UNIVERSITY OF GOTHENBURG

DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

AFRICAN ELEPHANTS' EFFECT ON THE TEMPORAL USE OF ELEPHANT HIGHWAY BY PREDATOR AND PREY

Makgadikgadi Pans National Park

Rebecka Relfsson

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Supervisor: Søren Faurby, Department of Biological and Environmental Sciences

Extern: Kate Evans, Elephants for Africa

Examiner: Mats Olsson, Department of Biological and Environmental Sciences

Image: African savanna elephant (*Loxondonta africana*) on an elephant highway (camera trap picture) ©Elephants for Africa

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Abstract

African savanna elephants (*Loxondonta africana*) are the world's largest land-mammal and are considered a keystone species. The effect they have on vegetation and their environment is well known, but their effect on other animal species is less studied. Knowledge about a species and its effect on other species is important for both conservation work and human-wildlife conflict management. This study investigates how elephant presence on so-called elephant highways affects the presence of other herbivore species as well as predator species. Additionally, it examines if the elephants are used as predation avoidance by other herbivores. This is done using approximately four years of data from camera traps that were set up along the elephant highways near the Boteti River in the Makgadikgadi Pans National Park in Botswana. The herbivore species included in the study were giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), and impala (*Aepyceros melampus*). The predators were investigated as a group (consisting of the five largest African predator species). Lions (*Panthera leo*) were also examined, separately from the other predators. Logistic regression models testing the presence of each of the herbivore species on the elephant highways against the presence of elephants and predators showed that elephants affected the presence of giraffes positively, while the presence of kudu and impala were unaffected. The presence of predators was almost exclusively non-significant, although almost none of the herbivore species were caught on the camera traps close in time to a predator. Logistic regression models testing predator presence against elephant presence showed no significant effect of elephant presence on predator presence. The study shows that larger herbivores such as giraffes tend to be drawn to elephants, but further studies need to be done to better investigate the elephants' effect on the smaller herbivores and the predators.

Key words: African savanna elephant, elephant highways, interspecies interactions, predation avoidance, predator-prey interaction, temporal activity

Abstract (SE)

Den afrikanska savannelefanten (*Loxondonta africana*) är världens största landlevande däggdjur och anses vara en nyckelart. Deras påverkan på den omgivande vegetationen och landskapet är väl studerat, men deras påverkan på andra djurarter är mindre utforskat. Kunskap om en art och dess påverkan på andra arter är viktigt för såväl bevarandearbete som konflikthantering mellan människor och djur. I denna studie undersöks hur närvaron av elefanter på så kallade elefantstigar påverkar närvaron av andra herbivorer och även rovdjur. Dessutom undersöks det om elefanter kan användas av andra herbivorer som ett sätt att undvika rovdjur. Detta görs med hjälp av ca fyra års data från kamerafällor uppsatta längs elefantstigarna nära Boteti floden i Makgadikgadi Pans nationalpark i Botswana. Herbivorerna som undersöktes i denna studie var giraff (*Giraffa camelopardalis*), större kudu (*Tragelaphus strepsiceros*) och impala (*Aepyceros melampus*). Rovdjuren undersöktes som en grupp (bestående av de fem största afrikanska rovdjuren). Lejon (*Panthera leo*) undersöktes också separat från de övriga rovdjuren. Logistiska regressionsmodeller som testade närvaron av de olika herbivorerna på elefantstigarna mot närvaron av elefanter och rovdjur visade att elefanterna påverkade giraffernas närvaro positivt, medan närvaron av kudu och impala förblev opåverkad. Närvaron av rovdjur hade en nästan uteslutande icke-signifikant påverkan, även om nästan inga herbivorer blev fångade på bild i nära anslutning till ett rovdjur. Logistiska regressionsmodeller som testade närvaron av rovdjur på elefantstigarna mot närvaron av elefanter visade att inga signifikanta effekter utav närvaron av elefanter kunde ses på rovdjuren. Studien visar att större herbivorer så som giraffer tenderar att hålla sig nära elefanter, men ytterligare studier behövs för att bättre undersöka elefanters effekt på de mindre herbivorerna samt på rovdjuren.

Nyckelord: Afrikansk savannelefant, dygnsaktivitet, elefantstigar, interaktion mellan arter, predationsundvikande, rovdjur-bytesdjurinteraktioner

Introduction

Predation avoidance

The co-existence and coevolution of predators and prey have played an important role in why we have such a rich diversity among species (Ito et al., 2013; Jones & Ellner, 2007; Tien & Ellner, 2012). It has not only been the driving factor behind much physical evolution, but also resulted in a vast behavioural diversity among both prey and predators. The anti-predator behaviours and responses of prey can vary greatly depending on the species, body size and age, environmental factors, time of day, vegetation, and presence of other species (Davies et al., 2016; Tambling et al., 2013).

One way to reduce the predation risk is for the prey to change their activity pattern and behaviour so it is harder for predators to spot or capture them (Davies et al., 2016; Tambling et al., 2015; van Der Meer et al., 2012). This can include the prey shifting their use of the habitat and their behaviour in different environments (Davies et al., 2016; Tambling et al., 2015). For example, studies of African herbivores have shown that greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*) and giraffes (*Giraffa camelopardalis*) all shift their behaviour to be more vigilant near waterholes (Périquet et al., 2010; van Der Meer et al., 2012) since this is a place with higher predation risk (Davidson et al., 2013; De Boer et al., 2010; Périquet et al., 2010).

Temporal partitioning

Temporal partitioning is another way of predation avoidance. Temporal partitioning is a mechanism of coexistence among species in ecological communities where animals shift their activity rhythm to avoid conflict (Kronfeld-Schor & Dayan, 2003; Schoener, 1974). Temporal partitioning can be found both within and between species (Kronfeld-Schor & Dayan, 2003), either between competitors or as a way to avoid predation (Hayward & Slotow, 2009; Kronfeld-Schor & Dayan, 2003; Schoener, 1974). Between competitors, this is a rather rare method of coexisting, with habitat and food partitioning being more common (Schoener, 1974), and is still relatively unstudied.

Species have evolved to be active during certain periods of time that optimize the timing of certain behaviours, such as food scavenging, predation avoidance, mating, etc., that are necessary for survival and reproduction (Hayward & Slotow, 2009). With this, some physiological adaptations have evolved, that will limit changes in the activity pattern (Kronfeld-Schor & Dayan, 2003). Therefore, it is very unusual that species shift their activity into the opposite of their preferred activity phase as a result of temporal partitioning, but it is not uncommon that they shift their activity within the preferred activity phase (Kronfeld-Schor & Dayan, 2003). This is true for temporal partitioning as a result of both predation and competition avoidance (Kronfeld-Schor & Dayan, 2003).

The diel activity pattern in a species depends upon both the circadian rhythm and various environmental stimuli (Kronfeld-Schor & Dayan, 2003). The circadian rhythm is mostly fixed within a species, but can be adjusted on an individual basis based on, for example past experiences and the environment (Kronfeld-Schor & Dayan, 2003). Studies have shown that the circadian rhythm can predict environmental changes to some degree, and subsequently letting the animal change its behaviour before the environmental change happens (Kronfeld-Schor & Dayan, 2003). Mostly, an animals rest and activity time will corelate to their circadian rhythm, but this can be cognitively overridden and activity time can shift without changing the circadian rhythm (Kronfeld-Schor & Dayan, 2003).

The environmental stimulus can consist of several different factors, such as food availability, predation risk, competition, temperature, weather, etc., but the most predictable and important environmental cue is the change between day and night (Kronfeld-Schor & Dayan, 2003). This change between day and night (or light and dark) is what normally controls the circadian rhythm (Kronfeld-Schor & Dayan, 2003) and allows the animal to develop a more or less fixed circadian programming of both behaviours and physiological traits (Kronfeld-Schor & Dayan, 2003).

Temperature, whether it is caused by weather, seasons, or time of day, has a large effect on when animals are active (Kronfeld-Schor & Dayan, 2003). Nocturnal animals are usually more adapted to the cold or more sensitive to the heat (Hayward & Slotow, 2009; Kronfeld-Schor & Dayan, 2003), while diurnal animals generally handle heat better but are more sensitive to cold (Kronfeld-Schor & Dayan, 2003). In areas where the temperatures get very high, even the diurnal animals avoid being active during the hottest hours and can instead compensate by being more active at dusk, night or dawn (Kronfeld-Schor & Dayan, 2003).

There are multiple studies which show that prey change their activity pattern to avoid predation (Kronfeld-Schor & Dayan, 2003; Mandelik et al., 2003; Tambling et al., 2015). This is most noticeable when there are nocturnal predators active, since prey will shift their activity so as not to overlap with the predators resulting in more diurnal and less nocturnal activity (Tambling et al., 2015). A good example of this are the large mammals in Africa. All the large predators in Africa; lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyaena (*Crocuta Crocuta*)*,* brown hyaena (*Parahyaena brunnea*), cheetah (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*), have crepuscular activity, with wild dogs being strictly crepuscular, cheetahs being mostly crepuscular, whilst the others are typically nocturnal with varying degree of crepuscular activity (Hayward & Slotow, 2009). The nocturnal predators are usually less active during the darkest part of the night and more active during nights with bright moonlight (Hayward & Slotow, 2009). In contrast most African herbivores are diurnal, especially when predators are in the area (Tambling et al., 2015), which might be a form of predation avoidance through temporal partitioning since being active at a different time than the predators will result in lower predation risk (Tambling et al., 2015).

As with the temporal partitioning among competitors, relatively few studies exist about temporal partitioning between prey and predators. When it comes to whether or not prey activity change predator activity, different studies show conflicting things (Kronfeld-Schor & Dayan, 2003). This might be a sign that the temporal partitioning here is less common, more subtle, or simply only present in certain species or ecosystems.

Grouping

Another anti-predator behaviour is something called grouping (Alexander, 1974; Davies et al., 2016; Périquet et al., 2010). This includes changing group sizes as a response to predation risk (Davies et al., 2016; Schmitt et al., 2014). Being in a large herd lowers the predation risk and allows the prey to spend less time being vigilant and more time on other behaviours, such as feeding and drinking (Davies et al., 2016; Périquet et al., 2010; Scheel, 1993; Schmitt et al., 2014). The group does not have to consist of only one species, several studies have shown that the predation risk lowers in interspecies groups (Ferry, 2018; Périquet et al., 2010; Scheel, 1993; Schmitt et al., 2016; van Der Meer et al., 2012). Studies have also shown that time spent being vigilant decreases among herbivores in interspecies groups, both in wild species such as zebras, kudu, impala (Périquet et al., 2010; Schmitt et al., 2014; van Der Meer et al., 2012), but also among domesticated herbivores such as cattle (Kluever et al., 2009).

In an interspecies group, not only does the total group size increase, resulting in lower predation risk, but the species can benefit from each other's anti-predator behaviours and different strengths in order to detect and avoid predation (Schmitt et al., 2016). This can be one sided, such as zebras (*Equus quagga*) spending time around giraffes to benefit from their height, that allows them to detect predators easier (Schmitt et al., 2016), or a mutual benefit to combine the strength of two different species for better predator detection, such as zebras, that have good eyesight, and wildebeest (*Connochaetes taurinus*), that have good hearing (Schmitt et al., 2014). How much each species can afford to lower their vigilance when in interspecies groups also depend on if they have a common predator and which of the species is preferred by the predators (Scheel, 1993; Schmitt et al., 2014). Herbivores that share a common predator, such as zebras and wildebeest (both preferred by lions), are less vigilant together (Schmitt et al., 2014), while zebras together with impala are more vigilant, since impala are not preferred by lions (Schmitt et al., 2014). On the other hand can species that are less preferred by a common predator, such as warthogs (*Phacochoerus africanus*), be safer in a group with more preferred prey, such as zebras, since the predator (in this case lions) will go for the more preferred prey instead (Scheel, 1993).

Size in relation to predation

When it comes to interactions between predators and prey, the size of both parties is of importance (Claessen et al., 2002; Lundvall et al., 1999; Owen-Smith & Mills, 2008; Tsai et al., 2016). Predators tend to prefer prey that are of a certain size, the so-called preferred predator-prey mass ratio (PPMR) (Tsai et al., 2016), which often is the same size or slightly larger than the predator itself (Hayward & Slotow, 2009; Owen-Smith & Mills, 2008). This PPMR can shift within a species and is mostly dependent on the size of each individual predators (Tsai et al., 2016).

When choosing prey, a predator has two factors to consider: gain and cost. For maximum gain, the predator should choose the biggest prey that will give them the most amount of food (DeLong & Luhring, 2018). The upper size of prey a predator can hunt is determined by the predators' physical abilities, such as their ability to catch and kill the prey as well as their ability to process the food (jaw strengths, feeding apparatus etc) (Lundvall et al., 1999; Tsai et al., 2016). It is also reasonable to assume that it is determined by external factors, such as how much of the carcass the predator can eat before the meat goes bad or scavengers steal it.

For minimal cost, however, the largest possible prey might not be the best choice. The number of hunts a predator has to do in order to successfully catch a prey increases with prey size (Lundvall et al., 1999), which lead to higher energy loss for the predator (DeLong & Luhring, 2018; Lundvall et al., 1999). Since larger prey has a lower capture success for predators (Claessen et al., 2002; Lundvall et al., 1999), smaller prey that is easier to catch might be preferable to the predator (DeLong & Luhring, 2018; Lundvall et al., 1999). There is also a lower limit to prey size, where the prey is too small to be able to detect and catch easily (Lundvall et al., 1999) and is too small to give enough energy to the predator (Tsai et al., 2016).

The optimal prey size for a predator is therefore a balance between the cost and gain. It can be described as a dome shape, where a prey's mortality is a function of their size (Lundvall et al., 1999) and predators hunt prey that are large enough to give them sufficient energy, but small enough to be able to catch without losing too much energy (DeLong & Luhring, 2018; Lundvall et al., 1999; Tsai et al., 2016).

Elephant interactions

African savanna elephants (*Loxondonta africana*), from here on referred to as elephants, are the largest land-living animal, and it is no surprise that they affect their surroundings. They are so called ecosystem engineers that shape their environment and have a large effect on the vegetation and landscape, as shown in several studies (Ferry, 2018; Makhabu et al., 2006; Tambling et al., 2013). The effects of elephants on vegetation are well studied, but due to their size they are also expected to have a large impact on other animals, although this is less studied.

Elephants and predators

Elephants are big enough that they fall outside all the African predators preferred prey size and therefore seldom have to worry about being hunted by any of the predators (Ferry, 2018; Power & Shem Compion, 2009; Tambling et al., 2015). There are however cases when lions have killed elephants (Davidson et al., 2013; Power & Shem Compion, 2009; Shannon et al., 2022; Tambling et al., 2015). However, lions are mostly only a threat to calves and younger elephants (Power & Shem Compion, 2009; Shannon et al., 2022; Tambling et al., 2015) or elephants weakened by drought for example (Davidson et al., 2013; Power & Shem Compion, 2009), where male elephants seem to be more vulnerable than females (Power & Shem Compion, 2009). Successful elephant hunts almost only occur when the lions are in a large group (Power & Shem Compion, 2009; Shannon et al., 2022).

Thus lions are perceived as a threat to elephants and when they are near the elephants often engage in protective behaviours, such as bunching or mobbing (Ferry, 2018; Power & Shem Compion, 2009; Shannon et al., 2022), or aggressive behaviours, such as charging, trumpeting and throwing things at the lions (Ferry et al., 2016; Londolozi Game Reserve, 2014; Power & Shem Compion, 2009). Elephants chase away lions, as well as other predators, even when they are not currently hunting or threatening the elephants, which can result in other prey being 'saved' and getting away from the predators (Ferry et al., 2016; Londolozi Game Reserve, 2014).

Elephants and herbivores

Although elephants' effect on other herbivores are not thoroughly studied, it has been shown that they have both direct and indirect effects on populations as well as individual herbivores (Ferry, 2018; Tambling et al., 2013).

The indirect effects are the most well studied. Since elephants affect their environment and the vegetation around them, that causes a ripple effect which affects all herbivores in the area. Elephants eating trees affects tree height and causes more young shoots to grow, which in turn facilitates browsing amongst smaller herbivories (Makhabu et al., 2006). For example, both greater kudu and impala prefer to eat trees that have been affected by elephants, since the young shoots are more nutritious and grow closer to the ground, making them more accessible for the smaller browsers (Makhabu et al., 2006), and especially impala tend to choose habitats with elephants over those without (Ferry, 2018).

Studies have shown that herbivores tend to keep close to elephants when they are near waterholes (Ferry et al., 2016), especially during the dry season when they are most vulnerable to predators by the water (Davidson et al., 2013; Périquet et al., 2010). While, in a study by Ferry (2018), zebras did not show any visible decrease in vigilance as a response to lion sounds when they were around elephants, Ferry did theorize that herbivores kept close to the elephants as a predation avoidance method. Ferry's studies also showed that the population size of several herbivores was affected by the presence and size of elephant populations in the area, and that no segregation between elephants and other herbivores could be detected.

While elephants' effect on the behaviour of other animals are still relatively unstudied, it could be an important part of understanding the complex ecosystem they live in. A better understanding of animals and their ecosystems can be beneficial in many different cases, such as conservation work and handling human-wildlife conflicts (Elephants for Africa, 2016c). Many African mammals are threatened or endangered (IUCN, 2023), and while working on conservation actions for them it is important to understand how other animals affect them and how they in turn affect other animals (Elephants for Africa, 2016c). Similarly, a tool to preventing human-wildlife conflict is to understand the animals and how they behave and affect each other (Elephants for Africa, 2016c). If actions to prevent the conflicts by altering an animal's behaviour (such as putting up a fence or otherwise forcing animals to take different routes than they would normally do) are taken, it is important to understand how this could affect other species as well.

Aim and Research Questions

The aim of this study is to investigate how elephants can affect the activity pattern of predators and herbivores, and to look at if they play a part in predation avoidance amongst herbivores in the Makgadikgadi Pans National Park in Botswana.

The following three hypothesis are tested:

H_A – Herbivores are less likely to be active at the same time as predators
H_B – Predators are less likely to be active at the same time as elephants
H_C – Herbivores are more likely to be active at the same time as elephants

Material and method

Location

The study was conducted in Makgadikgadi Pans National Park (MPNP) in Botswana (Appendix 2) with data provided by the NGO Elephants for Africa (EfA). Botswana is home to a relatively large elephant population with approximately 150 000 individuals in northern Botswana (Elephants for Africa, 2016a) and the population in MPNP has increased since the water returned to the Boteti River, which marks the western border of the MPNP, in 2009 after a 19 year dry period (Evans, 2019). MPNP has a predominately male elephant population, with 98% of all elephant sightings being male (Evans, 2019).

Within the MPNP the study took place along the elephant highways near the Boteti River (Fig. 1). The elephant highways are permanent paths formed over time by elephants traveling habitual routes (Presotto et al., 2019; Von Gerhardt et al., 2014). The highways are clear of vegetation (Allen et al., 2021; Von Gerhardt et al., 2014), less than a meter wide (mean width 84.8 cm (Allen et al., 2020)), and often connect places of resources such as feeding areas and waterholes or rivers (Von Gerhardt et al., 2014). These highways are used regularly by many different species (Elephants for Africa, 2016b; Von Gerhardt et al., 2014) making them informative study sites to interspecies studies.

Camera traps

The study used footage from camera traps set up by EfA, placed on eight different elephant highways (Fig. 2), from June 2014 until April 2017, with a break from April 2016 until July 2016.

Figure 1. Examples of elephant highways near the Boteti River in Makgadikgadi Pans National Park in Botswana (photo: R. Relfsson).

The cameras were all the brand Reconyx HC600 Hyperfire (except EfA06 during June 2014 until April 2016, which was Bushnell 119435C). They were continuously taking images and triggered by movements.

The data from the cameras were collected and compiled in an excel file by citizen scientists via the organisation SnapshotSafaris (SnapshotSafaris). The file rows contained information about each photo taken by the camera traps. Each row contained a link to the picture, the site (EfA02-EfA09), capture date, capture time, the identified species on the picture, as well as other information not relevant to this study.

The citizen scientists from SnapshotSafaris also identified what species each picture depicted. Multiple people identified each picture (at least 10 people per picture) and a p value over the stability of observed species was recorded, where p = 1 meant 100% of the people identified the same species in the picture, p = 0.5 meant 50% identified the same species etc. This p value was included in the excel file.

Species

To test the hypotheses, predator and herbivore species that uses the elephant highways in MPNP (apart from elephants) needed to be chosen for the study. The species included (Table 1) were

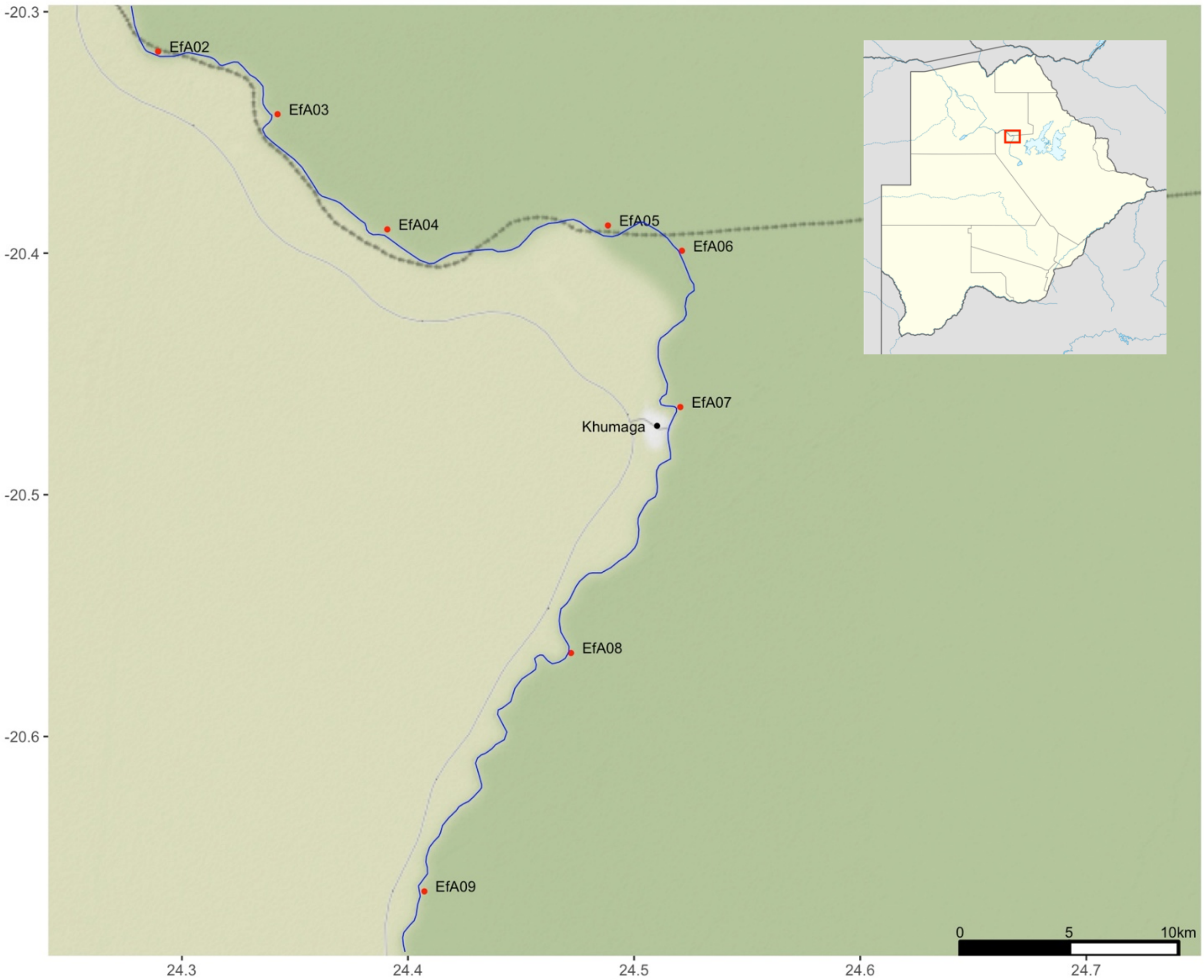

Figure 2. Map of study area. Camera positions are marked with red dots, Khumaga village is represented by a black dot and the Boteti River by the blue line. The darker green represents Makgadikgadi Pans National Park, while the lighter green represents unprotected land. The inlay shows the maps position within Botswana represented by a red rectangle.

chosen based on multiple conditions: all non-mammals and domesticated species were excluded from the study; since zebras and wildebeests are migratory species and only reside in the MPNP periodically during the year (Bennitt et al., 2022), they were excluded from the study; and finally to ensure a large enough sample size for the analyses, herbivore species that appeared in the dataset from the cameras less than a hundred times (with a p value of at least 0.8) were excluded from the study. This process left three suitable herbivore species: giraffe, greater kudu and impala.

To be able to test if the chosen herbivores avoid predators (hypothesis H_A), it was important that the chosen predators were species that might pose a threat to the chosen herbivores. Therefore, due to the size of the chosen herbivores, the predators chosen for this study were the five big predators in southern Africa; lions, leopards, hyaenas (spotted hyaena, brown hyaena), cheetahs, and wild dogs (Hayward & Slotow, 2009). These five predators have a large dietary overlap, with lions and hyaenas hunting the largest herbivores (Hayward & Slotow, 2009; Owen-Smith & Mills, 2008). While adult giraffes almost exclusively are killed by lions, the calves can be hunted and killed by the other four as well (Owen-Smith & Mills, 2008). Kudu are a favoured prey by lions, and hyaenas also tend to select them as prey. Impala are more favoured as prey by the smaller predators, such as leopards, cheetahs, and wild dogs, due to their size, but there is often such an abundance of them that they make up a substantial part of the diets of lions and hyaenas as well (Owen-Smith & Mills, 2008).

Of these large predators, only lions were captured on the camera traps more than a hundred times and were subsequently the only predator used in the study. However, during the statistical analyses, in addition to lions, predators were also looked at as a group, in which all five of the big predators were included.

Statistics

The collected data for this study was compiled in excel files and all statistics were made in the program R version 4.2.3 (R Core Team, 2023) using RStudio (Posit team, 2023). Logistic regression models were used to test the hypotheses, and see if the appearance of the species included in the study could be predicted by the appearance of elephants and/or predators within a short timespan before the species appearance.

To do this, the study period (24-06-2014 – 11-04-2017) was divided into hourlong intervals, with the first interval starting at 00:00:00 24-06-2014 and ending at 00:59:59 24-06-2014. This resulted in 24 552 intervals. Each interval was repeated 8 times, for the 8 different camera sites, resulting in 196 416 separate intervals.

For each camera site, the sightings of species within each interval were transformed into a binary of 1/0 (presence/absence), based on if the species were caught on the camera during that period ($p >= 0.8$). This was done for each of the following species: elephant, impala, kudu, giraffe, lion, all predators (included lion, leopard, hyaena, cheetah, or wild dog sightings), as well as different combinations of herbivores (giraffe/impala, kudu/giraffe, and impala/kudu) where presence would be noted if any of the two species were caught on camera. No matter the number of individuals captured on the camera traps during an interval it would be recorded as present (1), not taking multiple sightings at the same site within an interval into account. Presence of each species during the intervals is described in table 1.

Table 1. Species included in the study. “Total” shows the total number of sightings from the camera traps, “p >= 0.8” shows the number of sightings that had been identified with a p value of 0.8 or higher. “Interval sightings” shows in how many of the separate intervals each species appears. Predators include all the mentioned predators (lion, cheetah, leopard, wild painted dog, spotted and brown hyaena).

Species	Total	p >= 0.8	Interval sightings
Elephant	24 571	24 445	9 742
Impala	453	266	126
Kudu	1 167	654	393
Giraffe	1 187	1 159	482
Lion	211	179	126
Cheetah	1	0	0
Leopard	6	1	1
Wild painted dog	6	3	2
Hyaena spotted	15	8	6
Hyaena brown	21	6	6
Predators	260	197	141

Since the sightings of the different species varied both between hours of the days and months of the year (Appendix 3 and 4), these two factors were included as control factors in the logistic regression model. To account for the circular nature of time the values (0-23 for hours and 1-12 for months) had to be converted. Several different models were tried on the hour intervals to find the best fitting one: a half sinus-cycle with only positive values, placing midnight (interval 0) at the value 0 and noon (interval 12) at the value 1. The monthly patten was harder to interpret, since the months opposite of each other (i.e., December and June etc.) does not necessarily have opposite characteristics the same way noon and midnight have. Instead, the months (1-12) were converted both to a sinus curve and a cosines curve, and both scales were included in the model.

Weather data

To make sure the logistic regression model would not show false correlations between herbivore and elephant/predator appearances caused by weather conditions, the model included several weather conditions as control factors.

Weather data was collected during the study period by EfA staff members and compiled in an excel file. The file included daily rainfall data (in mm), minimum and maximum temperature both inside (of EfA camp buildings) and outside, and minimum and maximum relative humidity (RH). Due to different people recording the weather conditions over the years, some formatting was done to make it unison. Some of the rainfall data included a < or >, and these were treated as if the extra symbol was not there (i.e., if the rainfall was recorded as <2 mm it was treated as 2 mm). Based on the rainfall data, a daily rainfall amount was calculated showing the total amount of rain (in mm) during the previous 30 days. This was to account for any changes in the animals' use of the elephant highways based on if the river was their only source of water or not.

Due to outside influence (such as snakes by the weather station and monkeys destroying equipment) the outside temperature was not as regularly recorded as the inside temperature. Working under the assumption that the outside and inside temperatures are correlated, a mean difference between inside and outside maximum temperature was calculated, and in those cases an inside but not an outside temperature was recorded, the outside temperature was marked as the inside temperature with the mean difference added. The same was done for the minimum temperature.

The weather has not always been continuously recorded during the study period, resulting approximately 25% of missing data in each category. However, the missing data was not randomly distributed, but instead seemed to be clustered to certain time periods (for example during holidays when EfA staff were not in camp to record the weather) where all weather data was missing (Appendix 5).

Logistic regression model

Two different types of logistic regression models were used. The first one was a model for the herbivores (kudu, impala, and giraffe) to test hypotheses H_A and H_C. The presence of each of these species on the elephant highways at any of the camera sites and any given time interval was tested in separate models against the presence of elephants and predators at the same camera site.

Both the predators as a group (including all five predators) and lions were first tested in the models, but since they had a high correlation (shown by a variance inflation factor (VIF) > 10) due to the large number of lions and small number of the other predators, only one of them could be included in the final model. When testing the model with the lion-group and the predators-group separate, no noticeable change in result could be detected depending on which of the two groups were included. Therefore, the predators-group were chosen to be included in the model, since all the predators in the group could potentially be seen as a threat to the herbivores.

The model included the presence of elephants and predators both within the same time interval as the herbivore (this factor was named "Elephant/Predator") and within the previous time interval (named "Elephant prev/Predator prev"). This was because the presence or absence in any given time interval did not indicate when the animal was sighted within the interval. Therefore, a herbivore could be sighted early in the interval and an elephant or predator at the end of the interval. This would not answer the question if herbivores avoided or was drawn to elephants or predators, since said animals would have been at the highway after the herbivore. Testing instead against presence or absence the previous interval guarantees that the herbivore is at the elephant highway after the elephant or predator. On the other hand, if an elephant or predator appeared at the beginning of the previous interval and the herbivore at the end of the interval, it could go up to almost 2 hours between these sightings, which could be too long for any correlation. The presence or absence between the two intervals was not overly correlated (a pairwise correlation showed 0.31 for elephants and 0.04 for predators) so both were included in the model. The model was also run separately with only one of the two intervals (i.e., only the same time interval or only the previous time interval) included, to examine if this made any difference to the results, but no noticeable change was detected.

For each of the three herbivore species, the model also included the presence of the two other species (i.e., giraffe/impala were included in the kudu model, kudu/giraffe in the impala model, and impala/kudu in the giraffe model). For these groups both presence during the same and previous interval were tested, just as with the elephants and predators (correlation was 0.1 for giraffe/impala, 0.07 for kudu/giraffe, and 0.06 for impala/kudu).

To control for external factors that might influence herbivore sightings, the following control factors were also included in the model: outside maximum temperature, maximum RH (minimum outside temperature and RH excluded due to high correlation with other factors and VIF > 5), rainfall per day and for a previous 30-days period, camera site, as well as time of day (as half sinus cycle) and months (as both sinus and cosines curves) as previously explained. All variables were scaled, except camera site since it was categorical data.

The second type of logistic regression model was for the predators, to test the H_B hypothesis. For this, two models were used, one testing all predator species in the study as a group, and the other testing just lions. The predator's presence was tested against the elephant presence, both in the same and previous time interval. The same control factors as in the herbivore models were used. However, neither predator nor herbivore presence were included in these models.

Results

Herbivores

Giraffe

The presence of giraffes at elephant highways (Fig. 3) was positively affected by the presence of elephants, both during the same time interval (estimate 0.113, $p < 0.01$, n=62) and the previous time interval (0.109, $p < 0.01$, n=69). During the same time interval, giraffes appeared after elephants in ca 60% of the cases, and at 6 occasions a giraffe and an elephant was caught in the same picture. The predators had a negative effect on the giraffe presence but was not significant,

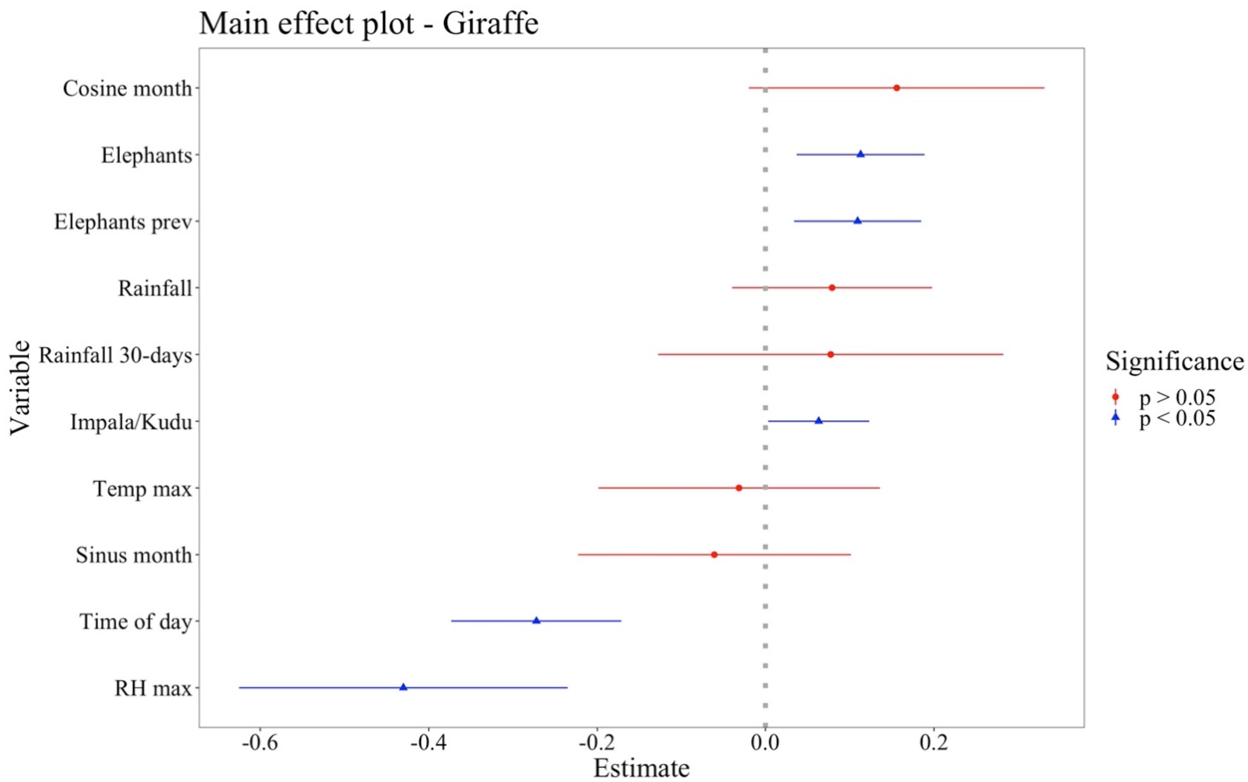

Figure 3. Variables with a significant ($p < 0.05$) effect on giraffe presence on the elephant highways as blue triangles. Non-significant variables as red circles. Error bars: +/- 2 standard errors. The variables "Predator", "Predator prev" and "Impala/Kudu prev" excluded from graph due to SE over 10.

however a giraffe was never caught on the camera traps if a predator had been sighted the same or previous time interval. The presence of the other herbivores (impala/kudu) had a positive effect during the same time interval (0.063, $p < 0.05$, n=3) but was not significant during the previous time interval. Of the factors that significantly affected the presence of giraffes, maximum RH (-0.430, $p < 0.001$) had the strongest effect. Camera site effect shown in appendix 6.

Kudu

The presence of kudu at elephant highways (Fig. 4) was positively affected by the presence of elephants, but not significantly (during the same time interval the estimate was 0.053, $p = 0.281$, n=42; the previous time interval, 0.011, $p = 0.830$, n=37). During the same time interval, kudu appeared after elephants in ca 43% of the cases. The predators had a positive effect on the kudu presence during the same time interval (0.059, $p < 0.05$, n=1), but a negative and non-significant effect during the previous time interval. However, a kudu was only sighted once within the same time interval as a predator, 9 minutes after a lion and heading in the opposite direction. Kudu was never sighted if a predator was sighted in the previous time interval. The presence of the other herbivores (giraffe/impala) had a positive effect both during the same time interval (0.092, $p < 0.001$, n=8) and the previous time interval (0.079, $p < 0.05$, n=7). Of the factors that significantly affected the presence of kudu, time of day (1.044, $p < 0.001$) had the strongest effect. Camera site effect shown in appendix 6.

Impala

The presence of impala at elephant highways (Fig. 5) was positively affected by the presence of elephants during the same time interval (estimate 0.100, $p = 0.266$, n=12) and negatively affected

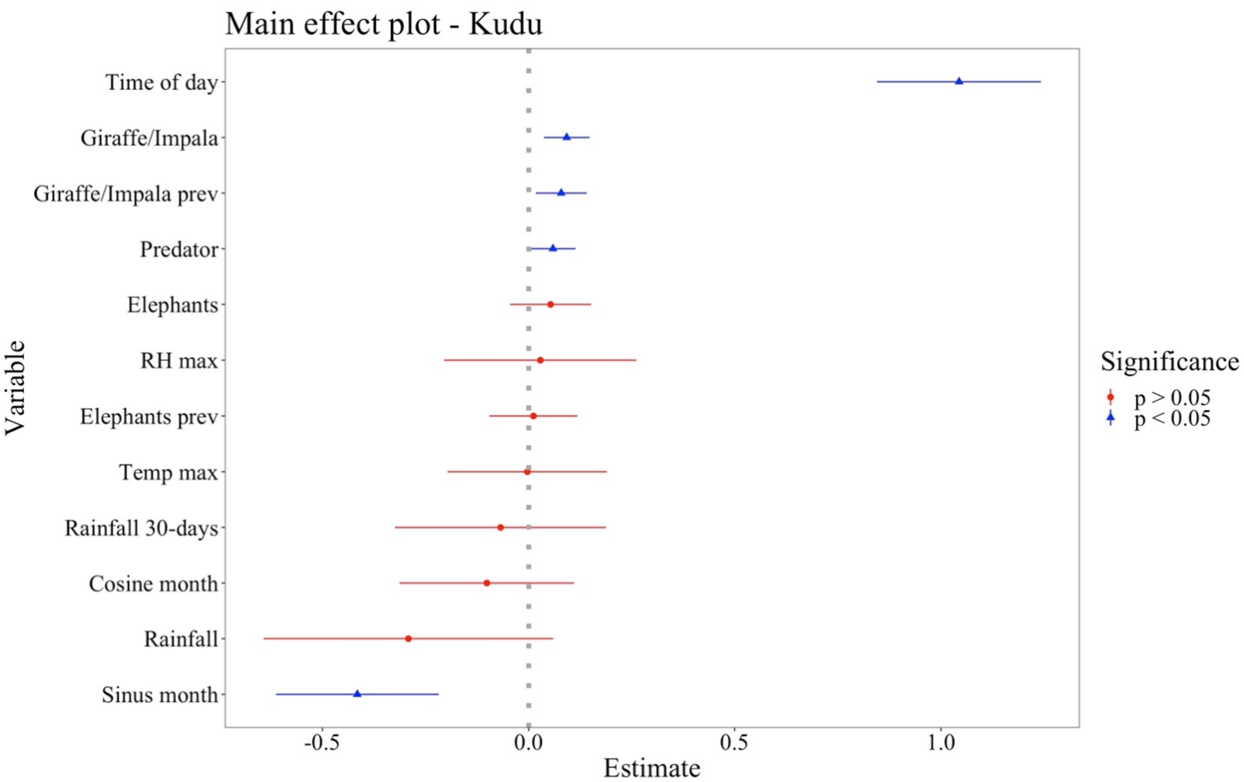

Figure 4. Variables with a significant ($p < 0.05$) effect on kudu presence on the elephant highways as blue triangles. Non-significant variables as red circles. Error bars: +/- 2 standard errors. The variable “Predator prev” excluded from graph due to SE over 5.

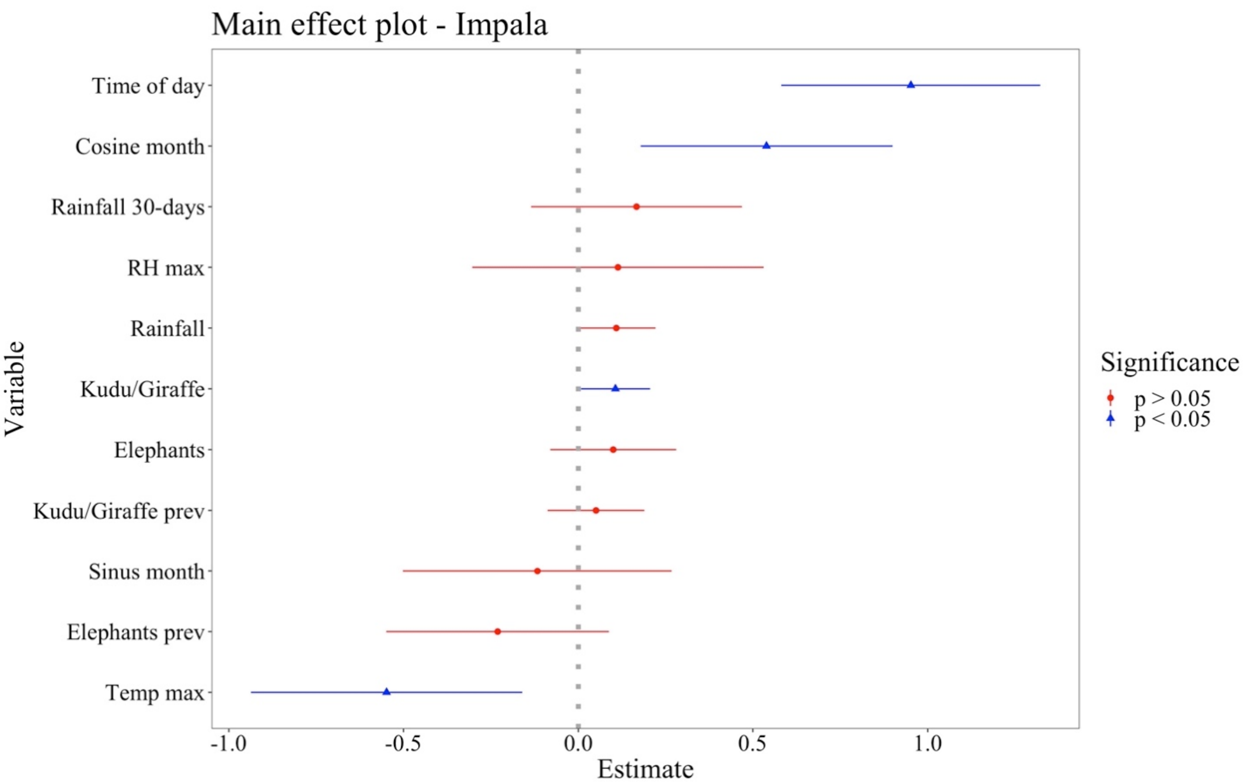

Figure 5. Variables with a significant ($p < 0.05$) effect on impala presence on the elephant highways as blue triangles. Non-significant variables as red circles. Error bars: +/- 2 standard errors. The variables "Predator" and “Predator prev” excluded from graph due to SE over 10.

by elephant presence during the previous time interval (-0.231, p = 0.148, n=11), although both are non-significant. During the same time interval, impala appeared after elephants in ca 67% of the cases, and at 3 occasions an impala and an elephant was caught in the same picture. The predators had a negative effect on the impala presence, but this was not significant, although an impala was never sighted if a predator had been sighted the same or previous time interval. The presence of the other herbivores (kudu/giraffe) had a positive effect both during the same time interval (0.106, p < 0.05, n=5) and the previous time interval (0.050, p = 0.466, n=3), although non-significant in the later. Of the factors that significantly affected the presence of impala, time of day (0.952, p < 0.001) had the strongest effect. Camera site (Appendix 6) was non-significant.

Predators

The presence of predators as a group at elephant highways (Fig. 6) was positively but non-significantly affected by the presence of elephants both during the same time interval (estimate 0.050, p = 0.471, n=19) and the previous time interval (0.072, p = 0.275, n=32). Of the sightings in the same time interval as elephants, ca 53% of them occurred before the elephant sighting and 47% after. Of the factors that affected the presence of predators significantly, time of day (-0.659, p < 0.001) had the strongest effect. Camera site effect shown in appendix 6.

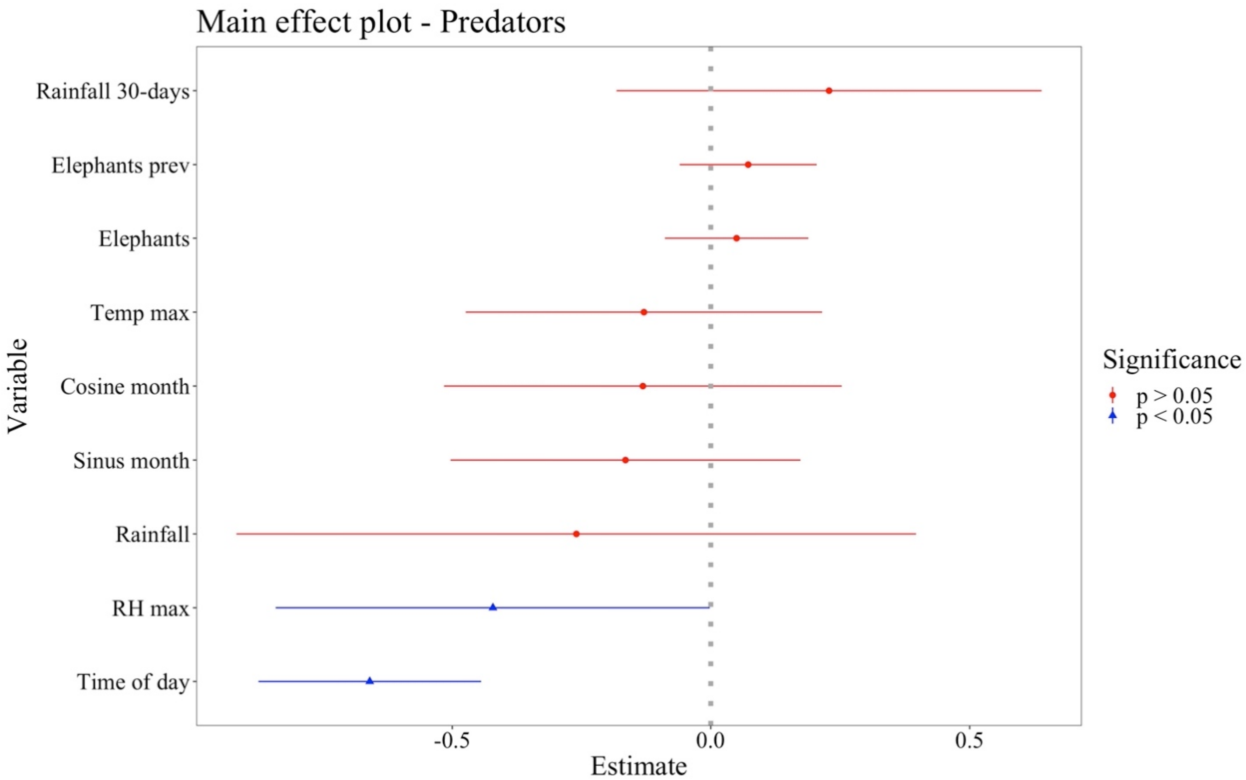

Figure 6. Tested variables effect on predator presence on elephant highways, significant (p < 0.05) as blue triangles and non-significant as red circles. Error bars: +/- 2 standard errors.

Lion

The presence of lions at elephant highways (Fig. 7) was positively but non-significantly affected by the presence of elephants both during the same time interval (estimate 0.011, p = 0.883, n=17) and the previous time interval (0.093, p = 0.160, n=32). All the sightings in the same time interval as elephants occurred between 18:00 and 02:00. Of the factors that affected the presence of predators significantly, time of day (-0.709, $p < 0.001$) had the strongest effect. Camera site effect shown in appendix 6.

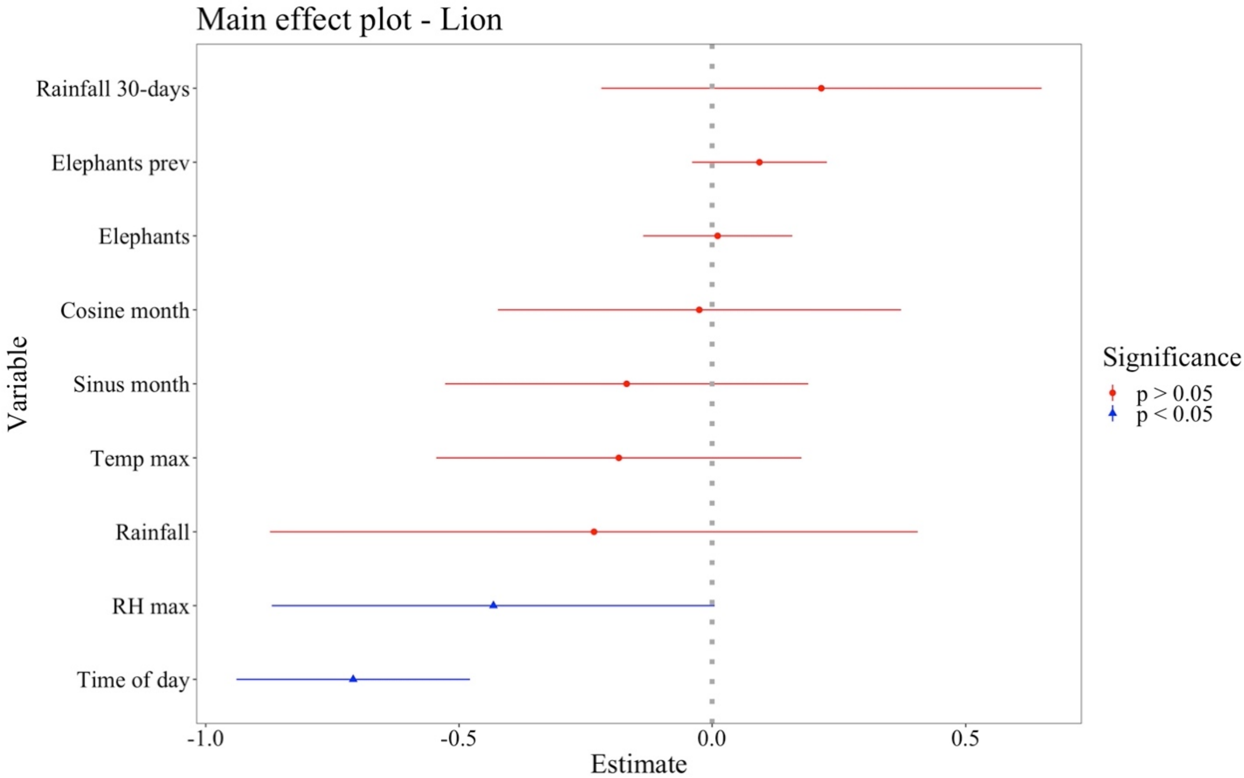

Figure 7. Tested variables effect on lion presence on elephant highways, significant ($p < 0.05$) as blue triangles and non-significant as red circles. Error bars: +/- 2 standard errors

Discussion

The H_A hypothesis about herbivores avoiding predators could not be supported by the logistic regression model, however there are still evidence supporting this hypothesis. No herbivores (except the elephants) where caught on the camera traps when a predator had been caught on camera in the same or previous time interval. The only exception of this was kudu, where on one occasion a kudu was sighted during the same time interval as a lion. However, although this single occasion was enough to make the effect significant (due to the relatively low number of sightings of both animals, the expected random effect would be 0.3 sightings of kudu in the same interval as predators, making 1 sighting significant) it is still only one single occasion and is not enough to draw any real conclusions from. Additionally, during this single occasion, although the kudu appeared after the lion, it was heading in the opposite direction from the lion, further proving the sentiment that this is not a sign of kudu being drawn to lions.

The fact that no herbivores were sighted in the same or following interval as predators could of course be an effect of the herbivores and predators normally being active at different times of the day (Appendix 3)(Hayward & Slotow, 2009; Tambling et al., 2015) and not strictly an effect of herbivores avoiding predators. However, their different activity times might be an evolutionary effect of herbivores avoiding predators in itself (Kronfeld-Schor & Dayan, 2003; Tambling et al., 2015), so these facts are not directly contrary.

The H_B hypothesis about predators avoiding elephants has not been supported in this study. There were tendencies of a positive correlation between the two, especially with lion and elephants in the previous time interval, although this correlation was non-significant ($p = 0.160$).

The hypothesis was based on the idea that since elephants are known to chase away predators, especially lions (Ferry et al., 2016; Londolozi Game Reserve, 2014; Power & Shem Compion, 2009; Shannon et al., 2022), the predators would want to avoid them. However, as the results show, this assumption might not be correct. First of all, it is mostly young elephants that are threatened by lions (Power & Shem Compion, 2009; Shannon et al., 2022; Tambling et al., 2015), and breeding herds of elephants tend to be more aggressive and protective than male groups, which are the predominant sex utilising the MPNP (Evans, 2019). It could be the case that the male elephants in MPNP do not see lions as a threat and therefor do not chase them, leading to the lions having no reason to avoid the elephants. On the other hand, while elephant calves are more vulnerable to predators than adult elephants (Power & Shem Compion, 2009; Shannon et al., 2022; Tambling et al., 2015), the most vulnerable group is young male elephants that travel alone or have recently left their mothers (Power & Shem Compion, 2009), since they no longer have the protection of the herd. This cohort are frequently sighted in the MPNP (Evans, 2019), which should make this park an ideal place for lions hunting elephants and a reason for the elephants in MPNP to be extra cautious of lions. However, lions only seem to successfully hunt elephants when they are in large prides (Power & Shem Compion, 2009; Shannon et al., 2022), and no large lion prides have been observed in the MPNP (Elephants for Africa, personal communication). This again, could be a reason for the elephants to not perceive the lions here as a threat and not bother chasing them.

The lions might also perceive the chance of getting prey close to the elephants as worth the risk of potentially getting chased by the elephants. If prey is indeed attracted to the elephants, it might be a good strategy by the predators to follow the elephants and therefore find the prey as well. It might also be the case that the movement of elephants, especially when they are in a large group, stir up animals that move out of the way of the elephants, making them easier to detect for the predators. The prey animals might also be distracted by the elephants, making them less vigilant, and therefore easier to catch for the predators.

There might also be other factors that affect the results. After a closer examination of the occasions a predator had been sighted within the same time interval as an elephant, it turned out that about half of the times the predator appeared before the elephant, not after. This could mean that the effect of the elephant presence shown by the results is a spurious correlation and that some other factor is causing this effect. One possible reason is time of day. The predators that appeared in the same interval as elephants (lions and hyaenas) are both nocturnal (Hayward & Slotow, 2009) and all observations happened while the sun was down. Although time of day was included in the model to avoid this kind of false correlation, it was represented as a half sinus curve which might not be the best fit for when these species are active. Elephants for example were captured on the camera traps quite frequently during the evening and until midnight, and these times also had frequent lion activity (Appendix 3). This similarity in capture rate during the same times of the day might be what is responsible for the slight increase of predator sightings in the same and following time interval as elephants in the model.

Another possible affect is the season, since all the observations of the predators and elephants within the same time interval happened during the dry season, between the months of March and September, when the Boteti River is the most important source of water in the western MPNP. Both elephants and lions had a peek in sightings during July-September (Appendix 4) which might be an explanation for their co-occurrence during these months.

The H_C hypothesis about herbivores being attracted to elephants have been partly supported. In the case of the giraffes, they show a clear tendency to be captured on the camera traps after elephants. The giraffes showed up after elephants in 60% of the cases, which strengthen the finding that giraffes are more likely to be at the elephant highways after elephants. Amongst impala and kudu however, no change in their presence on the elephant highways could be detected based on the presence or absence of elephants.

A change in effect of elephant presence on the different species of herbivores would have been expected due to their respective attractiveness as prey to predators. Giraffe and kudu are both preferred prey by lions, while impala, although occasionally hunted by lions, are more preferred by the smaller predators such as cheetah, wild dogs, and leopards (Hayward & Slotow, 2009; Owen-Smith & Mills, 2008; Power & Shem Compion, 2009). These smaller predators are never a threat to elephants (Owen-Smith & Mills, 2008; Tambling et al., 2015) and the elephants therefore might not bother to react at all, much less charge or warn, when they are near, as they might do with lions. This would mean that species who are mainly hunted by lions would be safer around elephants, or at least they might benefit from the elephants as extra individuals that can be vigilant and warn about approaching lions. However, species whose main predator is something smaller than a lion would not gain the same benefits from being around elephants and would therefore have no cause to change their activity pattern to stay close to elephants. Based on this, it would be expected that giraffe and kudu stay near elephants, while impala are not affected. While the results do show an increase of giraffes after elephant presence, both kudu and impala remain mainly unaffected.

Previous studies have shown that both impala and kudu are drawn to areas with elephants since they benefit from the new nutritious shoots that appear after elephants have browsed the trees (Ferry, 2018; Makhabu et al., 2006). If this was the main reason the herbivores stayed close to the elephants in this study, it would be expected that the effect would be strongest amongst impala and kudu, but weaker in giraffes. Since it is instead giraffes that show the strongest effect of elephants, this explanation is unlikely. The fact that the effect of elephant presence could be seen in giraffe but not in kudu or impala is more in line with the idea that staying close to the elephants might be a predation avoidance behaviour, although that is still not a well-supported idea. It would be advisable to look at if the effect of elephant presence to herbivores change in areas with and without large predators, and with the prey preference of the predators in the area. If this is an effect of a predation avoidance amongst the herbivores, it would be expected that the effect is small or non-existence in an area that has not have predators for a long time, and that the effect would be larger after predators were introduced, or in a similar area that has had predators for a long time. It would also be expected that the prey most preferred by lions in the area would be most affected by the elephant presence. However, this will only be true if the predation avoidance strategy is learnt and not genetic.

Although the effect of elephant presence was not significant in kudu and impala, the effect of the other herbivores presence (giraffe/impala for kudu, kudu/giraffe for impala, and impala/kudu for giraffe) were significant in most of the cases. This could imply that while the herbivores do not stay near elephants, they do stay near other herbivores, which could be a sign of the predation avoidance method grouping.

The different size of the herbivore species can also be an explanation as to why they are captured on the camera traps in the quantity that this study showed. In the MPNP, of the three herbivore species examined in this study, impala are the most numerous, followed by kudu and lastly giraffe

(Elephants for Africa, unpublished data). However, when looking at the numbers caught on the camera traps (Table 1), the exact opposite is true, with giraffes caught most often, followed by kudu and lastly impala. This can be a cause of their respective sizes. The larger animals, such as giraffes, would have a harder time moving around in the thicker under-vegetation and would benefit from following the vegetation free elephant highways. Impala, however, are much smaller and would have an easier time moving through the under-vegetation, thus not needing to follow the elephant highways as often or much as the larger animals. Kudu, being larger than impala and smaller than giraffes, would benefit from following the highways, but could also move through the under-vegetation when it is not too thick, thus being captured on the camera traps more than impala and less than giraffe, which is what happened.

The camera traps were also set up for elephants, which makes them more likely to be triggered by larger animals and increase the risk that smaller herbivores, such as impala and to some extent kudu, are not caught on the camera traps when they pass by. This could be an explanation of the results, where significant effect of elephant presence was only found in giraffes, which was the species most often caught on the camera traps of the three herbivores. It is possible that the significant effect is due to the larger sample size and that if more kudu and impala were caught on the camera traps, they too would show effect of elephant presence. To further investigate this, it would be advisable to set up cameras at different heights, to better catch the smaller species on camera and get a more real representation of the species utilizing the elephant highways.

It could also be worth reworking the logistic regression model. Firstly, fitting the 24-hour cycle to a half-sinus curve was the model that was deemed best in this study, but other ways to measure time of day, such as amount of light, should be examined. If more detailed weather data could be obtained, such as hourly temperature and relative humidity, it would be good to include it in the model instead of the daily measurements that were used in this study. Rainfall was used in the model to control for the animals' access to water, since they are more dependent on the Boteti River when the area is dry and water are hard to find elsewhere, thus making the elephant highways to the river more used. Other ways to control for the dry season could be used, such as including Normalized Difference Vegetation Index (NDVI) of the area.

Lastly, the model could be reworked to not include hour-long intervals. In almost 50% of the occasions where elephants have been caught on the camera traps in the same interval as a herbivore or predator, the elephant appeared after the herbivore or predator. This makes any affect during the time interval unsure, since it does not exclusively reflect the effect of elephant presence, which was the focus of this study. Instead, it would be desirable to investigate each occurrence where a herbivore or predator is caught on the camera traps and then observe the previous hour for elephant occurrences. This way the results would be clearer since the model would only include herbivores or predators that appear after the elephants. A model like this could also investigate the effect of elephant presence over time.

An alternative is to investigate shorter time periods than an hour, maybe as short as 10-15 minutes. Although this would not guarantee that the elephant appeared first in the interval, it would account for the occurrence of herbivores traveling with an elephant herd. This was observed multiple times in the study: on nine occasions a herbivore and an elephant appeared together in the same camera trap picture and multiple times a herbivore appeared both following and being followed by elephants within a few minutes of its appearance.

In conclusion, the presence of elephants in the MPNP affects the animals around them, especially the larger herbivores such as giraffes, although exactly how and why remains unclear. Further studies with an improved method need to be done to better investigate the effect of elephant presence on the smaller herbivores as well as the predators.

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References

Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual review of ecology and systematics, 5*(1), 325-383. doi:10.1146/annurev.es.05.110174.001545

Allen, C. R., Brent, L. J., Motsentwa, T., & Croft, D. P. (2021). Field evidence supporting monitoring of chemical information on pathways by male African elephants. *Animal Behaviour, 176*, 193-206.

Allen, C. R., Brent, L. J., Motsentwa, T., Weiss, M. N., & Croft, D. P. (2020). Importance of old bulls: leaders and followers in collective movements of all-male groups in African savannah elephants (Loxodonta africana). *Scientific reports, 10*(1), 13996.

Bennitt, E. (2016). *About Elephants for Africa - Study area*. Retrieved 18-04-2023 from https://www.elephantsforafrica.org/about-elephants-for-africa/study-sites/

Bennitt, E., Bradley, J., Bartlam-Brooks, H. L. A., Hubel, T. Y., & Wilson, A. M. (2022). Effects of artificial water provision on migratory blue wildebeest and zebra in the Makgadikgadi Pans ecosystem, Botswana. *Biological conservation, 268*, 109502. doi:10.1016/j.biocon.2022.109502

Claessen, D., Van Oss, C., de Roos, A. M., & Persson, L. (2002). The Impact of Size-Dependent Predation on Population Dynamics and Individual Life History. *Ecology (Durham), 83*(6), 1660-1675. doi:10.1890/0012-9658(2002)083[1660:TIOSDP]2.0.CO 2

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2013). Seasonal Diet and Prey Preference of the African Lion in a Waterhole-Driven Semi-Arid Savanna. *PloS one, 8*(2), e55182-e55182. doi:10.1371/journal.pone.0055182

Davies, A. B., Tambling, C. J., Kerley, G. I., & Asner, G. P. (2016). Limited spatial response to direct predation risk by African herbivores following predator reintroduction. *Ecology and Evolution, 6*(16), 5728-5748.

De Boer, W. F., Vis, M. J., De Knegt, H. J., Rowles, C., Kohi, E. M., Van Langevelde, F., . . . Slotow, R. (2010). Spatial distribution of lion kills determined by the water dependency of prey species. *Journal of Mammalogy, 91*(5), 1280-1286.

DeLong, J. P., & Luhring, T. M. (2018). Size-dependent predation and correlated life history traits alter eco-evolutionary dynamics and selection for faster individual growth. *Population ecology, 60*(1-2), 9-20. doi:10.1007/s10144-018-0608-7

Elephants for Africa. (2016a). *About Elephants for Africa - Study area*. Retrieved 27-05-2023 from https://www.elephantsforafrica.org/about-elephants-for-africa/study-sites/

Elephants for Africa. (2016b). *Coexistence*. Retrieved 30-04-2023 from https://www.elephantsforafrica.org/conservation/

Elephants for Africa. (2016c). *Research*. Retrieved 30-04-2023 from https://www.elephantsforafrica.org/research/about-our-research/

Evans, K. (2019). Elephants for Africa: male Savannah elephant Loxodonta africana sociality, the Makgadikgadi and resource competition. *International Zoo Yearbook, 53*(1), 200-207.

Ferry, N. (2018). *Processes involved in the functioning of large mammal communities: the role of the African elephant in the ecology of predator-prey relationships* [PhD thesis]. Université de Lyon.

Ferry, N., Dray, S., Fritz, H., & Valeix, M. (2016). Interspecific interference competition at the resource patch scale: do large herbivores spatially avoid elephants while accessing water? *Journal of Animal Ecology, 85*(6), 1574-1585.

Hayward, M. W., & Slotow, R. (2009). Temporal partitioning of activity in large African carnivores : tests of multiple hypotheses : research article. *South African Journal of Wildlife Research - 24-month delayed open access, 39*(2), 109-125. doi:doi:10.10520/EJC117325

Ito, T., Pilat, M. L., Suzuki, R., & Arita, T. (2013). ALife approach for body-behavior predator–prey coevolution: body first or behavior first? *Artificial life and robotics, 18*(1-2), 36-40. doi:10.1007/s10015-013-0096-y

IUCN. (2023). *The IUCN Red List of Threatened Species*. Retrieved 30-04-2023 from https://www.iucnredlist.org

Jones, L. E., & Ellner, S. P. (2007). Effects of rapid prey evolution on predator-prey cycles. *Journal of mathematical biology, 55*(4), 541-573. doi:10.1007/s00285-007-0094-6

Kluever, B. M., Howery, L. D., Breck, S. W., & Bergman, D. L. (2009). Predator and heterospecific stimuli alter behaviour in cattle. *Behavioural Processes, 81*(1), 85-91.

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of Time as an Ecological Resource. *Annu. Rev. Ecol. Evol. Syst, 34*, 153-181. doi:10.1146/annurev.ecolsys.34.011802.132435

Londolozi Game Reserve (Writer). (2014). Elephants Chase Lion Pride - Londolozi TV [Video file]. In.

Lundvall, D., Svanbäck, R., Persson, L., & Byström, P. (1999). Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian journal of fisheries and aquatic sciences, 56*(7), 1285-1292. doi:10.1139/f99-058

Makhabu, S. W., Skarpe, C., & Hytteborn, H. (2006). Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta oecologica (Montrouge), 30*(2), 136-146. doi:10.1016/j.actao.2006.02.005

Mandelik, Y., Jones, M., & Dayan, T. (2003). Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk. *Evolutionary Ecology Research, 5*(4), 501-515.

Owen-Smith, N., & Mills, M. G. (2008). Predator–prey size relationships in an African large-mammal food web. *Journal of Animal Ecology, 77*(1), 173-183.

Périquet, S., Valeix, M., Loveridge, A. J., Madzikanda, H., Macdonald, D. W., & Fritz, H. (2010). Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour, 79*(3), 665-671.

Posit team. (2023). RStudio: Integrated Development Environment for R. Boston, MA: Posit Software, PBC. Retrieved from http://www.posit.co/

Power, R. J., & Shem Compion, R. X. (2009). Lion Predation on Elephants in the Savuti, Chobe National Park, Botswana. *African zoology, 44*(1), 36-44. doi:10.3377/004.044.0104

Presotto, A., Fayrer-Hosken, R., Curry, C., & Madden, M. (2019). Spatial mapping shows that some African elephants use cognitive maps to navigate the core but not the periphery of their home ranges. *Animal Cognition, 22*, 251-263.

R Core Team. (2023). R: A Language and Environment for Statistical Computing (Version 4.2.3 (2023-03-15)). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Scheel, D. (1993). Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Animal Behaviour, 46*(4), 695-704.

Schmitt, M. H., Stears, K., & Shrader, A. M. (2016). Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behavioral ecology, 27*(4), 1073-1077. doi:10.1093/beheco/arw015

Schmitt, M. H., Stears, K., Wilmers, C. C., & Shrader, A. M. (2014). Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. *Animal Behaviour, 96*, 151-158.

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science, 185*(4145), 27-39.

Shannon, G., Cordes, L. S., Slotow, R., Moss, C., & McComb, K. (2022). Social Disruption Impairs Predatory Threat Assessment in African Elephants. *Animals (Basel), 12*(4), 495. doi:10.3390/ani12040495

SnapshotSafaris. *Snapshots Elephants for Africa*. from https://www.zooniverse.org/projects/shuebner729/snapshot-elephants-for-africa

Tambling, C. J., Minnie, L., Adendorff, J., & Kerley, G. I. H. (2013). Elephants facilitate impact of large predators on small ungulate prey species. *Basic and Applied Ecology, 14*(8), 694-701. doi:https://doi.org/10.1016/j.baae.2013.09.010

Tambling, C. J., Minnie, L., Meyer, J., Freeman, E. W., Santymire, R. M., Adendorff, J., & Kerley, G. I. H. (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology, 69*(7), 1153-1161. doi:10.1007/s00265-015-1929-6

Tien, R. J., & Ellner, S. P. (2012). Variable cost of prey defense and coevolution in predator-prey systems. *Ecological monographs, 82*(4), 491-504. doi:10.1890/11-2168.1

Tsai, C. H., Hsieh, C. h., Nakazawa, T., & Lusseau, D. (2016). Predator—prey mass ratio revisited: does preference of relative prey body size depend on individual predator size? *Functional ecology, 30*(12), 1979-1987. doi:10.1111/1365-2435.12680

van Der Meer, E., Pays, O., & Fritz, H. (2012). The Effect of Simulated A frican Wild Dog Presence on Anti-predator Behaviour of Kudu and Impala. *Ethology, 118*(10), 1018-1027.

Von Gerhardt, K., Van Niekerk, A., Kidd, M., Samways, M., & Hanks, J. (2014). The role of elephant Loxodonta africana pathways as a spatial variable in crop-raiding location. *Oryx, 48*(3), 436-444.

Appendix 1 Popular science summary

Elephants as bodyguards?

Have you ever seen a video of an elephant chasing away a lion? It's not an uncommon thing and there are lots of videos of it circulating on the internet. And sometimes when they charge against a lion, they even save another prey animal from the lion in the process. So, could it be the case that other animals hang out close to the elephants to use them as a sort of bodyguard against the predators? Well, that's what I wanted to figure out in this study.

The African savanna elephant (*Loxondonta africana*) is a huge animal, so it comes as no surprise that it affects everything around it, from vegetation to other animals and humans. Elephants often travel on permanent paths, used by generations of elephants, called elephant highways. These highways are free from most vegetation and often lead to places of resource, such as water or food. This makes them excellent travel paths not only for elephants, but many other African animals as well. And if a lot of different animals travel there, well, that makes them a great place to study how elephants interact with and affect other animals.

To find out if other animals use the elephants to avoid predators, I first needed to figure out if predators avoided the elephants. If an animal as huge as the elephant had the habit of charging against me, I would certainly try my best to avoid it, but do the predators? And if they do, that leads to the second part of my question: Do prey animals stay close to the elephants to avoid the predators? In order to answer these questions, I looked at four years of camera trap footage from the elephant highways in a national park in Botswana and if elephants' presence there makes other animals more or less likely to also be there. I looked at giraffes and two kinds of antelopes (kudu and impala) for the prey species, and mostly lions for the predators. Right from the start, it was obvious that elephants definitely influenced these animals. But the question was how?

Well for giraffes, this was easy to answer. If there was an elephant, they were more likely to be there as well. Kudu was not as clear, but they too seemed to prefer to hang out near the elephants. Impala were a bit trickier, my results were inconclusive, and I couldn't really find out if they liked to hang out with elephants or not. This could be because they were the smallest of the animals I looked at and could travel through the bushes much easier than kudu or giraffes, so they didn't travel on the highways and therefore wasn't caught on the cameras as much.

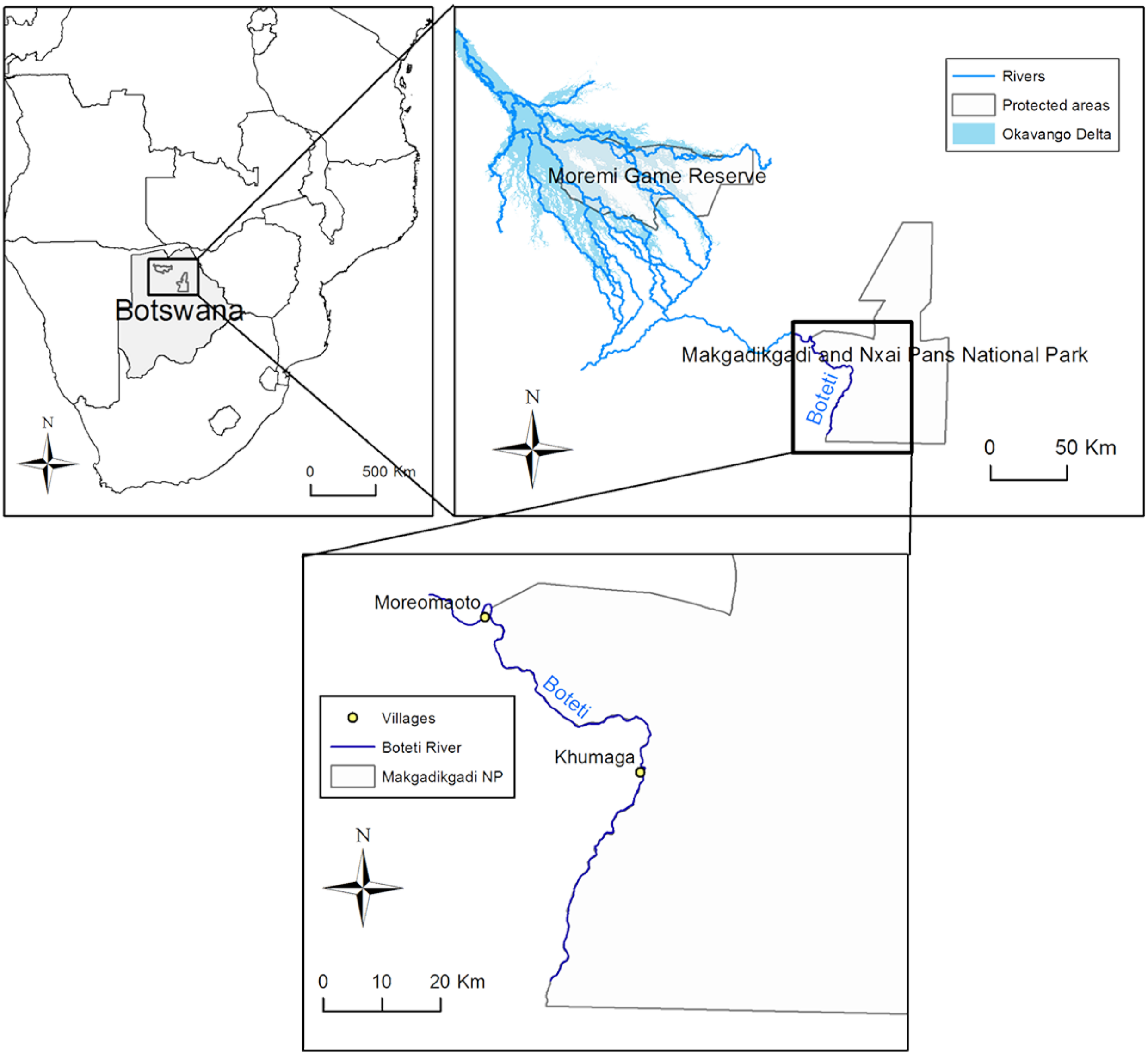
The big surprise was the predators. When I looked at the footage of lions, as well as other predators such as hyenas, leopards, and wild dogs, they also seemed to show up more frequently after an elephant had passed by. Maybe they knew that the prey animals would be close to the elephants and thought the risk of getting chased was worth the chance of getting a meal? Or maybe something different lays behind this?

But why is this important? Well, understanding how animals affect each other can be of great help in many cases, such as when it comes to conservation of endangered species. For example, the elephants are an endangered species and that are rapidly declining in numbers. If they disappear from an area, and for example giraffes have benefited from the elephants by using their highways and staying close to them to avoid predators, will the giraffes also be threatened and start to decline when the elephants disappear?

In the end, I might not have gotten a clear answer to if prey animals use elephants to avoid predators, but I did find out that the presence of elephants influence the presence and behaviours of both prey and predators. Everything in nature is pieces of the large complex puzzle that is our planet, and although we might never fully know how everything is connected, each small part is a step towards knowing how our world works.

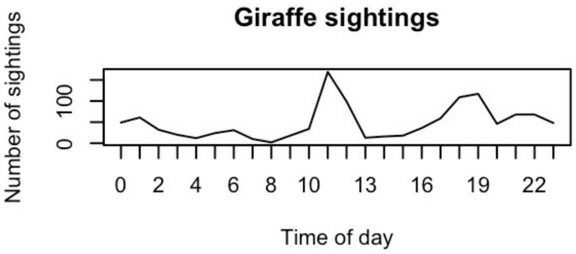
Appendix 2 Study Area

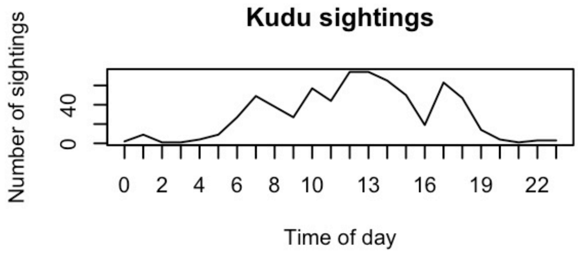
A map of the study area, Makgadikgadi Pans National Park (MPNP) in Botswana. Map is from the Elephants for Africa website (Bennitt, 2016).

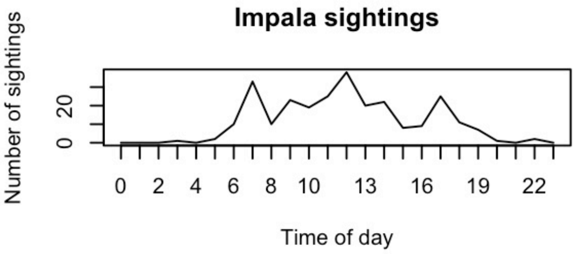


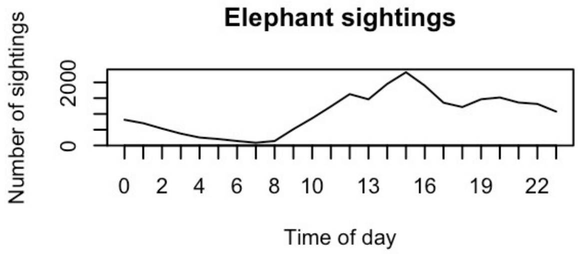
Appendix 3 Hourly sightings

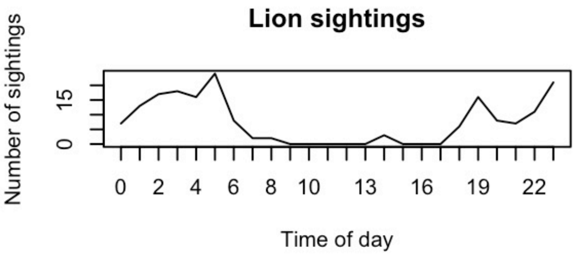
Graphs showing the total number of sightings (p>=0.8), of each of the studied species, per each hour of the day.





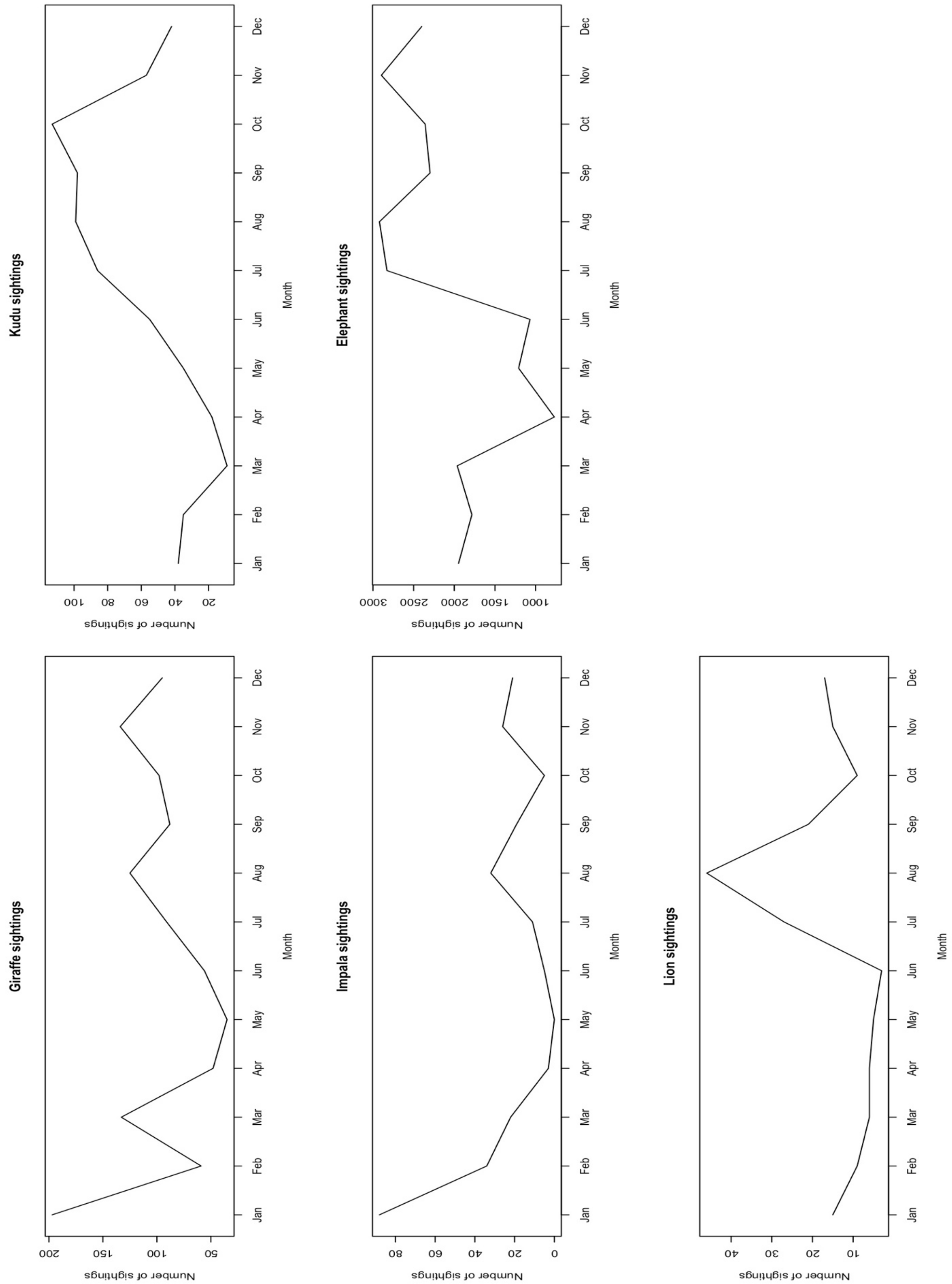






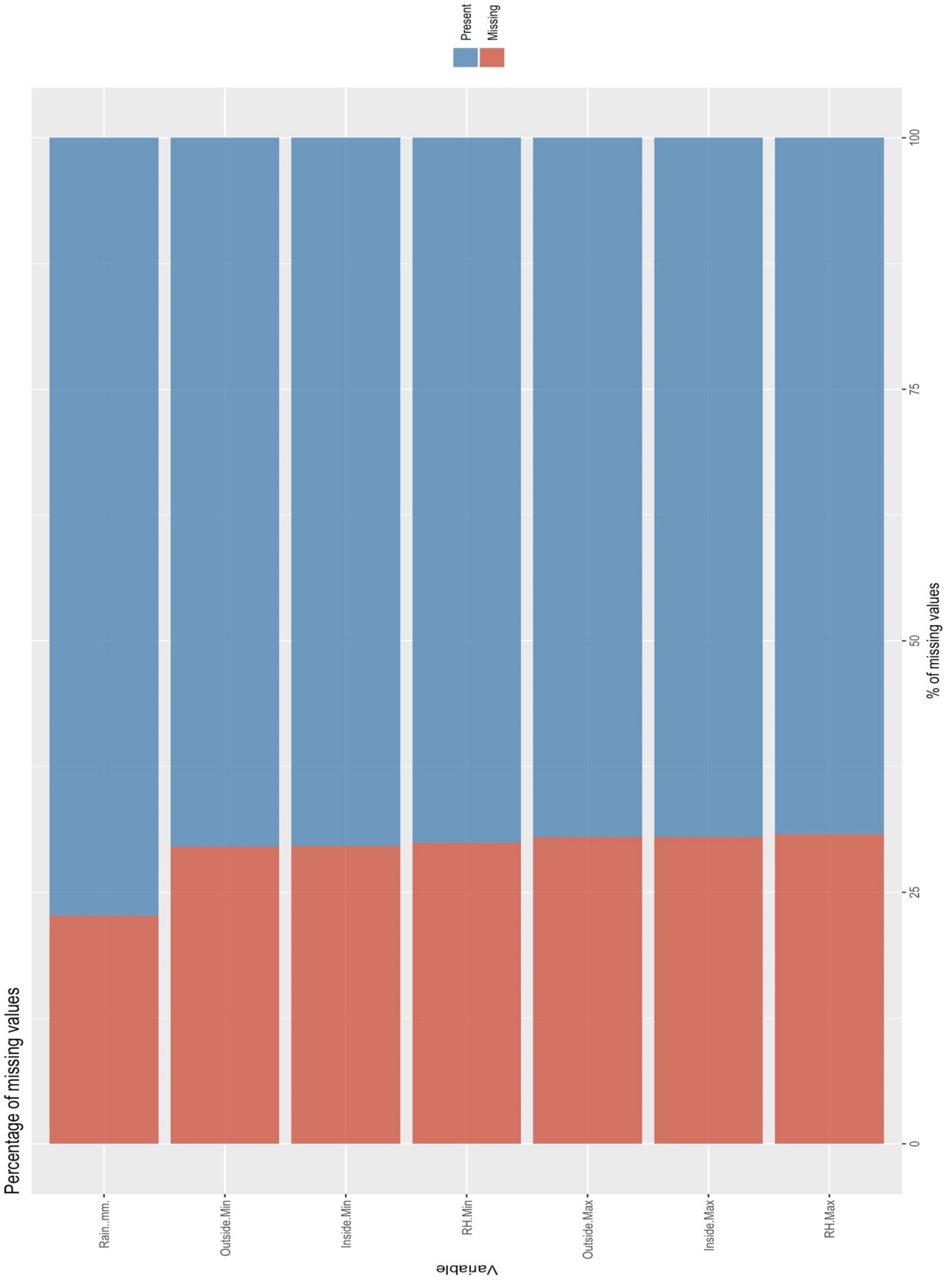
Appendix 4 Monthly sightings

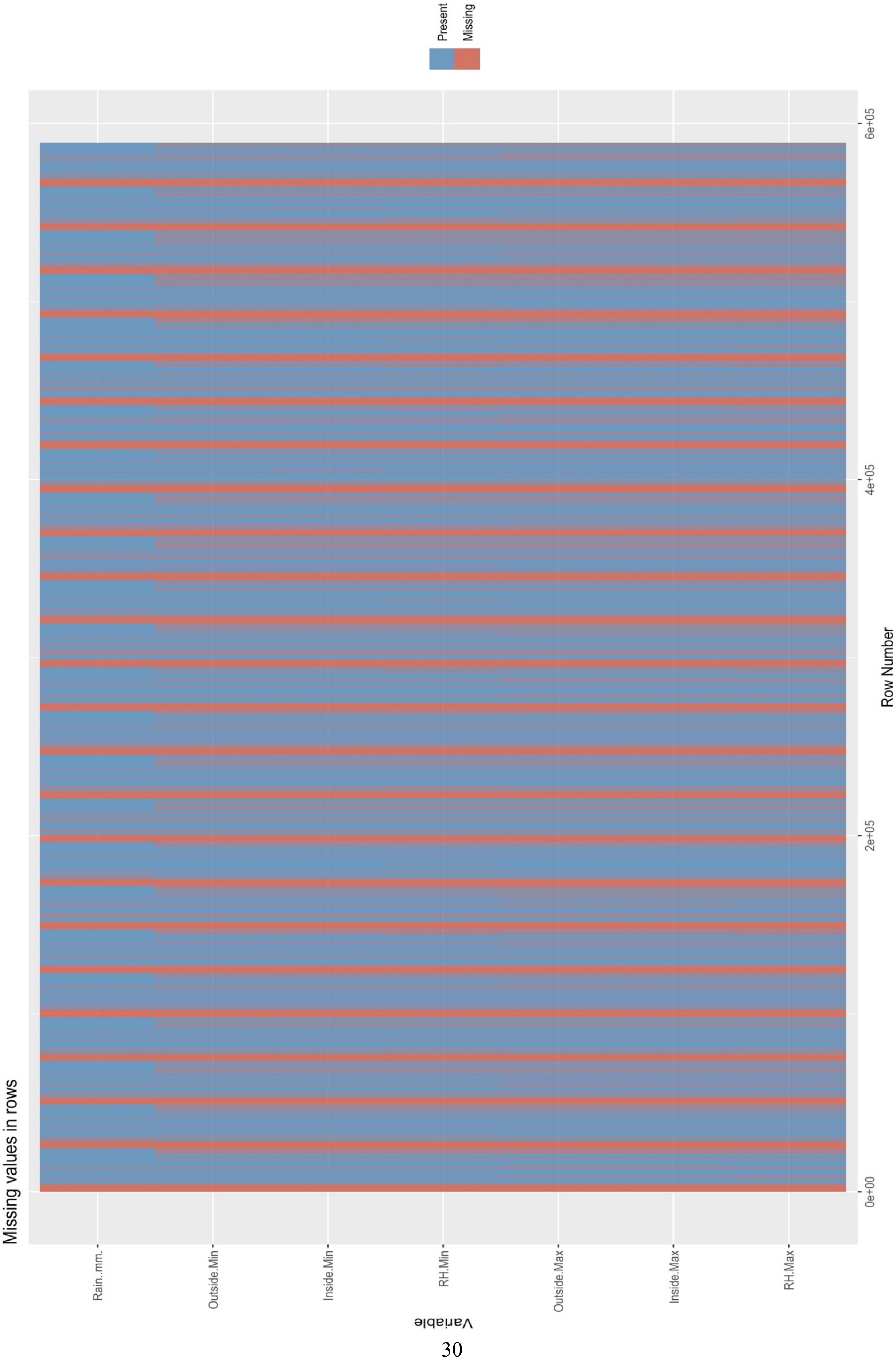
Graphs showing the total number of sightings (p>=0.8), of each of the studied species, per each month of the year. The number of sightings for all species is lower in April-June due to fewer of those months being included in the study period.



Appendix 5 Missing values

Graphs showing missing weather data during the study period as percentage of missing data and missing data per time interval.





Missing values in rows
Present
Missing
Rain..mm.
Outside.Min
Inside.Min
RH.Min
Outside.Max
Inside.Max
RH.Max
Variable
0e+00
2e+05
4e+05
6e+05
Row Number

Appendix 6 Effect of camera site

The effect of the different camera sites (EFA02-EFA09, in the figure referred to as Camera 2-Camera 9) on giraffe, kudu, impala, lion and predators from the logistic regression model. For each camera site estimate from the model, standard error (SE) and p-value is included.

Species	Variable	Estimate	SE	p
Giraffe	Camera 2	-6,926	0,725	1,23 E-21
	Camera 3	-7,269	0,739	8,17 E-23
	Camera 4	-6,480	0,711	7,87 E-20
	Camera 5	-5,860	0,699	5,31 E-17
	Camera 6	-6,907	0,720	8,25 E-22
	Camera 7	-5,335	0,693	1,41 E-14
	Camera 8	-5,977	0,699	1,28 E-17
	Camera 9	-5,621	0,696	6,78 E-16
Kudu	Camera 2	-6,793	0,268	3,04 E-141
	Camera 3	-6,830	0,270	9,60 E-141
	Camera 4	-6,796	0,268	1,94 E-141
	Camera 5	-7,012	0,282	8,18 E-137
	Camera 6	-7,069	0,284	7,36 E-137
	Camera 7	-7,310	0,300	1,09 E-130
	Camera 8	-5,929	0,231	1,14 E-144
	Camera 9	-6,575	0,255	1,02 E-146
Impala	Camera 2	-25,016	972,077	0,979
	Camera 3	-25,013	971,038	0,979
	Camera 4	-10,259	12,718	0,420
	Camera 5	-7,786	12,682	0,539
	Camera 6	-7,037	12,680	0,579
	Camera 7	-6,796	12,680	0,592
	Camera 8	-9,565	12,698	0,451
	Camera 9	-25,026	970,789	0,979
Lion	Camera 2	-23,828	599,826	0,968
	Camera 3	-10,037	1,006	1,99 E-23
	Camera 4	-9,338	0,716	7,41 E-39
	Camera 5	-8,644	0,513	9,47 E-64
	Camera 6	-7,531	0,302	1,88 E-137
	Camera 7	-9,018	0,590	1,22 E-52
	Camera 8	-6,170	0,187	7,66 E-238
	Camera 9	-23,830	599,895	0,968
Predator	Camera 2	-8,219	0,422	1,60 E-84
	Camera 3	-10,014	1,005	2,31 E-23
	Camera 4	-9,315	0,715	8,69 E-39
	Camera 5	-8,621	0,511	8,75 E-64

	Camera 6	-7,307	0,274	9,42 E-157
	Camera 7	-9,004	0,589	1,01 E-52
	Camera 8	-6,159	0,183	4,10 E-247
	Camera 9	-22,813	364,756	0,950