transformed
wilcox.test(group_se$GS ~ group_se$Season)
# W = 308040, p-value = 0.0001627

# t-Test on BC(GS, 0.5) ----
t.test(group_se$BC_GS ~ group_se$Season)
#t = 3.4362, df = 1321.7, p-value = 0.0006083

# Comparing relationship between Age and Group size ----
# BC tranformation of GS ----
BC <- function(x, p) {
  if(p == 0){
    log(x)
  } else{
    (x^p - 1) / p
  }
}

qq.plot <- function(p) {
  OP <- par(mfrow = c(1, 1))
  qqnorm(BC(ageVgs.df$Number_Of_Elephants, p))
  qqline(BC(ageVgs.df$Number_Of_Elephants,p))
  par(OP)
```

```
}

manipulate(
  qq.plot(p = round(p.slider, 2)),
  p.slider = slider(-3, 3, step = 0.1, initial = 0)
)

#Kruskal-Wallis test between GS of age groups
ageVgs.df <- alldata2 %>%
  filter(Indv_Sex == "M",
         Age_Range_ID != "NA",
         Age_Range_ID != "10",
         Age_Range_ID != "2") %>%
  mutate(Age_Range_ID = recode(Age_Range_ID,
                               "3" = "5-9",
                               "4" = "10-15",
                               "5" = "16-20",
                               "6" = "21-25",
                               "7" = "26-35",
                               "8" = "36+"),
         Age_Range_ID = droplevels(Age_Range_ID),
         Age_Range_ID = factor(Age_Range_ID, levels = c("5-9",
"10-15", "16-20",
                                                        "21-25",
"26-35", "36+"), ordered=TRUE),
         log_GS = log(Number_Of_Elephants)) %>%
  arrange(Age_Range_ID, log_GS) %>%
  select(Age_Range_ID, log_GS, Number_Of_Elephants) %>%
  na.omit()


kruskal.test(ageVgs.df$Number_Of_Elephants ~
ageVgs.df$Age_Range_ID)
#Kruskal-Wallis chi-squared = 159.96, df = 5, p-value < 2.2e-16

# Jonckheere-Terpstra of group size across age classes
library(clinfun)

jonckheere.test(ageVgs.df$log_GS, ageVgs.df$Age_Range_ID,
                alternative = "decreasing", nperm=1000)
# p-value = 0.001
# alternative hypothesis: decreasing

#PHYSICAL CONDITION VS GROUP SIZE ----
datPC <- alldata2 %>%
  filter(Indv_Sex == "M") %>%
  subset(Physical_Condition_ID == 2 |
           Physical_Condition_ID == 2.5 |
           Physical_Condition_ID == 3 |
           Physical_Condition_ID == 3.5 |
           Physical_Condition_ID == 4 |
           Physical_Condition_ID == 4.5) %>%
```

```
  mutate(PC_grouped = case_when(Physical_Condition_ID == 2 ~
                                      "Low",
                                Physical_Condition_ID == 2.5 ~ "Low",
                                Physical_Condition_ID == 3 ~
                                      "Intermediate",
                                Physical_Condition_ID == 3.5 ~
                                      "Intermediate",
                                Physical_Condition_ID == 4 ~ "High",
                                Physical_Condition_ID == 5 ~ "High"),
         PC_grouped = factor(PC_grouped, levels = c("Low",
                                                    "Intermediate",
                                                       "High"),
                                                    ordered = TRUE),
         log_GS = log(Number_Of_Elephants))

# ANOVA & TukeyHSD between groups sizes by physical condition
res.aov4 <- aov(log(datPC$Number_Of_Elephants) ~
datPC$PC_grouped)
summary(res.aov4)

TukeyHSD(res.aov4))

# JT test of group size along physical condition
jonckheere.test(datPC$log_GS,
                datPC$PC_grouped,
                alternative = "two.sided", nperm=1000)

#PHYSICAL CONDITION AND GROUP SIZE BY SEASON ----
# t-test by Physical condition
# Low PC
t.test(log_GS[PC_grouped == "Low"] ~ Season[PC_grouped == "Low"],
data = datPC)

# Intermediate PC
t.test(log_GS[PC_grouped == "Intermediate"] ~ Season[PC_grouped
== "Intermediate"], data = datPC)

#High PC
t.test(log_GS[PC_grouped == "High"] ~ Season[PC_grouped ==
"High"],
data = datPC)

#JT test of group size across physical condition split by season
# Dry Season
jonckheere.test(datPC$log_GS[datPC$Season == "Dry"],
                datPC$PC_grouped[datPC$Season == "Dry"],
                alternative = "two.sided", nperm=1000)

# Wet Season
jonckheere.test(datPC$log_GS[datPC$Season == "Wet"],
                datPC$PC_grouped[datPC$Season == "Wet"],
                alternative = "two.sided", nperm=1000)
```

```
# AGE AND DISTANCE TO WATER ----
# Load excel file with the distance data
Dist_water <- read_excel("./Data_frames/Dist_perm_water.xls")

# Join to other variables
spatial.df <- Dist_water %>%
  rename("Elephant_ID" = "Elephant_I",
         "Age_Range_ID" = "Age_Range_",
         "Physical_Condition_ID" = "Physical_C",
         "Activity_ID" = "Activity_I",
         "Number_Of_Elephants" = "Number_Of_",
         "Water_dist" = "NEAR_DIST",
         "Water_feature" = "NEAR_FC") %>%
  mutate(Elephant_ID = if_else(Elephant_ID == "-", NA_character_,
Elephant_ID),
         Season = as.factor(Season),
         Physical_Condition_ID =
as.factor(Physical_Condition_ID),
         Age_Range_ID = as.factor(Age_Range_ID),
         Activity_ID = as.factor(Activity_ID),
         Social_ID = as.factor(Social_ID),
         Habitat_ID = as.factor(Habitat_ID),
         Indv_Sex = as.factor(Indv_Sex),
         Number_Of_Elephants = as.numeric(Number_Of_Elephants),
         In_musth = to_logical(In_musth),
         Year = year(Date),
         Month = month(Date, label = TRUE),
         log_GS = log(Number_Of_Elephants),
         log_WD = log(Water_dist, base = 10),
         BC_GS = BC(Number_Of_Elephants, 0.1),
         BC_WD = BC(Water_dist, -0.5))

# Code for age groups
spatial.df3 <- spatial.df %>%
  filter(Age_Range_ID != "NA",
         Age_Range_ID != "10",
         Age_Range_ID != "2",
         Age_Range_ID != "0") %>%
  mutate(Age_Range_ID = recode(Age_Range_ID,
                               "3" = "5-9",
                               "4" = "10-15",
                               "5" = "16-20",
                               "6" = "21-25",
                               "7" = "26-35",
                               "8" = "36+"),
         Age_Range_ID = droplevels(Age_Range_ID),
         Age_grouped = case_when(Age_Range_ID == "5-9" ~ "Less
                                      than/Equal to 25",
                                 Age_Range_ID == "10-15" ~ "Less
                                      than/Equal to 25",
```

```
                                 Age_Range_ID == "16-20" ~ "Less
                                      than/Equal to 25",
                                 Age_Range_ID == "21-25" ~ "Less
                                      than/Equal to 25",
                                 Age_Range_ID == "26-35" ~
                                      "Greater than 25",
                                 Age_Range_ID == "36+" ~ "Greater
                                      than 25"),
         Age_grouped = factor(Age_grouped, levels = c("Less
                           than/Equal to 25", "Greater than 25"),
                              ordered = TRUE))

# T-TEST
t.test(BC_WD ~ Age_grouped, data = spatial.df3 )


#### END OF SCRIPT ####
```