CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access

WILEY

Assessing the potential of conspecific playbacks as a post-translocation management tool for white rhinoceros

Vera Pfannerstill[1] [ORCID] | Niko Balkenhol[1] | Emily Bennitt[2] |
Onkgopotse Somalia Maboga[3] | Marina Scheumann[4]

[1]Wildlife Sciences, University of Goettingen, Göttingen, Germany

[2]Okavango Research Institute, University of Botswana, Maun, Botswana

[3]Rhinos Without Borders, Maun, Botswana

[4]Institute of Zoology, University of Veterinary Medicine Hannover, Hanover, Germany

Correspondence
Vera Pfannerstill, Wildlife Sciences, University of Goettingen, Büsgenweg 3, 37077 Göttingen, Germany.
Email: vpfanne@gwdg.de

Abstract

Translocations can be a useful management tool to support endangered species. Translocated white rhinoceroses sometimes disperse from their release sites and leave protected areas, requiring sedation and return transport by vehicles. To avoid stressful transportation, less invasive management tools are needed to get animals back to the release site. We tested whether playbacks of white rhinoceros calls can influence their movements and thereby offer a potential management tool. We performed 200 experiments with 26 free-roaming white rhinoceroses in two reserves in Botswana and recorded response intensity and duration, including body movement toward and away from the loudspeaker in response to a socio-positive and a socio-negative call. Rhinoceroses responded more to conspecific calls than to control sounds but did not show consistent behavioral responses across all experiments per call type. Males approached the loudspeaker more often than females. The intensity of responses was higher for calls recorded from unfamiliar than from familiar callers and behavioral responses differed between reserves. Further research is necessary to develop an applicable design for a combination of playbacks that would more reliably lead to directed body movement responses.

KEYWORDS
bioacoustics, conservation behavior, mammal, playback, socio-negative, socio-positive, vocalization

1 | INTRODUCTION

In species conservation, knowledge of animal behavior is an important basis for management decisions (Bro-Jørgensen et al., 2019; Greggor et al., 2016) and can help to avoid ecological traps, reduce human-wildlife conflicts, halt spreading of invasive species, and improve translocation success (Elmer et al., 2021; Greggor et al., 2016). Translocations, the intentional movement of species from one part of their natural range to another (IUCN Species Survival Commission, 2013), are important tools in wildlife management (Soorae, 2018). Translocation success relies on understanding species-specific movement patterns and social behaviors to avoid problems, for example, long-distance dispersal (Knox & Monks, 2014; le Gouar et al., 2012), homing behavior (Miller & Ballard, 1982), selection of unsuitable home ranges (Stamps & Swaisgood, 2007) and intraspecific

conflicts (Goldenberg et al., 2019; Linklater & Swaisgood, 2008; Shier & Swaisgood, 2012).

Animal behavior research has successfully been applied to manipulate animal movement patterns, for example using wildlife road crossing structures and deterring animals with species-specific cues (Blackwell et al., 2016; Greggor et al., 2016). The advantage of using species-specific cues is that they only weakly affect non-target species (Blackwell et al., 2016). At long distances, acoustic cues can be well suited to manipulate animal movement. For example, whistles have been used to direct reintroduced cheetahs to suitable habitats (Hayward et al., 2007), pingers are used to deter harbor porpoises from fishing nets (Larsen & Eigaard, 2014), and bee swarm playbacks to deter elephants from crop fields (Ngama et al., 2016). Conspecific playbacks have successfully been used to attract amphibians (James et al., 2015) and birds (Ahlering et al., 2010; Bradley et al., 2011; Molles et al., 2008) by demonstrating the high quality of a habitat through the presence of conspecifics (Kiester, 1979) and mating partners (Szostek et al., 2014). Studies with mammals are rare but also indicate that animals can be attracted by conspecific playbacks (Bryant et al., 2016; Filatova et al., 2011; Knörnschild et al., 2017). In contrast, alarm call playbacks can be used to train predator avoidance in predator-naïve species (Morris et al., 2021). Thus, playbacks of conspecific calls can be used to attract ("socio-positive calls") but also to deter ("socio-negative calls") animals and can therefore be important management tools for translocations.

The southern white rhinoceros (*Ceratotherium simum simum*), hereafter called "rhino(s)," is an endangered species that is regularly translocated to ensure genetic exchange between populations and to establish populations in new reserves (Emslie et al., 2009). These translocations are nowadays common practice and highly successful when rhinos are released into fenced reserves (Patton et al., 2010; Sheil & Kirkby, 2018). However, translocations of rhinos into open systems, such as the Okavango Delta in Botswana, have resulted in long-distance dispersal of a few individuals (Pfannerstill et al., 2022; Støen et al., 2009). Released rhinos are usually monitored, so dispersers can be captured and transported back by truck, but this procedure is stressful and potentially harmful for the animals (Linklater et al., 2010), costly, and time-consuming. Based on the natal habitat preference theory (Stamps & Swaisgood, 2007), artificial distribution of the rhinos' own dung could improve settlement in their new environment (Hitchins et al., 1972; Pienaar, 1994). However, this theory was not supported by a study of Linklater et al. (2006),

where translocated rhinos were attracted to dung from other rhinos, while their own dung led to more post-release dispersal. Penny et al. (2019) found no effect of olfactory cues on rhino movement but an effect of drones or siren sounds, suggesting that acoustic stimuli have a higher potential to guide rhino movement than olfactory stimuli. However, drones and sirens would also affect other species. In contrast, conspecific calls would probably only affect rhinos and be less stressful than artificial sounds.

Southern white rhinos have the largest vocal repertoire of all rhino species (Policht et al., 2008) with 11 different vocal signals described in Owen-Smith (1973). Two of the most common calls are Pant and Hiss calls (Jenikejew et al., 2020). The Pant consists of a sequence of inhalations and exhalations, produced in socio-positive contexts to initiate contact to other conspecifics. The Hiss (formerly named "threat") is produced in a socio-negative context to warn or displace other rhinos. Thus, Pants have the potential to attract whereas Hisses have the potential to deter rhinos. The first step in applying playbacks as management tools are to test whether animals respond to conspecific calls as expected. To date, playback studies with rhinos focussed on contact or mating calls (Pants and Hics; Cinková & Policht, 2016; Cinková & Shrader, 2020, 2022), whereas socio-negative calls have not been investigated. Both sexes approached the loudspeaker in response to Pant calls; territorial males also responded with dung or urine marking, showing the possibility to stimulate territorial behavior with playbacks (Cinková & Shrader, 2020). Wild anoestrous females reacted more intensively to Pants of unfamiliar senders than to controls (Cinková & Shrader, 2022), so the familiarity may affect responses, as shown in elephants (McComb et al., 2000).

The aim of this study was to test whether rhinos show distinct responses to socio-positive and socio-negative conspecific call types, and how those responses are affected by familiarity. We hypothesized that (i) rhinos will display a higher intensity and longer response duration toward conspecific calls than to control sounds, including being attracted by Pants and deterred by Hisses; (ii) responses will be consistent between sexes; (iii) rhino behavioral responses will vary in intensity between playbacks from familiar and unfamiliar callers, but (iv) responses will be consistent across populations, here represented by reserves. Moreover, we investigate to which extent ecological factors that impact sound propagation (wind, distance; Bradbury & Vehrencamp, 2011; Maciej et al., 2011) and social factors (behavioral state, presence of surrounding rhinos) affect rhino behavioral responses to playbacks.

2 | METHODS

2.1 | Ethics statement

This article contains data derived from playback experiments influencing behavior of wild white rhinos, but no animal was handled directly for the study. A research permit (ENT 8/36/4 XXXXII 58) was issued by the Ministry of Environment, Natural Resources Conservation and Tourism of Botswana.

2.2 | Study area and subjects

The study was conducted between May and December 2020 with free-roaming white rhinos in two private reserves in Botswana. The names and exact locations of the reserves are not stated for security reasons (Clements et al., 2020). In reserve A, the vegetation consisted of grasslands and mixed savannah bushland. We tested 11 rhinos (eight females, three males) that were habituated to cars due to daily monitoring and met regularly in different group compositions of up to eight individuals. All females, except one subadult, had calves. In reserve B, the vegetation was dense savannah bushland with grassy meadows and stony desert parts. Of the 15 rhinos (eight females, seven males) that we tested, older individuals were mainly solitary while younger rhinos moved in groups of three to four individuals. Only two females had calves. There were artificial water holes and feeding stations at which the rhinos were given additional lucerne *(Medicago sativa)* because the vegetation did not provide enough forage. The rhinos were not habituated to cars or humans but to the artificial feeding stations and water holes and therefore data were often collected at these places. Two rhinos, one male and one female, were kept in an enclosure of approximately 2 km² to ensure breeding and were only tested when feeding from the supplementary lucerne. Rhinos had individual ear notches for identification.

2.3 | Recording, preparation, and presentation of playback stimuli

For playback experiments, we used the rhino call types Hiss and Pant, and bird calls as control stimuli. Details of the recording procedure and the preparation of the stimuli can be found in the Supporting Information Method S1. To test a wide range of senders, we used male (Pant: 3, Hiss: 4), female (Pant: 5, Hiss: 7), and juvenile calls (Pant: 1) (Table S1). Rhinos were tested only once with the same call to avoid pseudoreplication. In the case when a rhino potentially listened to a playback stimulus that was planned for another focal animal, a different playback stimulus was used, or the observation of the response of the respective subject was excluded from the analyses. This led to an unbalanced dataset across senders. Therefore, senders were pooled across call types. Playbacks were played from a JBL Xtreme 2 loudspeaker connected via Bluetooth with a laptop (HP 250 G7 Notebook PC) in uncompressed .wav format. To standardize loudness, the playback stimuli were leveled to the same sound pressure of 85 dB at a 1 m distance (Brüel & Kjaer, Type 2233 with microphone type 4155). The behavior of the animal was videotaped using a digital camera (Sony α 65, Germany, or Medion M86641, USA).

2.4 | Experimental procedure of playback experiments

Experiments were performed in semi-randomized order with one to four focal individuals per day. In reserve A, we approached the rhinos with the car and placed the loudspeaker on the bonnet, resulting in a playback height of approximately 1.20 m. In reserve B, where rhinos were less habituated to humans and ran away from cars, we stopped the car where we found a rhino track and approached the rhinos on foot against the wind or we waited at feeding places or water holes until rhinos approached. The loudspeaker was placed at approximately 1-m-height, either held by the experimenter or attached to a tree. The playbacks for the two individuals in the enclosure were performed with the experimenter standing in front of the fence. Each playback trial was videotaped for 5 min (Cinková & Policht, 2016). When other rhinos next to the focal individual were visible throughout the entire video, then the responses of all visible rhinos were encoded and counted as separate playback trials, but we included the presence of other rhinos as a possible confounding variable in the statistical analysis. We decided to include these trials in the analyses to increase sample size and to account for all playback trials the animals were exposed to.

We performed the experiments in three blocks (Table 1). In the first block, we tested how 11 rhinos in reserve A reacted to playbacks of familiar conspecific calls in comparison to control calls (92 trials). We played back socio-positive Pants and socio-negative Hisses; and calls from birds recorded in the same reserve. Rhinos were not tested with their own calls. In the second block, we played back unfamiliar Pants and Hisses (recorded in a different reserve during a pilot study) to the same 11 individuals in reserve A to test for the effect of familiarity (21 trials). In the third block, we tested the 15 subjects of reserve B by playing back unfamiliar Pants and

TABLE 1 Overview of datasets used for analyses of the variable of interest in bold and additional predictor variables, levels of each variable, and number of stimuli per call type are indicated in the brackets.

Dataset	Blocks of experiments	Number of experiments	Number of individuals	Predictor variables (levels (number of stimuli))
1	Block 1 (reserve A)	92	8 females, 3 males	**Stimulus** (control (6), Hiss (6), Pant (5)) * sex (female, male)
2	Block 1 without control + Block 2 (reserve A)	88	8 females, 3 males	**Familiarity** (familiar, unfamiliar) * sex (female, male) * stimulus (Hiss (8), Pant (7))
3	Block 2 (Reserve A) + Block 3 (reserve B)	108	16 females, 10 males	**Reserve** (reserve A, reserve B) * sex (female, male) * stimulus (Hiss (7), Pant (7))

Hisses recorded in reserve A (87 trials) for comparisons between reserves.

Furthermore, we noted the following potentially confounding methodological variables for each playback trial to test for effects of these variables in the statistical analyses: (1) Other rhinos present: We noted whether the animal was *alone* or *in a group* with other rhinos during the playback. (2) Wind condition: Since wind speed can influence sound propagation, we classified wind speed into three categories: *almost no wind*, *low wind*, and *high wind* as subjectively experienced by the experimenter. (3) Distance: Since distance from the rhino to the loudspeaker might influence perceived loudness, we measured the distance with a range finder and scored two distance categories for the analysis: *up to 20 m* or *more than 20 m*.

2.5 | Video analysis of playback experiments

We conducted a video analysis for each playback trial using the software Observer XT (version 12, Noldus, Netherlands; Noldus, 1991) and analyzed rhino responses for 2 min after stimulus onset because preliminary video screening showed almost no further responses after that. We coded the following point behaviors: ear movement, ears turned to the speaker, head moved up, head turned more than 45° to the speaker, body moved at least one to max. three steps toward or away from the speaker, body moved more than three steps toward or away from the speaker, alert behavior (head lifted and not chewing), vocalizations, and urination as a sign of excitement (Table S2). Furthermore, we noted the response duration. We defined the start of a response as when the rhino changed its behavior or body position from that before the playback (e.g., ear or head movement) and the end as when the rhino returned to its previous behavior and body

position. When the rhino did not return to its previous behavior and body position within the 2 min of observation time, then the duration of the response was counted until the end of the observation (2 min).

We scored the response intensity by giving a point for the first occurrence of each response behavior, similar to Cinková and Policht (2016) and Cinková and Shrader (2020, 2022). The sum of the points per playback trial within the response duration was taken as response score for the further analyses. We restricted the response intensity score to the response duration to prevent the inclusion of body movements not associated with the playback. For example, when the rhino lifted its head, then returned to its previous behavior of grazing and moved away after 3 s of grazing, no point was given for "body moved away." We recorded the direction of body movement to describe whether the rhino approached or avoided the loudspeaker. Although we had aimed to only perform experiments when the focal was in a relaxed body position and behavior, rhinos sometimes changed their behavior shortly before the playback sequence started. Therefore, we also coded the following behavioral states before the playback: *alert*, *feeding*, *locomoting*, or *resting*, and included the behavior as another potentially confounding variable.

To ensure reliability of the behavior encoding, 25% of the trials were compared to coding of a second observer with Cohen's Kappa coefficient. Inter-observer reliability was high (Kappa 0.92).

2.6 | Statistical analysis

We used three data sets (Table 1) to test the effects of three variables of interest (VOI): stimulus, familiarity, and reserve. Using dataset 1, we investigated effects of the rhino call types Hiss and Pant in comparison to controls. Using dataset 2, we compared familiar and unfamiliar rhino calls. Using dataset 3, we tested

consistency between reserves by comparing behavioral responses in reserve A and reserve B.

For the statistical analyses on each data set, we performed a two-step approach to exclude interactions between the VOI with potentially confounding variables. For each confounding variable (wind, distance, other rhinos present, behavior before playback), we ran a generalized linear mixed model (glmm) for each of the behavioral response measurements (score, duration) as dependent variables, the VOI and the confounding variable and the interaction between them as predictor variables. If confounding variables with more than two levels showed a significant impact on the model, pairwise comparisons were conducted to explain the effect of the confounding variable using the false discovery rate (fdr) adjustment (Benjamini & Hochberg, 1995) to control for multiple testing. If an interaction between the VOI and the confounding variable was significant in the model comparison, we performed a break-down analysis splitting the dataset to the levels of the confounding variable for the further analyses. If no interaction between the VOI and a potential confounding variable was found, the confounding variable was not included in subsequent analyses. In each model, we included the individual as a random effect to account for the repeated measurements with all individuals. We further included the position of the loudspeaker as a random effect because the approach direction was unpredictable and moving the car could result in alerting the rhinos. Thus, we were not able to standardize the position of the loudspeaker relative to the rhino for most trials and instead coded it as *front*, *side*, or *back*.

Second, we tested the impact of the VOI and sex for each dataset. We ran the full model using the behavioral measurement (score, duration) as dependent variable and the VOI, sex, and their interaction as predictor variables, controlling for individual and position of the loudspeaker by including them as random factors. For the VOIs familiarity and reserve, we included the call type additionally as a potential interaction variable, because Hiss and Pant might be affected differently by familiarity and reserve. We used a backward stepwise elimination procedure to determine the minimum adequate model (final model, Zuur et al., 2009). In each step, we calculated a reduced model excluding the highest interaction with the highest nonsignificant *p*-value and tested whether the two models were significantly different using the Wald test ("Anova" command; Zuur et al., 2009). We stopped the elimination procedure when the following criteria were fulfilled: (1) Wald statistics indicated a significant difference between models, (2) only significant interactions or main terms remained in the model. For significant predictor variables with more than two levels, pairwise comparisons were conducted using fdr adjustments.

Body movement as a response to playbacks was only rarely observed and statistical analysis with linear mixed models was challenged by zero inflation. Thus, we pooled the body movement responses across all individuals and used Chi-square tests comparing the number of occurrences of approaching and avoiding in the different datasets. For visualization, we used an index subtracting the number of avoidances from the number of approaches and dividing it by the total number of body movement occurrences (adapted from Scheumann & Zimmermann, 2008). Thus, we obtained values between −1 and 1, negative indicating avoidance and positive values representing approaching.

All statistical analyses were performed in R (v4.0.3 [October 10, 2020], The R Foundation for Statistical Computing), using the packages tidyverse (Wickham et al., 2019), ggplot2 (Wickham, 2016), ggsignif (Ahlmann-Eltze & Patil, 2021), nlme (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) and car (Fox & Weisberg, 2019). Due to the high number of statistical tests, we report only significant results of the final models in the results section, but full reports can be found in the Tables S3–S14. *p*-values <.05 were considered as statistically significant.

3 | RESULTS

3.1 | Familiar conspecific call versus control

Investigating methodological variables, we found no effect for other rhinos present and distance, and no interaction with stimulus for the two behavioral measurements. For behavior before playback, an effect was found on duration (Chi^2 = 26.49, *df* = 3, *p* < .001), but no interaction with the Stimulus. Rhinos showed a shorter duration for playbacks when they were feeding compared to alert or resting behavior (*alert* vs. *feeding* estimate = 28.48 ± 10.1, CI = 0.91–56.05, *t*(55) = 2.83, *p* = .020; *feeding* vs. *resting* estimate:= − 25.00 ± 7.40, CI = −45.26 to −4.75, *t*(55) = −3.38. *p* = .008, Table S4). For wind condition, we found a significant interaction between stimulus and wind for both behavioral measurements (score: Chi^2 ≥ 10.95, *df* = 4, *p* = .027; duration: Chi^2 = 10.23, *df* = 4, *p* = .037) suggesting that wind condition affected the perception of the stimuli (Figure 1). Therefore, for the further analyses of score and duration, we analyzed the dataset for the three wind conditions separately. Nevertheless, in all eight models, the stimulus had a significant effect on the behavioral measurements (score: Chi2 ≥ 9.57, *p* ≤ .008; duration: Chi2 ≥ 7.77, *p* ≤ .020; Table S3).

For the *almost no wind* condition, we found a significant interaction between stimulus and sex on both behavioral measurements (score: Chi^2 = 6.68, *df* = 2, *p* = .036;
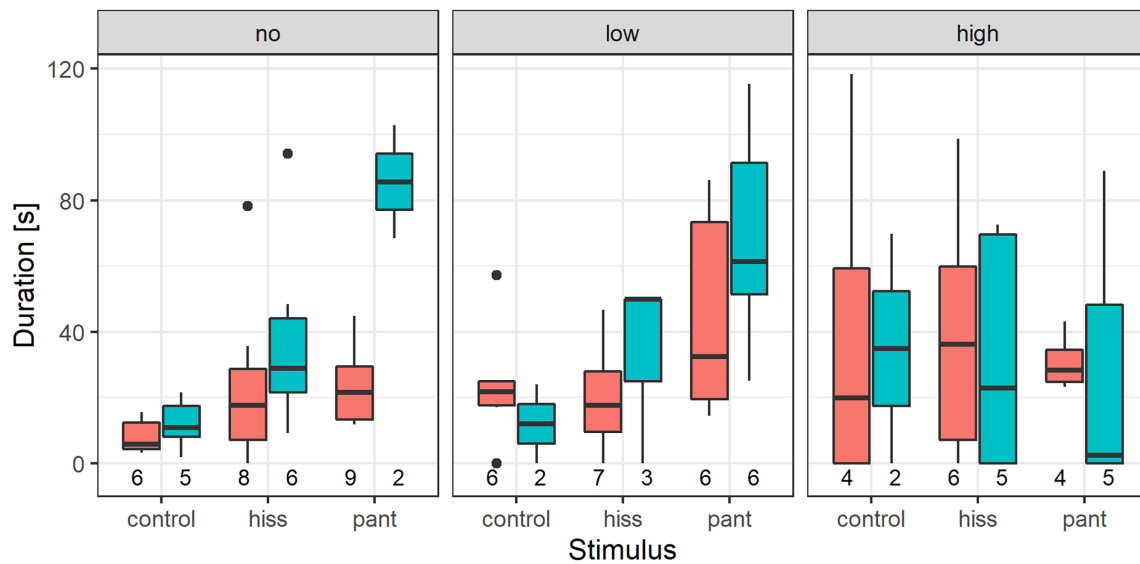
FIGURE 1 Effect of stimulus on response duration of 11 rhinos (eight females, three males) for the three wind conditions no = almost no wind, low = low wind, high = high wind speed in 92 experiments. The number of experiments per condition is indicated below the boxplots. Boxplots represent lower and upper quartile; a thick black line is the median. Red = females, blue = males.

duration: $Chi^2 = 12.45$, $df = 2$, $p = .002$; Figure 1, Table S4). Males showed higher scores toward Pants and Hisses than toward control playbacks (*control* vs. *pant*: estimate = -3.50 ± 0.57, CI = -6.28 to -0.72, $t(3) = -6.108$, $p = .016$; *control* vs. *hiss*: estimate = -2.41 ± 0.42, CI = -4.47 to -0.35, $t(3) = -5.675$, $p = .016$, Table S5) and a tendency for a longer duration toward Pants compared to controls (estimate = -75.5 ± 19.2, CI = -168.9 to 17.9, $t(3) = -3.93$, $p = .088$) whereas females showed no significant effect of stimulus. For the *low wind* condition, a significant effect of stimulus was found for both behavioral measurements (score: $Chi^2 = 21.72$, $df = 2$, $p < .001$; duration $Chi^2 = 11.56$, $df = 2$, $p = .003$). Rhinos showed a higher score and longer durations for Pants compared to playbacks of controls or Hisses (score: *control* vs. *pant*: estimate = -2.75 ± 0.72, CI = -4.86 to -0.64, $t(9) = -3.83$, $p = .001$, *hiss* vs. *pant*: estimate = -2.36 ± 0.67, CI = -4.33 to -0.39, $t(9) = -3.52$, $p = .001$; duration: *control* vs. *pant*: estimate = -32.7 ± 12.1, CI = -68.2 to 2.81, $p = .038$, *hiss* vs. *pant*: estimate = -30.29 ± 11.3, CI = -63.4 to 2.82, $t(9) = -2.68$, $p = .038$, Table S5). For the *high wind* condition, no effect of stimulus or sex was found either for the score or for the duration.

In 47 playback experiments, rhinos responded with body movement (toward [$n = 31$] or away [$n = 16$] from the loudspeaker). There was no significant difference between approaching and avoidance of the loudspeaker depending on the playback stimuli (Table S6). However, there were significant differences between males and females for the two conspecific rhino call types (Hiss:

$Chi^2 = 5.92$, $df = 1$, $p = .015$; Pant: $Chi^2 = 4.92$, $df = 1$, $p = .027$) but not for the control (index$_{female} = 0$, index$_{male} = 0.20$). In response to Hisses, females moved away (index$_{female} = -0.60$, Figure 2), whereas males approached the loudspeaker (index$_{male} = 0.75$). In response to Pants, males always approached the loudspeaker (index$_{male} = 1.00$), while females showed only a tendency to approach (index$_{female} = 0.17$).

3.2 | Familiar versus unfamiliar conspecific calls

Investigating methodological variables, we found no effect for wind and other rhinos present on the two behavioral measurements. For behavior before playback, there was an effect for both behavioral measurements (score: $Chi^2 = 8.52$, $df = 3$, $p = .036$; duration: $Chi^2 = 26.47$, $df = 3$, $p < .001$), but no interaction with familiarity. Rhinos showed a longer response duration when alert and resting compared to feeding and locomoting (*alert* vs. *feeding* estimate = -33.22 ± 10.8, CI = 3.57–62.86, $t(53) = 3.07$, $p = .020$; *alert* vs. *locomoting* estimate = -39.93 ± 16.8, CI = -6.00 to 85.86, $t(53) = 2.38$, $p = .031$; *feeding* vs. *resting* estimate = -47.86 ± 17.1, CI = -94.73 to -1.00, $t(53) = -2.80$, $p = .021$; *locomoting* vs. *resting* estimate = -54.58 ± 21.3, CI = -112.99 to 3.84, $t(53) = -2.56$, $p = .027$, Table S8). The effect of behavior before playback on the score was not significant in the pairwise comparisons. Distance had no effect on the score, but for duration, we found a significant
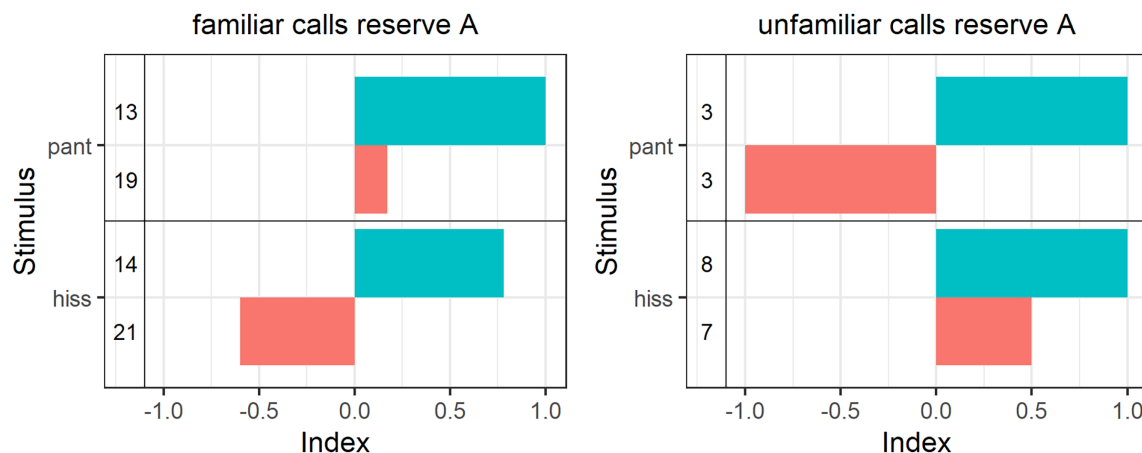
FIGURE 2 Index of body movement direction of 11 rhinos (eight females, three males) in response to familiar and unfamiliar calls in 88 experiments. The number of experiments per condition is indicated on the left side of the graphs. -1 = away from the loudspeaker, 1 = toward the loudspeaker. Red = females, blue = males.
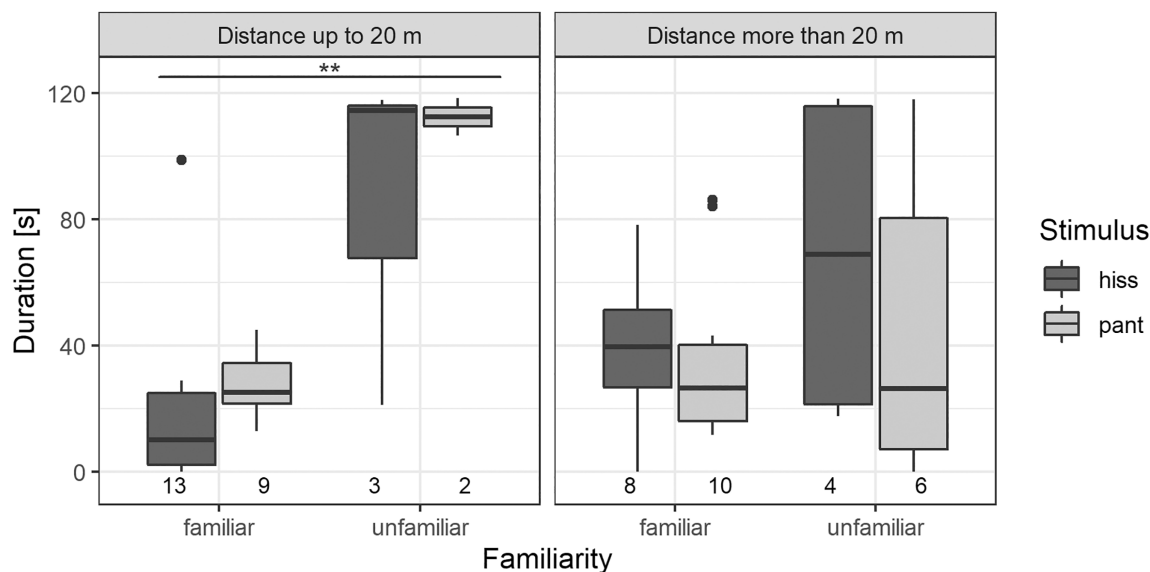
FIGURE 3 Effect of familiarity on response duration of eight female rhinos for the two distance categories in 55 experiments. The number of experiments per condition is indicated below the boxplots. Boxplots represent lower and upper quartile; a thick black line is the median.

interaction between familiarity and distance (Chi^2 = 12.16, df = 1, p < .001) suggesting that the distance affected the response duration. Nevertheless, in almost all models, the effect of familiarity on the behavioral response measurements was significant (score: Chi^2 ≥ 3.99, p ≤ .046; duration: Chi^2 ≥ 5.52, p ≤ .019; Table S7), except for the model with wind and score, where only a tendency was found.

For the score, the final model showed a strong effect of familiarity with a higher score for unfamiliar compared to familiar calls (Chi^2 = 5.43, df = 1, p = .020, estimate = 0.99 ± 0.44, CI = 0.14–1.84, Table S9), but no strong effect of sex and Stimulus.

For the duration, we analyzed the dataset for the two distance categories separately due to the above-mentioned

interaction. Unfortunately, for males, the data distribution did not allow statistical analyses within the distance subsets. Thus, we focussed this analysis on females only. For *up to 20 m*, females responded longer to unfamiliar than to familiar calls (Chi^2 = 37.73, df = 1, p < .001, estimate = 73.68 ± 12.72, CI = 47.28–100.08, Figure 3, Table S9) but no effect of stimulus was found. For *more than 20 m* the effect of familiarity on the duration was lost, but there was a significant effect of the stimulus with a shorter duration for Pants compared to Hisses (Chi^2 = 12.46, df = 1, p < .001, estimate = -30.93 ± 9.27, $t(12)$ = -3.34, p = .006, CI = -50.21 to -11.64).

Comparing the total number of playback trials with body movements, no significant effect of familiarity was
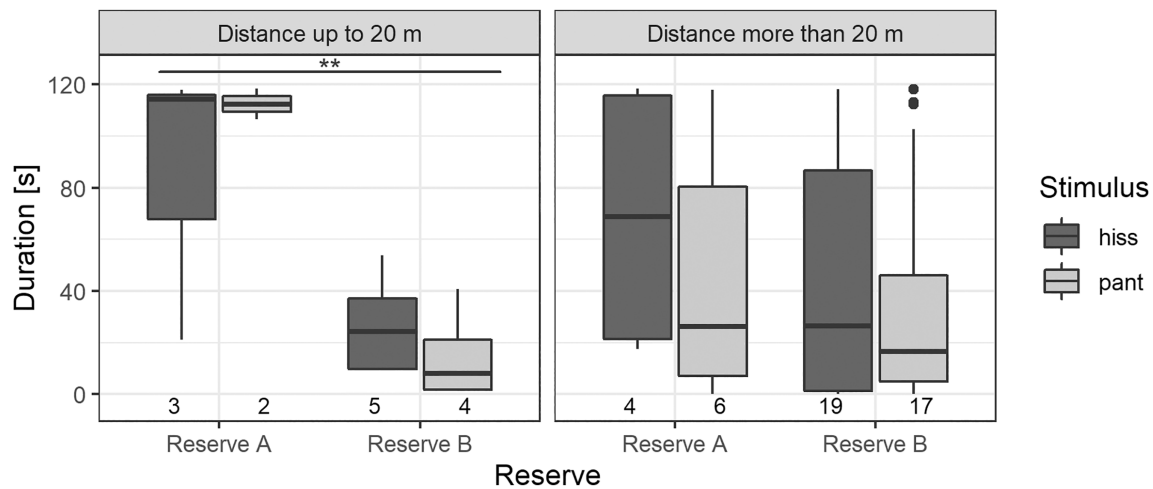
FIGURE 4 Effect of reserve on response duration of 16 female rhinos for the two distance categories in 60 experiments. The number of experiments per condition is indicated below the boxplots. Boxplots represent lower and upper quartile; a thick black line is the median.

TABLE 2 Summary of predictor and confounding variables that significantly impacted rhino behavioral responses to playbacks of conspecific calls based on the output of generalized linear mixed models with data from 200 experiments with 26 rhinos (16 females, 10 males).

Predictor variable	Response variable	Confounding variable	Biological meaning
Stimulus	Score	Wind	Rhinos respond under low wind conditions more to rhino calls than to control sounds
	Duration	Behavior before playback	Rhinos show shorter responses when feeding
		Wind	Rhinos show under low wind conditions longer responses to rhino calls than to controls
Familiarity	Score		Rhinos show stronger responses to unfamiliar than to familiar calls
	Duration	Behavior before playback	Rhinos show shorter responses when feeding or locomoting
		Distance	Females show at close distances longer responses to unfamiliar than to familiar calls
Reserve	Score		Habituated rhinos show stronger responses than non-habituated rhinos
	Duration	Behavior before playback	Rhinos show longer responses when alert
		Distance	Habituated females show at close distances longer responses than non-habituated females
Sex	Score	Wind	Males show under almost no wind conditions stronger responses than females
	Duration		Males tend to respond to familiar calls longer than females
	Body movement		Males approach the loudspeaker in response to all call types. Females approach the loudspeaker for familiar Pants and unfamiliar Hisses and avoid the loudspeaker in response to familiar Hisses and unfamiliar Pants

revealed (Table S10). However, in response to unfamiliar Pants, females avoided the loudspeaker (index$_{\text{female}}$ = −1) significantly more often compared to familiar Pants where

they were more likely to approach the loudspeaker (index$_{\text{female}}$ = 0.17; Chi^2 = 4.96, df = 1, p = .026, Figure 2). Males, on the other hand, approached the loudspeaker in

response to unfamiliar Pants (index$_{male}$ = 1.00; Chi^2 = 7, df = 1, p = .008, Figure 2).

3.3 | Effect of reserve: Reserve A versus reserve B

Investigating methodological variables, we found no effect for wind on the two behavioral measurements. For behavior before playback, an effect was found on duration (Chi^2 = 16.85, df = 3, p < .001), but no interaction with reserve and no effect on the score. Rhinos showed a longer duration for playbacks when they were alert compared to feeding (estimate = 36.34 ± 11.3, CI = 5.37–67.3, $t(49)$ = 3.23, p = .013, Table S12). For other rhinos present, there was an effect on the score (Chi^2 = 6.57, df = 1, p = .010), which was not supported by pairwise comparison, and no effect on duration. Distance had no effect on the score, but for duration, we found a significant interaction between reserve and distance (Chi^2 = 5.76, df = 1, p = .016) suggesting that the distance affected response duration. Nevertheless, in all eight models, the reserve had a significant effect on the behavioral measurements (score: Chi^2 ≥ 13.44, p ≤ .001; duration: Chi^2 ≥ 3.85, p ≤ .050; Table S11).

For the score, the final model showed a strong effect of reserve with a higher score in reserve A compared to reserve B (Chi^2 = 13.80, df = 1, p < .001, estimate = −1.77 ± 0.49, CI = −2.73 to −0.81), but no effect of stimulus and sex.

For the duration, we analyzed the dataset for the two distance categories separately due to the above-mentioned interaction. Again, only females were analyzed because the data distribution among the distance categories did not allow statistical analyses for the male subsets. For *up to 20 m*, females showed a strong effect of reserve with longer durations in reserve A compared to reserve B (Chi^2 = 7.73, df = 1, p = .005, estimate = −71.24 ± 28.91, CI = −152.81 to 10.33, Figure 4, Table S13) but no effect of stimulus. For *more than 20 m*, there was no significant effect of reserve or stimulus on duration.

Comparing the total number of playback experiments where rhinos approached versus avoided the loudspeaker, no differences between the two reserves were revealed (Table S14) even if separated for call type and sex. A summary of the most important results is given in Table 2.

4 | DISCUSSION

In this study, we performed experiments to test whether playbacks of conspecific calls have the potential to direct movements in southern white rhinos. As expected, rhinos responded more intensely and for longer to rhino calls than to control stimuli. However, we found no significant difference in body movement responses between socio-positive and socio-negative call types. Instead, we found an effect of sex with males approaching the loudspeaker more often than females. As predicted, the familiarity of the tested rhino with the playback caller affected behavioral responses with a higher intensity and duration toward unfamiliar callers. Responses differed between reserves in intensity, but not in body movement direction. Some methodological factors influenced the behavioral responses and should be considered when developing playbacks of conspecific calls as a management tool. Our study is, therefore, exemplifying the relevance of behavior studies for conservation.

Our first two hypotheses, that rhinos responded more intensely and for longer to rhino calls than to control calls and that responses are consistent between sexes, were partly supported. Both sexes responded more strongly to Pants than to control stimuli, supporting previous studies (Cinková & Policht, 2016; Cinková & Shrader, 2020, 2022). Rhinos reacted more intensely and longer to Pants than to Hisses. However, with our sample size, there was no significant difference in the direction of body movements between call types. Instead, we found a significant effect of sex on the body movement for both conspecific calls. Males approached the loudspeaker more often than females in response to Pants. This phenomenon has been observed for other species as well, for example, collared pika (*Ochotona collaris*) males were three times more likely to approach the loudspeaker than females (Trefry & Hik, 2009) and male chimpanzees (*Pan troglodytes*) generally reacted more strongly to playbacks than females (Herbinger et al., 2009). Interestingly, females avoided while males approached the loudspeaker in response to Hisses. Sex-specific differences regarding the Hiss were also observed in Jenikejew et al. (2021), whereby Hisses were mainly produced by females and mainly directed at males. Thus, Hisses might be attractive for males, signaling the presence of a female or a potential rival. Further studies are needed to investigate sex-specific responses to conspecific stimuli and the effect of the sex of the sender on the responses.

Investigating the effect of familiarity, our third hypothesis was supported. Rhinos responded with higher intensity to playbacks of calls from unfamiliar compared to familiar senders. Females avoided unfamiliar but approached the loudspeaker for familiar Pants. All tested females, except the subadult, had calves and thus likely avoided unfamiliar individuals to prevent conflicts, whereas familiar individuals were approached because the calves were already socialized with them. However,

we only found the effect of familiarity for experiments performed at close distances. It is possible that the acoustic nuances differentiating calls individually are not audible over larger distances (Maciej et al., 2011) or that unfamiliar calls are only meaningful at close distances. Overall, our findings on the effect of familiarity must be treated with caution because we were only able to test rhinos in one reserve and had a small sample size for experiments with unfamiliar calls.

Rhino behavioral responses to playbacks differed between the two reserves with a higher intensity and longer durations in reserve A, where rhinos were habituated. The responses in reserve A were likely a more representative sample biologically than the responses in reserve B, as responses in the latter often seemed to be masked by fear. In reserve B, rhinos were afraid of humans and avoided them when they detected them, except for one bull and the rhinos in the paddock. Therefore, we tried to approach the rhinos against the wind to prevent being detected. However, this was not always successful, and often rhinos ran away when they detected the experimenters. In other cases, the experimenters were not detected, but it was also unclear whether the rhino had perceived the playback or whether the distance had been too large and the vegetation too dense. Nevertheless, in both reserves, males approached the loudspeaker for both call types. When avoiding the loudspeaker, rhinos in both reserves moved in a direction where the vegetation allowed free movement. This indicates that the general behavioral response was similar between both reserves. To avoid possible observer effects, playback setups without human presence should be considered in the development of management tools.

Although the effect of the stimulus was always present independent of the methodological confounding factors, our results showed that wind speed and distance affected the perception and therefore the reaction of the rhinos to the playback stimuli. When wind speed and distance were high, behavioral response differences between conspecific calls and the control disappeared, suggesting that stimulus perception was impaired. Hisses were apparently more easily attenuated by wind than Pants. Another possibility is that Hisses are only relevant to the subject in short-distance contexts, whereas Pants are suggested to function also as long-distance signals (Cinková & Policht, 2014; Policht et al., 2008). Additionally, the behavioral responses depended on the behavior before the playback. The most intense and longest responses were observed when the rhino was already alert or standing, scanning the surroundings, and ready to change its behavior. We also observed that the time to respond was longer when rhinos were feeding before the playback, possibly because sound produced by chewing masked the playback sound. Thus,

not only stimulus and sex influenced the behavioral responses of rhinos to playbacks of conspecific calls, but also distance, wind, and behavior before the playback. Sound dispersion can also be affected by temperature (Bradbury & Vehrencamp, 2011; Garstang et al., 1995) but we excluded this variable from our analyses as we found no strong effect in an exploratory analysis. Thus, confounding factors should be considered when developing playbacks as a management tool, for example by placing loudspeakers strategically at places where rhinos pass at a close distance.

Our results indicate that rhinos showed specific responses to conspecific calls but these rarely lasted longer than 2 min, often only consisted of a lifting of the head for several seconds, and body movements toward or away from the loudspeaker were rarely observed. When we played calls from the same location, such as in reserve B for the two rhinos in a paddock, the animals got habituated to the experiment, and responses attenuated with repetition. Thus, further experiments are needed to improve stimulus presentation to elicit long-lasting behavioral responses and to test a design that would be successful after translocations.

Drone and siren sounds (Penny et al., 2019) are promising possibilities to manage the behavior of rhinos but could also result in habituation and stress (Fàbregas et al., 2021). A combination of playbacks with visual and olfactory cues could be more effective for long-lasting responses (King, 2015; Madliger, 2012) but this requires a more complex design of the management intervention, which we were trying to simplify with our approach of using conspecific playbacks only. In future experiments, we suggest playing one call, followed by another from the same individual after the response by the targeted individual has been observed. These interactive playback designs as suggested by King (2015) would allow a more natural communicative situation instead of a repetition of the same stimulus. By adapting the second stimulus to the subject's response, habituation could be avoided, and a stronger response could be elicited. This could be used as an addition when a team on the ground herds a dispersing rhino back by car, trying to reduce the stress from chasing. Here, the personnel would know the individual and could play back specific calls in an interactive manner and could intervene when responses are not as expected or when the rhino moves away from the desired location.

To avoid observer effects, automated behavioral response systems as developed by Suraci et al. (2017) could be efficient. Such systems could negate the effects of wind and distance to the loudspeaker, as the rhinos would pass by at close distances, and operate in the absence of personnel. Rhinos may then associate the location with the playback and learn to avoid that

area. However, automated systems are static and triggered by movement, so would need to be placed along known dispersal paths or at very high densities; such limitations mean that successful deployment may only be possible in small reserves. Familiar Pant calls would be the optimal stimulus since both sexes responded by approaching the speaker, and familiar calls are less likely to cause aggression and stress (Herbinger et al., 2009; McComb et al., 2000). Alternatively, the system could be combined with an identification software based around artificial intelligence to adapt the playback to the target individual. Automated behavioral response systems could be a useful experimental setup for future studies, but further research and development are needed before such systems could be rolled out, and they may not be effective in large, unfenced areas similar to reserve A. For future studies and management applications of automated playback systems, it would also be advantageous to equip the rhinos with GPS trackers to monitor their movement and the duration of the effect of the playback.

As an application that can be derived from this study, playbacks would be useful in rhino monitoring to identify individuals because rhinos commonly responded by pointing their ears toward the loudspeaker, thereby facilitating the identification of their ear notches.

To conclude, we found that rhinos of both sexes do respond to playbacks of conspecific calls, with sex-specific and call type-specific responses. Further research is necessary to develop a successful application design.

CONFLICT OF INTEREST STATEMENT
The authors declare no known conflict of interest.

DATA AVAILABILITY STATEMENT
Video and audio data are stored at the Institute of Zoology of the University of Veterinary Medicine in Hanover and can be provided by the authors upon reasonable request. Tables with raw data can be accessed at DOI 10.5281/zenodo.6979981.

ORCID
Vera Pfannerstill https://orcid.org/0000-0002-4146-6486

REFERENCES

Ahlering, M. A., Arlt, D., Betts, M. G., Fletcher, R. J., Nocera, J. J., & Ward, M. P. (2010). Research needs and recommendations for the use of conspecific-attraction methods in the conservation of migratory songbirds. *The Condor*, 112(2), 252–264. https://doi.org/10.1525/cond.2010.090239

Ahlmann-Eltze, C., & Patil, I. (2021). ggsignif: R Package for Displaying Significance Brackets for 'ggplot2'. https://doi.org/10.31234/osf.io/7awm6

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57(1), 289–300 Retrieved from http://www.jstor.org/stable/2346101

Blackwell, B. F., DeVault, T. L., Fernández-Juricic, E., Gese, E. M., Gilbert-Norton, L., & Breck, S. W. (2016). No single solution: Application of behavioural principles in mitigating human–wildlife conflict. *Animal Behaviour*, 120, 245–254. https://doi.org/10.1016/j.anbehav.2016.07.013

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sinauer Associates.

Bradley, D. W., Ninnes, C. E., Valderrama, S. V., & Waas, J. R. (2011). Does 'acoustic anchoring' reduce post-translocation dispersal of North Island robins? *Wildlife Research*, 38(1), 69. https://doi.org/10.1071/WR10173

Bro-Jørgensen, J., Franks, D. W., & Meise, K. (2019). Linking behaviour to dynamics of populations and communities: Application of novel approaches in behavioural ecology to conservation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 374(1781), 20190008. https://doi.org/10.1098/rstb.2019.0008

Bryant, J. V., Brulé, A., Wong, M. H. G., Hong, X., Zhou, Z., Han, W., Jeffree, T. E., & Turvey, S. T. (2016). Detection of a new Hainan gibbon (*Nomascus hainanus*) group using acoustic call playback. *International Journal of Primatology*, 37(4–5), 534–547. https://doi.org/10.1007/s10764-016-9919-8

Cinková, I., & Policht, R. (2014). Contact calls of the northern and southern white rhinoceros allow for individual and species identification. *PLoS One*, 9(6), e98475. https://doi.org/10.1371/journal.pone.0098475

Cinková, I., & Policht, R. (2016). Sex and species recognition by wild male southern white rhinoceros using contact pant calls. *Animal Cognition*, 19(2), 375–386. https://doi.org/10.1007/s10071-015-0940-7

Cinková, I., & Shrader, A. M. (2020). Rival assessment by territorial southern white rhinoceros males via eavesdropping on the contact and courtship calls. *Animal Behaviour*, 166, 19–31. https://doi.org/10.1016/j.anbehav.2020.05.013

Cinková, I., & Shrader, A. M. (2022). Individuality, species-specific features, and female discrimination of male southern white rhinoceros courtship calls. *Animal Cognition*, 1–14, 769–782. https://doi.org/10.1007/s10071-021-01591-4

12 of 14 | WILEY— Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access

PFANNERSTILL ET AL.

Clements, H. S., Knight, M., Jones, P., & Balfour, D. (2020). Private rhino conservation: Diverse strategies adopted in response to the poaching crisis. *Conservation Letters*, *13*(6), e12741. https://doi.org/10.1111/conl.12741

Elmer, L. K., Madliger, C. L., Blumstein, D. T., Elvidge, C. K., Fernández-Juricic, E., Horodysky, A. Z., Johnson, N. S., McGuire, L. P., Swaisgood, R. R., & Cooke, S. J. (2021). Exploiting common senses: Sensory ecology meets wildlife conservation and management. *Conservation Physiology*, *9*(1), coab002. https://doi.org/10.1093/conphys/coab002

Emslie, R., Amin, R., & Kock, R. (2009). Guidelines for the in situ re-introduction and translocation of African and Asian rhinoceros (1st ed.). Occasional paper of the IUCN species survival commission: no. 39. Gland Switzerland: IUCN.

Fàbregas, M. C., Fosgate, G. T., Ganswindt, A., Bertschinger, H., & Meyer, L. C. R. (2021). Unforeseen consequences of conservation management practices: Case study on herding rhino as an anti-poaching measure. *Animal Conservation*, *24*(3), 412–423. https://doi.org/10.1111/acv.12646

Filatova, O. A., Fedutin, I. D., Burdin, A. M., & Hoyt, E. (2011). Responses of Kamchatkan fish-eating killer whales to playbacks of conspecific calls. *Marine Mammal Science*, *27*(2), E26–E42. https://doi.org/10.1111/j.1748-7692.2010.00433.x

Fox, J., & Weisberg, S. (2019). An R companion to applied regression (version third edition) [computer software]. Sage, Thousand Oaks, CA. Retrieved from https://cran.r-project.org/web/packages/car/citation.html

Garstang, M., Larom, D., Raspet, R., & Lindeque, M. (1995). Atmospheric controls on elephant communication. *Journal of Experimental Biology*, *198*(Pt 4), 939–951. https://doi.org/10.1242/jeb.198.4.939

Goldenberg, S. Z., Owen, M. A., Brown, J. L., Wittemyer, G., Oo, Z. M., & Leimgruber, P. (2019). Increasing conservation translocation success by building social functionality in released populations. *Global Ecology and Conservation*, *18*, e00604. https://doi.org/10.1016/j.gecco.2019.e00604

Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., Clair, C. C. S., Crooks, K., de Silva, S., Fernández-Juricic, E., Goldenberg, S. Z., Mesnick, S. L., Owen, M., Price, C. J., Saltz, D., Schell, C. J., Suarez, A. V., Swaisgood, R. R., Winchell, C. S., ... Sutherland, W. J. (2016). Research priorities from animal behaviour for maximising conservation Progress. *Trends in Ecology & Evolution*, *31*(12), 953–964. https://doi.org/10.1016/j.tree.2016.09.001

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-Douglas, A., Bissett, C., Moolman, L. C., Bean, P., Fogarty, A., Howarth, D., Slater, R., & Kerley, G. I. (2007). Practical considerations for the reintroduction of large, Terrestrial, Mammalian predators based on reintroductions to South Africa's eastern Cape Province. *The Open Conservation Biology Journal*, *1*(1), 1–11. https://doi.org/10.2174/1874839200701010001

Herbinger, I., Papworth, S., Boesch, C., & Zuberbühler, K. (2009). Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: A playback study. *Animal Behaviour*, *78*(6), 1389–1396. https://doi.org/10.1016/j.anbehav.2009.09.010

Hitchins, P. M., Keep, M. E., & Rochat, K. (1972). The capture of black rhinoceros in Hluhluwe game reserve and their translocation to the Kruger National Park. *Lammergeyer*, *17*, 18–30.

IUCN Species Survival Commission. (2013). *Guidelines for reintroductions and other conservation translocations*: Version 1.0 (viiii + 57 pp). Gland, Switzerland. Retrieved from https://www.iucn.org/content/guidelines-reintroductions-and-other-conservation-translocations

James, M. S., Stockwell, M. P., Clulow, J., Clulow, S., & Mahony, M. J. (2015). Investigating behaviour for conservation goals: Conspecific call playback can be used to alter amphibian distributions within ponds. *Biological Conservation*, *192*, 287–293. https://doi.org/10.1016/j.biocon.2015.10.001

Jenikejew, J., Chaignon, B., Linn, S., & Scheumann, M. (2020). Proximity-based vocal networks reveal social relationships in the southern white rhinoceros. *Scientific Reports*, *10*(1), 15104. https://doi.org/10.1038/s41598-020-72052-0

Jenikejew, J., Wauters, J., Dehnhard, M., & Scheumann, M. (2021). The female effect—How female receptivity influences faecal testosterone metabolite levels, socio-positive behaviour and vocalization in male southern white rhinoceroses. *Conservation Physiology*, *9*(1), 1–15. https://doi.org/10.1093/conphys/coab026

Kiester, A. R. (1979). Conspecifics as cues: A mechanism for habitat selection in the Panamanian grass anole (*Anolis auratus*). *Behavioral Ecology and Sociobiology*, *5*(4), 323–330. https://doi.org/10.1007/BF00292522

King, S. L. (2015). You talkin' to me? Interactive playback is a powerful yet underused tool in animal communication research. *Biology Letters*, *11*(7), 20150403. https://doi.org/10.1098/rsbl.2015.0403

Knörnschild, M., Blüml, S., Steidl, P., Eckenweber, M., & Nagy, M. (2017). Bat songs as acoustic beacons—male territorial songs attract dispersing females. *Scientific Reports*, *7*(1), 13918. https://doi.org/10.1038/s41598-017-14434-5

Knox, C. D., & Monks, J. M. (2014). Penning prior to release decreases post-translocation dispersal of jewelled geckos. *Animal Conservation*, *17*, 18–26. https://doi.org/10.1111/acv.12149

Larsen, F., & Eigaard, O. R. (2014). Acoustic alarms reduce bycatch of harbour porpoises in Danish North Sea gillnet fisheries. *Fisheries Research*, *153*, 108–112. https://doi.org/10.1016/j.fishres.2014.01.010

le Gouar, P., Mihoub, J.-B., & Sarrazin, F. (2012). Dispersal and habitat selection: Behavioral and spatial constraints for animal translocations. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), *Reintroduction biology: Integrating science and management* (pp. 138–164). Blackwell Publishing Ltd.. https://doi.org/10.1002/9781444355833.ch5

Linklater, W. L., Flamand, J., Rochat, Q., Zekela, N., MacDonald, E., Swaisgood, R., Airton, D. F., Kelly, C. P., Bond, K., Schmid, I., & Morgan, S. (2006). Preliminary analyses of the free-release and scent-broadcasting strategies for black rhinoceros reintroduction. *CCA Ecological Journal*, 7, 26–34 Retrieved from http://www.rhinoresourcecenter.com/pdf_files/121/1211876244.pdf

Linklater, W. L., MacDonald, E. A., Flamand, J. R. B., & Czekala, N. M. (2010). Declining and low fecal corticoids

are associated with distress, not acclimation to stress, during the translocation of African rhinoceros. *Animal Conservation*, 13(1), 104–111. https://doi.org/10.1111/j.1469-1795.2009.00308.x

Linklater, W. L., & Swaisgood, R. R. (2008). Reserve size, conspecific density, and translocation success for black rhinoceros. *The Journal of Wildlife Management*, 72(5), 1059–1068. https://doi.org/10.2193/2007-398

Maciej, P., Fischer, J., & Hammerschmidt, K. (2011). Transmission characteristics of primate vocalizations: Implications for acoustic analyses. *PLoS One*, 6(8), e23015. https://doi.org/10.1371/journal.pone.0023015

Madliger, C. L. (2012). Toward improved conservation management: A consideration of sensory ecology. *Biodiversity and Conservation*, 21(13), 3277–3286. https://doi.org/10.1007/s10531-012-0363-6

McComb, K., Moss, C., Sayialel, S., & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour*, 59(6), 1103–1109. https://doi.org/10.1006/anbe.2000.1406

Miller, S. D., & Ballard, W. B. (1982). Homing of transplanted Alaskan brown bears. *The Journal of Wildlife Management*, 46(4), 869. https://doi.org/10.2307/3808219

Molles, L., Calcott, A., Peters, D., Delamare, G., Hudson, J. D., Innes, J., Flux, I., & Waas, J. R. (2008). "Acoustic anchoring" and the successful translocation of North Island kokako (*Callaeas cinerea wilsoni*) to a New Zealand mainland management site within continuous forest. *Notornis*, 55, 57–68 Retrieved from http://researcharchive.lincoln.ac.nz/handle/10182/7369

Morris, V., Pitcher, B. J., & Chariton, A. (2021). A cause for alarm: Increasing translocation success of captive individuals through alarm communication. *Frontiers in Conservation Science*, 2, 2. https://doi.org/10.3389/fcosc.2021.626311

Ngama, S., Korte, L., Bindelle, J., Vermeulen, C., & Poulsen, J. R. (2016). How bees deter elephants: Beehive trials with forest elephants (*Loxodonta africana cyclotis*) in Gabon. *PLoS One*, 11(5), e0155690. https://doi.org/10.1371/journal.pone.0155690

Noldus, L. P. J. J. (1991). The observer: A software system for collection and analysis of observational data. *Behavior Research Methods, Instruments, & Computers*, 23(3), 415–429. https://doi.org/10.3758/BF03203406

Owen-Smith, N. (1973). The behavioural ecology of the white rhinoceros (Dissertation). University of Wisconsin. PhD thesis. Retrieved from http://www.rhinoresourcecenter.com/pdf_files/132/1320739004.pdf

Patton, F., Mulama, M. S., Mutisya, S., & Campbell, P. E. (2010). The colonization of a new area in the first six months following 'same-day' free release translocation of black rhinos in Kenya. *Pachyderm*, 47, 66–79 Retrieved from https://pachydermjournal.org/index.php/pachyderm/article/view/213

Penny, S. G., White, R. L., Scott, D. M., MacTavish, L., & Pernetta, A. P. (2019). Using drones and sirens to elicit avoidance behaviour in white rhinoceros as an anti-poaching tactic. *Proceedings Biological Sciences*, 286(1907), 20191135. https://doi.org/10.1098/rspb.2019.1135

Pfannerstill, V., Signer, J., Fitt, M., Burger, K., Balkenhol, N., & Bennitt, E. (2022). Effects of age and sex on site fidelity, movement ranges and home ranges of white and black rhinoceros translocated to the Okavango Delta, Botswana. *African Journal of Ecology*. Advance online publication, 60, 344–356. https://doi.org/10.1111/aje.13011

Pienaar, D. J. (Ed.). (1994). *Social organization and behaviour of the white rhinoceros*. South African Veterinary Association Retrieved from http://www.rhinoresourcecenter.com/pdf_files/124/1245152449.pdf

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2017). nlme: Linear and Nonlinear Mixed Effects Models (Version R package version 3.1–131) [Computer software]. Comprehensive R Archive Network (CRAN): Comprehensive R Archive Network (CRAN). Retrieved from https://cran.r-project.org/web/packages/nlme/index.html

Policht, R., Tomášová, K., Holečková, D., & Frynta, D. (2008). The vocal repertoire in northern white rhinoceros *Ceratotherium simum cottoni* as recorded in the last surviving herd. *Bioacoustics*, 18(1), 69–96. https://doi.org/10.1080/09524622.2008.9753591

Scheumann, M., & Zimmermann, E. (2008). Sex-specific asymmetries in communication sound perception are not related to hand preference in an early primate. *BMC Biology*, 6(1), 3. https://doi.org/10.1186/1741-7007-6-3

Sheil, D., & Kirkby, A. E. (2018). Observations on southern White rhinoceros *Ceratotherium simum simum* translocated to Uganda. *Tropical Conservation Science*, 11, 194008291880680. https://doi.org/10.1177/1940082918806805

Shier, D. M., & Swaisgood, R. R. (2012). Fitness costs of neighborhood disruption in translocations of a solitary mammal. *Conservation Biology*, 26(1), 116–123. https://doi.org/10.1111/j.1523-1739.2011.01748.x

Soorae, P. S. (2018). *Global reintroduction perspectives: 2018: Case studies from around the globe* (6th edition, xiv +286pp). Gland, Switzerland: IUCN/SSC Reintroduction Specialist Group, Environment Agency, Abu Dhabi, UAE.

Stamps, J. A., & Swaisgood, R. R. (2007). Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science*, 102(3–4), 392–409. https://doi.org/10.1016/j.applanim.2006.05.038

Støen, O.-G., Pitlagano, M. L., & Moe, S. R. (2009). Same-site multiple releases of translocated white rhinoceroses *Ceratotherium simum* may increase the risk of unwanted dispersal. *Oryx*, 43(4), 580. https://doi.org/10.1017/s0030605309990202

Suraci, J. P., Clinchy, M., Mugerwa, B., Delsey, M., Macdonald, D. W., Smith, J. A., Wilmers, C. C., & Zanette, L. Y. (2017). A new automated cehavioural response system to integrate playback experiments into camera trap studies. *Methods in Ecology and Evolution*, 8(8), 957–964. https://doi.org/10.1111/2041-210X.12711

Szostek, K. L., Schaub, M., & Becker, P. H. (2014). Immigrants are attracted by local pre-breeders and recruits in a seabird colony. *Journal of Animal Ecology*, 83(5), 1015–1024. https://doi.org/10.1111/1365-2656.12206

Trefry, S. A., & Hik, D. S. (2009). Eavesdropping on the neighbourhood: Collared pika (*Ochotona collaris*) responses to playback calls

of conspecifics and heterospecifics. *Ethology*, *115*(10), 928–938. https://doi.org/10.1111/j.1439-0310.2009.01675.x

Wickham, H. (2016). *Ggplot2: Elegant graphics for data analysis* (2nd ed.). *Use R!*. Springer.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Zuur, A. F., Ieno, E. N., Walker, N., Ahlering, M. A., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer. https://doi.org/10.1007/978-0-387-87458-6

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.