UNIVERSITY OF GOTHENBURG

DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

INVESTIGATING THE USE OF OLFACTORY CUES TO RE-DIRECT AFRICAN SAVANNAH ELEPHANT PATHWAYS

A potential conflict mitigation tool

Vera Ruijs

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Supervisors: Søren Faurby, Department of Biological and Environmental Sciences
Kate Evans, Elephants for Africa

Examiner: Mats Olsson, Biological and Environmental Sciences

Picture taken by Vera Ruijs

Index (table of contents)

Abstract 2
Introduction 3
Methods 6
  Description of the experimental area 6
  Experimental apparatus and procedure 7
  Data collection 9
  Statistical Analyses 10
  Ethical declaration 12
Results 12
  General overview of the data 12
  Results of the statistical analyses 13
Discussion 15
  Main findings on elephant movement 15
  Interpretation of the results 15
  Future recommendations 16
Conclusion 18
Acknowledgements 18
References 19
Appendix 1 Popular science summary
Appendix 2 Coordinates of the experimental sites
Appendix 3 Dimensions of the experimental sites
Appendix 4 Model summary of all sites separately
Appendix 5 Model summary not corrected for groups
Appendix 6 Model summary of elephants travelling solo

Abstract

Human-elephant conflict resulting from, for example crop raiding behaviour, poses a significant threat to the conservation of African savannah elephants (*Loxodonta africana*). These conflicts can lead to fatalities in both humans and elephants. When a crop field is located in the proximity of an elephant pathway, the chances of it being raided are higher. To mitigate these problems, this study investigated the potential of using olfactory cues in elephant pathway soil to re-direct elephant pathways away from crops and human settlements. In an attempt to manipulate elephant movement, a treatment of soil with olfactory cues was placed on the side that was initially less used in pathway branching events, aiming at stimulating the usage of these less used sides. The 1500 elephant sightings, captured by camera traps on pathways towards the Boteti River in the Makgadikgadi Pans National Park, gave data for elephant pathway usage in the study. There was considerable variation in pathway usage by individual elephants and groups, as well as in usage during the day and night. A logistic regression in time series analyses revealed no significant immediate or sustained effect of the treatments on pathway usage. This could be due to the pre-existing olfactory cues on established pathways overshadowing the treatments, or that elephants have a better understanding of the park than previously assumed. Additionally, the elephants may have smelled the Boteti River water nearby, reducing their attention to the pathway treatments. Furthermore, the study found that elephants have an even greater preference for the initially more used pathways during darkness. This suggests that the elephants have a stronger dependence on olfactory cues during the night. Overall, this study is the first step in creating a new method to mitigate human-elephant conflict, and it highlights the need to better understand the factors influencing elephants' movement patterns.

Keywords: *African savannah elephants – conflict mitigation – elephant pathways – human-elephant conflict – olfactory cues*

Introduction

Population growth is forcing humans to expand their territories. As human populations expand, they require more land for housing and agriculture. This often results in the conversion of natural habitats into human settlements or farmland, which can displace wildlife and reduce their available habitat (Mmbaga et al., 2017; Dejene et al., 2021). The loss of habitat can have particularly severe impacts on large mammals since they require large areas of land to find enough resources to survive (Dejene et al., 2021). Therefore, populations of the African savannah elephant (*Loxodonta africana*) (referred to as elephants from here on in) are facing increasing threats of habitat loss and human-elephant conflict (De Boer et al., 2013). The habitat available to elephants in Africa is becoming smaller and more fragmented, thus making many elephant populations vulnerable to extinction (Okello & Kiringe, 2004; Mmbaga et al., 2017). Moreover, research has shown that elephants are restricted to using just a small fraction of the suitable habitat, due to anthropogenic and climatic factors (Dejene et al., 2021; Wall et al., 2021). On top of this, the demand for ivory has led to a rise in poaching activities across Africa, especially in areas where elephant populations are concentrated and law enforcement is weak (Wittemyer et al., 2014). The outcome of these threats to survival is that many remaining elephant populations are decreasing rapidly, therefore, the African savannah elephant is listed as Endangered on the IUCN Red List of Threatened Species (Gobush et al., 2022).

Elephants serve a crucial role as keystone species in maintaining terrestrial biodiversity in their ecosystem (Asner et al., 2009; Osborne et al., 2018; Hyvarinen et al., 2021). In addition to their ecological importance, the habitats of elephants also provide humans with important services and goods, such as water, food, and tourism (Osborne et al., 2018). Protecting the elephants is therefore not only crucial for the health of ecosystems, but also for the livelihoods and well-being of humans who depend on these ecosystems. Thus, conservation efforts are necessary to protect the elephant, and the ecosystems and thus rich biodiversity they support as keystone species.

Botswana is a unique case among the range states of elephants, as its elephant population has been increasing rather than declining due to successful conservation strategies and the firm anti-poaching attitude of the government (Figure 1) (Thouless et al., 2016). In fact, approximately one third of all African savannah elephants reside in Botswana, making it one of the last strongholds for this species (Thouless et al., 2016). The western boundary of the Makgadikgadi Pans National Park (MPNP) in Botswana is an area where both humans and elephants rely on the water of the Boteti River (Evans, 2019). However, as the elephant range overlaps with that of the local communities, the frequency of human-elephant conflict is increasing (Evans, 2019). Besides, the MPNP area has seen an increase in human-elephant conflict since the resurgence of the Boteti River in 2009, after having been dry for 19 years (Evans, 2019). Elephants are recolonising the area and the cultural knowledge of the local communities on how to deal with elephants is lost due to this 19 year gap.

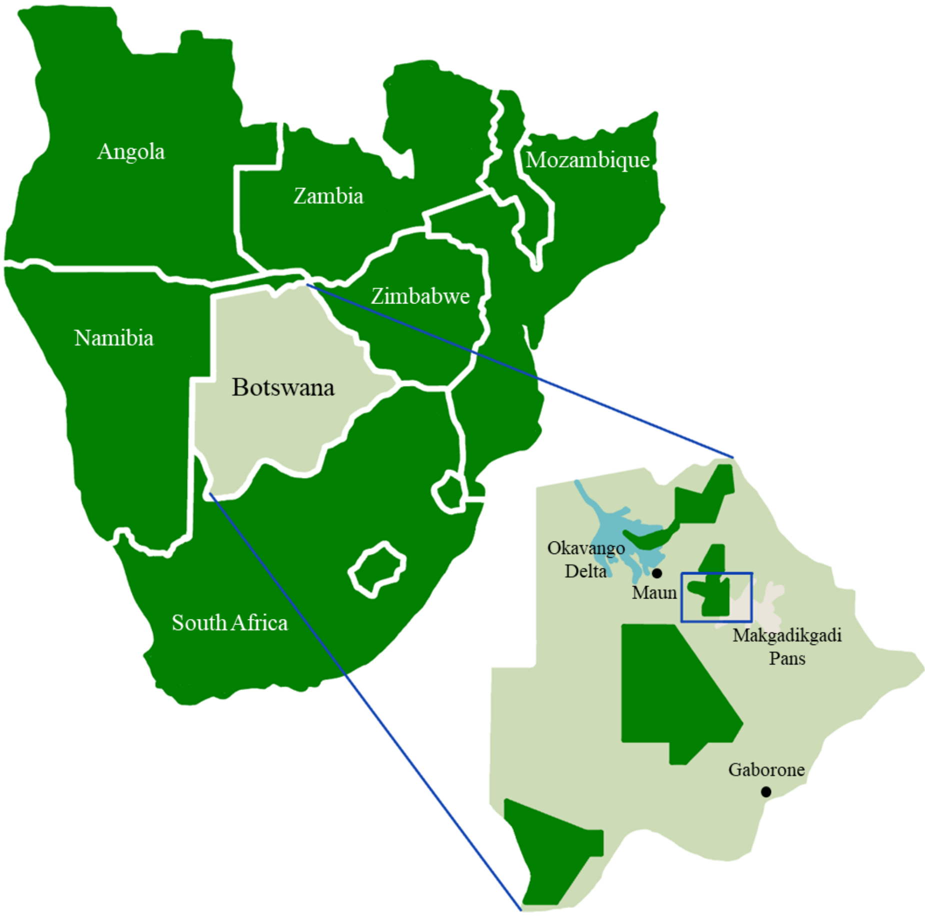

Figure 1: Map of Southern Africa. Within Botswana, its national parks are indicated with dark green. Furthermore, the Okavango Delta and the Makgadikgadi salt pans are shown. The MPNP is indicated with the blue square.

Elephants have large nutritional requirements and are bulk feeders, which can lead them to risk raiding highly nutritious crop fields as the rewards of a successful raid are high (Osborn, 2004; Chiyo & Cochrane, 2005; Schmitt et al., 2018). This behaviour is primarily seen in adult male elephants because they are more likely to take risks compared to female elephants (Hoare, 1999). The MPNP is considered a 'bull area' as over 90% of the elephant sightings in the national park are male, and therefore crop raiding has become a serious problem in this region (Evans, 2019). It is estimated that over 40% of the potential annual harvest in the region bordering the MPNP is destroyed by crop-raiding elephants (Chamberlain, 2016; Stevens, 2018).

In addition to the loss of crops, there is a great deal of fear and disruption to the daily lives of members of the local community as a result of living in close proximity to elephants since it can lead to dangerous situations for both elephants and humans, with fatalities on both sides (Sitati, 2003; Mayberry et al., 2017; Elephants for Africa unpublished data). These negative experiences with elephants do not improve the local community's understanding of the importance of elephant conservation. By finding ways to reduce conflict and promote coexistence, we can protect both elephants and the people who live in their range.

Conflict mitigation methods are paramount in improving human-elephant coexistence. Throughout the elephant range, multiple simple and cost-effective conflict mitigation methods have been tested to protect local farms. Some are human-made physical barriers like electrical fences (Thouless & Sakwa, 1995), but there are also methods based on natural signals, such as the use of beehive fences (King et al., 2017) and burning chilli peppers (Pozo et al., 2017). An even more natural method would be placing predator dung (Valenta et al., 2020), since this is based on cues that elephants also come across in their natural habitat. These methods have in common that they are often based on ‘negative’ and deterring stimuli. While they can be effective in deterring elephants, the sustainability and effectiveness of these methods are questionable, and many are only temporary solutions (Sitati & Walpole, 2006; Enukwa, 2017; Pozo et al., 2017; Ball et al., 2022). To illustrate the example of burning chilli peppers: chilli peppers release capsaicin in the air which irritates the sensitive trunks, and this deters elephants (Pozo et al., 2017). However, the chilli peppers would have to be kept burning continuously in order to maintain their effectiveness since many elephants will return after the capsaicin in the atmosphere is gone (Pozo et al., 2017). Common traits among many of the existing conflict mitigation methods are that they are transient and not sustainable in the long term (Sitati & Walpole, 2006; Enukwa, 2017; Pozo et al., 2017; Ball et al., 2022). Therefore, having a variety of methods to mitigate human-elephant conflict is essential.

Within the core of their extensive range, elephants use a type of mental map, known as a Euclidean map, to familiarize themselves with their surroundings and the location of resources (Presotto et al., 2019). However, the MPNP is based in the periphery of the usual range of the elephant and additionally, in this area a lot of male elephants are transitory meaning that the elephants here are less familiar with their surroundings (Thouless et al., 2016; Pitfield, 2017; Allen et al., 2021). In these unfamiliar areas elephants tend to travel along habitual routes called elephant pathways, and they are established towards and from resources (Presotto et al., 2019; Allen et al., 2021).

Research has shown that on these pathways in unfamiliar areas, elephants rely on the scent trail of other elephants that have travelled there previously to navigate and locate resources (Von Gerhardt, 2014; Plotnik et al., 2019; Allen et al., 2021). Furthermore, it has also been observed that male elephant lone travellers are more responsive to olfactory cues along these pathways in comparison to elephants in groups (Allen et al., 2021). While elephants possess a moderate degree of visual acuity, their eyesight is relatively poorer compared to their sense of smell (Pettigrew et al., 2010; Plotnik et al., 2019; Allen et al., 2021). With an extensive collection of functional olfactory receptors, surpassing any other known species today, elephants prioritize their sense of smell over their sense of vision when following these pathways (Niimura et al., 2014; Plotnik et al., 2019; Allen et al., 2021).

By relying on olfactory cues, elephants acquire valuable information for foraging decisions (Niimura et al., 2014; Plotnik et al., 2019). Using olfactory information, elephants possess the ability to distinguish between food quantities (Plotnik et al., 2019). Additionally, elephants can track down water sources by relying on olfactory cues alone, potentially at distances beyond their visual range (Wood et al., 2022). The scents of urine and dung provide elephants with information regarding the depositors’ age class, kin, sex, reproductive status, and approximate location (Poole & Moss, 1989; Bates et al., 2008; Allen et al., 2021). For instance, elephants can track down changes in the hormone levels associated with the reproductive state, i.e., musth males find oestrous female elephants by smelling their urine, while oestrous females can track down musth males by following their urine trails (Poole & Moss, 1989). Thus, the sense of smell is a valuable tool for elephants, and by following the scent trails of other elephants on pathways, they can acquire a substantial amount of information from the urine and dung deposits (Bates et al., 2008; Allen et al., 2021).

When an agricultural field is located in close proximity to these pathways, the field is at a higher risk of being raided by elephants compared to fields that lie further away (Von Gerhardt et al., 2014; Songhurst et al., 2016). It is known that elephants rely heavily on olfactory cues in scent trails deposited by other elephants to navigate along established pathways, so the aim of this research is to make optimal use of this trait. Olfactory cues in pathway soil could be used to manipulate elephant movement and ultimately re-direct the pathways away from crops and human settlements and connect landscapes by leading elephants around the human communities to their resources (Allen et al., 2021). Additionally, the allocation of olfactory cues to corridors could enhance the effectiveness of these corridors in connecting protected areas (Allen et al., 2021). By reducing the opportunities for conflict between humans and elephants, this method could ultimately create an environment for improved human-elephant coexistence.

Therefore, the research question for this project: Can African savannah elephant (*Loxodonta africana*) movement on established elephant pathways be manipulated using olfactory cues in the Makgadikgadi Pans National Park?

Methods

Description of the experimental area

The African savannah elephant was observed and studied along the western boundary of the Makgadikgadi Pans National Park (MPNP) in Botswana (Figure 2a,b). The western boundary of the park is an important area of elephant movement as it gives access to the Boteti River, a valuable resource for both humans and elephants (Evans, 2019). The MPNP has numerous elephant pathways, and a predominantly male elephant population, and this makes it an ideal location for this experiment (Evans, 2019). The vegetation in the MPNP is dominated by grasses and scattered shrubs and trees such as *Vachellia tortilis* and *V. erioloba*, which are all well adapted to the extreme conditions of the region. The field work was conducted during the rainy season from February 2023 to April 2023, during which the maximum daily temperatures ranged from 21.6 °C to 37.6 °C, with a mean maximum daily temperature of 32.4 °C. Precipitation is very localised in the region, and during the study, 17 days of rainfall were recorded at the research camp (Figure 2a). The average precipitation of these 17 days was 8.6 mm and the highest daily precipitation during the experimental period was recorded at 25 mm.

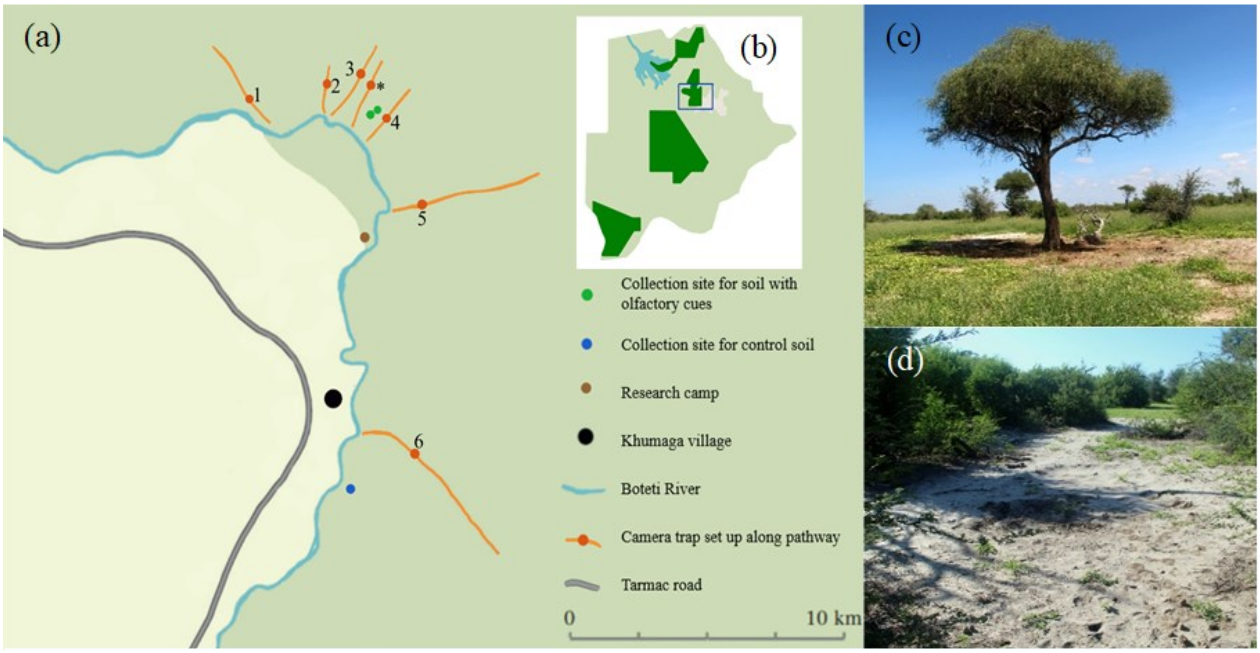

Figure 2: (a) Locations of the camera trap sites on the seven active elephant pathways used for the experiment. The western boundary of the MPNP protected area is represented by the green colour, and the light green represents the community land. Soil for the treatments with olfactory cues were taken from two highly trafficked spots under two Vachellia sps. *trees, indicated by green dots, and the control soil was taken from an open area, not trafficked by elephants. The weather data was collected at the research camp. The seven sites are numbered, although one of the sites (indicated by an asterisk) did not have any elephant sightings travelling in the right direction and thus it was removed from the analyses. Exact coordinates of the locations can be found in Appendix 2. Figure adapted from Allen et al., 2021. (b) Map of Botswana showing its national parks, the Okavango Delta, and the Makgadikgadi salt pans. The MPNP, in which the experimental sites are located, is indicated with the square. (c) One of the two* Vachellia sps. *trees in the MPNP under which the soil was taken. Under the tree a layer of elephant dung is visible, this indicates that the soil should contain olfactory cues. (d) The open spot inside the MPNP where the soil for the control phase was taken.*

Experimental apparatus and procedure

At times, elephant pathways branch off and bypass obstacles such as small trees or bushes before re-joining after a short distance (Figure 3). The branching events of the elephant pathways can result in one side of the path being used more frequently than the other. In this study, I aimed to assess whether it is possible to manipulate the elephants' usage of these elephant pathways, i.e., encourage the elephants to use one side more often than the other. To do this, I conducted an experiment in which I applied olfactory cues from areas of high elephant use to the less used side of the branching event in an attempt to encourage elephants to use these less used paths (Figure 3). If it is possible to stimulate and increase the usage of less used pathways, it means that elephant movement on the pathways can be manipulated.

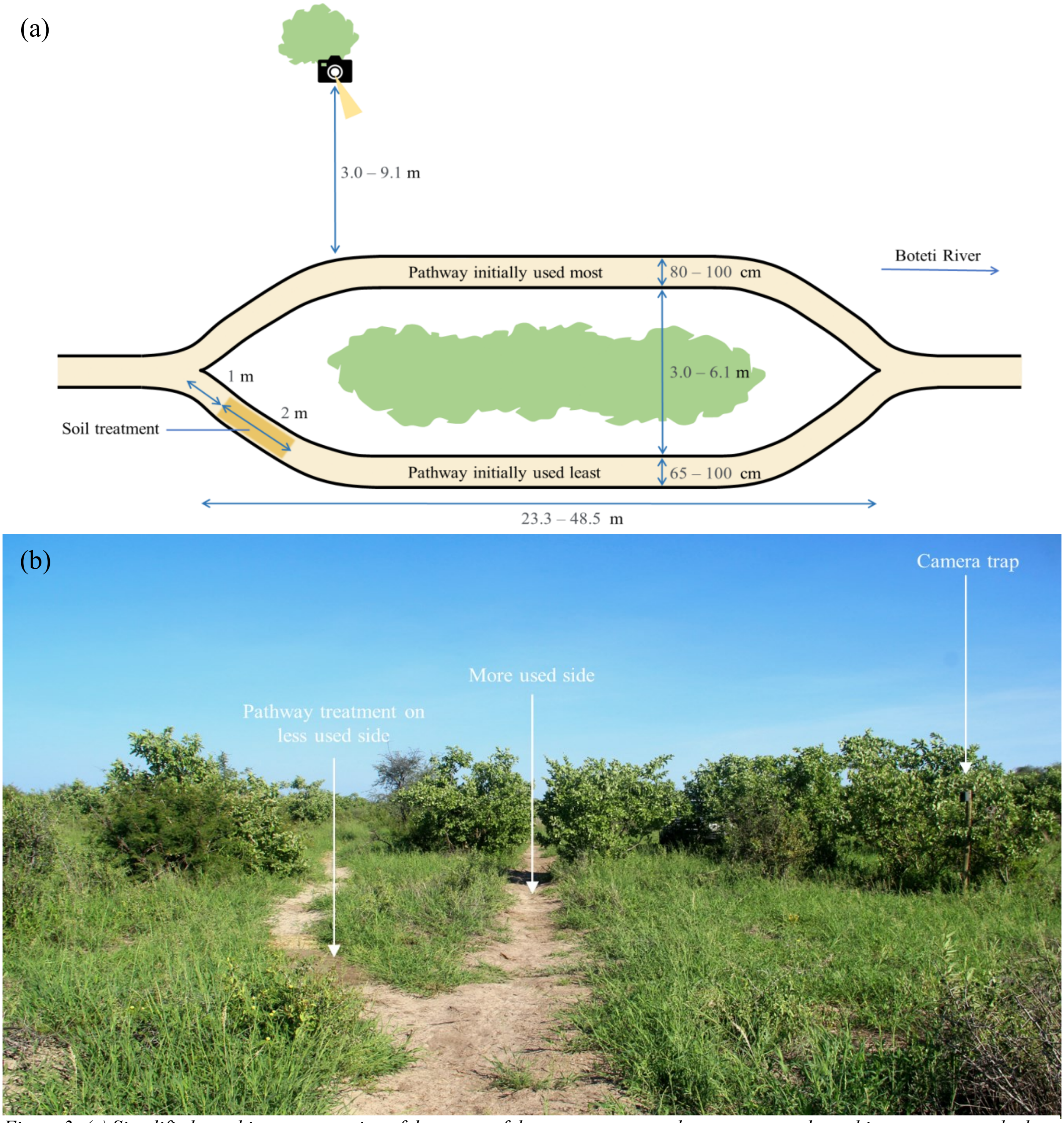

Figure 3: (a) Simplified graphic representation of the set-up of the camera traps and treatment on a branching event on an elephant pathway in the MPNP. The elephants travel in both directions on the pathways towards and from the Boteti River, the treatment was applied to assess elephants travelling towards the Boteti River. Exact average pathway measurements can be found in Appendix 3. (b) Camera set-up at a branching event, showing the initially more and less used side of the pathway, as well as the pathway treatment on the less used side.

Before the experimental period, I assessed whether one side of these branching events was used less frequently than the other. This was done using several methods, such as counting elephant footprints and dung on the pathways, investigating the depth of the indentation of the pathway relative to the surroundings, and comparing the amount of vegetation growing on the pathways. Once I had identified the less used sides of branching events, I carried out a control treatment. For this, soil was collected from a spot inside the park with no pathways and elephant tracks nearby, thus assumed to contain fewer olfactory cues (Figure 2a,c). This control treatment was used as a reference to compare the results of my experiment to assess the effectiveness of the olfactory cues in promoting the use of less used pathways. Then, for the pathway treatments during the test phase after the control period, I collected olfactory cues from a heavily used spot inside the park: two trees where groups of elephants frequently rested in their shade (Figure 2a,d). Under these trees, elephants were often observed urinating and defecating, meaning that the soil samples taken from here were assumed to contain a high concentration of olfactory cues from urine and dung.

In order to ensure that the olfactory-cue-rich soil samples were sufficiently and equally different from the soil on each of the studied pathways that were to be treated, the two trees from under which samples were collected were not located near any of the pathways used in this experiment. The soil was collected from the top layer of the ground since it was assumed that urine seeps down into the ground approximately 5 cm. Touching the sand with bare hands was avoided, with the soil being collected and transported in seven 9 L buckets using a shovel. One bucket was used per pathway, to ensure that each treatment on each of the seven pathways was done with the same amount of sand. The approximately 9 L of sand was then scattered on the pathways (Figure 3).

The treatment was done at the start of the pathway after the split as a clue for elephants that another elephant had used it to entice the other elephants to use it as well. It was assumed that it was sufficient to only place the treatment at the start of the pathway since I expected that once an elephant has chosen to follow the pathway on one side, he would not go back to the other side. The treatment started 1 m into the branching event to lead the elephants onto the path: I hypothesized that putting it not directly at the start of the split would encourage the elephants to go onto the pathway with the treatment. For logistic reasons I could not conduct the treatment for the full length of the pathway branch. Based on the stride length of elephants (average 1.8 m, range: 0.77 m – 2.60 m), I decided to do the treatments for a length of 2 m over the full width of the pathway (Figure 3) (Hutchinson et al., 2006).

The experiment was conducted in two phases, the control phase and treatment phase. The first phase lasted for 32 days. During this phase, the less used sides of the pathways were treated with the control soil that contained little to no olfactory cues, and elephants' usage of the two pathway branches was assessed through remote camera traps by counting the number of elephant sightings using each side travelling towards the river. This was to control for the visual cue of the soil of the treatment itself and our human presence, and whether this was affecting the behaviour of the elephants. In the second phase, which lasted for 30 days, olfactory-cue-rich soil was applied from an area trafficked heavily by elephants to the less used side of the pathway and again the elephants' usage of the pathways was assessed. During both phases of the experiment, I applied the soil (either control or olfactory-rich) to the pathway twice a week on Tuesday and Friday mornings, and simultaneously retrieved the camera trap images and/or changed batteries of the cameras approximately every one to two weeks. The process of treating and assessing the pathway was repeated for seven different branching events located on distinct elephant pathways to ensure that an elephant travelling to the Boteti River does not encounter multiple experimental sites on the same pathway (Figure 2a).

Data on the elephants' usage of the pathways and their behaviour was collected using camera traps. One camera was set up by each of the pathway branching events to assess which branch the elephants utilised (Figure 3). I considered that the elephants travel on the pathways in both directions from and towards the river, and elephants seem to pay an equal amount of attention to olfactory cues on pathways regardless of the direction in which they travel (Allen, pers. comms.). However, it would have been too laborious to do pathway treatments for elephants travelling in both directions to and from the river, since double the number of buckets with sand would not all fit in the research vehicle. So, for consistency, I decided to solely assess the elephants travelling towards the Boteti River as the river is a valuable resource for elephants (Figure 3a). Since the pathways and their surroundings were highly variable, I individually assessed each of the sites for how to angle the camera towards the pathways to capture as much of the pathway as possible, and to allow enough time for the camera trap to be triggered when an elephant was in front of it.

Data collection

The camera traps used for image collection were Reconyx HyperFire 2 Professional Covert IR Camera OD Green. Once an elephant triggered the sensor, the cameras were set to immediately take a picture with no time interval, and for each trigger, the cameras took three pictures with one second in between each image. During each research session in the field, I had at least one assistant with me to help with the treatments and for safety.

The camera trap images were assessed for whether the elephant, travelling towards the Boteti River, in the picture was on the more or the less used pathway side. Every time, the date and timestamp of when the elephant first entered the picture frame was noted. It was also noted on which of the seven pathway sites the elephant was travelling. Finally, I also assessed whether the elephant was travelling solo, in a pair, or in groups of three or more individuals.

I established, based on previous research, that a ten-minute gap between the sighting of the last elephant in a group and the appearance of the next one serves as an appropriate cut-off period to signify the beginning of a new group/individual elephant/pair (Allen, 2021). Furthermore, following the findings of Allen et al. (2020), I assumed that the first individual in a group decides the travel direction, thus for the analyses a group of elephants was deduced to just one sighting (the first elephant in the group) and thus one data point.

I also investigated the effect of the time of day on the decision of elephants to choose the treated or untreated pathway. I assumed that the sense of smell would be the primary factor influencing their decision, rather than their vision (Plotnik et al., 2019; Allen et al., 2021). This was done since although their visual acuity is moderate for animals, it is relatively poorer than their sense of smell and potentially, at night or in low light conditions, their vision could be further impaired (Pettigrew et al., 2010).

Camera traps were initially set up in the middle of the split of the pathways, with two cameras whereby each camera was angled towards one pathway branch, so that a simple count of elephants on each camera should give me the data (Figure 4). However, this was not successful, and six cameras where lost due to the elephants pulling them down. After eight days, the methodology was adapted in the hope to decrease elephants' interest in cameras. Instead of placing two cameras in between the two pathway branches, I used one camera placed between 3.0 m and 10.1 m to the side of the pathways, where it could simultaneously capture both branches of the elephant pathway.

Figure 4: Old camera trap set up where two cameras were used to capture both sides of the branching event. The split where the pathway branches off is not visible but located behind the bush.

During the control phase, the camera at the site indicated with an asterisk in Figure 2a did capture elephants, but none that were travelling towards the river on the pathway. Therefore, it was impossible to perform a statistical comparison between the control phase and the test phase for this site. Additionally, during the test phase, only six elephant sightings were recorded, which is considerably lower compared to the other six sites. Perhaps, the distance of the camera to the pathway was too big (10.1 m; Appendix 3) and occasionally caused the sensor to not be triggered. Due to the low levels of data, this site was excluded from the analyses. Elephants were occasionally interested in the cameras, resulting in the cameras being removed by the elephants. The camera trap at site 1 was removed by elephants three times during the control period, resulting in gaps in the data from 06-02-23 23:13:31 to 07-02-23 10:27:10, from 11-02-23 21:12:32 to 14-02-23 10:15:38, and from 17-02-23 20:09:13 to 21-02-23 10:06:41. The camera trap at site 6 malfunctioned between 01-03-23 and 21-03-23 which resulted in gaps in the data due to the camera being down for most of the time (during this period, the camera was set up again every time after being down a total of four times, but then the camera was consistently down again later the same day or the day after).

Statistical Analyses

Once all data were collected, interrupted time series analyses were used to statistically analyse the results (Equation 1) (Fusi & Lecy, n.d.). I used a logistic regression in a time series analysis since the dependent variable is binary, and so the data was binomially distributed. This allowed me to model the relationship between a binary dependent variable, and the independent variables for the time series analysis. The logistic regression model estimates the probability of the binary outcome based on the values of the independent variables. This method was appropriate for the study since I was interested in predicting the probability of an elephant choosing the initially less used pathway before and after the implementation of the pathway treatments with olfactory cues.

Equation 1: Logistic regression equation for a time series model (based on Fusi & Lecy, n.d.).

$$ln\left(\frac{p}{1-p}\right) = b_0 + b_1T + b_2D + b_3E$$

Using an interrupted time series analysis allowed me to determine whether the use of olfactory cues is an effective method for encouraging elephants to use less used pathways, and whether it has an immediate effect and/or a sustained effect. The start of the treatments with olfactory cues on the pathways, is called the intervention in a time series analysis. In this formula, the dependent variable is binary and modelled using a logistic function (Equation 1). Here, p is the probability of an elephant using the less used pathway. So, the dependent variable $ln(p/(1-p))$ represents the natural logarithm of the odds ratio between the probability of the event occurring (elephant choosing the less used side), to the probability of the event not occurring (elephant choosing the more used side).

T is a variable that represents the passage of time since the beginning of the observation period (in this case, it is measured in days), and it takes on continuous values. D is a binary variable that distinguishes observations that were made prior to the intervention (=0) from those that were made after the intervention (=1). It is a dummy variable that allowed me to compare the outcomes of interest between the two groups. E is also a continuous variable that measures the elapsed time since the implementation of the intervention. Prior to the intervention, the value of E is zero.

The baseline level (intercept) is represented by b_0, while b_1 is the rate at which the outcome variable changes over time before the intervention occurs. Furthermore, b_2 refers to the immediate change in the outcome variable that occurs immediately after the intervention. It quantifies the difference between the outcome level at the last observation before the intervention and the first observation after the intervention. On the other hand, b_3 captures the difference between the rate of change in the outcome variable before the intervention and the rate of change after the intervention. This variable reflects the sustained effect of the intervention on the outcome.

To account for potential site-specific differences in the use of pathways, I included the site as a random effect in the time series analyses. In other words, this way I accounted for the fact that the effect of the intervention on the elephants' decision may vary across various locations, for example due to differences in vegetation or other environmental factors. By including the site as a random effect besides the fixed effects (T, D, E), I was able to model the variation in pathway usage that was specific to each location, while still being able to estimate the overall effect of the intervention on pathway usage.

The R Statistical Software was used to conduct a binomial regression analysis of the data (v4.2.2; R Core Team, 2022). Specifically, the *glm* function from the stats R package (v4.2.2; R Core Team, 2022) to fit a logistic regression model to the data for analysing each site separately, and the *glmer* function from the lme4 R package (v1.1.31; Bates et al., 2015) was used to fit a mixed-effects logistic regression model from to the data for analysing all sites together allowing me to model the random effects and estimate the fixed effects simultaneously.

To investigate the results further, I performed additional analyses. One analysis was done where I included all sightings without correcting for groups to ensure that this assumption based on the research of Allen et al. (2021) was not affecting the outcome of the analysis. I chose not to investigate the consistent selection of the same pathway side by elephants travelling in pairs. The reason is that it is difficult to definitively determine whether these two elephants are genuinely travelling together or merely coincidentally in close proximity to each other for a brief period at the location of the camera trap. On the other hand, when elephants travel in a group of three or more, there is a higher likelihood that they are indeed travelling together instead of three or more separate individuals coincidentally together for a brief moment. Furthermore, an additional analysis was conducted specifically examining solo-traveling elephants, and thus excluded elephants travelling in pairs and groups of three or more. This was carried out due to the fact that elephants travelling individually exhibit a higher level of attentiveness to olfactory cues compared to elephants in groups.

I assessed the goodness of fit of the models to detect whether the models accurately represent the data so reliable predictions could be made. Potential issues such as overdispersion were investigated, which occurs when there is more variability in the data than expected under the assumed statistical model and can cause biased estimates. Therefore, I used the *check_overdispersion* function from the performance R package (v0.10.0; Lüdecke et al., 2021) which calculated the ratio of the residual deviance to the residual degrees of freedom of the fitted models. Moreover, I examined the assumption of independence of observations in logistic regression models. Temporal autocorrelation arises when there is a correlation between the residuals of a model at different time points, violating the assumption of independence. This can lead to biased estimates of the standard errors and p-values, resulting in incorrect conclusions. Therefore, I used the *acf* function from the stats R package to visualise the autocorrelation of the model residuals and check for violations of the independence assumption, which is important in ensuring the validity of the results. Additionally, I evaluated the assumption of linearity between the independent variables and the log-odds of the dependent variable. This assumption implies that the effect of the independent variables on the probability of the event occurring (in this case, the elephant choosing the less used pathway) remains constant across different levels of the independent variables. To assess linearity, I examined diagnostic plots, including an observed versus predicted probabilities plot and a residuals versus predicted values plot. Finally, the Wats R package (v1.0.1; Rodgers et al., 2014) was used to visualise the results in time series plots.

Ethical declaration

The fieldwork was conducted with permission of the Research & Development Unit of the Ministry of Environment, Natural Resources, Conservation & Tourism of Botswana, under research permit ENT 8/36/ 4 LIV (6). Entrance to the Makgadikgadi Pans National Park was granted by the Department of Wildlife and National Parks of Botswana, under supplementary research permit WP/RES 15/2/2 XXXV (25). Finally, approval for the collection of soil inside the park was granted by the Department of Wildlife and National Parks of Botswana, under the sample collection permit WP/RES 15/2/2 XXXV (16).

Results

General overview of the data

During the 62 days that the fieldwork was conducted, a total of 1500 sightings of elephants on the pathways travelling towards the Boteti River were captured by the camera traps. The seven sites differed from each other in number of sightings captured by the camera traps (Table 1). During the test phase, a considerably larger number of elephants were sighted by the cameras than during the control phase (Table 1a). 625 sightings were captured by the camera traps during the day, and during the night the camera traps captured a total of 875 elephant sightings (Table 1a). At sites 1 and 2, more elephants were captured travelling during the day, whereas sites 3, 4, 5, and 6 had more elephant sightings captured during the night. Furthermore, the cameras captured 326 sightings of elephants travelling solo, 234 elephants were captured travelling together with one other elephant, and a total of 940 sightings of elephants travelling in groups of three or more individuals (Table 1b). The cameras captured 170 occurrences of groups of three or more elephants travelling together (Table 1b). It should be noted that these instances may not represent 170 distinct groups, as the cameras might have captured the same groups multiple times. The same goes for solo travellers and elephants travelling in pairs along the seven pathways that might have been sighted multiple times during the 62 day experimental period.

*Table 1: Overview of the elephant sightings captured by the camera traps at the seven sites. The sightings of the excluded site (marked by * and indicated in italics), were not included in the analyses. (a) The sightings during the control and test phase are compared, as well as the sightings during the day and night. (b) An overview of the travel modes of elephants: number of elephants travelling alone, travelling with another elephant, and travelling in a group of three or more elephants. Additionally, the table shows how many individuals in groups followed the same side of the pathway as the first individual of the group, and how many groups had differences within the group in choosing the treated or untreated side.*

(a)	Phase:		Time of day:		
Site	Control phase	Test phase	Day	Night	Total
1	68	346	291	123	414
2	42	159	110	91	201
3	7	66	32	41	73
4	21	131	65	87	152
5	61	503	81	483	564
6	23	67	42	48	90
*	*0*	*6*	*4*	*2*	*6*
Total	222	1278	625	875	1500

(b)	No. of elephants travelling:			No. of times where individuals in a group:		
Site	Alone	In a pair	In a group	All chose the same side	Chose different sides	Total group sightings
1	75	61	278	24	26	50
2	51	30	120	20	8	28
3	23	11	39	4	4	8
4	53	34	65	10	5	15
5	107	72	385	55	4	59
6	16	22	52	7	2	9
*	*1*	*4*	*1*	*0*	*1*	*1*
Total	326	234	940	120	50	170

Results of the statistical analyses

A time series analysis was conducted on six of the seven sites to investigate the effects of pathway treatments on the decision-making of elephants to choose the treated pathway, the initially less used side. The analysis was performed on all six sites together, with the sites being included into the model as random effects. The model summary of the analysis, as shown in Table 2, revealed that the results were non-significant. This indicates that the pathway treatments did not have any immediate and/or sustained effect on the decision of elephants to choose the treated side over the untreated side.

Table 2: Summary of the model where the sightings are corrected for elephants travelling in groups.

	Estimate	Std. Error	P-value
Intercept	-1.233	0.682	0.071
Days since start (T)	-0.025	0.023	0.262
Treatment (D)	0.418	0.564	0.458
Days since treatment (E)	-0.039	0.032	0.225

The positive estimate of the *Treatment* variable indicates that there seems to be a small immediate effect where elephants choose the less used side more frequent right after the intervention when the treatments commenced, however the p-value indicates that this effect is not significant and thus likely due to chance (Table 2). The slightly negative estimate of the *Days since treatment* variable suggests that the usage of the rare side of the pathway with the treatment decreased somewhat over time. However, the p-value indicates that this effect was not statistically significant, and thus it may be due to chance.

Tests to check for linearity, autocorrelation and overdispersion were also conducted. The results showed linearity and no significant autocorrelation in the data, indicating that the observations were independent of each other over time. I found evidence of overdispersion at sites 1, 2, and 4, but not when all sites were analysed together. Nonetheless, given the non-significant results obtained, the issue of overdispersion was not further addressed.

For the investigation into the effect of the time of day on the decision of elephants to choose the treated or untreated pathway, no significant immediate and/or sustained effects of the treatments were found, regardless of whether the elephants were travelling during the day or during the night (Table 3). However, the p-value of the intercept of the analysis for the night is significant. This indicates that during the night, elephants decide against using the less used side of the pathway even more than during the day.

Table 3: Summary of the model where time of the day is considered, 'day' signifies any sighting that happened between sunrise and sunset, 'night' signifies the time between sunset and sunrise. The sightings are corrected for elephants travelling in groups. Significant value ($p < 0.05$) is indicated in bold.

	Time of day	Estimate	Std. Error	P-value
Intercept	Day	-0.700	0.784	0.372
	Night	-2.025	0.983	**0.040**
Days since start (T)	Day	-0.037	0.032	0.249
	Night	-0.022	0.035	0.525
Treatment (D)	Day	0.686	0.761	0.367
	Night	0.536	0.890	0.547
Days since treatment (E)	Day	-0.054	0.044	0.219
	Night	-0.039	0.050	0.438

Although the sites were already included in the model as random effects, I performed analyses on all sites separately as well to further investigate the non-significant results of the immediate and sustained effects. The model summary of these analyses can be found in Appendix 4. This was done since the pathway usage on each site varied considerably (Table 1). This allowed me to examine whether the lack of significance was consistent across all sites or whether some sites did show a significant effect of the treatments on the pathway usage. However, despite the differences between the sites, the results of the separate analyses were consistent with the overall analysis in that they showed no significant effect, indicating that the pathway treatments did not have any significant effect on the elephants' decision in any of the sites (Appendix 4). The results of the analysis do indicate a significant effect of the *Days since start* variable in site 1. However, it is important to note that the conventional threshold for statistical significance is a p-value of 0.05, which means that there is a 1 in 20 chance of observing a significant effect due to random variation or factors other than the pathway treatment.

Additional analyses were conducted in an attempt to investigate the results even further. One analysis was performed where I included all sightings without correcting for groups (Appendix 5). Another analysis was done to solely examine solo-travelling elephants (Appendix 6). However, the immediate and sustained effects of the treatments on the decision-making of elephants remained non-significant in both analyses. In both analyses, I found a significant value for the intercept, indicating that the more used side is significantly used more than the less used side.

Discussion

Main findings on elephant movement

The study recorded a total of 1500 sightings of elephants on the elephant pathways leading towards the Boteti River. This substantial number of sightings provides valuable insights into the movement patterns of elephants in the experimental area. I observed considerable variability in the number of sightings across the seven sites I surveyed. This diversity in elephant presence suggests that various site-specific factors may play a role in shaping the elephants' pathway usage and behavioural choices. Such site-specific factors could include the vegetation composition, water source availability and the presence of human activities in the vicinity.

The time series analyses aimed at investigating my hypothesis on the effectiveness of using olfactory cues derived from urine and dung in the soil as pathway treatments, specifically focusing on their impact on elephants' decision-making regarding travel direction. The results of the analyses investigating the immediate and sustained effect of the treatments were non-significant, indicating that the treatment on the pathways did not have either an immediate nor a sustained effect on the elephants' decision on going to the treated or untreated pathway side. Despite my initial expectations, the absence of statistical significance suggests that the method of introducing olfactory cues from elephant urine and dung on the pathways did not cause a discernible change in the decision-making process of an elephant.

Interestingly, I found a notable difference in the number of elephant sightings between the test phase, when pathway treatments with olfactory cues were applied, and the control phase, when I implemented pathway treatments without olfactory cues. During the test phase, there was a considerably higher number of elephant sightings recorded by the camera traps compared to the control phase. While this difference might initially suggest that the pathway treatments have influenced the elephant abundance, it is more likely that the increased number of sightings during the test phase is a result of dryer conditions rather than the olfactory cues in the pathway treatments. The rainy season did not bring substantial rainfall, leading to water scarcity in the region encompassing the MPNP. As a result, as time progressed, more elephants were likely drawn towards the Boteti River which is a vital water source in the area. This could have resulted in more sightings being recorded at the seven pathways, all leading towards the river. These findings highlight the significance of environmental factors, such as rainfall, in shaping elephant movement.

Interpretation of the results

One explanation for the lack of significant effects of the pathway treatments on pathway usage could be that the presence of other olfactory cues overshadowed the new cues introduced through the treatments. It is plausible that the quantity of olfactory cues I used, 9 L of soil with cues derived from elephant urine and dung, was overridden by the abundance of pre-existing olfactory cues already present along the well-established pathways. Possibly, the 9 L of soil with olfactory cues was not enough to make the elephants choose the treated pathway. In some cases, elephant pathways have remained in the exact location since at least 2004, from when the Boteti River ran dry (Allen et al., 2021). This indicates that the continuous usage of these pathways by elephants has likely contributed to the accumulation of an intricate olfactory landscape along the established pathways, acting as a positive feedback loop (Allen et al., 2021).

The investigation into the effect of the absence and presence of daylight on elephant decision-making revealed no significant immediate or sustained effects of treatments on their choice of pathway sides during either the day or the night. However, it is important to note that I observed a significant intercept for the analysis done for elephants travelling during the night, indicating an even stronger aversion to the less used, treated pathway side in an absence of daylight. This significant finding may be attributed to the suggestion that already present olfactory cues overshadow the cues in the pathway treatments. Elephants may rely more heavily on their sense of smell during the low-light conditions when their visual perception is more limited, compared to when they are travelling during the day (Pettigrew et al., 2010). Under these circumstances, the elephants might favour the already present olfactory cues along the more frequently used side of the pathway even more than during the day when some visual cues may also come into play.

Furthermore, my assumption that elephants would perceive the treated and untreated sides of the pathway as distinct branches leading to distinct destinations (instead of joining back together shortly) may not hold true in the MPNP. This assumption was based on the understanding that the Boteti River area is being recolonised by elephants, and thus relatively new for elephants due to the resurgence of the Boteti River in 2009, after having been dry for 19 years (Evans, 2019). This 19 year gap did show some elephants in the area, however not in such high numbers. Additionally, the area is primarily inhabited by male elephants whose home ranges are large and so they may have not seen this area for extended periods of time, meaning they could be transitory or less familiar with the area. However, elephants in the MPNP may possess a deeper spatial understanding of the MPNP than I assumed. It could be possible that a higher portion of the elephants than expected were aware that both sides of the pathways would ultimately re-join and lead to the Boteti River, regardless of the presence of olfactory cues. Their familiarity with the area and its pathways could render the olfactory cues less influential in their decision-making process. This explanation gains support from the observation that out of the 170 instances where groups of three or more elephants were observed by the cameras, I noticed that in 50 instances not all individuals within a group chose the same side of the pathway (Table 1b), contrary to the assumption that once the first individual chose a side, all others would follow.

Another potential explanation for the lack of significant immediate and sustained effects of the pathway treatments could be the presence of additional types of olfactory cues. It is possible that elephants, with their exceptional sense of smell, were capable of detecting the presence of the Boteti River from the experimental sites (Wood et al., 2022). The site that was located furthest away from the river was approximately 1300 m away, whereas the closest was approximately at 400 m. Although unknown at which spatial scale, the olfactory cues coming from the river water itself were possibly strong enough to guide the elephants in their decision-making process, thereby diminishing the impact of the olfactory cues derived from other elephants through the pathway treatments (Wood et al., 2022). This scenario suggests that the perception of the river's presence, rather than the olfactory cues from conspecifics, may have played a more significant role in the elephants' decision-making process than initially assumed. Additionally, it could be another explanation for why the elephants did not all choose the same side of the pathway when travelling in groups.

Future recommendations

To address the limitations and unanswered questions raised by this study, several key areas for future research should be prioritized. These areas focus on optimizing the use of olfactory cues as a conflict mitigation method and expanding its applications. Despite the non-significant results for immediate and sustained effects of the pathway treatments obtained in this study, it is important to emphasize the need to persevere in finding ways to optimize the effectiveness of olfactory cues as a conflict mitigation method. It is well known that smell is an important sense to elephants, and thus their olfactory worlds may offer some novel solutions for conflict mitigation, specifically in manipulating where they travel and the areas they utilise. This study signifies the first step to finding ways to realise this novel conflict mitigation method. The method I trialled, which relies on natural positive chemical signalling instead of negative stimuli, has the potential to create a positive feedback loop, wherein the treated pathways stimulate more elephants to travel on them (Allen et al., 2021). As these elephants add their own olfactory cues to the pathway, it can attract and influence more elephants to follow suit, thereby creating a self-reinforcing cycle. This positive feedback loop can contribute to the establishment of a novel, sustainable and effective conflict mitigation method, and can be used alongside the existing conflict mitigation methods.

Moreover, it is important to consider the broader applications of this method beyond diverting established pathways away from crop fields and local communities. Exploring its potential in increasing the efficacy of wildlife corridors between protected areas could be a promising opportunity, as suggested by Allen et al. (2021). By using olfactory cues to guide elephant movement and facilitate ecological connectivity, this approach can help reduce human-elephant conflict on a larger scale while promoting coexistence. Potentially not only within the African savannah elephant range, but also in the Asian elephant (*Elephas maximus*) range where similar challenges are faced (Webber et al., 2011).

Alternative and stronger olfactory cues for pathway treatments should be explored, given the possibility that the pathway treatments may have been overshadowed by pre-existing olfactory cues. One way is to investigate the placement of a greater quantity of soil with olfactory cues, or potentially directly using elephant dung and/or urine instead of soil contaminated with these waste materials. This may provide a more powerful signal for elephants. Potentially, as is done for African wild dogs (*Lycaon pictus*), the molecular signature of the different chemicals that make up the elephant urine and dung could be identified (Apps et al., 2013). The specific compounds in the scent trails that elephants follow could be synthetically produced and used in mass as pathway treatments. Additionally, increasing the quantity of these cues along the entire length of the pathway, rather than just at the beginning, could enhance their effectiveness. Also, placing the treatments more frequently than twice a week could be explored. By ensuring a stronger and more pervasive olfactory presence, the influence of the treatments on elephant decision-making may be amplified. Furthermore, another key area to investigate is to discourage elephants from using the initially more used path. This could be achieved by finding ways to remove the existing olfactory cues or masking them with other scents (while at the same time avoiding the introduction of harsh chemicals, since the MPNP is a protected area) (Allen et al., 2021). Additionally, considering the use of predator dung as a deterrent could prove to be an effective, natural strategy (Valenta et al., 2020).

To evaluate the long-term effects of pathway treatments, conducting longitudinal studies is recommended. These studies should encompass multiple seasons, including both dry and rainy seasons, to account for the variations in environmental conditions and resource availability. This study took place during the rainy season. The rains make the vegetation grow which makes elephant pathways, which are mainly devoid of vegetation, visually stand out more from their surroundings. So, visual cues might be more important during the rainy season compared to the dry season. By observing how the olfactory cues persist and influence elephant movement patterns over time, a comprehensive understanding of the long-term efficacy of this approach can be gained. Furthermore, it is valuable to conduct comparative studies across various locations with varying resource availability. This comparative analysis will provide a broader understanding of how elephants utilize pathways in diverse environments. By considering the range of available resources and their impact on elephant decision-making, a more comprehensive approach to mitigating human-elephant conflict can be developed.

To gain a broad understanding of elephant movement patterns and design effective conflict mitigation strategies, future research should investigate factors that influence an elephants' decision to choose one side of the pathway over the other, such as age, sex, and social rank (Allen et al., 2020). E.g., young male elephants could have different demands for pathways than older male elephants that are in musth. It is also crucial to understand why some groups of elephants all choose to follow the same side, while others split up over the two branches. Additionally, an analysis could be performed where the odds are investigated of whether the second individual or the last individual in a male elephant group follows the same side as the first individual. Insights gained from research towards elephant movement and male group dynamics could inform targeted treatment of pathways based on demographic characteristics of the elephants using them. Additionally, understanding which groups of elephants use specific pathways and during which times of day can provide insights into the social dynamics and behaviour of the elephant population in the MPNP.

Finally, the angle in which the pathway branches off could also influence the decision of elephants on which side to go. The branch that is less used often branches off at an angle, whereas the more used branch continues straight (Figure 2b). This might discourage the elephants to choose the less used side as it would disrupt the flow in which they are travelling. For developing a conflict mitigation method based on olfactory cues where the goal is to move pathways away from human settlements, it would be useful to also investigate the angle in which the new pathway should cut off from the original pathway, as a sharp angle might discourage elephants to follow it.

Conclusion

In conclusion, this study aimed to manipulate African savannah elephant movement on established pathways in the Makgadikgadi Pans National Park (MPNP) using olfactory cues. However, the introduction of olfactory cues derived from urine and dung as pathway treatments did not have a discernible effect on elephant decision-making. Factors such as drought conditions, pre-existing olfactory cues, and elephants' familiarity with the area, likely overshadowed the olfactory cues introduced through the treatments. While the study did not provide conclusive evidence of the effectiveness of olfactory cues in manipulating elephant movement on established pathways in the MPNP, it contributes to our understanding of the complexities of elephant behaviour and the challenges of modifying their pathway usage. Furthermore, the substantial number of elephant sightings recorded provides valuable insights into their movement patterns in the study area. It is important to persevere in finding ways to optimize the use of olfactory cues as a conflict mitigation method. The sense of smell of elephants is a powerful tool and thus should be utilized and investigated further as a mitigation tool. The outcome of this study serves as a valuable foundation for future research. By further exploring and optimizing the use of olfactory cues as a conflict mitigation method, we can work towards sustainable and effective strategies for managing human-elephant conflict and promoting coexistence in the MPNP and similar ecosystems.

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Appendix 1 Popular science summary

A smelly tool in the box to help with human-elephant conflict

African savannah elephants have an excellent sense of smell; this is not unexpected with their iconic trunks. But what if I tell you we can use this great sense of smell to protect the elephants? This might sound a bit abstract, but I will explain it thoroughly in this summary. All over Africa, the human population is growing, and this results in overlapping habitats with that of the elephants. Elephants are attracted to the crop fields: they raid the crops for food which often leads to dangerous situations for both the elephants and humans. Both sides lose their lives over this. I am researching a way to prevent these conflicts by keeping the elephants away from human settlements, and I will do this by using the sense of smell of elephants.

Elephant pathways

Often, elephants travel on elephant pathways. They do use their vision to follow these paths, but research shows us that they mainly rely on olfactory cues. Olfactory cues are smells that the elephants pick up in their surroundings. There is a lot of valuable information captured within the urine and dung of elephants. For example, the smell of urine teaches an elephant about the depositors' age class, whether the urine came from a male or female and also their reproductive status, whether they are related, and it even tells them about the approximate location of the depositor. So, it is the scent trail of others that most elephants follow to find their resources.

Informative soil

In the Makgadikgadi Pans National Park (MPNP), young males frequently choose to follow older males. This is likely because the old bulls have more knowledge of where to go and where to find valuable resources. However, when travelling solo, they can also smell where the old bulls have gone before them. So, they could choose to follow this scent trail. The soil of the elephant pathways is full of smells: elephants urinate and defecate everywhere! The pathway soil is full of the olfactory cues that they smell and follow, and I want to use this soil to create new pathways.

> ***Did you know?*** *Over 95% of the sighting in the MPNP are male. This contradicts the common view that we should only focus on matriarchal groups. A lot is still unknown about male elephant behaviour in male-dominated areas.*

Elephant conservation

Creating new pathways would be a valuable new method for preventing human-elephant conflict. If we find a way that elephant movement on pathways can be manipulated, then we can potentially create new pathways to lead elephants away from human settlements and crop fields. Other conflict mitigation methods that are already in use today, depend on negative, deterring smells. For example, people can burn chilli peppers around their crop fields, and this will release a substance in the air that irritates the sensitive trunks of elephants. However, my method would instead attempt to use the olfactory cues in elephant pathway soil as positive stimuli which are already familiar to the elephants. Using the olfactory cues this way will protect rural communities and benefit elephant conservation.

Appendix 2 Coordinates of the experimental sites

Coordinates of all the locations used in the experiment.

Site	Coordinates
1	-20.382449, 24.479347
2	-20.383422, 24.504261
3	-20.378529, 24.51254
4	-20.387946, 24.522086
5	-20.416031, 24.531981
6	-20.487118, 24.530564
*	-20.379654, 24.51493
Research camp	-20.42695, 24.521333
Collection site for soil with olfactory cues 1	-20.387238, 24.517694
Collection site for soil with olfactory cues 2	-20.386321, 24.518387
Collection site for control soil	-20.502408, 24.511519

Appendix 3 Dimensions of the experimental sites

Dimensions of the six sites, as well as the removed site that is depicted with an asterisk. The removed site is not included in the average.

Site	Max. distance between both sides (m)	Length, split to split (m)	Distance between camera and closest pathway	Width more used side (cm)	Width less used side (cm)
1	3.0	46.0	3.0	100	100
2	3.2	43.0	7.9	80	60
3	6.1	43.0	9.1	80	65
7	5.5	42.0	6.0	100	80
5	6.0	48.5	6.7	100	70
6	3.5	23.3	4.5	100	75
*	*4.2*	*18.5*	*10.1*	*80*	*60*
Avg.	4.6	41.0	6.2	93	75

Appendix 4 Model summary of all sites separately

Model summary values of all sites separately, corrected for elephants travelling in groups. Significant value ($p < 0.05$) is indicated in bold.

	Site	Estimate	Std. Error	P-value
Intercept	1	0.728	0.608	0.231
	2	-19.870	4.286×10^3	0.996
	3	-25.570	2.069×10^5	1.000
	4	0.354	1.179	0.764
	5	-22.236	24.362	0.361
	6	-0.619	0.990	0.532
Days since start (T)	1	-0.076	0.038	**0.048**
	2	0.003	2.276×10^2	1.000
	3	0.000	1.303×10^4	1.000
	4	0.000	0.050	0.998
	5	0.642	0.787	0.414
	6	-0.049	0.105	0.642
Treatment (D)	1	1.498	0.977	0.125
	2	18.990	4.849×10^3	0.997
	3	-0.437	3.133×10^5	1.000
	4	-0.653	1.019	0.521
	5	-1.430	1.600	0.371
	6	-19.010	1.652×10^4	0.999
Days since treatment (E)	1	0.023	0.049	0.643
	2	-0.162	2.276×10^2	0.999
	3	0.004	1.493×10^4	1.000
	4	-0.080	0.071	0.263
	5	-0.688	0.789	0.384
	6	0.060	7.789×10^2	1.000

Appendix 5 Model summary not corrected for groups

Model summary values of all sites together, not corrected for elephants travelling in groups. Significant value ($p < 0.05$) is indicated in bold.

	Estimate	Std. Error	P-value
Intercept	-1.501	0.572	**0.009**
Days since start (T)	-0.030	0.019	0.113
Treatment (D)	0.607	0.466	0.193
Days since treatment (E)	-0.024	0.025	0.343

Appendix 6 Model summary of elephants travelling solo

Model summary values of the analysis done for elephants travelling solo, and so all elephants travelling in duos or groups are excluded. The analysis is with all sites together. Significant value ($p < 0.05$) is indicated in bold.

	Estimate	Std. Error	P
Intercept	-1.924	0.913	**0.035**
Days since start (T)	-0.016	0.030	0.606
Treatment (D)	0.506	0.705	0.473
Days since treatment (E)	-0.042	0.042	0.324