DEPARTMENT OF BIOLOGICAL
AND ENVIRONMENTAL
SCIENCES

INVESTIGATING THE COVARIANCE BETWEEN RAINFALL AND MALE ELEPHANT MOVEMENT

To Reduce Human-Elephant Conflict

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Cover photo: elephants at the Boteti River, Botswana. Photo by Kate Evans, Elephants for Africa

1 Abstract

Human-wildlife conflict threatens the survival of a range of species, including the savannah elephant (*Loxodonta africana*). Villages bordering the Makgadikgadi Pans National Park in Botswana are among the most affected by human-elephant conflict, and it is crucial to identify contributing factors to develop mitigation strategies. Researchers in the area have suspected a potential covariance between rainfall and elephant movement. However, it is difficult to separate patterns that are directly related to rainfall from those that are primarily governed by circannual cycles related to elephant life history, because rainfall is highly seasonal in this region. This study investigated the relative effect of rainfall versus time of year on movement patterns, specifically among males in musth (a condition of heightened testosterone recognized by secretion from temporal glands) and older males, since these are the most prone to aggression and crop raiding, respectively. Data on rainfall and elephant sighting collected between 2012 and 2022 were analyzed using generalized additive models (GAMs), controlling for day of year and moving averages of rainfall. Results showed that all response variables were mainly associated with day of year rather than rainfall. Although rain was slightly associated with the probability of a sighting including an older male, this partial covariation was minimal compared to that of day of year. The probability of a sighting including a musth male showed no association with rain. When modelling partial effect of day of year, the probability of a sighting including a musth male was highest in March/April (corresponding to the middle of the farming season) and lowest in September (end of the dry season). The probability of a sighting containing an older male showed the opposite pattern to that of musth males, which is surprising considering older males are the main crop raiders. It is possible, however, that this pattern does not reflect the experience of locals since the research area is slightly removed from the farms. Further studies are required to investigate reasons for the different movement patterns shown by older males and males in musth, as well as the overall probability of encountering an older male when total number of sightings is taken into account.

Keywords:

Loxodonta africana, Elephants, Botswana, Human-Elephant Conflict, HEC, Human-Wildlife Conflict, HWC, Conservation, Musth, Bulls, Rainfall

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3 Introduction

Human-wildlife conflict is one of the biggest challenges for biodiversity and wildlife conservation today (Dickman, 2010). As human populations have expanded and encroached on wildlife habitats, competition for space and resources has become increasingly common around the world, with humans suffering loss of livelihoods, property, food security, and life, and animals in turn facing retaliatory shootings and sometimes complete extinction (Chamberlain, 2016; WWF, n.d.). As human-wildlife conflict mostly affects people below the poverty line, reducing human-wildlife conflict is important both for conservation and development purposes (WWF, n.d.). Although it is a global concern, solutions need to be context-specific to identify the underlying causes in each individual case and develop mitigation strategies that fit local circumstances. Successful mitigation necessitates understanding both the ecological and social aspects of these conflicts, with the long-term goal of reducing tension between human livelihoods and wildlife conservation.

One case of human-wildlife conflict is that of the keystone species African savannah elephant (*Loxodonta africana*), whose vast home ranges have become fragmented as human land-use has increased. Human-elephant conflict takes the form of crop raiding, injury, and death, as well as hidden impacts such as consistent fear and opportunity costs (Hoare, 1999; Mayberry, Hovorka & Evans, 2017). This study focuses on Botswana, which has the biggest savannah elephant population in Africa with approximately 130,000 elephants as of 2016 (Chase et al., 2016). A team of researchers in north-eastern Botswana are working on developing mitigation strategies for human-elephant conflict in Makgadikgadi Pans National Park, focusing on bull elephants, since older males and males in musth are the most prone to crop raiding and aggression, respectively. One important part of reducing human-elephant conflict is predicting when and where encounters with these demographical groups of elephants are most likely to occur, which in turn requires an understanding of elephant movement patterns and knowledge about which environmental cues predict them in a particular area. Several factors are suspected to play a role in the timing and frequency of elephant encounters, including elephant breeding patterns, timing of crop maturation, vegetation abundance, and water availability. Previous studies have theorized that rainfall could play a role in elephant movement on both large and small scales (Garstang et al., 2014), but we do not know how and to what extent rain affects elephant behavior in the Makgadikgadi Pans National Park. This study aims to fill that knowledge gap by analyzing data about rainfall and elephant movement in the area, specifically among older bulls and males in musth.

4 Background

Elephants are often referred to as ecosystem engineers (Haynes, 2012). They shape the landscape by knocking down trees, make water accessible to other animals by digging up groundwater, and spread seeds long distances through their diet (Dudley, 2003; Fritz, 2017; Haynes, 2012; Kerley et al., 2008). Although some species are negatively impacted by elephants (Kerley et al., 2008; O'Connor, Goodman & Clegg, 2007), elephants may have an important role in maintaining long-term biodiversity (International Fund for Animal Welfare, 2021; Herremans, 1995; Kerley et al., 2008), which is further supported by the ecological cascades and species loss following the extinction of their prehistoric relatives (Haynes, 2012). Elephants are also a flagship species, acting as an ambassador for other wildlife and bringing light to the urgency of wildlife conservation (Lee and Graham, 2006 in Chamberlain, 2016). As such they also contribute to the tourism industry which benefits the economies of the countries they inhabit. As of 2021, the tourism industry made up 12 % of Botswana's GDP (Adams et al, 2021). However, the communities most at risk of human-elephant conflict rarely benefit from this, as they largely rely on subsistence farming (DEA & CAR, 2010).

4.1 Human-Elephant Conflict: Impact on Humans

The negative effects that elephants have on people's livelihoods, food security and safety contribute to hostile perceptions of elephants that can hinder conservation efforts. In the village of Khumaga, located on the western border of the Makgadikgadi Pans National Park

(Figure 4 and Figure 5) ancestral knowledge about elephant behavior has been lost after elephants were hunted from the area in the 19th century (Skarpe et al., 2004). When elephants have recolonized the area in recent times (Thouless et al., 2016) due to immigration, population growth, and, most recently, the resurgence of the Boteti River in 2009 (Chamberlain, 2016; DEA & CAR, 2010; Evans, 2019), many people no longer know how to live alongside them safely (Evans, 2019). Since the electric fence that used to serve as a barrier between the Makgadikgadi Pans National Park and the Boteti River has fallen into disrepair, elephants frequently cross the river into community lands (Chamberlain, 2016) where they raid crops and interrupt daily tasks such as fetching water, walking to school, gathering firewood and veld products, tending to livestock, and visiting friends and family (Mayberry, Hovorka & Evans, 2017). In the period 2020-2022, two humans and four elephants were killed in the area (Kate Evans, personal communication 9 Jan 2023). Crop raiding also has serious consequences, with the average loss per farmer each year being 65.7 % (Chamberlain, 2016) affecting food security. Lastly, there are hidden impacts such as opportunity costs and intense fear (Mayberry, Hovorka & Evans, 2017). Opportunity costs present themselves as time stolen from important tasks and activities, such as pursuing alternative incomes due to the extra time needed on farming to compensate crop loss (Evans, 2019) or fetching water due to elephants blocking paths (Mayberry, Hovorka & Evans, 2017). Improved knowledge about elephant behavior, including movement patterns, might allow locals to adjust their daily routines to minimize risk of conflict and reduce fear.

4.2 Elephant Ecology

Below I list some factors that could contribute to the timing and frequency of human-elephant conflict, including timing of crop raids, timing of musth, and reproduction patterns. I also present some previous studies about elephants and rainfall.

4.2.1 Timing of crop raids

Several studies have shown that crop raiding in savannah habitats is most common at the end of the rainy season (Hoare 1995, Osborn 1998, 2004 in Chamberlain, 2016). In 2015, the growing season for farmers in the Boteti area lasted from January to June, and crop raids occurred during the whole period (Figure 1); however, March was highly overrepresented, containing more than half of all crop raids (Chamberlain, 2016). This is likely to be because March is both the start of the dry season (which is accompanied by a decline in natural forage) and the month where crops are mature. Since 2015, rainfall has become increasingly unpredictable and the start of the rainy season has often been delayed (Evans, personal communication, 24 Mar 2022), which means that identifying the relative importance of natural forage abundance (impacted by rain) and crop availability in the timing of crop raids could be increasingly important in optimizing mitigation efforts.

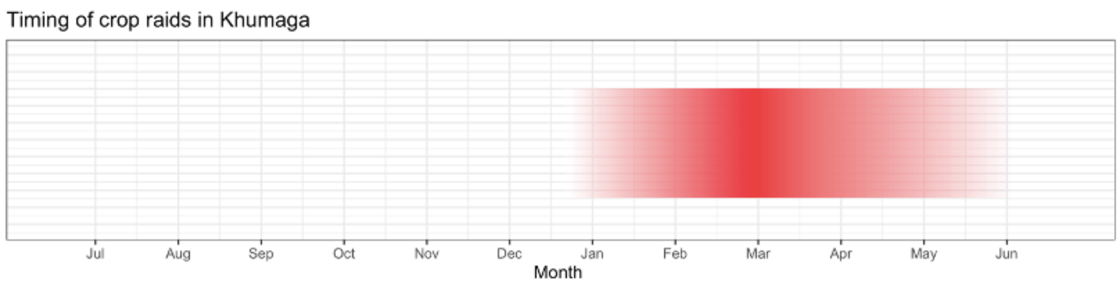


Figure 1: Plot showing approximate timing of crop raids in Khumaga, with most crop raids occurring in March.

4.2.2 *Timing of reproduction*

Elephants can breed year-round, but some seasonality in reproduction has been observed. Hufenus et al (2018) carried out a meta-analysis on studies that investigated elephant reproduction patterns and stated that most studies found a “moderate yet distinct seasonal breeding pattern” (p. 261). It is likely that this seasonality has evolved to increase calf survival, since calves that are born during a time of year when food is plentiful for mothers are more likely to survive. Hufenus et al (2018) concluded that elephants seem to be so called long-day breeders - breeding at times of year when days are longer - although other factors such as body condition, stress levels and rainfall can override this photoperiodic cueing. For example, conception peaks differed between studies depending on e.g. latitude, species (Asian or African elephant – the study did not distinguish between the two African species), captivity status, and number of rainy seasons per year. For free-ranging African elephants, conception peaks in most studies analyzed tended to occur at the onset of rainy seasons. In Botswana, this would approximately correspond to November and December (Figure 2). December is also the month where days are longest in the southern hemisphere, and there is a possibility that photoperiodic cueing could be a contributing factor to breeding patterns in Botswana, since days there are almost four hours longer in December than in June (Sunrise Sunset Times Lookup, n.d.). If the elephants in Makgadikgadi Pans National Park follow this pattern, reproductive males could be expected to leave the research area – which predominantly consists of bulls - to seek out females at the beginning of the rainy season, with a potential peak in December (Figure 2). If mating in December is successful, calves will be born in October (since the gestation time is 22 months), coinciding with the start of the rainy season and the subsequent flourishing of grasses and trees.

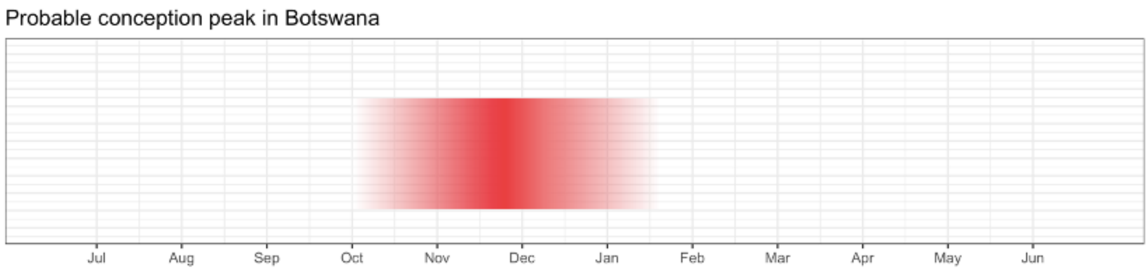


Figure 2: Illustration of the probable mating period among elephants in Botswana, based on findings by Hufenus et al (2018).

4.2.3 *Timing of musth*

Musth is a condition of heightened testosterone exhibited by some older males on an annual or diannual basis, and is recognized by secretion from temporal glands, dripping of urine (Hall-Martin, 1987; Poole & Moss, 1981), longer travelled distances, and aggression. Musth males have been known to kill other musth males, female elephants and even rhinos. Hall-Martin (1987) writes “A further testament to the aggression of musth bulls is the record of one bull who broke a tusk, killing a non-musth bull, broke his other tusk killing a cow and was then in turn killed by another musth bull” (p. 619). Musth males are likely overrepresented in human killings, as indicated by a study on elephant-caused deaths in Nepal where more than half of the involved elephants were in musth (Ram et al., 2021).

It has been shown that androgens activate musth whereas glucocorticoids suppress it (Rasmussen et al., 2008a). In female African elephants, an increase in glucocorticoids has been observed especially during dry periods when body condition is poorer (Wittemyer et al., 2007; Foley et al., 2001), but studies showing similar seasonal patterns in males are few. The presence of oestrous females seems to have an effect, producing an increase in androgens occurring in males that are already in musth and an increase in glucocorticoids in subordinate males. The latter also happens to younger, subordinate males in the presence of older, dominant males (Rasmussen et al., 2008a). As a result, older musth males have the highest breeding success of all males (Rasmussen et al., 2008b).

Poole (1987) has demonstrated that whether older bulls go into musth in the dry or wet season, they consistently go into musth at the same time every year. Elephants thus seem to have “an internal annual clock announcing when their time slot has come up” (Rasmussen, 2008a, p. 547). This slot can be any time of year, but seems to be more commonly associated with the rainy season – a study by Poole (1987) in Kenya found that it is most common during and right after the wet seasons, and two studies carried out by Ganswindt et al (2010) and Hall-Martin (1987) in South Africa found that musth was somewhat more common at the onset of the wet seasons. This aligns with the data on reproduction presented by Hufenus et al (2018). The combined findings by Poole (1987), Ganswindt et al (2010) and Hall-Martin (1987) are illustrated in Figure 3.

Musth is a relatively uncommon occurrence since its benefits to reproduction must be weighed against its physiological costs for the elephant (Hall-Martin, 1987), and indeed, sightings in the research area are rare (Kate Evans, personal communication, 2022). However, when musth does occur, it poses a severe threat to anyone who crosses the musth male’s path.

The local rarity of musth male sightings could further be attributed to the fact that the elephant population in our focal research area is primarily made up of bulls (Evans, 2019), since males generally prefer to associate with females when they are in musth (Hall-Martin, 1987). If Makgadikgadi Pans National Park follows the patterns of musth occurrence discovered by Ganswindt et al (2010), Hall-Martin (1987) and Poole (1987), the proportion of sightings including musth males in the study area could be expected to be lower during the period illustrated in Figure 3.

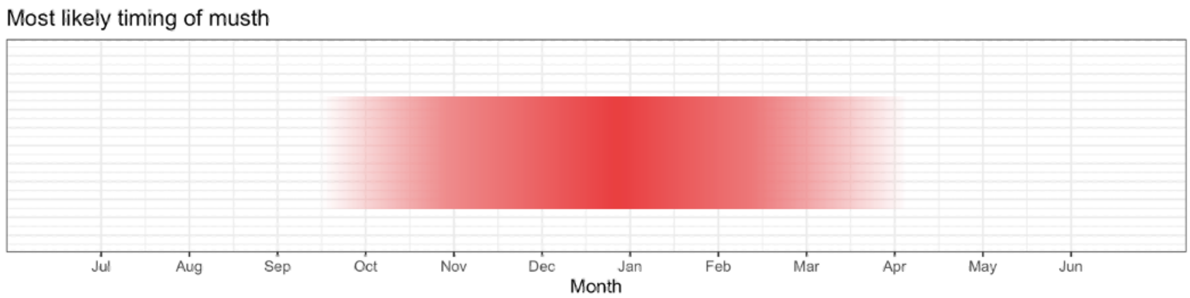


Figure 3: Illustration of the most likely timing of musth in male elephants, based on the findings by Ganswindt et al (2010), Hall-Martin (1987) and Poole (1987) mentioned above.

4.2.4 Effect of rainfall

Elephants need to drink every 1-3 days (Moss, 1994) and are frequent visitors at the Boteti River, which is the main water source in the area, especially during dry periods (Kate Evans, personal communication 9 Jan 2023). Factors that affect water abundance, including rainfall, should therefore have some effect on elephant presence around the river. The vegetation growth caused by rain could also play a role in elephant movement.

There is some evidence that rainfall itself can have an influence on elephant movement. Garstang et al (2014) found that elephants in Namibia equipped with radio collars changed directions near simultaneously shortly after rainfall as far as 300 km from their respective locations. They theorized that this could be triggered by a common perception of thunder, which would have been within hearing range for all the elephants. However, in the study by Garstang et al (2014) there were more significant changes in movement in the 24 days prior to the onset of the wet season compared to the 24 days after, suggesting that thunder cannot account for all changes in movement associated with rainfall. Garstang et al (2014) noted that the pre-rainfall movement could be connected to changes in vegetation, because vegetation growth is not only triggered by rain, but also by other factors like solar insolation and length of day which can change before the rain starts. On the other hand, that could not account for the near simultaneous responses to distant rainfall occurring in the middle of the dry seasons. It must be noted, in any case, that the changes in movement detected by Garstang et al (2014) were not necessarily in the direction of the rain. They conclude that further studies are needed to better understand the covariation between elephant movement and rainfall.

It is also unclear which effect, if any, rain has on elephant crop-raiding. Hoare (1999) found that crop-raiding elephants in Zimbabwe prefer the mature growth stages of crops, but that neither inter-annual differences in rainfall nor the resulting difference in crop quality was statistically associated with the number of crop raids in a year; rather, elephants ate what was available. This suggests that intra-annual rainfall variation might not have a big impact on timing of crop raids either, but there are no studies about this to my knowledge.

4.3 Aim

The general knowledge about elephant behavior and rainfall presented above is not enough to determine patterns in a such a specific location as the Khumaga area. In developing mitigation strategies for human elephant conflict, risks need to be assessed locally. The aim of this study is to visualize and quantify partial effects of time of year and rainfall in the Khumaga area, to see which has the greater effect on elephant presence and to what extent they can be used as predictors for encountering older males and males in musth.

5 Methods

5.1 Study Site

The study site is located on the western border of Makgadikgadi Pans National Park in north-eastern Botswana, separated from nearby villages by the Boteti River. The village of Khumaga, where most of the human-elephant conflict in this study was reported, lies just across the river from the Elephants for Africa (EfA) research camp (Figure 4 and Figure 5). The Makgadikgadi Pans is a 12,000 km^2 saline wetland system surrounded by semi-arid savannah (Spriggs, 2016) and linked to the Okavango Delta in the northwest through the Boteti River (DEA & CAR, 2010). Its unique saline environment has given rise to some endemic species, and the area is also a biodiversity hotspot (DEA & CAR, 2010). The EfA research camp, whose focus is on bull elephants, relocated here from the usually bull-dominated Okavango Delta in 2012 due to ecological shifts that caused males to become more common in the Makgadikgadi Pans (Evans, 2019). Today, 98 % of sightings in the Khumaga area are of males.

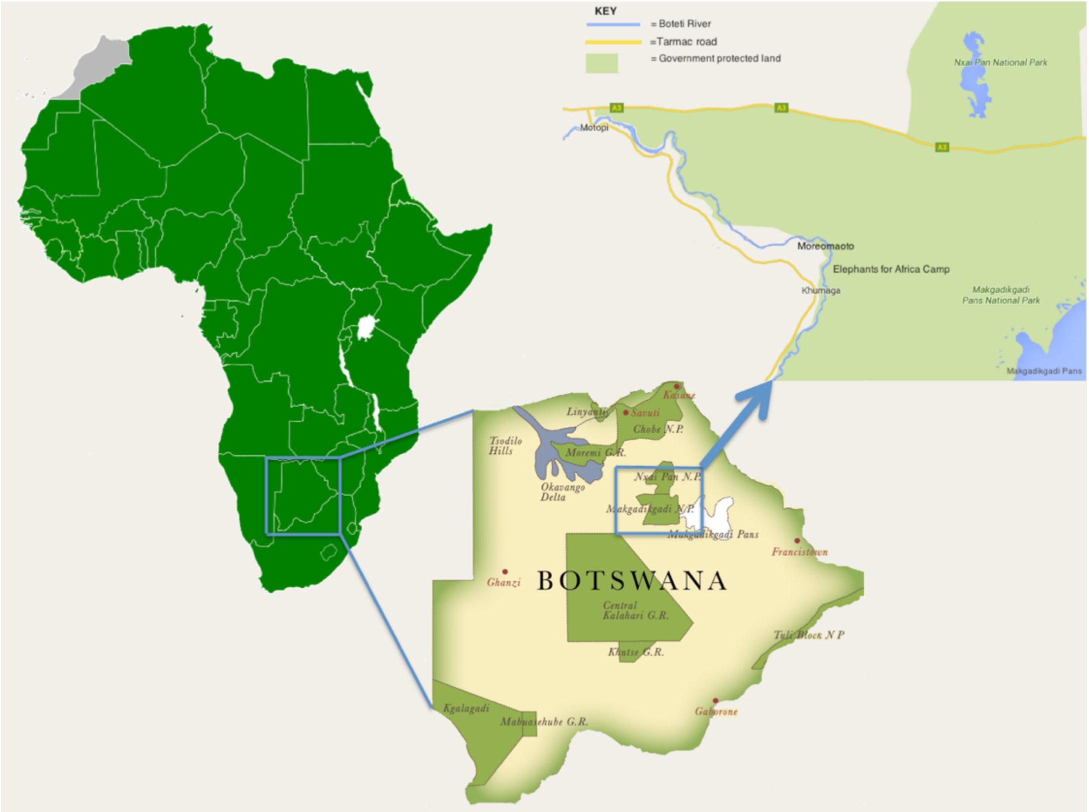


Figure 4: Map of research location. Elephants for Africa, 2022

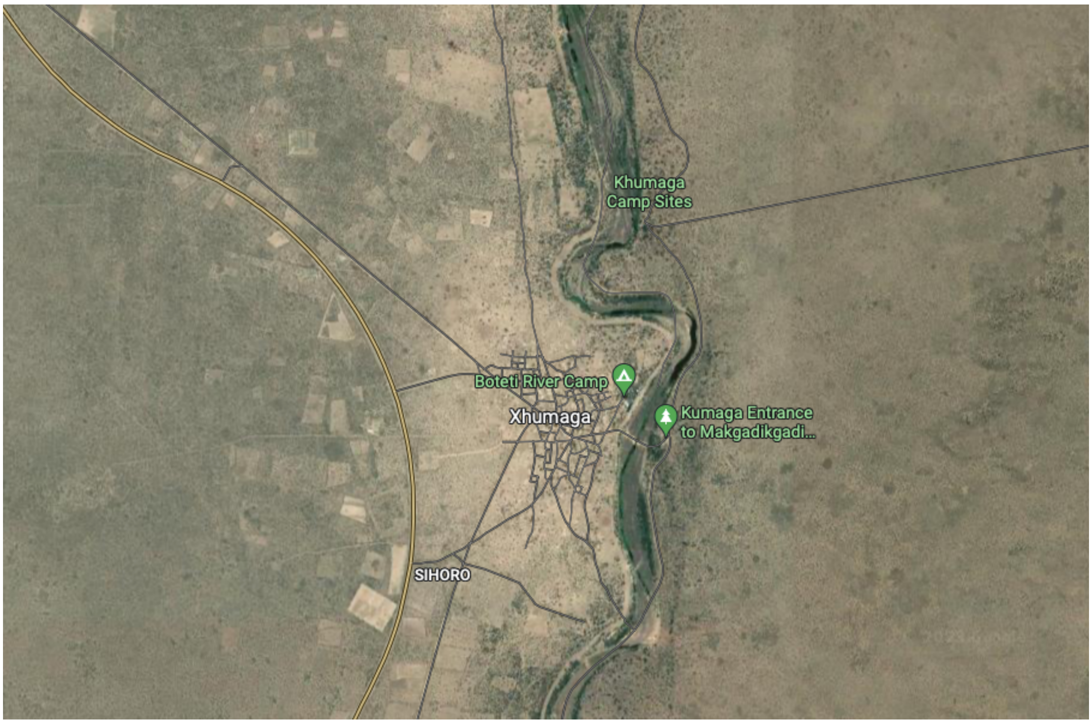


Figure 5: Close-up of the area surrounding the Khumaga research camp. Crop fields can be seen on the western side of the river. Google Maps, 2023.

The area has one primary rainy season per year (Statistics Botswana, 2022), which has traditionally started around November and lasted until March or April. However, it has been less predictable in recent years, sometimes starting as late as January (Evans, personal communication, 24 Mar 2022), and can be expected to become even more unpredictable in the future as climate change proceeds (Climate Risk Profile: Botswana, 2020).

5.2 Data Collection

Data was collected by a team of researchers on a regular basis between 2012 and 2022, driving established routes in the Makgadikgadi Pans National Park. The data collected include rainfall per day, number of elephants per sighting, group size certainty (on a rank from 1 to 3, where 1 is high certainty and 3 is low certainty), date, GPS coordinates, musth male presence, sex, age, and number of elephants per age category and sighting. Age was divided into the categories 0-1 years, 1-4 years, 5-9 years, 10-15 years, 16-20 years, 21-25 years, 26-35 years, 36+ years, as well as Unknown, Subadult, and Adult for elephants where age was harder to determine.

A large number of records with ambiguous dates were detected among data recorded in 2013. Therefore, 2013 was excluded from the analyses to avoid incorrectly ascribing the wrong day of year to observations. The entire year was excluded since the remaining records, which were distributed unevenly throughout the year, would otherwise have risked skewing the results.

There is also a 2–3-week data gap every Christmas and New Year, during which the camp is closed.

5.3 Data Analyses

The choice of response variables was based on the aggression and crop raiding tendencies exhibited by these categories of elephants, with older males being the most responsible for crop raids and musth males being the most aggressive. Older males were defined as those belonging to categories 26-35 yr, 36+ yr or Adult. Three response variables were chosen: 1) probability of a sighting including a male in musth, 2) probability of an encountered group containing an older male, and 3) probability of an encountered lone elephant being an older male.

I chose to analyze lone older elephants and groups of older elephants separately as it could provide valuable insight on male elephant ecology – almost half of all crop-raids are carried out by lone males; however, the average group size is 2.6 elephants (Stevens, 2018), and it would be interesting to investigate if groups behave differently. However, it is worth noting that only 50 % of sightings of lone elephants were given a group size certainty of 1 (81 % if certainty 2 is included).

Number of elephants per age category is visualized in Figure 6. During the research period, the number of elephants identified as belonging to the older male category was 3493, accounting for approximately 20 % of total individual sightings (or 26 % of individuals where age and sex was possible to determine - 19 % of elephants were of unknown age). During the same period, only 45 males were observed in musth.

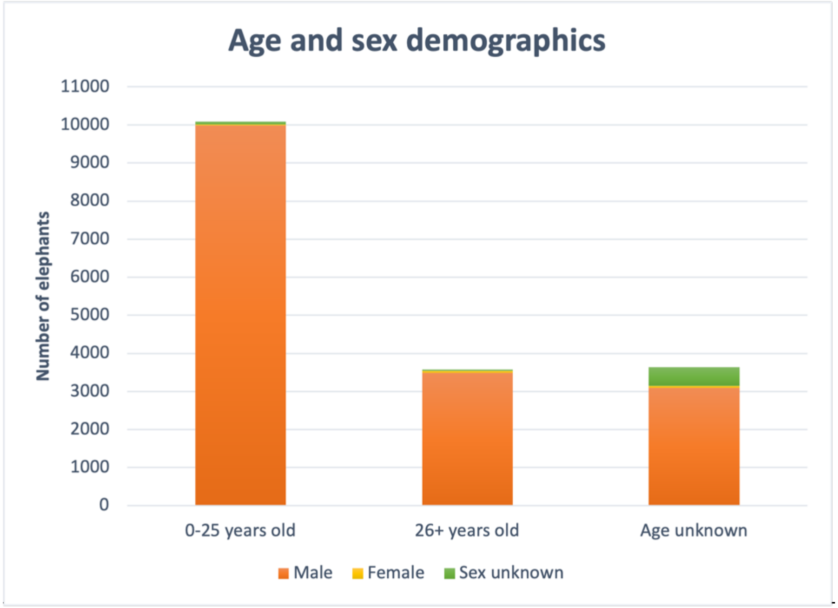


Figure 6: Age and sex categories of elephants counted between 2012 and 2022.

To determine the relative importance of rain versus time of year on elephant movement, two predictors were chosen: day of year and moving average of rain. Two different moving averages were evaluated; a 30-day moving average of rain and a 5-day moving average of rain. The 30-day moving average would roughly correspond to the time it takes for vegetation to respond to repeated rainfall (Kate Evans, personal communication, 2022) and thus give an indication of the importance of a given year's vegetation, whereas the 5-day moving average would correspond better to the effect of rainfall itself on elephant behavior.

A visualization of the 30-day moving average of rain can be seen in Figure 7. Years 2017 and 2021 experienced moving averages of as much as 10 mm per day, but overall, the moving averages rarely exceeded 5 mm per day. Figure 8 shows 5-day moving averages of rain for the same period.

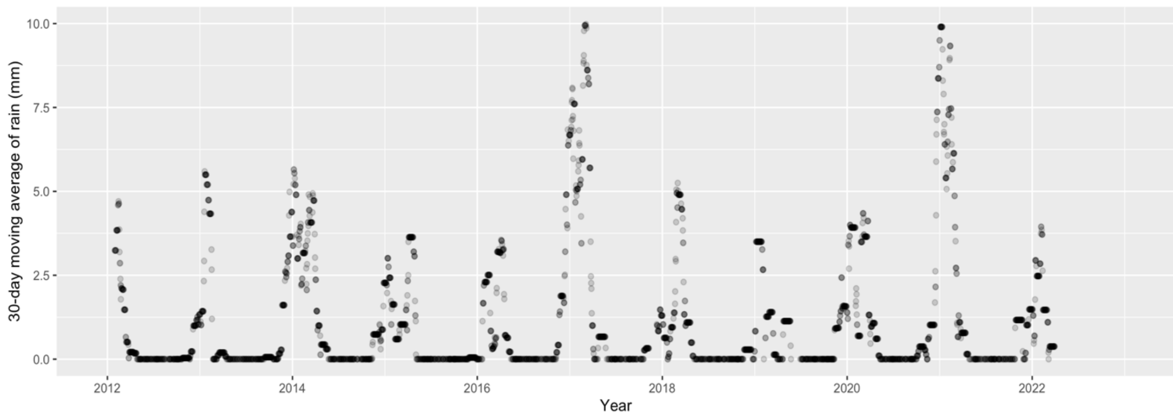


Figure 7: 30-day moving average of rain from 2012 to 2022. There is one dot per day, where each dot represents the average of the last 30 days.

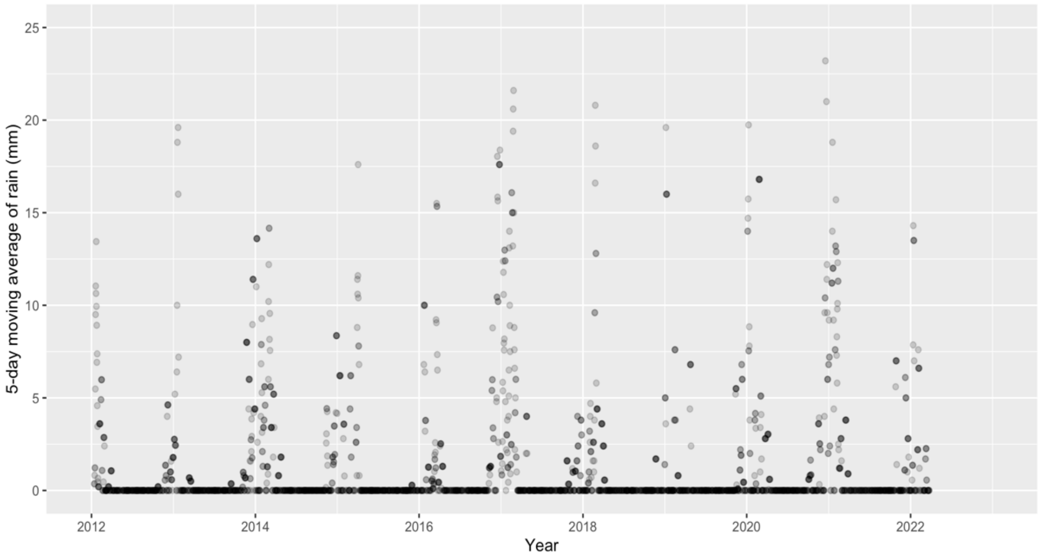


Figure 8: 5-day moving average of rain from 2012 to 2022. There is one dot per day, where each dot represents the average of the last 30 days.

I also prepared plots with total numbers of elephants per day and rainfall per day; I present these presented together with the results for easy comparison.

5.4 Generalized Additive Models (GAMs)

To quantify changes in elephant activity over time, I fitted hierarchical generalized additive models (GAMs) (Pedersen et al, 2019) in R 4.1.3 (R Core Team, 2022), using the packages mgcv 1.8.39 (Wood, 2011) and tidyverse 1.3.1 (Wickham et al., 2019). GAMs are used to quantify and visualize complex non-linear relationships by fitting a number of typically nonparametric smoothing functions. The latter are penalized according to degree of complexity to avoid overfitting. In this study, cyclic cubic regression splines were chosen as the smoother, since one of the predictors (day of year) is of a cyclical nature. As recommended by Pedersen et al (2019), the restricted maximum likelihood (REML) algorithm was chosen as the variance estimator.

Two GAMs were fitted for each response variable: one with a 30-day moving average of rain and one with a 5-day moving average of rain. Each GAM was then visualized as two plots, showing partial effect of rain and day of year, respectively.

6 Results

The model fitting worked well for both the probability of a sighting including a musth male and the probability of a sighting including an older male. Partial effect of day of year and partial effect of rain are illustrated in Figure 11 and Figure 12, followed by summary statistics in Table 1, Table 2, Table 3. The GAMs with 5-day moving average of rain show nearly identical patterns to the GAMs with 30-day moving average of rain (which is to be expected since they both aim to isolate the effect of day of year), so for simplicity I chose to only present the latter (Figure 11).

Plots showing total number of elephants per day (Figure 9) and rainfall per day (Figure 10) are included for comparison purposes. These are based on data from 2012-2022 just like the GAMs. The total number of elephants is important to keep in mind when talking about total probability of encountering any of the variables, since the GAMs only quantify the binomial probability of encountering a particular category of elephant given a sighting.

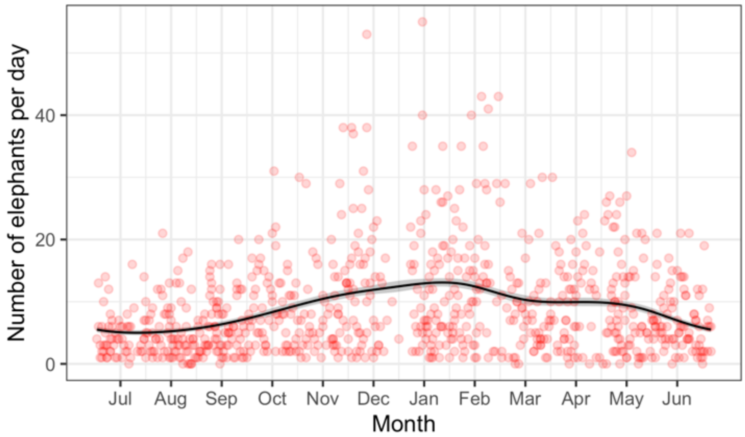


Figure 9: Plot showing number of elephants per day across years, made from a GAM. Each point represents a day's elephant count. The line is a smoother that represents the best fit smoothed line across the 10-year study period, and the narrow gray ribbon around the line is the 95 % confidence interval for the prediction.

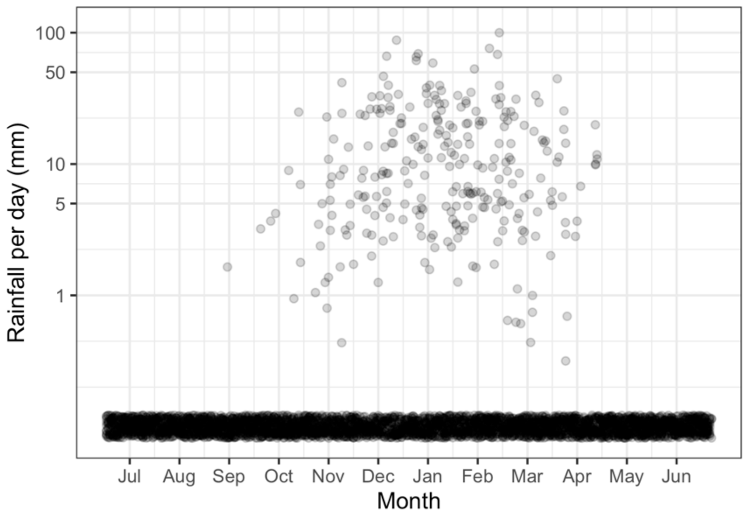
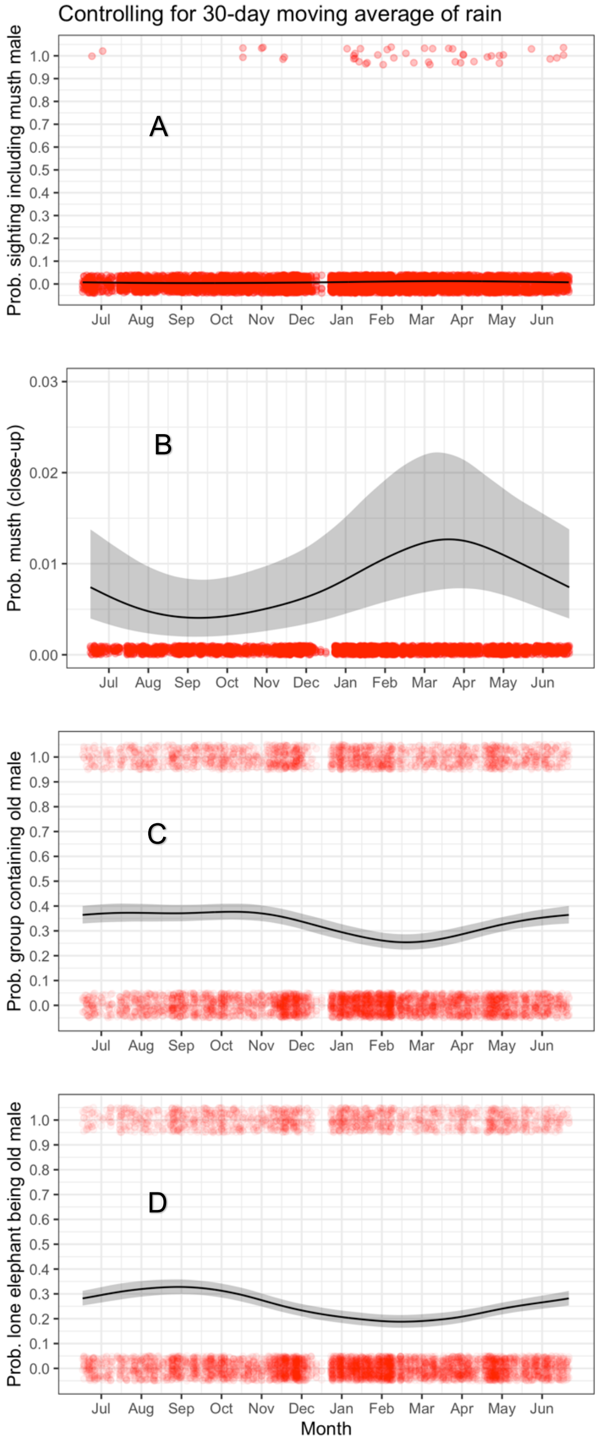


Figure 10: Plot showing observed rainfall per day (as opposed to moving average) for the entire dataset. The plot is log transformed to make low amounts of rainfall visible, and the points jittered to make the many observations with zero rain visible. No smoother is applied.

6.1 Partial Effect of Day of Year

The partial effect of day of year on all three variables is illustrated in Figure 11, controlling for 30-day moving average of rain.



The probability of encountering a male in musth in the research area is very low year-round (Figure 11A), with only 45 musth male sightings recorded during the 10-year research period. However, there is a slight and significant association with day of year, which is statistically significant at the 0.05 level (Table 2). According to this pattern, the probability of a sighting including a musth male peaks around March and April, when it is almost three times higher than at its lowest point in September (Figure 11B). Note that not a single musth male was observed between August and October (Figure 11A).

For the probability of a group containing an older male, the partial effect of day of year hovers consistently at almost 40 % throughout the dry season, but starts to decrease in November, reaching its lowest point around February/March at 25 %, and then returning to almost 40 % again by June (Figure 11C). This pattern roughly corresponds to the farming season. It also overlaps with the breeding season (Figure 2).

The partial effect of day of year on the probability of a lone elephant being an older male (Figure 11D) shows a similar pattern to the one on a group containing an older male (Figure 11C), but it is consistently a few percent lower. There was a higher-than-average probability from May to November, which corresponds to the dry season. The probability peaks in September at just above 30 % and is lowest in February/March at around 20 %.

Figure 11: Partial effect of day of year, controlling for 30-day moving average of rain. The response variables are from top to bottom: A) probability of a sighting including a male in musth, B) close-up of the probability of a sighting including a male in musth, C) probability of a group containing an older male, and D) probability of a lone elephant being an older male. The points are sightings, assigned a value of 1 if they contained the relevant class of male and a 0 if they did not. All points are jittered, meaning that they are assigned small random deviations from their actual values to make them more distinguishable - this is for visualization only and does not affect the model. The lines are smoothers, and the ribbons are 95 % confidence intervals. The predictions are generated assuming a moving average for rain of 0, but the patterns are similar regardless of the precise rainfall value chosen.

6.2 Partial Effect of Rain

The partial effects of rainfall in each model are visualized in Figure 12. Neither the 30-day moving average nor the 5-day moving average was associated with the probability of a sighting including a male in musth (Figure 12A and 12B; Table 1). However, rain did seem to influence the other two response variables. The probability of a group containing an older male showed a moderate positive association with both 30-day and 5-day moving average (Figure 12C and 12D; Table 2), and the probability of a lone elephant being an older male showed an even stronger association with 30-day moving average of rain (Figure 12E; Table 3), increasing by 19 % from 0 to 8 mm and by 11 % from 0 to 5 mm. However, the probability of a lone elephant being an older male showed no association at all with the 5-day moving average of rain (Figure 12F; Table 3).

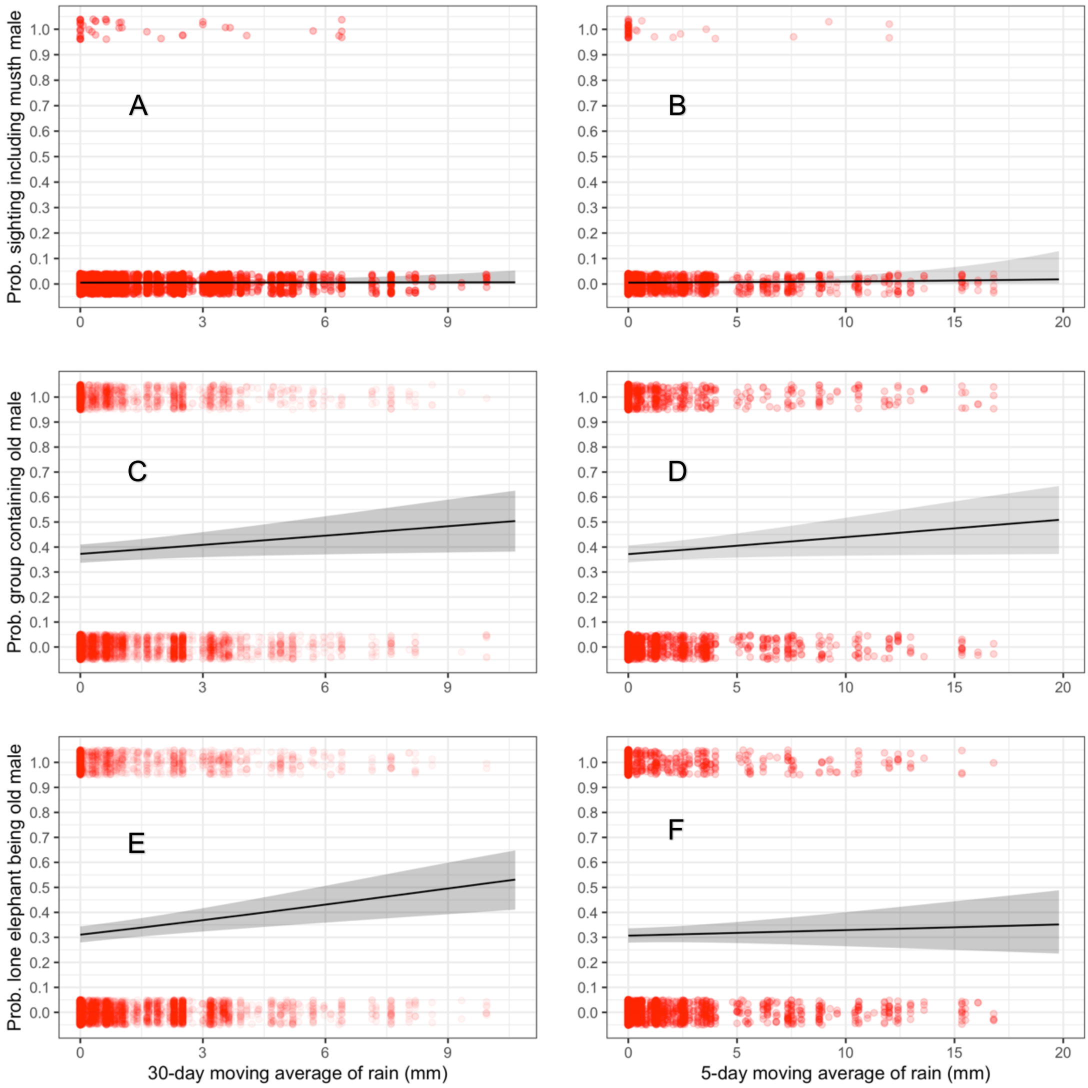


Figure 12: Partial effect of 30-day moving average of rain (left) and 5-day moving average of rain (right), both controlling for day of year, for the three response variables. From top to bottom: probability of a sighting including a male in musth (A and B), probability of an encountered group containing an older male (C and D), and probability of a lone elephant being an older male (E and F). Points are sightings, assigned a value of 1 if contained the relevant class of male and a 0 if they did not. The points are jittered, meaning that they are assigned small random deviations from their actual values to make them more distinguishable, but this is for visualization only and does not affect the model. The lines are smoothers, and the ribbons are 95 % confidence intervals around the predictions. These predictions are generated for day 32 but the patterns are consistent regardless of the day of year chosen to generate the prediction.

6.3 Summary Statistics

Table 1: Model summaries for the fixed effects and smoothers for the GAMs modelling probability of a sighting including a male in musth. Rain30days and Rain5days are the partial effects of 30-day moving average and 5-day moving average of rain, respectively. s(Date) is the partial effect of day of year (s stands for smoother).

30-day moving average				
Fixed effects (LM)	***Estimate***	***SE***	***Z-value***	***P-value***
Intercept	-4.83899	0.19727	-24.530	<0.001
Rain30days	0.02107	0.09466	0.223	0.824
Smoother (GAM)	***EDF***	***Red.df***	***Chi.sq***	***P-value***
s(Date)	1.988	13	6.377	0.0205
5-day moving average				
Fixed effects (LM)	***Estimate***	***SE***	***Z-value***	***P-value***
Intercept	-4.89459	0.16893	-28.974	<0.001
Rain5days	0.06224	0.05042	1.234	0.217
Smoother (GAM)	***EDF***	***Red.df***	***Chi.sq***	***P-value***
s(Date)	2.042	13	7.413	0.0119

Table 2: Model summaries for the fixed effects and smoothers for the GAMs modelling probability of a group containing an older male. Rain30days and Rain5days are the partial effects of 30-day moving average and 5-day moving average of rain, respectively. s(Date) is the partial effect of day of year (s stands for smoother).

30-day moving average				
Fixed effects (LM)	***Estimate***	***SE***	***Z-value***	***P-value***
Intercept	-0.75900	0.03940	-19.266	<0.001
Rain30days	0.05042	0.02235	2.256	0.0241
Smoother (GAM)	***EDF***	***Red.df***	***Chi.sq***	***P-value***
s(Date)	4.08	13	33.91	< 0.001
5-day moving average				
Fixed effects (LM)	***Estimate***	***SE***	***Z-value***	***P-value***
Intercept	-0.72095	0.03102	-23.243	<0.001
Rain5days	0.02828	0.01381	2.049	0.0405
Smoother (GAM)	***EDF***	***Red.df***	***Chi.sq***	***P-value***
s(Date)	3.556	13	32.62	<0.001

Table 3: Model summaries for the fixed effects and smoothers for the GAMs modelling probability of a lone elephant being an older male. Rain30days and Rain5days are the partial effects of 30-day moving average and 5-day moving average of rain, respectively. s(Date) is the partial effect of day of year (s stands for smoother).

30-day moving average				
Fixed effects (LM)	***Estimate***	***SE***	***Z-value***	***P-value***
Intercept	-1.14132	0.03947	-28.917	<0.001
Rain30days	0.08650	0.02180	3.969	<0.001
Smoother (GAM)	***EDF***	***Red.df***	***Chi.sq***	***P-value***
s(Date)	3.951	13	52.03	<0.001
5-day moving average				
Fixed effects (LM)	***Estimate***	***SE***	***Z-value***	***P-value***
Intercept	-1.04018	0.03075	-33.828	<0.001
Rain5days	0.01020	0.01407	0.725	0.469
Smoother (GAM)	***EDF***	***Red.df***	***Chi.sq***	***P-value***
s(Date)	3.208	13	35.33	<0.001

7 Discussion

I found strong evidence that the probability of a sighting containing an older male depends on both the day of year and recent rainfall, although the association with day of year was generally stronger. In the case of groups with older males, there was a slight association with both the 5-day and 30-day moving average of rain; in the case of lone older males, there was no association at all with 5-day moving average, but a strong association with 30-day moving average of rain. The probability of a sighting containing a male in musth seemed to only depend on day of year. In sections 7.1-7.2 I discuss possible reasons for these findings, particularly with regards to the timing of events mentioned in the background (section 4).

Before proceeding with the discussion, a few disclaimers might be of pertinence. As discussed in section 5.3 in Methods, the rain predictor was divided into 5-day and 30-day moving average to give a rough indication of the relative importance of rain itself (5-day moving average) and indirect effects of rain, mainly vegetation (30-day moving average). However, I have not controlled for other potentially confounding factors, and there is no guarantee that statistical significance indicates a causal relationship with either rain or vegetation growth, as there are many other cyclical biological phenomena that could coincide with moving averages of rain and which could theoretically have a greater impact on elephant behavior than either rain itself or rain-induced vegetation changes.

It should also be noted that the probabilities of encounter detected in this study are based on data collected during research drives on the national park side of the Boteti River and are not necessarily the same as villagers' probabilities of encounter. First of all, researchers actively search for elephants and cover a large area during drives, which could increase their overall probability of encounter compared to villagers, who remain relatively stationary in comparison. This overall probability of encounter is not the goal of my study, which has as its focus to investigate probability of encountering a certain category of elephant given a sighting, but it is worth keeping in mind.

That said, even the probability of encountering a particular class of elephant given a sighting could differ between researchers and villagers, even though their respective locations are very close and the overall sighting probability is controlled for, simply because the environment differs between the two sides of the river. For example, elephants are at risk of retaliatory shootings on the community side, which is not the case on the research side; on the other hand, the community side offers nutritious crops during farming season, which the research side does not. The findings in this study were meant to serve as a proxy for the risks experienced by locals, but there are undeniably limitations to the confidence with which conclusions can be drawn.

7.1 Males in musth

The probability of a sighting including a male in musth was close to zero year-round, with only 45 out of 6570 sightings including a musth male. There was no association with either 5-day moving average or 30-day moving average of rain; however, there was a slight association with day of year (Figure 11 and Table 1). The highest probability was around March and April, which is normally the end of the wet season as well as the peak in crop raiding incidence. The lowest probability was in September, which is close to the end of the dry season (Figure 11B).

This pattern is somewhat bewildering, as it does not seem to correspond closely to any of the phenomena discussed in the background: reproduction patterns, timing of crop raids, or previous studies' findings of the timing of the musth condition itself. As noted under 4.2.3, existing literature suggests that the most likely time for a male to be in musth is between the onset of the wet season and the period right after the wet season. My prediction was that the probability of a sighting including a musth male would be lower in the research area during this period, during which they would have best reproduction success if they pursued females. According to my results, however, there does not seem to be any clear association between the most likely timing of musth based on literature and the probability of a sighting including a musth male in the research area - if anything, the farming season appears to be the most closely associated (Figure 13A and 13D). One possibility is that musth males – usually a sub-category of older males – take part in crop raiding, and that crops are thus a stronger driving force shaping elephant spatial behavior than the marginal increase in estrous females elsewhere that might attract musth males away from our study site. On the other hand, if that was the case, the pattern would have been expected to be the same as that shown by older males, which is not the case – in fact, these patterns appear to be each other's opposites (Figure 11B, 11C and 11D). Also, males have been known to eat less during musth (Hall-Martin, 1987) which, if true for these elephants as well, would make crop maturation an unlikely driving force.

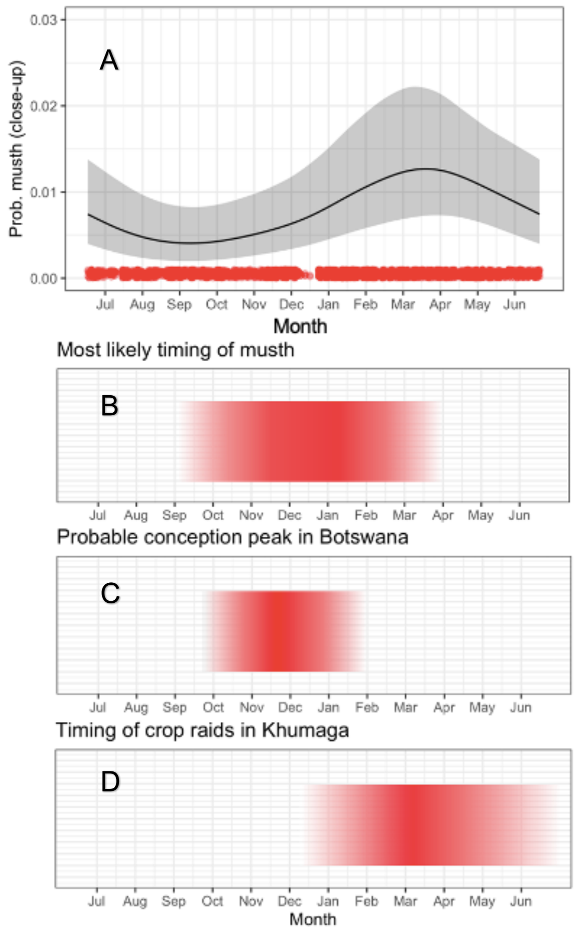


Figure 13: The partial effect of day of year for the probability of a sighting including a male in musth, juxtaposed with plots illustrating the most likely timing of musth, the probable peak mating season in Botswana, and timing of crop raids in Khumaga.

It could be the case that the probability of a sighting including a musth male is not a reflection of the *movement patterns* exhibited by musth males, but rather a reflection of the local timing of the musth condition itself among the males already present, and thus reflects a similarity to the findings made by Poole (1987) as opposed to those made by Ganswindt et al (2010) and Hall-Martin (1987). The latter two found that musth was more common at the onset of the rainy season, whereas Poole (1987) found that it was most common during and right after the rainy season, which corresponds slightly with my findings (Figure 13A and 13B). Furthermore, it is possible that the actual peak in probability of a sighting including a musth male occurs a bit earlier than my results suggest, considering there is a gap in data for several weeks each Christmas and New Year. If musth males were missed during that time, the actual pattern would be shifted to the left, making it fit even better with Poole's findings (1987).

Regardless of the exact timing of the peak in probability of an encountered elephant in the research area being in musth and the reasons behind that timing, my data indicate that the probability of a sighting including a musth male in the research area is lowest at the end of the dry season. This pattern is also likely to correspond quite well with the overall probability of encountering a male in musth, since the total number of elephants is also lowest in the dry season (Figure 9).

7.2 Older males

The probability of a group containing an older male and the probability of a lone individual being an older male showed similar patterns. In the case of groups with older males, there was a slight association with both the 5-day and 30-day moving average of rain, suggesting that both direct and indirect effects of rain could play a role in the decisions that groups with older males make about when to visit the river and riverine forest, where the data collection was focused. In the case of lone older males, there was no association at all with 5-day moving average, which suggests that rain itself might not play a role; however, the association with 30-day moving average of rain was even stronger than for groups with older males. For lone older males, the partial effect of 30-day moving average and the partial effect of day of year showed probability changes in the same order of magnitude: in the plot showing partial effect of day of year (Figure 11D), the probability decreases by 13 % from September to February, and in the plot showing partial effect of 30-day moving average of rain (Figure 12E), it increases by 11 % from 0 to 5 mm. However, since a 30-day moving average of 5 mm is relatively uncommon (Figure 7), in an average year, the partial effect of rainfall might still not be very noticeable compared to that of day of year. In other words, most days of the year the moving average of rain is so low that any changes in probability associated with it do not come close to changes in probability associated with a shift in season.

Having concluded that the partial association with rain, even when statistically significant, is likely weaker than that with day of year, it appears that the overall probability of a sighting including an older male decreases during the wet season and farming season. This is somewhat surprising - the probability of a sighting including an older male could have been expected to be higher during the farming season, since older males are the main crop raiders, and the research camp is located only a few kilometers away from farms (Figure 5). There could be several reasons why the results instead show a decrease in probability during this time. Below is a non-exclusive list of possible explanations.

1) One possible explanation is that older males choose to stay on the community side of the river when crops are ready to harvest – it could be that natural forage, although most abundant by the river, is available in sufficient amounts on the community lands when combined with nutritious crops. If that is the case, it might be more energy-efficient for elephants to stay on the side where crops are available. Studies in other areas have shown that elephants crop raid mainly at night and return to protected areas during the day to avoid people (Graham et al., 2010), but the elephants in Makgadikgadi Pans National Park are particularly unperturbed by humans (Kate Evans, personal communication, 2023), which could mean that they feel safe enough to stay on the community side during the day and thus remain undetected during research drives. If that is true, it would mean that the decrease in probability of a sighting including an older male as experienced by researchers is an inaccurate reflection of the actual change in probability experienced by locals, for whom the probability might instead *increase*

during the farming season. To investigate this, research drives would likely need to be extended to the community side of the river.

2) Another possible explanation is that it is an increase in younger males, rather than a decrease in older males, that accounts for the reduced probability of a sighting including an older male in the crop-raiding season – perhaps because younger males are less likely to mate during the breeding season than older males and thus have more incentive than older males to visit the abundant forage in the Boteti area. This is further supported by the plot with elephants per day (Figure 9) which shows an increase in total number of elephants during the rainy season – the influx of elephants could be primarily made up of younger bulls. However, further analyses are required to confirm this.

3) A third possible reason for the decreased probability of a sighting including an older male during the farming season is that they are more drawn to females than crops, since the farming season at least partly overlaps with the peak breeding season as suggested by previous literature (Figure 14C and 14D). The increase in crop-raids would thus be explained by the presence of crops in combination with a change in behavior among the older males that remain in Makgadikgadi Pans, rather than an influx of older males to the area. This hypothesis is supported by the fact that older males ought to leave the area at some point if they want to reproduce, and the best time to do that is when females are most likely to be receptive. However, it is strange that musth males do not follow the same pattern (Figure 11) – both categories of males should be interested in finding females during this time.

The complete explanation behind the apparent decrease in probability of a sighting including an older male during the farming season could be a combination of some or all of the above-mentioned factors. It could for example be that the probability of a *group* containing an older male decreases because groups with older males stay on the community side of the river, whereas the probability of an encountered *lone* elephant being an older male decreases because lone older males leave the area in search for females. This speculation is based on the premise that older males interested in crop raiding quite often do so in groups (and most crop raiding occurs between January and June, which corresponds quite well with the plot concerning groups with older males (Figure 14A and 14C)), whereas older males interested in pursuing females are more likely to do so alone (and the breeding season and farming season when combined last approximately from October to June, which corresponds quite well with the plot concerning lone older males (Figure 14B and 14D)).

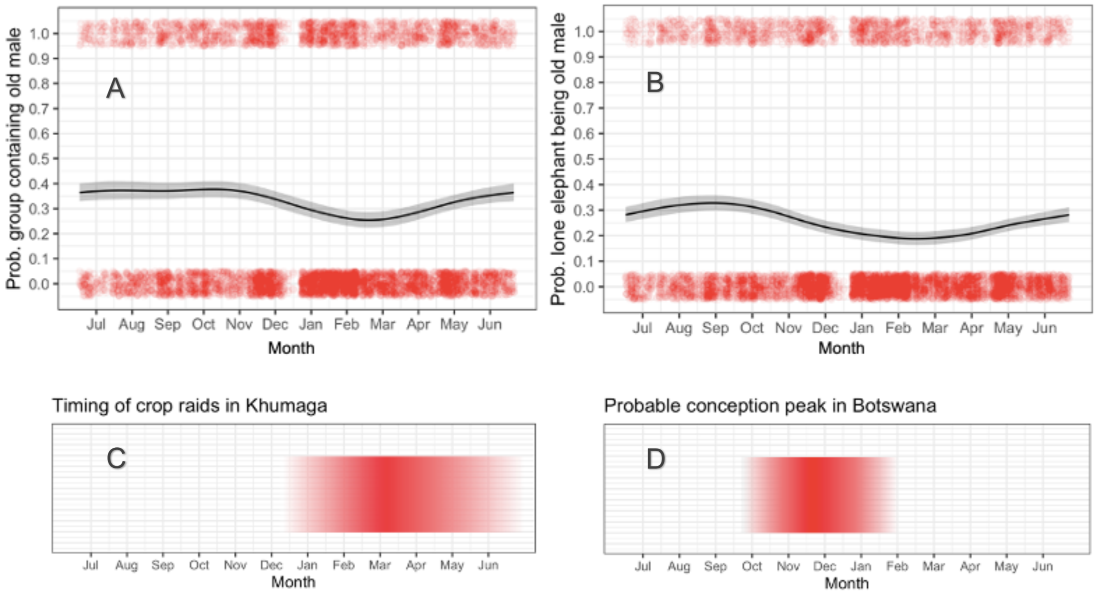


Figure 14: Partial effect of day of year for the probability of a group containing an older male (plot A) and a lone elephant being an older male (plot B), juxtaposed with plots showing timing of crop raids in Khumaga (plot C) and timing of conceptions as suggested by literature (plot D).

All in all, it is not yet possible to make definitive claims about what causes the apparent decrease in probability of sightings including older males during the farming season without further research. Furthermore, if one considers the fact that the total number of elephants in the area is greater during the rainy season than in the dry season (Figure 9), it is not safe to assume that the overall probability of encountering older males decreases during the rainy season even in the research area.

7.3 Further remarks

The underlying reasons behind the statistical significance of day of year for all three variables are likely complex. Even though the plots showing partial effect of day of year (Figure 11) controlled for observations of rainfall, the association between response variables and day of year could still be indirectly related to rainfall. This is because elephants, not least older males that have many years of experience, might have learned when and where the natural forage (influenced by rain) is usually most abundant. As such, they might move to certain areas at certain times based on habit rather than actual circumstances. Since younger males learn from bulls (Evans & Harris, 2008), this behavior would apply to younger males as well. If such habitual movement is the case, the effect of day of year might present differently in the future, if climate change causes consistent change and new averages of rain that give elephants new expectations. However, this change in movement patterns would be a more long-term shift, and not very useful for locals on a day-to-day basis in the foreseeable future.

Another reason behind the prominent association between response variables and day of year might be photoperiodic cueing, if Hufenus et al (2018) is correct in that elephants are long-day breeders. Since the number of daylight hours follows the same pattern every year, photoperiodic cueing could be part of the reason why day of year is a better predictor than rainfall. If day length affects elephant movement patterns in this area, the patterns found could be expected to remain similar regardless of impacts of future climate change. As discussed above, however, it is unclear from my results if reproductive cycles have any effect at all on elephant movement in the Makgadikgadi Pans National Park, especially when it comes to musth males.

Lastly, it could be that the association between elephant movement and rainfall is actually stronger than my results suggest, but it has been undetected due to the choice of predictor: as Garstang et al (2014) noted, "changes in the movement of elephants were found to both precede and follow the transition from dry to wet conditions" (p 10). As I have only investigated the association between sightings and rainfall preceding the sightings, I might not have been able to fully detect associations with rainfall succeeding sightings.

8 Conclusion

The partial effect of day of year is greater than the partial effect of rain for all three variables: the probability of a sighting including a musth male, the probability of an encountered group containing an older male and the probability of an encountered lone individual being an older male. Even though the partial association with rain was statistically significant for the probability of a sighting including an older male, especially for the probability of an encountered lone elephant being an older male for which 30-day moving average was strongly significant, that association is weak compared to that with day of year when actual amounts of rainfall are taken into account.

The probability of a sighting including a musth male was low year-round, but showed a clear pattern - it was highest at the end of the rainy season (March and April) and lowest at the end of the dry season (September). The reasons for this pattern are unclear, as it does not correspond clearly to any of the cyclical biological phenomena discussed in the background. However, the probability follows the curve with total number of elephants quite closely, meaning that the overall chance of encounter with musth males is likely to be similar to the pattern mentioned above. There is also no obvious reason to suspect that the detected pattern could be different on the community side, and the information could thus be useful in predicting musth male encounters.

The variables concerning older males showed an opposite pattern to that of musth males: both the probability concerning groups and that concerning lone elephants were lowest around February and March, when most crop raids occur. This is surprising, as older males dominate crop raids. One potential reason for this pattern could be that crop raiding males remain on the community side during the farming season, in which case locals would experience an increased probability of encountering an older male during this time. Alternatively, the reduced probability could be due to an influx of younger males and/or to older males leaving the area in search of females. In both latter cases, the locals would experience the same reduced probability of a sighting including an older male as the researchers do. However, the overall chance of encounter would still be unclear given that total number of sightings increases during the rainy season, counteracting some of the decrease in probability of sightings including older males shown during the farming season. The practical implications of the results concerning older males are thus unclear, as it is not known what causes the decrease in probability during the farming season and whether it shows the same pattern on the community side of the river.

Out of the two predictors investigated, the partial covariance with day of year was more prominent than the partial covariance with rain. In combination with further research, the partial covariance with day of year is thus a comparatively more useful tool for locals hoping to predict encounters and avoid conflict.

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