White rhinos decreased visitations and increased vigilance in response to human vocalizations

Zoliswa N. Nhleko[1, 2], Adrian M. Shrader[3], Sam M. Ferreira[2], Robert A. McCleery[3,4*]

[1]Interdisciplinary Program in Ecology, University of Florida, Gainesville, FL, 32611; [2]Savanna Node, Scientific Services, SANParks, Skukuza, 1350; [3]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa, [4] Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, 32611

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*Corresponding author: ramccleery@ufl.edi

mobile +1 352 214 3073

110 Newins-Ziegler Hall, PO Box 10430, Gainesville, FL 32611-0430

Abstract

Harnessing animals' fear of humans has the potential to aid in the conservation of wildlife. Most vertebrates perceive humans as 'super predators'. While predator cues are an important non-lethal management tool, the use of human cues for the management has rarely been implemented or experimentally tested. Extensive poaching is threatening the persistence of white rhinos (*Ceratotherium simum simum*), and there is a need to deter them from areas with elevated poaching risks. To investigate the feasibility of harnessing white rhinos' fear of humans to aid in their conservation, we conducted playback experiments at rhino middens. We broadcasted repeated human (treatment) and bird (control) vocalizations, and measured changes in visitations and anti-predator responses. We found overall rhino visitations did not change in response to controls but decreased by 46 % in response the human vocalizations. This pattern appears to be driven by the response of females, who decreased their visitations by 70% in response to human vocalizations, while male's visitation remained unchanged. This difference is likely related to male's defense of small exclusive territories. Providing evidence that changes in female visitation rates were a function of white rhino's perceived fear we found both sexes exhibited more vigilance in response to human vocalizations (males 69.5%, females 96%) compared to controls. We also saw a 63% reduction of other herbivores at treatment sites. Our findings provide evidence that female white rhinos, critical to population recovery, and other large herbivores' fear of humans can be used to alter their movements and behaviour.

Introduction

Animals' fear of predation is a powerful force that can reshape their behaviour, habitat use, and movement patterns (Laundre, Hernandez & Ripple, 2010; Ordiz *et al.*, 2011). Animals assess variation in their risk of predation using different cues (olfactory, vibrations, auditory, and visual) (Hermann and Thaler, 2014; Nersesian, Banks & McArthur, 2012) and show a heightened response to cues from the most lethal potential predators (Frid and Dill, 2002). In many landscapes, humans have replaced large carnivores as the most lethal predator (cliff *et al.*, 2012; Smith *et al.*, 2017; Suraci *et al.*, 2019), with most larger vertebrates perceiving humans as 'super predators' (Ciuti *et al.*, 2012; Smith *et al.*, 2017; Suraci *et al.*, 2019).

Animals' most energetically costly response to fear is to flee or avoid the area where they perceive a heightened risk (Frid and Dill, 2002). Alternatively, animals can use vigilance behaviour to mitigate their risk while still accessing food resources (Li, Jiang, Beauchamp, 2009; Ordiz *et al.*, 2011; Creel, Schuette & Christianson, 2014). Combined, the repeated use of these behavioural responses to non-lethal threats from humans can lead to reductions in animal fitness (Lima and Dill, 1990; Creel, 2018). However, there is a potential to harness animals' fear to aid in their conservation and management (Atkins *et al.*, 2017; Allen *et al.*, 2019; Miller and Schmitz, 2019). In fact, the use of predator cues to induce fear in animals and increase their perception of predation (i.e. landscape of fear) has become an important non-lethal management tool to reduce human conflict with potential nuisance species such as rodents, waterfowl, and scavenging birds (Baxter and Allan, 2006; Atkins *et al.*, 2017; Mahlaba *et al.*, 2017). Encouraging animals' fear response might also help reduce the number of animals selecting potentially dangerous areas with a higher risk of mortality (i.e. ecological traps; le Roex, Dryer & Ferreria 2020), or human conflict (Gaynor *et al.*, 2019). For example, elephant's (*Loxodonta africana*) fear of bees has been used, with some success, to deter them from raiding crops (King *et al.*, 2009; Vollrath and Douglas-Hamilton, 2002). Yet, the most effective management tool should elicit the greatest fear response, and for many animals, that response is likely to come from human cues (Ciuti *et al.*, 2012;

Smith *et al.*, 2017; Suraci *et al.*, 2019). While researchers have recognized the potential for using human cues for the management of wildlife (Cromsigt *et al.*, 2013; Kuijper *et al.*, 2019), rarely has this concept been implemented or experimentally tested.

Poaching (i.e. illegal hunting) of white rhino (*Ceratotherium simum simum*) in southern Africa has resulted in dramatic population declines, threatening their persistence (Ferreira *et al.*, 2018, Nhleko *et al.*, 2021). One strategy for mitigating the effects of poaching is transporting rhinos to safer areas (Ferreira *et al.*, 2018). However, there are substantial costs and risks (e.g. bovine tuberculosis) associated with these relocations (Miller *et al.*, 2018). As such, a cheaper, less invasive method for moving rhinos out of poaching hotspots is desirable. When rhinos encounter humans, their reactive response is to stand their ground or flee (Owen-Smith, 1987). While we know very little about how rhinos proactive respond to areas with frequent human activity, we expect they will avoid them (Creel, 2018).

Male and female rhino differ in their movement and social groupings. Female and subadult white rhinos maintain large annual home ranges (ca. $6 – 45$ km^2) (Owen-Smith, 1972; Pienaar *et al.*, 1993; Rachlow, Key & Berger 1999; Shrader and Owen-Smith, 2002), while males establish smaller, more permanent ranges between 0.8 and 2.6 km^2 (Owen-Smith,1971, 1988). Females and subadults forming groups of 2-7 individuals, while territorial adult males are solitary (Owen-Smith, 1974). All individuals regularly defecate in communal dung heaps, called middens (Owen-Smith, 1974; Marneweck, Jürgens, & Shrader *et al.*, 2017; Marneweck, Jürgens, & Shrader *et al.*, 2018a). Middens are often located around frequently used footpaths, waterholes, and territory boundaries (Marneweck, Jürgens, & Shrader, 2018a). Studies have suggested that white rhinos use middens to communicate amongst each other since dung odours can be used to transmit information (Rodgers *et al.*, 2015; Eppley, Ganzhorn & Donati 2016; Marneweck *et al.*, 2017). Territorial males frequent the middens throughout their territory (Marneweck, Jürgens, & Shrader, 2018b) and use the ones along territory boundaries to communicate territorial ownership (Owen-Smith, 1974), while females likely visit specific middens less frequently, using them to advertise their oestrous state (Marneweck *et al.*, 2017; Marneweck *et al.*, 2018a).

Due to the frequency with which they are visited, middens provide an opportunity to expose individuals to potentially fear inducing cues (Marneweck *et al.*, 2018a). Accordingly, the goal for this study was to experimentally investigate the feasibility of altering rhino behaviour by introducing human auditory cues at middens. Specifically, we wanted to determine if human auditory cues i) reduce visitations to specific middens and increase vigilance of white rhinos, ii) elicited sex-based behavioural responses in white rhinos, and iii) reduced the visitation rates of other herbivore species. We predicted a reduction in visitation rates of white rhinos and other herbivore species, and an increase in white rhino's vigilance behaviour in response to auditory cues from human activity (Frid and Dill, 2002; Gaynor *et al.*, 2018, Ciuti *et al.*, 2012; Dwinnell *et al.*, 2019). We also predicted white rhino's response (i.e. visitation, vigilance) to human cues would be more pronounced in female rhinos because they have less invested in the establishment and maintenance of their territories than the more localised males (Owen-Smith 1971, 1988).

Materials and methods

Study site

Our study was conducted in Marakele National Park (290.51 km^2, Marakele hereafter), located in the south-western part of the Limpopo province in South Africa (Figure 1). Marakele receives 556-630 mm annual rainfall in the summer months (October – March) with temperatures up to 32 °C (van Staden and Bredenkamp, 2005). Winters are cool (1ºC - 6ºC average temperatures) and dry with frost occurring in low lying areas (Novellie and Spies, 2014). The park is situated in the Savanna Biome and its vegetation includes Sour Bushveld, Mixed Bushveld, Sourish Mixed Bushveld and North-Eastern Mountain Sourveld (van Staden and Bredenkamp, 2005). The dominant grass species in the park include *Trachypogon spicatus, Themeda triandra, Eragrostis curvula,* and *Aristida transvaalensis* (van Staden and Bredenkamp, 2005). Marakele has a medium-sized (100 < 500) population of white rhino (Ferreir*a et al.*, 2017). Other common mammals in the park include elephant, black rhino (*Diceros bicornis minor*),

kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), zebra (*Equus quagga*), buffalo (*Syncerus caffer*), warthog (*Phacochoerus africanus*), and duiker (*Cephalophinae*) (Novellie and Spies, 2014).

Study Design

We used a Before-After-Control-Impact (BACI) experimental design to understand white rhino's behavioural responses to human vocalizations at middens. We evaluated white rhino's response with metrics of visitations before and after human treatments occurred and compared them to measurements taken before and after control (i.e. bird vocalizations) treatments (Valeix, 1991). Additionally, we recorded the changes in the visitations of other herbivores using the same BACI design.

We identified experimental sites by opportunistically searching for white rhino middens in areas of high rhino activity. At each midden we attached a camera (X-Change Color Model 1279, Cuddeback) to the nearest (5 - 15m) tree with an unobstructed view of the midden. We assumed no variation in vigilance behaviours prior to our treatments and set cameras to take pictures to capture baseline visitation rates. Using preliminary data, we determined that rhino did not stay at or return to the same midden after 15 minutes. Accordingly, we set the camera to have a 15 min delay between photo sequences and considered each sequence (3 pictures) to be an independent visitation (Brook, Johson & Ritchie, 2012). After 14 days of before-data, we selected sites with ≥10 rhino visitations that were ≥ 600 m apart as experimental treatments.

We identified 17 viable middens for manipulation. Expecting more variation in white rhinos' response to human vocalization, we randomly selected eleven sites for the treatment (humans) and 6 sites for the control (birds). We used auditory cues because sound can be easily manipulated, standardized across time and space, and elicits clear anti-predator responses in mammals (Blumstein *et al*., 2008, Clinchy *et al.*, 2011; Suraci *et al.*, 2016a; Smith *et al.*, 2017). To create environments with continuous and elevated levels of cues, we prepared 30 sec. playbacks of human vocalizations obtained online from local

radio stations' library archives. The human voices included both males and females speaking in six languages common in the area: isiZulu, isiPedi, English, Afrikaans, TshiVenda, and IsiShangaan. For controls we used 30-sec calls from common bird species that should not elicit a fear response (Epperly *et al.* 2021). During the day, we used calls from the African hoopoe (*Upupa Africana*) and at night, we used calls from the African Scops Owl (*Otus senegalensis*).

We sourced our recording of birds from collaborators and the Xeno-Canto website (www.xeno-canto.org). We cleaned (e.g. other voices, background music) all our recordings (human and control audio) using Audacity (version 2.3.3). We created 10 exemplars for each playback type (e.g. 10 hoopoe, 10 isiPedi etc.) for a total for 80 sound clips. Next, we created a 24-hour soundtrack made up of 30-sec sound clip (control or human) followed by 90 seconds of silence to minimize the likelihood of habituation to the audio recordings (Suraci *et al.*, 2016a). We randomized the order in which the sound clips were played using base R (version 3.6.1, RStudio Team) functions. We broadcasted the human and control vocalizations through solar powered speakers (Elzle, model BO-JDC01, China) for 14 days. Each midden had 1 speaker broadcasting the calls. The speaker was attached to a bush/tree within 2 m of the midden. Similar to other studies, we broadcasted the playbacks at a volume of 80 dB (Suraci *et al.*, 2019) and replaced used speakers with fully charged ones every 2 days. We kept the cameras in the same location throughout the experiment and switched them to video mode (30-sec long videos during the day and 20-sec during the night, the maximum video length the cameras can record at night) once the treatments began. At each site, we measured the number of independent white rhino visits, group sizes and the sex of individuals. In a similar manner we recorded the species and number of other herbivores that visited the middens. We received all necessary permits and ethical clearances from South African National Parks (SANParks).

Behaviour analysis

To detect measurable differences in white rhino behaviour once treatments began, we recorded and scored the behaviour of rhinos that were recorded for > 15 sec. To understand differences in vigilance behaviour, we recorded six behavioural responses as head up (head held higher than the knees), head down (head held below the knee), foraging, defecating/urinating, interacting with another individual, and alert (i.e. head up and scanning around with ears twitching). Alert white rhinos always had their heads up, but white rhinos often held their heads up without displaying alert behaviours. We consider both a raised head and alert behaviours (i.e. scanning) as clear indicators of vigilance (Hunter and Skinner, 1998; Childress and Lung, 2003; Li *et al.*, 2009; Shrader *et al.*, 2013; Dalerum and Belton, 2015) and similarly to other studies, we restricted our analyses the four most common and relevant behaviours (i.e. head up, head down, alert, and foraging; Dalerum and Belton, 2015; Palmer and Gross, 2018; Sura*ci et al*., 2016b).

We scored videos using the Solomon Coder software (19.08.02, Peter Andras). One observer reviewed videos from all the trials without knowledge of the treatment applied, a second observer independently scored a sample (25%) of the videos to confirm the scores by the first observer (Cinková and Shrader, 2020). We scored the behaviour of the focal rhino for the entire video. When we observed a mother and calf pair, we only scored the behaviour of the adult. We recorded all behaviours as events each being a minimum of 0.2 sec in length. We converted the total durations for all behaviours to percentages to account for difference in the total time the animal was recorded (Epperly et al. 2021), allowing us to compare full length videos with videos in which white rhinos disappeared before the end of the video clip (≥ 15 sec).

Statistical analysis

We compared white rhino's response to treatments combined by sex, and separately for males and females. This allowed us to determine if overall patterns were driven by differences in the response of each sex. To compare differences in rhino visitations to middens before and after treatments, we used

multiple-paired estimation (comparable to a repeated measures ANOVA; H*o et al*., 2019), coupled with a

nonparametric measure of effect size (Cliff's Delta). In addition, we generated Cumming's plots which

allowed for the visualization and estimation of the precision of the effect size via bootstrapping of the

95% CI (Cumming, 2012). Estimating effect size allowed us to assess the strength of the change between

the control and the treatment experiments (Tomczak and Tomczak, 2014). Cliff's delta ranges from -1

to 1, where a delta value of – 1 or 1 indicates no overlap in the data between experiments, and a

value of 0 indicates complete overlap (Cliff, 1993; Macbeth, Razumiejczyk, & Ledesma

2011). We fit rhino visitation models (combined and by sex) to a Poisson distribution using the dabest

package on Spyder (Python v. 3.7.6), and generated Cliff's delta using the package orddom (Rogmann,

2013) on the R platform (v. 3.4.3, R Core Team).

Similarly, to compare differences in visitations for other herbivore species, we again used

multiple paired estimation Cliff's delta and Cumming's plots. To compare overall differences between the

four common behavioural responses for white rhinos, we used a Friedman's repeated measure test from

the jmv package (Selker *et al.*, 2020) in R, to account for the non-parametric distribution of the data. Then

using the anovaRMNP function from the jmv package we conduced pairwise comparisons (Durbin-

Conover test) specifically between the broad head up and head down categories, and the more specific

alert and foraging categories.

Results

We recorded 197 individual rhino visitations from 140 observations (Males = 123, Females = 74).

Examining all white rhinos, we found that a difference between pre- and post-treatment visitation in

response to the human treatment (Cliff's delta = -0.413, sd = 0.155, p = 0.01) relative to the control

(Cliff's delta = -0.062, sd (delta's standard dev) = 0.240, p = 0.80), with overall rhino visits decreasing by

more than 5 visits per midden (46 %) during the human treatments (Figure 2A). Separating the visitation

data by sex, we found the human treatment had a strong influence on visitation (Cliff's delta = -0.595, sd

= 0.187, p = 0.004) on female white rhinos compared to the control (Cliff's delta = 0, sd = 0.343 p = 1), with female visits decreasing by at least 6 visits per site during human treatments (70%; Figure 2B). However, we found a non-significant difference in males' response to human treatments (Cliff's delta = -0.429, sd = 0.228, p = 0.07, Figure 2C) and controls (Cliff's delta = -0.222, sd (delta's standard dev) = 0.323, p = 0.51).

For all white rhinos, the main behavioural responses differed between the control and treatment experiments (Friedman's test, χ2 = 89.32, df = 3, p < 0.0001). We found a difference in our broad categories of head down and head up, with more white rhinos having their heads up during the human treatment than in the control treatment (test statistic = 2.71, p < 0.05). However, we did not find a difference between our more specific categories, foraging and alert (t statistic = 1.30, p = 0.20). Similar to our examination of all white rhinos, overall behaviours (Friedman's test, χ2 = 105.0, df = 3, p < 0.0001) and broad head up down and head up categorization differed between treatments for males (test statistic = 5.14, p < 0.01). Specifically, male white rhino had their head up by 69.5% more often in response to human treatments sites control treatments. Again, we found no difference between the more specific foraging and alert categories (t statistic = 0, p = 1.0).

The behavioural responses of female white rhinos were slightly different. Their responses also differed between the treatments (Friedman's test, χ2 = 16.25, df = 3, p < 0.01) but unlike males we found a difference between foraging and alert (t statistic = 2.34, p = 0.02) as well as head down and head up (test statistic = 2.52, p = 0.01). Female white rhinos spent a greater percentage of their time with their head up (96%) and alert (83.9% i.e. scanning) during the treatment experiments than during the control experiments.

Finally, we recorded 161 visits from other herbivore species including black rhino (14), kudu (27), and zebra (23; Appendix 1). As with all rhinos pooled and female white rhinos, we saw fewer visits after the human treatment experiments compared to before them (mean difference = -17; Cliff's delta = -0.44,

sd = 0.09, p = 0.001; Figure 2D). We found no difference in the visitation of herbivores before and after the control treatments (Cliff's delta = -0.01352, sd = 0.14383, p = 0.92).

Discussion

With humans now the dominant ecological force in most terrestrial landscapes, regular encounters with humans are likely to instil fear in a wide range of animals (Ciuti *et al.*, 2012; Gaynor *et al.*, 2018). We found clear evidence that white rhino's perceived fear of humans resulted in avoidance and increased vigilance at middens. Rhino responses to human auditory cues were consistent with our predictions and the growing body of literature showing that animals' fear of humans is ubiquitous (Ciuti *et al.*, 2012; Smith *et al.*, 2017; Dwinnell *et al.*, 2019). Moreover, our experimental findings showing that human auditory cues can alter the behaviour of white rhinos and other herbivores, suggest that while cues of human activity may lead to deleterious effects on populations of wild animal, they also hold tremendous potential to be harnessed in the management of threatened species.

Using auditory cues of humans, we were able to reduce white rhinos use of an important social resource, middens. However, most of the changes in visitations that we observed were from female white rhinos, with males returning to middens at similar rates regardless of the treatments. The difference in visitations was likely related to male's defence of small (about 2.6 km^2) exclusive territories. Male white rhinos rarely leave their territories, except to find water, in the dry season (Owen-Smith, 1971, 1972). Additionally, scent marking at middens informs intruding males of another's territory boundaries and reduce direct confrontations (Owen-Smith, 1971), and the freshness of these signals is likely important (Marneweck, Jürgens, & Shrader 2018). As such, the drive to regularly scent mark and maintain their territory was likely stronger than male white rhinos' fear of humans. On the other hand, female white rhinos are more tolerant to the presence of other rhinos in their home ranges (Owen-Smith, 1971), and since they have larger home ranges, they have the option to move to a different part of their home range to avoid a risky area.

Supporting our claim that changes in visitation rates were a function of rhino's perceived fear, we found that white rhinos of both sexes that visited middens with human treatments displayed more vigilance (i.e. head up) than white rhinos visiting control treatments. When grazing herbivores hold their heads up and away from the ground it is an indicator of vigilance (Childress and Lung, 2003; Dalerum and Belton, 2015; Hunter and Skinner, 1998; Li *et al.*, 2009). Studies have shown that some vigilance behaviour come at the cost of lost opportunities to mate and forage (Hunter and Skinner, 1998; Childress and Lung, 2003; Li *et al.*, 2009; Dalerum and Belton, 2015). However, large herbivores may be able to maintain a constant rate of food intake while exhibiting vigilance behaviours such as scanning the landscape for predators (Fortin *et al.*, 2004). Although male rhino's visitation rates did not change with human cues, they did alter their vigilance behaviour, suggesting the increased human presence instilled fear, just not enough to overcome their drive to defend their territory. Finally, the results suggest that the other herbivores observed in our study also avoid areas with increased cues of human activities (Creel *et al.*, 2014, Gaynor *et al.*, 2018).

Implementing fear as a management tool

Our findings highlight the potential for using animals' fear of humans as a cheaper, less invasive method than capturing and moving animals away from areas with potential for conflict. Poaching events are not homogenously distributed across the landscape. Rather, they are clustered, creating poaching hotspots (Haine*s et al*., 2012; Maingi *et al*., 2012; Rashidi *et al*., 2015). Ease of access and areas with high concentration of target species (i.e. watering holes) can create these poaching hotspots (Haines *et al.*, 2012; Maingi *et al.*, 2012). If these hotspots can be identified, our results suggest that the localized application of human vocalizations may reduce female rhinos' use of these ecological traps, potentially mitigate their risk to poaching. This is especially important because the survival of adult females is critical to the recovery of the white rhino populations (Nhleko *et al*., 2021). Additionally, females may be more prized by poachers because of their potentially longer horns than males (Pienaar *et al*., 1991).

The localized application of fear using human vocalizations also has the potential for reducing the activity of herbivores in areas where they have caused ecological damage and are in conflict with humans. For example, fenced populations of African elephant (Asner *et al.*, 2016; McCleery *et al.*, 2018), white-tailed deer (*Odocoileus virginianus*; Côté *et al.*, 2004), kangaroo (*Macropus giganteus*; Viggers and Hearn, 2005), and aggregations of other herbivores can degrade vegetation communities, threatening ecosystem function and reducing productivity (Asner *et al.*, 2016; Asner and Levick, 2012; Cromsigt *et al.*, 2013). These herbivore-induced impacts are often localized and using their fear of humans would allow managers to change their movement and behavioural patterns to reduce their use of sensitive or degraded areas (Cromsigt *et al.*, 2013).

Our study demonstrated the potential to alter female rhino movements and behaviour in localized areas over a 2-week period. The methods used here might have utility in moving females from localized hazards (i.e. fences, roads, ecological traps) where they could be in danger of being poached. However, this technique will be more valuable if it could move white rhinos across larger areas (> 500 m) and keep them away for longer periods. To do this, we would need to create an unpredictable landscape of fear by making the perception of danger spatially predictable yet temporally unpredictable (Cromsigt *et al.*, 2013). Prior to increasing the spatial and temporal scales of the human vocalization trials it would be critical to fill important informational gaps. For example, we would need to know how far white rhinos move to avoid human treatment sites, how long they avoided the sites after vocalizations end, and importantly, how much exposure leads to habituation. Rates of habituation are influenced by the temporal distribution of the stimulus, with infrequent presentation of the stimulus resulting in no habituation (Staddon, 1993). As such, we would have to examine different ratios of human vocalization to silence to determine habituation thresholds. It would also be important to determine the influence of volume and speaker density (i.e. distribution across the landscape) on the magnitude and spatial extent of white rhinos' response. Addressing these gaps would allow us to determine the length and spacing of treatments and maximize the potential of using rhino's fear of humans as a management tool.

The large-scale implementation of fear as a management tool would also have to address several logistical issues. For example, it would require speakers that can play for longer than 2 days without a need to change batteries. This could likely be achieved by pairing speakers with a solar panel or portable battery. Additionally, we suggest that it would be worth considering using food and human vocalizations as a potential management strategy. Ensuring that high quality resources (e.g. supplemental forage) exist in low poaching areas, may reduce the probability of animals returning to poaching hotspots with human vocalization treatments. However, additional measures (e.g. translocations) may still be needed to remove females from high poaching areas. Doing so would reduce the possibility of adult females leading subadult companions to these dangerous areas during probing excursions outside of established home ranges (Shrader and Owen-Smith, 2002).

In conclusion, we found the fear of humans to be an effective deterrent for female white rhinos and their young. Since the loss of a female has negative impacts on the lifetime reproductive potential of the population (Nhleko *et al.*, 2021), any technique that can deter females from high poaching areas is likely to aid conservation efforts. With refinements, this technique could be scaled temporally and spatially to become an effective tool for changing the behaviour of animals in high-risk areas and anti-poaching efforts.

Acknowledgements

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Figure captions

Figure 1. Location of Marakele National Park in South Africa. The polygons represents the sections where the rhino playback experiments were carried out from June to September 2019.

Figure 2. At the top of each pannel are Cumming plots, with each line representing the rhino visits to middens before and after bird vocalizations (Pre-Control, Post-Control) used as controls and before and after human vocalizations (Pre-Treat, Post-Treat). On the bottom of each pannel are boostraped distributions of the mean differences in midden visits at with bird (Post-Control – Pre-Control) and human vocalization. Distributions that contain 0 suggest no change. The pannels display visitations for (A) All rhinos (combined), (B) rhino females, (C) rhino males and (D) other herbivores.