

RESEARCH

Investigating the use of olfactory cues to redirect elephant pathways, Makgadikgadi Pans, Botswana

Vera Ruijs^{1,2}, Soren Faurby^{1,2}, Kate E Evans^{1,2,3*}

¹Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

²Gothenburg Global Biodiversity Centre, Gothenburg 40530, Sweden

³Elephants for Africa, Mailbox HAKb, Maun, Botswana

*corresponding author: kate@elephantsforafrica.org

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Abstract

Human-elephant conflict poses a threat to both elephants and humans. This study explored the potential of using olfactory cues on African savannah elephant pathways (*Loxodonta africana*), to divert elephants from crops and human settlements. Where selected pathways used by elephants branched, we applied a treatment of olfactory-cue-rich soil to the less frequently used side to assess whether this would influence the side the elephants used. Camera traps were placed adjacent to where the pathway split to capture which side the elephants chose. During the 62-day experiment, the camera traps recorded 1,500 sightings of elephants along seven selected pathways leading to the Boteti River in Makgadikgadi Pans National Park, Botswana. The results showed no immediate or sustained effect of the treatments on the usage of the pathways, possibly due to pre-existing olfactory cues on established pathways or the elephants' familiarity with the area. Elephants may have been drawn to the nearby Boteti River, reducing the potential impact of the treatments on the study-designated pathways. An interesting observation was that, at night, elephants exhibited a stronger preference for the pathways that, before the application of the treatments, had a higher rate of usage, possibly suggesting a stronger dependence on olfactory cues during darkness. While the application of the olfactory cues did not significantly impact how the elephants utilised the pathways, it is important to explore means by which we can communicate to elephants where high-risk areas are in a changing landscape and how to navigate these areas. This study highlights the need to better understand the factors that influence elephant movement patterns.

Additional Keywords: behavioural ecology, mitigation strategies, conservation management, sensory perception

Résumé

Les humains comme les éléphants sont menacés par les conflits qui les opposent. Dans notre étude, nous avons exploré le potentiel de l'utilisation de signaux olfactifs sur les passages empruntés par les éléphants de savane (*Loxodonta africana*) dans le but de détourner ces derniers des cultures et des zones habitées,

et de prévenir les conflits humains-éléphants. Lorsque les passages sélectionnés se divisaient, nous appliquions un traitement, composé de terre riche en signaux olfactifs, sur le côté le moins utilisé par les éléphants, afin d'évaluer si leur choix s'en trouvait influencé. Des pièges photographiques, installés près de l'embranchement, permettaient de saisir la direction choisie par les éléphants. Pendant l'expérience de 62 jours, les pièges photographiques ont enregistré 1 500 vues d'éléphants le long de sept sentiers menant à la rivière Boteti, dans le parc national du Pan de Makgadikgadi, au Botswana. Les résultats n'ont pas témoigné d'un effet immédiat ni durable du traitement sur l'utilisation des passages, peut-être en raison de signaux olfactifs préexistants sur des chemins établis, ou du fait que les éléphants connaissaient déjà la zone. Ils peuvent avoir été attirés par la proximité de la rivière Boteti, réduisant ainsi l'impact potentiel des traitements sur les zones désignées dans le cadre de l'étude. Il est intéressant d'observer que, pendant la nuit, les éléphants montraient une préférence plus marquée pour les sentiers qui, avant l'application des traitements, étaient parmi les plus empruntés. Cela suggère potentiellement une dépendance plus élevée aux signaux olfactifs dans l'obscurité. Bien que cette expérience n'ait pas eu d'impact significatif sur la manière dont les éléphants utilisent les chemins, il est important d'explorer les moyens permettant de leur communiquer l'emplacement des zones à haut risque dans un paysage en mutation, et la façon de s'orienter dans ces espaces. Cette étude met en lumière la nécessité de mieux comprendre les facteurs qui influencent les schémas de déplacement des éléphants.

Mots clés supplémentaires: écologie comportementale, stratégies d'atténuation, gestion de la conservation, perception sensorielle

Introduction

The African savannah elephant (*Loxodonta africana*) has large spatial requirements. They often cannot meet their ecological needs within protected areas (PAs), bringing them into contact and, thus, competition for resources with humans. Hence, habitat loss and human-elephant conflict (HEC) are threatening their survival (Dejene et al. 2021). Botswana is home to the largest remaining elephant population (Thouless et al. 2016), which is increasing in size and expanding into historical rangelands (Evans 2019). The expansion includes community land, with a resulting increase in HEC.

While physical barriers are useful in mitigating conflict in certain situations, they have limitations in effectively keeping elephants away from human settlements, often being damaged and requiring high maintenance (Erukwa 2017). Influencing elephant movement through olfactory cues offers an alternative that could impact elephant conservation, both in encouraging and enabling the use of wildlife corridors connecting PAs and diverting them away from cropland (Allen et al. 2021).

Studies on African wild dogs (*Lycaon pictus*) offer a compelling example of how olfactory cues can be used to manipulate wildlife movement for conservation purposes (Apps et al. 2013; Haring

et al. 2023). Wild dogs, which also face significant threats from human-wildlife conflict when they venture outside PAs, have been shown to respond to the scent of dominant predators such as lions (*Panthera leo*) (Haring et al. 2023). By deploying lion scat along the boundaries of wildlife farms, researchers successfully simulated the presence of lions, significantly reducing wild dog incursions (Haring et al. 2023). This indicates that olfactory cues can alter wild dog movement patterns by increasing their perception of risk in certain areas. Such non-invasive management strategies offer a promising approach to mitigating conflicts with farmers while conserving endangered species. The success observed in wild dogs suggests that similar methods could be adapted to influence elephant movements, thus reducing HEC and promoting coexistence in shared landscapes.

Within the core of their range, elephants rely on a mental Euclidean map to navigate and locate resources (Presotto et al. 2019). In contrast, elephants tend to travel along habitual routes called elephant pathways (referred to as pathways in this manuscript) in unfamiliar areas (Presotto et al. 2019; Allen et al. 2021). Research shows that on these pathways, elephants, particularly lone bulls, rely on scent trails left by previous elephants to make informed foraging and social decisions (Von Gerhardt 2014; Allen et al. 2021). Olfaction plays a central role in the way elephants perceive and interpret their environment.

They can distinguish between food quantities (Plotnik et al. 2019), locate water sources beyond their visual range (Wood et al. 2022), and gather detailed information about other elephants from urine and dung deposits, including age, kinship, sex, and reproductive status (Poole and Moss 1989; Bates et al. 2008; Allen et al. 2021).

At times, pathways exhibit branching locations to circumvent obstacles, such as small trees or bushes, before merging back together shortly after. These branching locations often have an asymmetric usage of the pathway, with one side of the path being used more frequently than the other. This study aimed to evaluate the possibility of influencing elephant movement along these pathways by promoting increased usage of the previously less utilised side. To test this, we conducted an experiment in which we applied olfactory cues from conspecifics to the less frequented sides of the branching locations, to encourage elephant utilisation of these less used paths (Fig. 2). This allowed us to investigate the potential to manipulate elephant movement along pathways for management and mitigation purposes, as pathways could be re-directed away from crops and human settlements, thus reducing the opportunities for HEC. Allocating olfactory cues to corridors could also enhance their effectiveness in connecting PAs (Allen et al. 2021). Therefore, adding to the toolbox of mitigation strategies that local and national stakeholders can use to reduce conflict and enable coexistence (HECx) in shared landscapes. Consequently, this study's central research question is: Can African savannah elephant (*Loxodonta africana*) movement on established elephant pathways be manipulated using olfactory cues in the Makgadikgadi Pans National Park (NP)? We hypothesized that elephant movement on the pathways can be manipulated with soil treatments consisting of olfactory cues of conspecifics and that it would stimulate and increase the usage of less-used pathways.

Materials and Methods

Study area

The study was conducted between January and April 2023 in Makgadikgadi Pans NP, Botswana (Figs. 1a, b), which is located on the southwestern

boundary of the Kavango Zambezi Transfrontier Conservation Area (KAZA). The area hosts a high proportion of male elephants (Evans 2019), who are known to actively utilise more peripheral areas and explore new habitats (Thouless et al. 2016; Allen et al. 2021). The resurgence of the Boteti River in 2009 after a 19-year dry period led to an increase of elephants in the area (Evans 2019). Consequently, crop raiding has become a serious issue in this region (Chamberlain 2016; Stevens 2018). In areas such as the Makgadikgadi Pans NP region, where agricultural fields are located in close proximity to a national park and to pathways leading to the river, the fields are at a higher risk of elephant foraging (Von Gerhardt et al. 2014; Songhurst et al. 2016).

Data collection

Data on pathway usage and elephant behaviour were collected using camera traps (Reconyx Hyperfire 2 Professional Covert IR Camera OD Green). A camera was set up by each of the pathway branching locations to assess which branch the elephants utilised, seven in all (Fig. 2). They were set to take three to four pictures upon triggering the sensor, with a second between each picture. Every one to two weeks, the batteries of the camera traps were replaced, and images were retrieved for data collection. We focused on elephants travelling towards the Boteti River from the east and north-east (Fig. 2a).

The data from the camera trap images were analysed to determine whether elephants travelling towards the Boteti River were on the more or the less frequented side of the pathway. The date and timestamp of when an elephant first entered the picture frame were recorded, along with the specific pathway site. Additionally, the sizes of the elephant groups were categorised as solo, pairs, or groups of three or more individuals. A ten minute gap between the last sighting of one group of elephants and the appearance of the next was considered an appropriate cut-off period to signify the start of a new group/individual elephant/pair, based on prior research in the study area where it was found that the majority of elephants in a group passed the camera trap within 10 minutes (Allen et al. 2020). Furthermore, following the findings of Allen et al. (2020), it was assumed that the first individual in a group decided the direction of travel; thus, group sightings were reduced to one data point, representing the first elephant in the group.

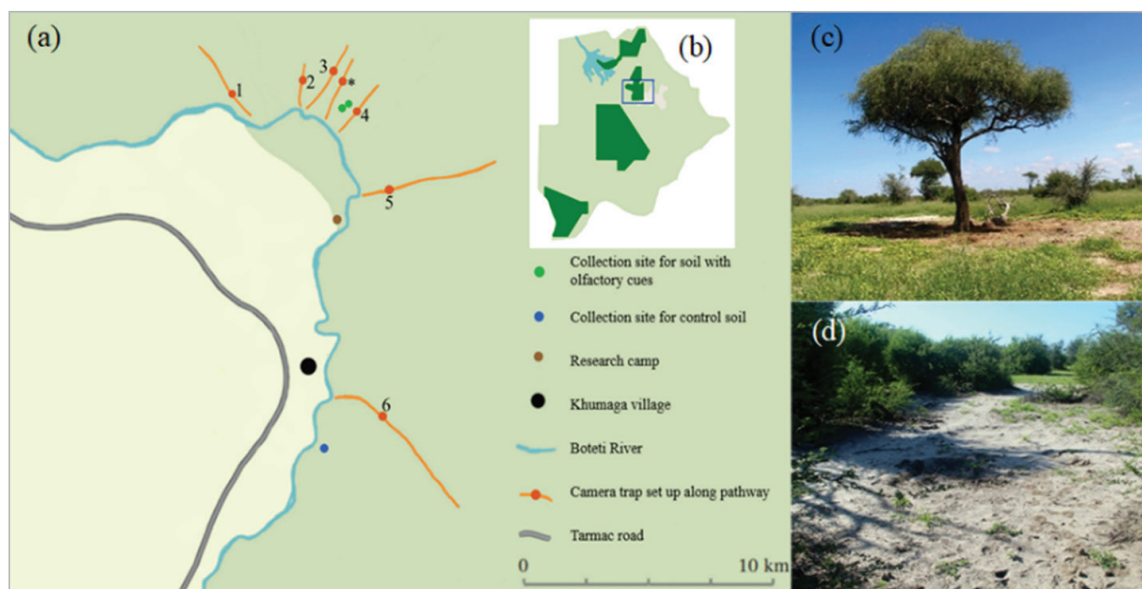


Figure 1. (a) Locations of the camera trap sites on the seven active pathways used for the experiment. The light green colour represents the Makgadikgadi Pans NP, and the light yellow represents community land. Khumaga village (black dot) is located at $-20.471, 24.511$ (decimal degrees). The soil for the treatments with olfactory cues was taken from two highly trafficked spots under two *Vachellia* spp. trees, indicated by green dots, and the control soil was taken from an open area of the Park, with low elephant traffic, indicated by the blue dot. The seven sites were numbered, although one of the sites (indicated by an asterisk) did not have any elephant sightings travelling in the right direction and was therefore removed from the analyses. Figure adapted from Allen et al. 2021. (b) Map of Botswana showing its national parks (dark green), the Okavango Delta (blue), and the Makgadikgadi salt pans (light grey). The Makgadikgadi Pans NP, where the experimental sites are located, is indicated with the square. (c) One of the *Vachellia* spp. trees, under which the soil was taken. (d) The open spot inside the Makgadikgadi Pans NP, from where the soil was taken for the control phase.

Experimental procedure

The experiment was set up with an interrupted time series framework, investigating whether there was an immediate or sustained effect of olfactory cues on elephant behaviour.

To establish a baseline, we conducted a control treatment using soils from an area within the Park without pathways or elephant tracks, assumed to have fewer olfactory cues (Figs. 1a, c). During the control phase (32 days), the less-used sides of the pathway were treated twice a week with the olfactory-cue-poor control soil to assess elephants' usage of the two branches of the pathway. Remote camera traps were used to collect data on elephants utilising each side of the pathway heading in the direction towards the river. In the treatment phase (30 days), olfactory-cue-rich soil was applied to the less-used pathway sides twice a week, and the elephants' usage of the pathways was assessed from the camera trap images. The olfactory-cue-rich soil was collected from well-used areas within the Park: two trees that were frequently

used by elephant groups for resting in the shade (Figs. 1a, d). Under these trees, elephants were often observed urinating and defecating, meaning that these areas were rich in elephant urine and dung, making the soil samples highly concentrated with olfactory cues. To confirm the freshness of the olfactory cues in the soil, a visual assessment was made each time that soil was collected from under these trees. The visual assessment consisted, among others, of searching for footprints and fresh piles of dung that would indicate recent elephant(s) visits. Furthermore, Goodwin et al. (2012) discuss that olfactory cues from the urine of male elephants last at least three days after urination. The process of treating the pathways was repeated at seven different branching locations along distinct pathways to prevent multiple experimental sites on the same pathway (Fig. 1a).

The treatment was applied at the start of each pathway after the split, as a signal to entice the elephants to use it. It was assumed that it was sufficient to place the treatment only at the start of the pathway since we expected that once an elephant chose a pathway,

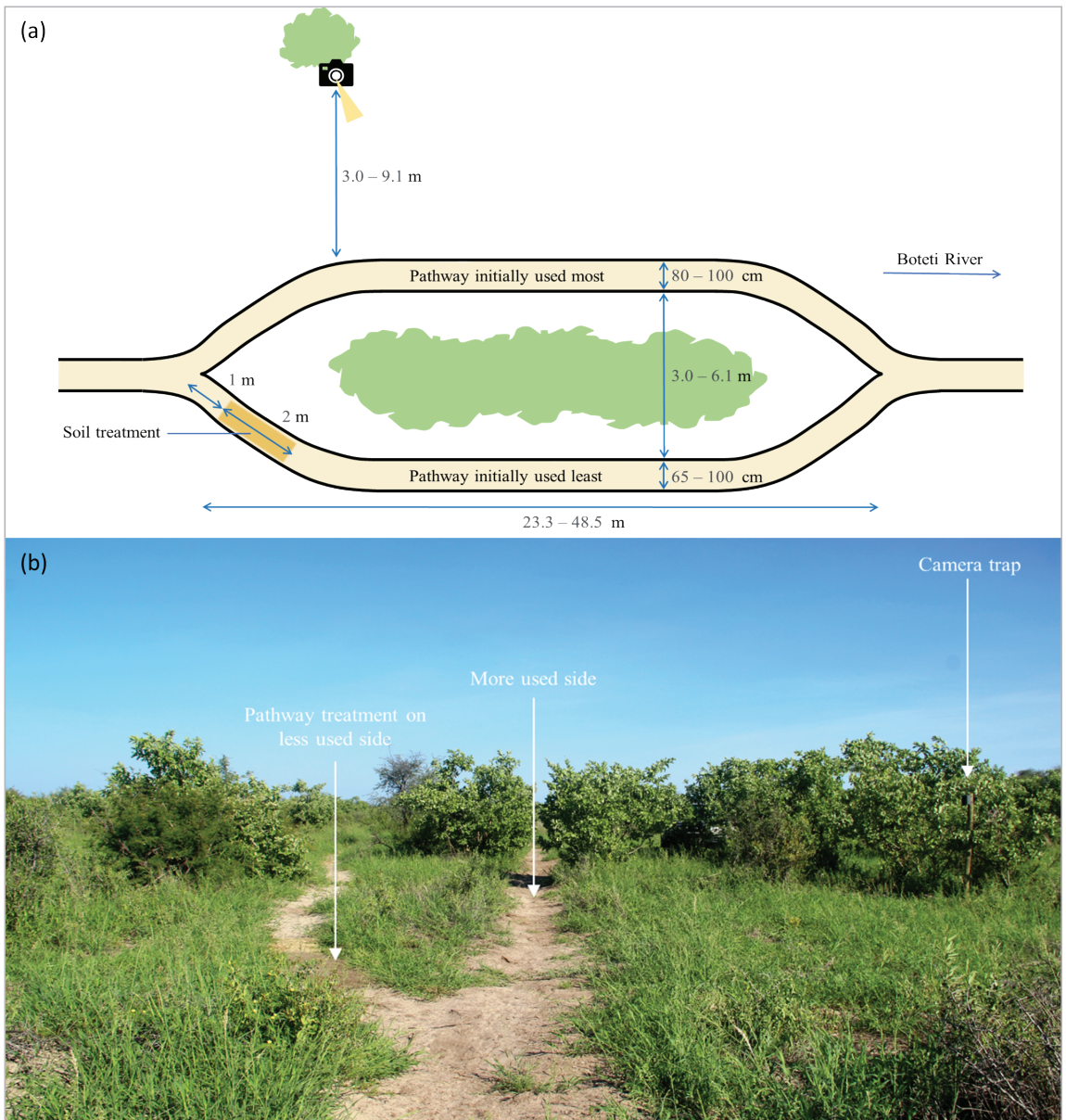


Figure 2. (a) Simplified graphic representation of the camera trap set-up and treatment on a branching location on a pathway in the Makgadikgadi Pans NP. The elephants travel in both directions on the pathways towards and from the Boteti River; the treatment was applied to assess elephants travelling towards the Boteti River. (b) Camera trap set-up at a branching location, showing the more (right) and less (left) used sides of the pathway.

they would not cross over to the other side. The treatment began 1 m above the branching location to encourage the elephants onto the path. Due to logistical constraints, the treatment could not cover the entire branch length of the pathway. Based on the stride length of elephants (average 1.8 m, range: 0.77 m–2.60 m (Hutchinson et al. 2006)), the treatments were applied for a length of 2m, spanning the entire pathway width (Fig. 2).

Statistical analyses

We were interested in predicting the probability that an elephant would choose the initially less-used pathway both before and after implementing the pathways with olfactory cue-based treatments (the intervention). So, we tested whether the probability of using the less used side was higher in the test phase than in the control phase. We analysed this using an interrupted time series framework. This type of analysis allowed us to differentiate between immediate and sustained effects. The following variables were part of the analysis: the passage of time from the beginning of the observation period (T), a variable that distinguishes observations that were made prior to the intervention from those that were made after the intervention (D) and thus the immediate effect of the intervention, and the elapsed time since the implementation of the intervention (E) and thus the sustained effect of the intervention (see also Equation 1). The dependent variable is binary and modelled using a logistic function. i.e. we were not modelling the change in observations, but rather we modelled the probability that any observation was on the least used side. Here, p is the probability that an elephant will use 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 (an elephant choosing the less used side), and the probability of the event not occurring (an elephant choosing the more used side). Two sets of analyses were conducted, one for each individual site and one combined, which included the site as a random effect (to account for the fact that the effect of the intervention on the elephants’ decision may vary across locations). All analyses were done in R v. 4.2.2. (R Core Team 2022) and the mixed effect

models were run in lme4 (v1.1.31; Bates et al. 2015).

Equation 1. Logistic regression equation for a time series model

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

The influence of time of day on the choice an elephant made of which pathway was also explored using the same equation with the same variables; however, the analysis was divided into one analysis solely accounting for observations made between sunrise and sunset (day), and one analysis accounting for the observations made between sunset and sunrise (night). Elephants generally rely more on olfaction than vision, but since their eyesight is moderate for mammals (Pettigrew et al. 2010), visual cues may also be relevant under adequate light conditions. Vision is slightly limited at night, and it is therefore plausible that the relative importance of olfactory cues is greater at night than during daylight hours. For this, the data were separated into observations made between sunrise and sunset, and vice versa.

Table 1. Overview of 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) Sightings during the control and test phases 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) Site	Phase:		Time of day:		Total
	Control phase	Test phase	Day	Night	
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
*	<i>0</i>	<i>6</i>	<i>4</i>	<i>2</i>	<i>6</i>
Total	222	1,278	625	875	1,500

(b) Site	Number of elephants travelling:			Number of times where individuals were in a group:		Total group sightings
	Alone	In a pair	In a group	All chose the same side	Chose different sides	
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

Table 2. Summary of the model in which all sites were combined and the site was considered as a random effect. The sightings are corrected for elephants travelling in groups (i.e. group sightings are reduced to one data point).

	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

Results

During the 62 days of fieldwork, the camera traps recorded 1,500 sightings of elephants on pathways leading to the Boteti River. The number of sightings varied across the seven sites, with considerably more sightings during the test phase compared to the control phase (Table 1a). Of these sightings, 625 were captured during the day, while 875 were recorded at night (Table 1a). Sites 1 and 2 had a higher number of daytime sightings, while sites 3, 4, 5, and 6 recorded more nighttime sightings. The cameras captured 326 sightings of elephants travelling alone, 234 elephants travelling in pairs, and 170 occurrences of groups of three or more elephants travelling together (Table 1b). It is important to note that the 170 group sightings may have included multiple observations of the same

Table 3. Summary of the model in which all sites were considered separately. The sightings are 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

Table 4. Summary of the model in which the time of the day is considered, 'day' signifies any sighting that happened between sunrise and sunset, and 'night' signifies the time between sunset and sunrise. The sightings are corrected for elephants travelling in groups. The 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

individuals. This also applies to solo travellers and pairs observed along the seven pathways during the 62-day experimental period. In some instances, not all individuals in a group chose the same side as the first (lead) elephant in the group (Table 1b). Furthermore, not all individuals in a group travelled directly along the pathway; some individuals travelled parallel to the pathway, while others were on it. The same applies to elephants travelling in pairs.

The results did not show any significant effect of the olfactory treatment on elephants' choice of pathway, analysed with all sites combined (Table 2), nor with all separately analysed sites (Table 3). With regard to the investigation into the effect of the time of day on the decision of elephants to choose the treated or untreated pathway, there were no significant immediate and/or sustained effects of the treatments (Table 4).

Discussion

The time series analyses aimed to assess the influence of introducing olfactory cues from elephant urine and dung as pathway treatments on the movement decisions elephants make. The results did not reveal any significant immediate and sustained effects of the treatments, suggesting

that these olfactory cues did not alter the decision-making processes of elephants.

Although our olfactory treatment of pathways had no significant effect on which side the elephant(s) chose to travel along, given their biology and reliance on the sense of smell, it is likely that the underlying method of using olfactory cues to manipulate elephant movement may be possible. Potentially, the quality and quantity of olfactory cues introduced were insufficient to influence the elephants' choice compared to the abundance of pre-existing cues along the well-established pathways. Additional olfactory cues, such as the Boteti River's water scent, may have allowed elephants to detect the river and guide their choices more than cues from conspecifics (Wood et al. 2022). It is also possible that elephants in the area possess a deeper spatial understanding than assumed, recognising that both sides ultimately lead to the Boteti River. This familiarity with the area's pathways could render olfactory cues less influential in their decision-making process, where the experiment was undertaken.

Furthermore, elephants could be neophobic and thus potentially scared away by the addition of an introduced soil, however, research on wild Asian elephants (*Elephas maximus*) suggests they can be neophilic-inclined (Jacobson et al. 2023), thus we do not think neophobia is a problem with this experiment. If this were a factor, it would likely reduce the use of the least used side in both the control and study period and would therefore likely not change our ability to see any potential effect of olfactory cues. Finally, the significant aversion to the less-used side of the treated pathway at night might be due to elephants relying more on their sense of smell in low-light conditions when visual perception is limited.

Future recommendations

Despite the non-significant results for immediate and sustained effects of pathway treatments, continued efforts to enhance the effectiveness of olfactory cues for conflict mitigation are crucial. This approach, based on positive chemical signalling, has the potential to create a self-reinforcing cycle where treated pathways attract and influence more elephants over time, offering a novel, sustainable mitigation method to work alongside existing strategies (Allen et al. 2021).

Alternative and stronger olfactory cues should be explored, such as using larger quantities of soil mixed

with elephant dung and urine olfactory cues. Potentially, as has been done for African wild dogs, the molecular signature of the different chemicals that make up elephant urine and dung could be identified (Apps et al. 2013). The specific compound in the scent trails that elephants follow could be synthetically produced and scaled up as pathway treatments. A more pervasive application along the entire pathway, an increased frequency of cue application, and the investigation of ways to remove or mask existing cues, are worth exploring (Allen et al. 2021). Additionally, predator dung (Valenta et al. 2020) or chillis (Pozo et al. 2017) could serve as a natural deterrent to prevent elephants from travelling on the more used sides, combined with promoting the use of the initially less used sides.

Conclusion

In conclusion, this study aimed to manipulate elephant movement on established pathways using olfactory cues. However, introducing urine and dung-derived olfactory cues as pathway treatments did not have a discernible effect on elephant behaviour. Factors such as drought conditions, pre-existing olfactory cues, and elephants' familiarity with the area and the nearby location of the river, likely overshadowed the olfactory cues introduced through the treatments. Despite these results, the study emphasises the importance of persisting in finding ways to optimize the use of olfactory cues as a conflict mitigation tool. The incredible sense of smell of elephants offers the potential for effective strategies. The outcome of this study serves as a valuable foundation for future research, encouraging further exploration and refinement of the use of olfactory cues in conflict mitigation. By doing so, we can work towards sustainable and effective strategies for managing HEC and promoting HECx in communities bordering the Makgadikgadi Pans NP and similar ecosystems.

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References

- Allen CRB, Brent LJJ, Motsentwa T, Weiss MN, Croft DP. 2020. Importance of old bulls: leaders and followers in collective movements of all-male groups in African savannah elephants (*Loxodonta africana*). *Scientific Reports* 10: 13996. <https://doi.org/10.1038/s41598-020-70682-y>
- Allen CRB, Brent LJJ, Motsentwa T, Croft DP. 2021. Field evidence supporting monitoring of chemical information on pathways by male African elephants. *Animal Behaviour* 176: 193–206. <https://psycnet.apa.org/doi/10.1016/j.anbehav.2021.04.004>
- Apps P, Mmualefe L, McNutt JW. 2013. A Reverse-Engineering Approach to Identifying Which Compounds to Bioassay for Signalling Activity in the Scent Marks of African Wild Dogs (*Lycaon pictus*). *Chemical Signals in Vertebrates* 12: 417–432. http://dx.doi.org/10.1007/978-1-4614-5927-9_33
- Bates LA, Sayialel KN, Njiraini NW, Poole JH, Moss CJ, Byrne RW. 2008. African elephants have expectations about the locations of out-of-sight family members. *Biology Letters* 4: 34–36. <https://doi.org/10.1098/rsbl.2007.0529>
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67 (1): 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Chamberlain AI. 2016. An Analysis of the Human Elephant Conflict Situation in the Boteti Area, Botswana: The Economic Cost of Elephant Crop Raiding. MSc thesis. University of Bristol, Bristol.
- Dejene SW, Mpakairi KS, Kanagaraj R, Wato YA, Mengistu S. 2021. Modelling continental range shift of the African elephant (*Loxodonta africana*) under a changing climate and land cover: implications

for future conservation of the species. *African Zoology* 56 (1): 25–34. <https://doi.org/10.1080/15627020.2020.1846617>

Enu kwa EH. 2017. Human-Elephant conflict mitigation methods: A review of effectiveness and sustainability. *Journal of Wildlife and Biodiversity* 1 (2): 69–78. <https://doi.org/10.22120/jwb.2017.28260>

Evans KE. 2019. Elephants for Africa: male Savannah elephant *Loxodonta africana* sociality, the Makgadikgadi and resource competition. *International Zoo Yearbook* 53 (1): 200–207. <https://doi.org/10.1111/izy.12238>

Goodwin TE, Broederdorf LJ, Burkert BA, Hirwa IH, Mark DB, Waldrip ZJ, Kopper RA, Sutherland MV, Freeman EW, Hollister-Smith JA, et al. 2012. Chemical signals of elephant musth: temporal aspects of microbially-mediated modifications. *Journal of Chemical Ecology* 38: 81–87. <https://doi.org/10.1007/s10886-011-0056-8>

Haring RD, Beverly G, Thompson PN, Taylor A, O'Dell JH. 2023. Evaluation of lion (*Panthera leo*) scat as a wild dog (*Lycaon pictus*) deterrent on game farms. *Wildlife Research* 50 (12): 1021–1030. <http://hdl.handle.net/2263/96679>

Hutchinson JR, Schwerda D, Famini DJ, Dale RHI, Fischer MS, Kram R. 2006. The locomotor kinematics of Asian and African elephants: changes with speed and size. *Journal of Experimental Biology* 209 (19): 3812–3827. <https://doi.org/10.1242/jeb.02443>

Jacobson SL, Dechanupong J, Horpiencharoen W, Yindee M, Plotnik JM. 2023. Innovating to solve a novel puzzle: wild Asian elephants vary in their ability to problem solve. *Animal Behaviour* 205: 227–239. <https://doi.org/10.1016/j.anbehav.2023.08.019>

Pettigrew JD, Bhagwandin A, Haagen sen M, Manger PR. 2010. Visual acuity and heterogeneities of retinal ganglion cell densities and the tapetum lucidum of the African elephant (*Loxodonta africana*). *Brain, Behaviour and Evolution* 75: 251–261. <https://doi.org/10.1159/000314898>

Plotnik et al. 2019. Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences* 116 (25): 12566–12571. <https://doi.org/10.1073/pnas.1818284116>

Poole JH and Moss CJ. 1989. Elephant mate

searching: group dynamics and vocal and olfactory communication. *Proceedings of the Symposia Zoological Society (London)* 61: 111–125.

Pozo RP, Coulson T, McCulloch G, Stronza A, Songhurst A. 2017. Chilli-briquettes modify the temporal behaviour of elephants, but not their numbers. *Oryx* 53 (1): 100–108. <https://doi.org/10.1017/S0030605317001235>

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. <https://psycnet.apa.org/doi/10.1007/s10071-019-01242-9>

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> [Accessed 25 April 2023]

Songhurst A, McCulloch G, Coulson T. 2016. Finding pathways to human-elephant coexistence: a risky business. *Oryx* 50 (4): 713–720.

Stevens J. 2018. Understanding human-elephant interactions in and around Makgadikgadi Pans National Park, Botswana. PhD thesis. University of Bristol, Bristol.

Thouless CR, Dublin HT, Blanc JJ, Skinner DP, Daniel TE, Taylor RD, Maisels SF, Frederick, HL, Bouche P. 2016. African elephant status report 2016: an update from the African Elephant Database. *IUCN Species Survival Commission No. 60*. Gland, Switzerland

Valenta K, Schmitt MH, Ayasse M, Nevo O. 2020. The sensory ecology of fear: African elephants show aversion to olfactory predator signals. *Conservation Science and Practice* 3. <https://doi.org/10.1111/csp2.333>

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.

Wood M, Chamaillé-Jammes S, Hammerbacher A, Shrader AM. 2022. African elephants can detect water from natural and artificial sources via olfactory cues. *Animal Cognition* 25: 53–61. <https://doi.org/10.1007/s10071-021-01531-2>