



White rhinos and other herbivores decrease visitations and increase vigilance in response to human vocalizations

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Harnessing the fear animals have 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 nonlethal management tool, the use of human cues for 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 the fear white rhinos have 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 antipredator responses. We found that overall rhino visitations did not change in response to controls but decreased by 46% in response to 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 visitations by males remained unchanged. This difference is likely related to males defending small exclusive territories. Providing evidence that changes in female visitation rates were a function of the perceived fear of white rhinos, we found that 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 the fear of humans can be used to alter the movements and behavior of female white rhinos, critical for population recovery, as well as other large herbivores.

Key words: behavior modification, *Ceratotherium simum*, middens, perceived risk, playback experiment

The fear animals have of predation is a powerful force that can reshape their behavior, habitat use, and movement patterns (Laundre et al. 2010; Ordiz et al. 2011). Animals assess variation in their risk of predation using different cues (olfactory, vibrations, auditory, and visual; Nersesian et al. 2012; Hermann and Thaler 2014) 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 (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).

The most energetically costly response of animals to fear is to flee or avoid the area where they perceive a heightened risk (Frid and Dill 2002). Alternatively, animals can use vigilance behavior to mitigate their risk while still accessing food

resources (Li et al. 2009; Ordiz et al. 2011; Creel et al. 2014). Combined, the repeated use of these behavioral responses to nonlethal threats from humans can lead to reductions in animal fitness (Lima and Dill 1990; Creel 2018). However, there is a potential to harness the fear of animals 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 risk (i.e., landscape of fear) has become an important nonlethal 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 an animals response to fear might also help reduce the number of animals selecting potentially dangerous areas with a higher risk of mortality (i.e., ecological traps; le

Roex et al. 2020), or human conflict (Gaynor et al. 2019). For example, the fear of elephants (*Loxodonta africana*) to bees has been used, with some success, to deter them from raiding crops (Vollrath and Douglas-Hamilton 2002; King et al. 2009). 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 respond proactively to areas with frequent human activity, we expect that they will avoid them (Creel 2018).

Male and female rhinos differ in their movement and social groupings. Female and subadult white rhinos maintain large annual home ranges (ca. 6–45 km²; Owen-Smith 1972; Pienaar et al. 1993; Rachlow et al. 1999; Shrader and Owen-Smith 2002), while males establish smaller, more permanent ranges between 0.8 and 2.6 km² (Owen-Smith 1971, 1988). Females and subadults form 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 et al. 2017, 2018a). Middens are often located around frequently used footpaths, waterholes, and territory boundaries (Marneweck et al. 2018a). Studies have suggested that white rhinos use middens to communicate among each other since dung odors can be used to transmit information (Rodgers et al. 2015; Eppley et al. 2016; Marneweck et al. 2017). Territorial males frequent the middens throughout their territory (Marneweck et al. 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 estrous 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 behavior 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-specific behavioral 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 the vigilance behavior of white rhinos in response to auditory cues from human activity (Frid and Dill 2002; Ciuti et al. 2012; Gaynor et al. 2018; Dwinnell et al. 2019). We also predicted that the response (i.e., visitation, vigilance) of white rhinos to human cues would be more pronounced in female rhinos because they are less invested in the establishment and maintenance of their territories than the more localized males (Owen-Smith 1971, 1988).

MATERIALS AND METHODS

Study site.—Our study was conducted in Marakele National Park (290.51 km², Marakele hereafter), located in the south-western part of the Limpopo province in South Africa (Fig. 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 (1°C–6°C 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 (Ferreira 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 the behavioral responses of white rhinos to human vocalizations at middens (Underwood 1991). We evaluated the response of white rhinos 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



Fig. 1.—Location of South Africa on the African continent and Marakele National Park within South Africa. The polygons represent the sections where the rhino playback experiments were carried out from June to September 2019.

2012). Additionally, we recorded the changes in 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 with a white “strobe flash” for color pictures at night) to the nearest (5–15 m) tree with an unobstructed view of the midden. We assumed no variation in vigilance behaviors prior to our treatments and set cameras to take pictures to capture baseline visitation rates. Using preliminary data, we determined that rhinos did not stay at or return to the same midden after 15 min. Accordingly, we set the camera to have a 15-min delay between photo sequences and considered each sequence (three pictures) to be an independent visitation (Brook et al. 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 the response of white rhinos to human vocalization, we randomly selected 11 sites for the treatment (humans) and six sites for the control (birds). We used auditory cues because sound can be easily manipulated, standardized across time and space, and elicits clear antipredator 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-s playbacks of human vocalizations obtained online from a library of local radio station 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-s 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 recordings 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-h soundtrack made up of 30-s sound clip (control or human) followed by 90 s 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 one 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-s long videos during the day and 20-s 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 by groups (group size = 1–4) and the sex of adults. We sexed adults during both day and night based on the presence of accompanying young (female) and genitalia. In a similar manner, for all other larger herbivores (>12 kg) we recorded the species, the number of independent groups (group size = 1–60), and individuals that visited the middens. Our research practices followed ASM guidelines (Sikes et al. 2016) for the use of wild mammals in research and we received all necessary permits and ethical clearances from South African National Parks (SANParks).

Behavior analysis.—To detect measurable differences in white rhino behavior once treatments began, we recorded and scored the behavior of rhinos that were recorded for > 15 s. To understand differences in vigilance behavior, we recorded six behavioral 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 behaviors. We considered both a raised head and alert behaviors (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). Similar to other studies, we restricted our analyses to the four most common and relevant behaviors (i.e., head up, head down, alert, and foraging; Dalerum and Belton 2015; Suraci et al. 2016b; Palmer and Gross 2018).

We scored videos using the Solomon Coder software (19.08.02, Peter Andras). One observer reviewed videos from all trials without knowledge of the treatment applied, and 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 behavior of the focal rhino (i.e., entered the frame first) for the entire video. When we observed a mother and calf pair, we only scored the behavior of the adult. We recorded all behaviors as events each being a minimum of 0.2 s in length. We converted the total durations for all behaviors 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 (minimum time ≥ 15 s).

Statistical analysis.—We compared the response of white rhinos 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; Ho et al. 2019), coupled with a nonparametric measure of effect size (Cliff’s delta). In addition, we generated Cumming 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 et al. 2011). We fit rhino visitation models (combined and by sex) using the dabest package on Spyder (Python Software Foundation, Python 3.7.6 2022), and generated Cliff's delta using the package orddom (Rogmann 2013) on the R platform (v. 3.4.3; R Core Team 2019).

Similarly, to compare differences between independent 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 behavioral responses for white rhinos, we used a Friedman's repeated measure test from the jmv package (Selker et al. 2022) in R, to account for the nonparametric distribution of the data. Finally, using the anovaRMNP function from the jmv package we conducted 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 (males = 123, females = 74) adult rhino from 140 independent visits. Examining all white rhinos, we found a difference in independent visits between pre- and posttreatment in response to the human treatment (Cliff's delta = -0.41 , SD [delta's standard deviation] = 0.16 , $P = 0.01$) relative to the control (Cliff's delta = -0.06 , $SD = 0.24$, $P = 0.80$), with overall rhino visits decreasing by more than 5 visits per midden (46%) during the human treatments (Fig. 2A). Separating the visitation data by sex, we found that the human treatment had a strong influence on visitation (Cliff's delta = -0.60 , $SD = 0.19$, $P = 0.004$) on female white rhinos compared to controls (Cliff's delta = 0 , $SD = 0.34$, $P = 1$), with female visits decreasing by at least 6 visits per site during human treatments (70%; Fig. 2B). We also found that the visitations of males decreased in response to human treatments; however, this pattern was not significantly different (Cliff's delta = -0.429 , $SD = 0.23$, $P = 0.07$; Fig. 2C) than controls (Cliff's delta = -0.22 , $SD = 0.32$, $P = 0.51$).

For all white rhinos, the main behavioral responses differed between the control and treatment experiments (Friedman's test, $\chi^2 = 89.32$, d.f. = 3, $P < 0.001$). 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 treatments than in the control treatments (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 behaviors (Friedman's test, $\chi^2 = 105.0$, d.f. = 3, $P < 0.001$) and broad head up and down categorization differed between treatments for males (test statistic = 5.14 , $P < 0.01$). Specifically, male white rhinos had their head up 69.5% more often in response to human treatments than to control treatments. Again, we found no difference between the more specific foraging and alert categories (t -statistic = 0 , $P = 1.0$).

The behavioral responses of female white rhinos were slightly different to the population as a whole. Their responses also differed between the treatments (Friedman's test, $\chi^2 = 16.25$, d.f. = 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 (t -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 independent visits (of groups) from other herbivore species including black rhino (36), kudu (75), and zebra (81; Supplementary Data SD1). As with all 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 , $SD = 0.09$, $P = 0.001$; Fig. 2D). We found no difference in the visitation of other herbivores before and after the control treatments (Cliff's delta = -0.01 , $SD = 0.14$, $P = 0.92$).

DISCUSSION

With humans now the dominant ecological force in most terrestrial landscapes, regular encounters with humans are likely to instill fear in a wide range of animals (Ciuti et al. 2012; Gaynor et al. 2018). We found clear evidence that the perceived fear of white rhinos to 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 the fear of animals to 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 behavior of white rhinos and other herbivores suggest that while cues of human activity may lead to deleterious effects on populations of wild animals, 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, a larger portion of the changes in visitations that we observed were from female white rhinos, with males returning to middens at rates that were reduced, but not significantly different than controls. The difference in visitations between males and females was likely related to males defending 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). They define their territories by marking middens with scent (Owen-Smith 1971), and fresher scents are more likely to reduce confrontations with other males (Marneweck et al. 2018b). As such, the drive to regularly scent mark and maintain their territory was likely stronger than the fear of humans by male white rhinos. 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.

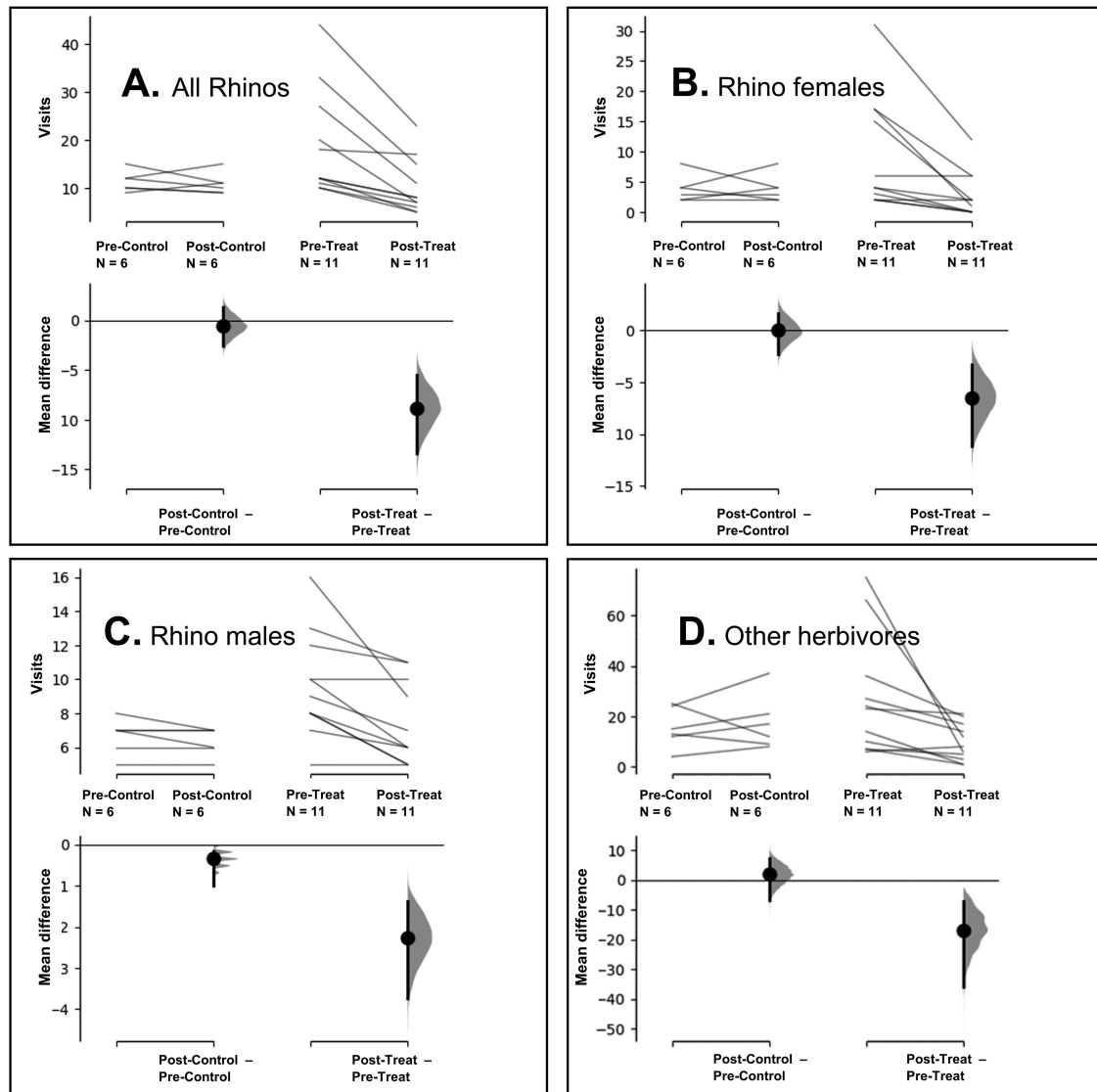


Fig. 2.—Panels contain Cumming plots, with lines representing the rhino visits to middens before and after bird vocalizations controls (pre-control, post-control), human vocalizations treatments (pretreat, posttreat), and bootstrapped distributions of the mean differences in midden visits. Distributions that contain 0 suggest no change. The panels display visitations for (A) all rhinos (combined), (B) rhino females, (C) rhino males, and (D) other herbivores.

Supporting our claim that changes in visitation rates were a function of perceived fear by rhinos, 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 (Hunter and Skinner 1998; Childress and Lung 2003; Li et al. 2009; Dalerum and Belton 2015). Studies have shown that some vigilance behavior comes 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 behaviors such as scanning the landscape for predators (Fortin et al. 2004). Although the visitation rates of male rhinos did not change with human cues, they did alter their vigilance behavior, suggesting

that the increased human presence instilled fear, just not enough to overcome their drive to defend their territories. 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).

Randomly assigning treatments, we found no evidence that the responses of rhinos to playbacks were confounded by environmental variation (e.g., water or vegetation); however, we did record more pretreatment visitation of rhinos on our treatment sites ($n = 11$, pretreatment $\bar{x} = 19.0$) than on our control site (pretreatment $\bar{x} = 10.5$). To adjust for this anomaly, we removed four sites with the highest number of pretreatment visitations from our analysis. Using this new data set ($n = 7$, pretreatment $\bar{x} = 12.1$) we still found that all rhinos (Cliff's delta = -0.58 , $SD = 0.16$, $P < 0.001$), and female rhinos (Cliff's delta = -0.76 , $SD = 0.24$, $P = 0.01$) reduced visitation in response to human vocalizations.

Implementing fear as a management tool.—Our findings highlight the potential for using the fear of animals to humans as a cheaper, less invasive method than capturing and moving animals away from areas with potential for conflict. Poaching events are not homogeneously distributed across the landscape. Rather, they are clustered, creating poaching hotspots (Haines 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 the use of female rhinos 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 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 and Levick 2012; Crooms et al. 2013; Asner et al. 2016). These herbivore-induced impacts are often localized and using their fear of humans would allow managers to change their movement and behavioral patterns to reduce their use of sensitive or degraded areas (Crooms et al. 2013).

Our study demonstrated the potential to alter female rhino movements and behavior 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 (Crooms 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 the response of white rhinos. Addressing these gaps

would allow us to determine the length and spacing of treatments and maximize the potential of using the fear of rhinos to 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, or the use of fire to enhance grass quality) 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 behavior of animals in high-risk areas and anti-poaching efforts.

ACKNOWLEDGMENTS

We are grateful to SANParks for financial and logistical support. We also thank the park manager and section rangers at Marakele National Park for access to the study sites. S. Khoza for logistical support and R. Mogoane, D. Morowane, and O. Matshona for field assistance. We also acknowledge M. Clinchy and L. Zanette for their help with the study design and A. Potash for assistance with coding. This work was supported by South African Parks and the University of Florida (U.S. National Institute of Food and Agriculture, Hatch project FLA-WEC-005125).

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—List of all herbivore species seen during the playback experiments in Marakele National Park.

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Submitted 16 December 2021. Accepted 20 July 2022.

Associate Editor was Rafael Reyna.