Improving rhinoceros conservation and management through behaviour-based research: Evidence from Botswana

Dissertation

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Preface

"If you truly want to grasp the situation faced by conservationists, do what a poacher does and look at a rhino and see a three-foot-long horn made of pure gold. Game rangers are in the unenviable and extremely hazardous position of trying to protect solid gold. What should be locked securely in a vault instead walks around on four legs in the bush."

Lawrence Anthony

"For the animal shall not be measured by man. In a world older than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear."

Henry Beston

Meinen Eltern… und den Nashörnern

Contents

Summary

Illegal wildlife trafficking is one of the major drivers of biodiversity loss. Some of the most targeted species of illegal wildlife trade are rhinoceroses ("rhinos"), which exist nowadays in distinct populations in several reserves. For genetic exchange between these meta-populations and to establish new populations, rhinos are commonly translocated. Spatial behaviour of rhinos after translocations is very variable and can result in long-distance dispersal, but the causes for this behaviour are not well known. Long-distance dispersal can be controlled by fences or through re-capture of the dispersing individual, but this is expensive and stressful for the animals. Cues from natural rhino communication could present more animal-friendly and cost-effective methods to keep rhinos at the release site. After translocation, the protection of the new population from illegal harvesting is very important. To reduce the attractiveness of rhinos to poachers, the animals can be dehorned, but the effects of horn removal on natural rhino behaviours have previously not been extensively studied. The aim of this thesis is to use behavioural research to evaluate rhino management methods and to contribute to their improvement.

The **first chapter** provides a general introduction and presents rhinos as a study species. To improve understanding of spatial behaviour of rhinos, several indicators for home range establishment are tested in **Supplementary study 1**. **Chapter 2** builds on Supplementary study 1 and analyses the movement data of 72 rhinos translocated to Botswana for site fidelity and movement range sizes after release. In white rhinos (*Ceratotherium simum*), differences in site fidelity depending on age were found, with higher site fidelity in adults than in subadults. There was no evidence for differences in site fidelity between age classes in black rhinos (*Diceros bicornis*). Movement range sizes of white rhinos were smaller at a confined release site compared to sites without movement restricting barriers, and range sizes of newly released individuals were larger than range sizes after one year. Fencing the release area during the explorative phase of rhino movement after translocations might therefore help to increase site fidelity, but the logistical efforts needed for fencing might outweigh the benefits, as all individuals in this study eventually established stable home ranges.

Chapter 3 examines the possibility to attract or deter rhinos through playbacks of conspecific calls, which might be applied as a management tool to reduce post-translocation dispersal. Playback experiments were performed with 25 free-roaming white rhinos in Botswana. The study subjects reacted to both socio-positive and socio-negative calls with head movements and calling but directed movement responses were rare and depended on a wide range of factors, i.e., the sex of the targeted rhino, wind conditions, the behaviour of the animal before the playback, and the familiarity of the tested individual with the caller. Males often approached the loudspeaker, while females escaped from playbacks with calls from unfamiliar senders. It would potentially be possible to use playbacks to guide rhino movement, but to evaluate the applicability, further research would be needed, ideally with automated behavioural response systems and the testing of long-term effects. **Supplementary study 2 and 3** present additional experiments with juvenile calls and analyses of vigilance behaviour durations and distances travelled before and after playback experiments.

Chapter 4 examines the impact of dehorning on natural rhino behaviour using data from focal animal sampling of nine rhinos. The focal subjects were observed for one month before and after a dehorning event. No effects of dehorning on resting, feeding and comfort behaviour were found. Females showed more locomotion after dehorning than before, which might reflect an avoidance of the observation vehicle, because the animals had been immobilised and therefore chased from the vehicle in preparation for the dehorning. The vocalisation rate of males was lower after dehorning than before because two males had vocalised continuously during a fight before dehorning. No fight was observed after dehorning, so this could either be a biased result or an indicator for reduced aggressive behaviour after dehorning. During the two months of behavioural observations, two rhinos in the study population gave birth. The births seemed to have much stronger effects on rhino behaviour than dehorning, because the females that gave birth changed from mainly feeding to mainly resting, and males that searched for the females when they had isolated themselves for giving birth showed increased locomotion. Therefore, social events might impact rhino behaviour more than dehorning and dehorning can be seen as a safe conservation method from an animal welfare point of view. Further research would be necessary to evaluate the effectiveness of dehorning in reducing poaching events.

This thesis contributes to the growing field of conservation behaviour, a discipline that aims to use behavioural ecological knowledge for successful and efficient conservation solutions. **Chapter 5** discusses the application of the main findings of this work in rhino management and in the larger context of adaptive management. Overall, the results of this thesis highlight research gaps in rhino conservation plans and report possible improvements of current management methods, which can be extended to other species and contribute to biodiversity conservation.

Zusammenfassung

Illegaler Wildtierhandel ist einer der großen Treiber der Biodiversitätskrise. Zu den am stärksten davon betroffenen Arten gehören Nashörner, die heute in verschiedenen Reservaten in isolierten Populationen leben. Für den genetischen Austausch zwischen diesen Meta-Populationen und zur Etablierung neuer Populationen werden Nashörner häufig umgesiedelt. Das räumliche Verhalten von Nashörnern nach Umsiedlungen ist sehr variabel und kann zur Ausbreitung über weite Entfernungen führen, doch die Ursachen für diese Verhaltensweisen sind unklar. Die Ausbreitung über weite Entfernungen kann durch Zäune oder durch den Wiederfang der abwandernden Tiere kontrolliert werden, doch das ist teuer und stressig für die Tiere. Signale aus der natürlichen Kommunikation von Nashörnern könnten möglicherweise als tierfreundlichere und kostengünstigere Methoden angewendet werden, um die Tiere an der Freilassungsstelle zu halten. Nach den Umsiedlungen ist der Schutz der neuen Populationen vor illegaler Jagd sehr wichtig. Um die Attraktivität von Nashörnern für Wildernde zu reduzieren, können die Tiere enthornt werden, aber die Auswirkungen des Enthornens auf natürliches Nashornverhalten wurden bisher noch nicht vollständig untersucht. Ziel dieser Arbeit ist es, verhaltensökologische Untersuchungen zu nutzen, um Managementmethoden für Nashörner zu evaluieren und zu deren Verbesserung beizutragen.

Das **erste Kapitel** enthält eine allgemeine Einleitung und stellt Nashörner als Studienart vor. Um das Verständnis für das räumliche Verhalten von Nashörnern zu verbessern, werden in **Zusatzstudie 1** mehrere Indikatoren für die Etablierung von stabilen Streifgebieten getestet. **Kapitel 2** baut darauf auf und analysiert die Bewegungsdaten die Bewegungsdaten von 72 Nashörnern, die nach Botswana umgesiedelt wurden, im Hinblick auf Standorttreue und Streifgebietsgrößen. Bei Breitmaulnashörnern (*Ceratotherium simum*) traten Unterschiede in der Standorttreue in Abhängigkeit vom Alter auf, wobei adulte Individuen höhere Standorttreue zeigten als subadulte. Bei Spitzmaulnashörnern (*Diceros bicornis*) gab es keinen signifikanten Einfluss des Alters auf die Standorttreue. Die Streifgebietsgrößen von Breitmaulnashörnern in einem eingegrenzten Freilassungsgebiet waren kleiner als in Freilassungsgebieten ohne bewegungseinschränkende Barrieren, und die Streifgebietsgrößen von neu freigelassenen Individuen waren größer als diejenigen nach einem Jahr. Das Umzäunen des Freilassungsgebietes während der explorativen Phase in den Bewegungsmustern von Nashörnern nach Umsiedlungen könnte daher helfen, die Standorttreue zu erhöhen. Die dafür notwendigen logistischen Kosten könnten aber die Vorteile übertreffen, da alle Nashörner in dieser Studie auch ohne Einzäunung schlussendlich stabile Streifgebiete etablierten.

Im **dritten Kapitel** wird getestet, ob Breitmaulnashörner mit Playbacks von Rufen von Artgenossen angelockt oder verjagt werden können, was als Managementmethode angewendet werden könnte, um Abwanderungen nach Umsiedlungen zu verhindern. Es wurden Playback-Experimente mit 25 wildlebenden Nashörnern in Botswana durchgeführt. Die Fokustiere reagierten sowohl auf sozio-positive als auch auf sozio-negative Rufe mit Kopfbewegungen und Vokalisation, doch gezielte Bewegungen waren nur selten Teil der Reaktionen und hingen von einer Vielzahl von Faktoren ab, z.B. dem Geschlecht des Fokustieres, den Windverhältnissen, dem Verhalten des Tieres vor dem

Experiment und der Vertrautheit des getesteten Individuums mit dem Rufenden. Männliche Nashörner näherten sich dem Lautsprecher häufig, während Weibchen vor Playbacks von Kontaktrufen unbekannter Nashörner flüchteten. Diese Ergebnisse deuten darauf hin, dass es möglich wäre, Playbacks zu nutzen, um die Bewegungen von Nashörnern zu beeinflussen, aber weitere Experimente idealerweise mit automatisierten Playbacks und Tests der Langzeiteffekte würden benötigt, um die tatsächliche Anwendbarkeit zu bewerten. In den **Zusatzstudien 2 und 3** werden zusätzliche Experimente mit Jungtierrufen sowie Analysen der Dauer des Wachsamkeitsverhaltens und zurückgelegte Entfernungen vor und nach den Playback-Experimenten vorgestellt.

Kapitel 4 untersucht die Auswirkungen des Enthornens auf das natürliche Verhalten von Nashörnern anhand von Fokustierbeobachtungen von neun Nashörnern. Die Fokustiere wurden während je eines Monats vor und nach dem Enthornen beobachtet. Bei Ruhe-, Fress- und Komfortverhalten wurden keine Effekte des Enthornens gefunden. Weibliche Nashörner zeigten nach dem Enthornen mehr Bewegungsverhalten als vorher, was wahrscheinlich durch das Ausweichen vor dem Beobachtungsfahrzeug ausgelöst wurde, weil die Tiere in Vorbereitung auf das Enthornen mit Fahrzeugen verfolgt von dort aus immobilisiert wurden. Die Vokalisationsraten waren bei männlichen Nashörnern nach dem Enthornen niedriger als davor, da zwei der Männchen vor dem Enthornen während eines Kampfes durchgängig vokalisiert hatten. Nach dem Enthornen wurde kein Kampf beobachtet, daher könnte dies entweder ein durch eine Einzelbeobachtung verzerrtes Ergebnis sein oder ein Hinweis auf weniger aggressive Interaktionen nach dem Enthornen. Während der zwei Beobachtungsmonate kalbten zwei Nashörner in der Studienpopulation. Diese Geburten schienen einen starken Einfluss auf das Verhalten der Nashörner zu haben, da deutliche Veränderungen von Fressverhalten zu Ruheverhalten bei den kalbenden Weibchen auftraten. Zudem gab es einen Anstieg im Bewegungsverhalten bei den Männchen, die nach den Weibchen suchten, als diese sich zum Gebären isoliert hatten. Soziale Ereignisse scheinen daher Nashornverhalten zu stärker beeinflussen als das Enthornen, was aus Tierwohlsicht das Enthornen als sichere Artenschutzmethode bestätigt. Weitere Forschung wäre nötig, um zu evaluieren, wie effizient das Enthornen zum Rückgang von Wilderei beiträgt.

Diese Studie trägt zu dem wachsenden Feld des *Conservation Behaviour* bei, einer Disziplin, die es sich zum Ziel gesetzt hat, verhaltensökologisches Wissen für effiziente und erfolgreiche Naturschutzlösungen anzuwenden. **Kapitel 5** erörtert die mögliche Anwendung der wichtigsten Ergebnisse dieser Arbeit im Nashornmanagement und im größeren Kontext des adaptiven Managements. Insgesamt zeigen die Ergebnisse dieser Arbeit Forschungslücken im Bereich des Nashornschutzes auf und berichten über mögliche Verbesserungen der derzeitigen Managementmethoden, welche auf weitere Arten übertragen werden und damit zum Biodiversitätsschutz beitragen können.

1. General Introduction

Wildlife trafficking as a driver for biodiversity loss

In the current era of the Anthropocene, wildlife populations are globally affected by human activities, which have caused a world-wide biodiversity crisis (Ripple et al., 2017). Among the major drivers of the biodiversity crisis are habitat loss and -degradation (Krauss et al., 2010; Wilson et al., 2016) and wildlife trafficking, i.e., illegal activities related to commercial exploitation and trade of wildlife specimens (all wild fauna, flora, and fungi) or their parts (‘t Sas-Rolfes et al., 2019). Data from seizures indicate that more than 6000 species and millions of animals are trafficked annually (United Nations Office on Drugs and Crime, 2020). Especially targeted species are elephants with 30.6% of total wildlife seizures, pangolins with 13.9% and rhinoceroses with 11.8% (United Nations Office on Drugs and Crime, 2020).

In addition to the impact on the traded species, wildlife trafficking is a way for unintentionally transporting pathogens and invasive species, and a multi-billion-dollar industry that is used to finance violent conflicts (Cardoso et al., 2021; Rosen & Smith, 2010). It is difficult to combat illegal wildlife trafficking because it is intertwined with other illegal activities that cause social conflict, and because the drivers of demand and supply are diverse and trade routes are complex (Douglas & Alie, 2014; Keskin et al., 2023). Conservationists and animal owners try to protect animals on site with fences, ranger patrols and aerial surveillance (Reuter & Bisschop, 2016), but this might not be sufficient or feasible in large, inaccessible, or high-risk areas (Haas & Ferreira, 2018). In these cases, animal translocations to safer locations may be an option.

Animal translocations

The intentional movement of animals from one area of their natural range to another with the aim of protecting the animals, reintroducing the species to its former range, or restocking populations, is called conservation translocation (IUCN/SSC Re-introduction Specialist Group, 1998). Although early translocations were often unsuccessful (Griffith et al., 1989), others have contributed substantially to the re-establishment of healthy populations (Seddon et al., 2014).

The translocation procedure itself is stressful for animals (Teixeira et al., 2007) and can, for example, lead to capture myopathy (Breed et al., 2019) or other injuries during transport. Furthermore, it is challenging for translocated animals to orientate themselves in a new area (Letty et al., 2007). Most animals engage in an exploratory phase after release when they search for suitable feeding and resting locations or for conspecifics, thus moving longer daily distances than typical for the species (Berger-Tal & Saltz, 2014). The exploratory phase leads into the settlement phase, when animals recurrently visit the same locations and restrict their movement to a home range, which can be seen as short-term translocation success (Berger-Tal & Saltz, 2014). Monitoring animal behaviour post release is therefore crucial to evaluate and increase translocation success (IUCN Species Survival Commission, 2013). In the long term, translocations are successful when they result in the establishment of self-sustaining populations (Griffith et al., 1989).

Conservation behaviour

Animal behaviour research has always aimed to understand causative and functional aspects of behaviours, explaining their fitness value, development in ontogeny, development in evolution and their mechanisms of control (Bateson & Laland, 2013; Tinbergen, 1963). The relatively young scientific discipline of conservation behaviour developed behaviour research into examinations of how proximate and ultimate aspects of behaviour can improve biodiversity conservation (Berger-Tal et al., 2011; Berger-Tal et al., 2016; Rabin et al., 2003).

Behaviours that increase an individual's fitness are expressed as the most immediate response to current environmental conditions (Maspons et al., 2019; Norris, 2004). When environmental conditions change, behavioural indicators can be used to measure changes in the natural behaviour and this way reveal conservation threats (Figure 1.1). As a response, behavioural-sensitive management can modify the problematic behaviour or reduce anthropogenic impacts on the animals (Buchholz, 2007). Furthermore, behaviour studies have the potential to test tools which could be applied by managers to overcome specific conservation problems (Berger-Tal et al., 2016; Durant et al., 2019).

Movement and space-use is one of the behavioural domains that are key for all species to achieve high fitness (Berger-Tal et al., 2011, Figure 1.1). In the context of growing human land use, understanding and finding ways to guide animal movement is important to prevent human-wildlife conflict, ensure successful habitat selection, and avoid long-distance dispersal after translocations (Greggor et al., 2016). Therefore, studying changes in movement patterns and experimental studies with tools that could guide animal movement towards desirable locations can both contribute to species conservation.

Animals have a variety of senses that enable them to recognise important environmental information and support behavioural responses that increase individual fitness (Elmer et al., 2021; Madliger, 2012). Management interventions can take advantage of species-specific behavioural responses by adapting tools to the senses of the target species and this way minimising impact on the environment and on other species (Buchinger et al., 2015). Individual behavioural responses to artificial signals or cues can still differ within a species and must therefore be tested experimentally prior to application (Blumstein & Berger-Tal, 2015).

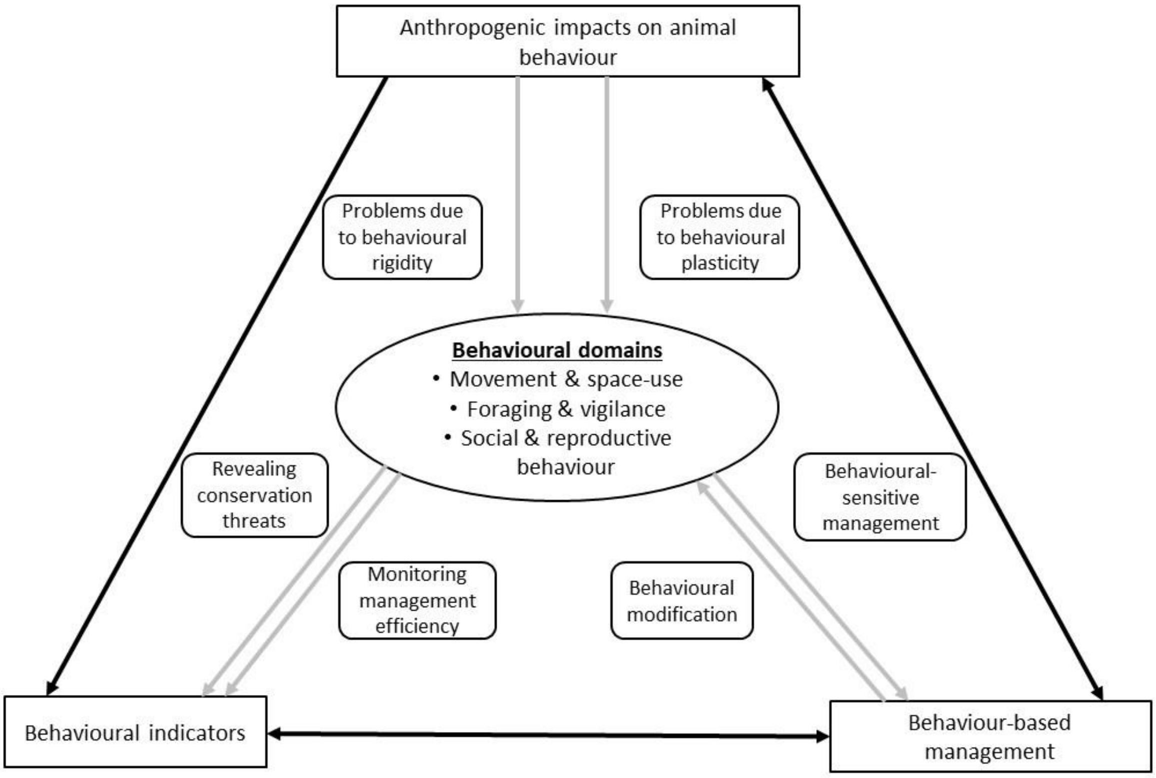

Figure 1.1 Conservation behaviour framework. Black arrows represent interactions between the conservation themes and grey arrows represent connections of themes to behavioural domains. Adapted from Berger-Tal et al., 2011.

However, the urgency of conservation problems can result in application of methods that could not be tested experimentally beforehand (Lindeque, 1990). In addition, management interventions can be successful in solving the immediate conservation problem but at the same time have unforeseen influences on other aspects of the animal's welfare. For example, herding is used in some sanctuaries to direct rhinoceroses between their night shelters and daytime grazing grounds, which helps to safeguard the animals at night from poaching but leads to more aggressive and discomfort behaviours during the herding (Fàbregas et al., 2021). Management interventions can thus cause desired and undesired behavioural changes and it is important to conduct comprehensive studies on effects of management activities that are in place and have not been examined before.

Rhinoceroses as study species

Rhinoceroses (hereafter referred to as "rhinos") are iconic animals that serve as flagship species for nature conservation. All five extant species are endangered due to poaching and habitat loss. Rhinos are poached for their horn to meet a consumer demand in Southeast Asia. The horn is used in traditional Chinese medicine mixed with other ingredients as remedy against mild illnesses and fever (Cheung et al., 2021; Dang Vu & Nielsen, 2018). The major driver of poaching is, however, increasing demand by a growing upper middle class that uses the horn as a status symbol and currency for luxury products, gift to authorities and powdered in ceremonial drinks to improve business relations (Dang Vu & Nielsen, 2018; Rademeyer, 2016). Nepal has successfully applied conservation schemes and campaigns to protect the greater one-horned rhino (*Rhinoceros unicornis*) (Acharya et al., 2020; Aryal et al., 2017), which therefore currently numbers approximately 4000 individuals in Nepal and India, recovered from less than 200 individuals in the early 20th century (Hutchins & Kreger, 2006). The Javan (*Rhinoceros sondaicus*; 76 individuals) and Sumatran (*Dicerorhinus sumatrensis;* approx. 40 individuals) rhinos, however, are close to extinction (Ferreira et al., 2022; Save The Rhino International, 2022).

African rhinos were widespread across large parts of the continent south of the Sahara until colonialists initiated trophy hunting (Player & Feely, 1960). Early records report observations of large groups of white rhinos, but also the rapid decrease in numbers once hunting started (Player, 1967; Player & Feely, 1960). Southern white rhinos (*Ceratotherium simum simum*) were reduced to only 20 to 50 animals by 1895 (Emslie & Brooks, 2002). Consequently, the last area of occurrence of the remaining white rhino population, Umfolozi, was declared a game reserve and rhino numbers recovered to more than 400 individuals by 1953 (Player & Feely, 1960). In an unmatched conservation action, rhinos were translocated from there to other reserves, national parks, and zoological gardens to create meta-populations and reduce the risk of local extinction (Player, 1967). The translocations were very successful and land transformations in South Africa from agriculture to game farms helped to create space for rhinos, while revenue from trophy hunting made private rhino ownership attractive (Hübschle, 2016). With growing tourism, the value of rhinos as charismatic animals, promoted as part of the “big five” for photographic safaris, was recognised (Lindsey et al., 2007). White rhino numbers increased to approx. 20 600 individuals in 2012 (Emslie et al., 2016). However, by the 1970s, the Asian demand for rhino horn combined with increasing globalisation had already created trade routes and international syndicates that spread poaching for rhino horn to Africa (Jakins, 2018). The black rhino (*Diceros bicornis*) population consisted of 65 000 animals in 1970, poached to 2300 individuals by 1992 (decrease of 96%) (Hutchins & Kreger, 2006). There are 6 195 adult black rhinos and 15 942 adult white rhinos alive at the time of writing (Ferreira et al., 2022). Most of them live in highly protected game reserves where rangers are confronted with organised international criminals in war-like situations (Rademeyer, 2016). Investment in anti-poaching patrols, sniffer dogs and technical equipment for the detection of poachers on site is necessary to protect individual rhinos (Kamminga et al., 2018; Moore et al., 2018; Reuter & Bisschop, 2016/2016).

From the ecological point of view, **white rhinos** are megaherbivores that shape the landscape for other endangered species through their grazing (Malmström, 2019). Their social system includes territorial males that defend minimally intersecting territories and subordinate males and females moving between territories in overlapping home ranges (Owen-Smith, 1973). White rhinos are considered the most social rhino species. They often move in groups and have the most complex vocal communication system among rhino species (Policht et al., 2008).

Black rhinos occupy a different ecological niche than white rhinos by browsing on shrubs and branches of trees (Oloo et al., 1994). Females, their calves and subadults can form stable groups whose individual home ranges overlap (Conway & Goodman, 1989; Lent & Fike, 2003). Home ranges of adult black rhino males mostly do not overlap (Cain et al., 2014; Tatman et al., 2000), but this seems to differ between reserves and depend on habitat quality, as other studies reported male home range overlap of up to 40% (Conway & Goodman, 1989; Goddard, 1967; Göttert et al., 2010; Lent & Fike, 2003).

Between 2006 and 2018, Botswana was considered a "safe haven" for wildlife as it had very low poaching numbers of both rhinos and elephants compared to surrounding countries and strong law enforcement against poachers (Mogomotsi & Madigele, 2017; Senyatso, 2021). To re-establish rhinos in Botswana, several conservation agencies and non-governmental organisations teamed up to translocate rhinos from high poaching areas to the presumed safe Okavango Delta in Botswana (Great Plains Foundation, 2022; The Wilderness Trust, 2019). These translocations differed from previous rhino translocations as the animals were released into a large, almost unfenced area where monitoring from the ground is difficult and no physical barriers stop the movement of rhinos when exploring their new surroundings. Little was known about rhino movement patterns after translocation and previous releases had resulted in long-distance dispersal of some individuals, which had to be recaptured (Pitlagano, 2007; Støen et al., 2009). Although the recaptures were successful and all rhinos eventually established home ranges, rhino immobilisation operations, which were necessary for recapture, are logistically challenging and expensive, especially in the vastness of the Okavango Delta with many inaccessible areas. Therefore, animal-friendly alternatives to recapture were sought that could guide rhinos back into, or to prevent them from leaving, protected areas.

The rhinos in the Okavango Delta were regularly monitored and showed good reproduction rates, resulting in a growing population (Rhino Conservation Botswana, personal communication). Compared to other countries, the loss of six individuals between 2006 and 2017 to poaching was very low (Environmental Investigation Agency, 2022). This changed starting from 2018, when 11 were killed, and increased to more than 30 rhinos poached in 2019 and 62 in 2020 (Environmental Investigation Agency, 2022; Senyatso, 2021). In 2020, the government decided to dehorn all rhinos (Mguni, 2020), whereby the major part of the horn is removed in a veterinary procedure, as this would reduce the reward from illegal sale and was presumed to diminish the attractiveness of the rhinos to poachers (du Toit & Anderson, 2013). However, the effects of dehorning on rhino behaviour including their general daytime activities were not well studied so far, which was important to evaluate the method from an animal welfare point of view.

Aim and structure of the thesis

The overall aim of this thesis is to contribute to improving rhino conservation practices through behaviour-based research. It seeks to optimise a well-known conservation practice by analysing differences in short-term translocation success, tests a novel method for an animal-friendly management tool, and studies effects of dehorning as a widely applied management measure on natural rhino behaviour.

Chapter 2 focuses on the spatial behaviour of translocated rhinos and examines how sex and age of the translocated individuals affect site fidelity and movement range sizes. The results suggest that in white rhinos, site fidelity is higher in adults than in subadults, and that movement range sizes can be controlled by fencing the release area. Since no significant differences in site fidelity were observed between age and sex classes of black rhinos, the applied translocation procedure and release method for black rhinos can be deemed ideal.

Chapter 3 demonstrates that playbacks of rhino vocalisations could potentially be applied as an animal-friendly tool to guide rhino movement, but several factors influence the behavioural responses to playbacks. It suggests that automated behavioural response systems, which can be adapted to the targeted individual, will be the most promising way to apply playbacks.

Chapter 4 illustrates that rhino general activities, comfort- and social behaviour are only weakly affected by dehorning, providing evidence for the safety of dehorning as a conservation measure from an animal welfare point of view.

Chapter 5 describes how findings of the chapters 2-4 can be applied in rhino management and sets them in the larger context of conservation behaviour and adaptive management.

In **Chapter 6**, supplementary studies are reported which were part of this doctoral project, but which were not submitted for publication in peer-reviewed journals due to insufficient data. They provide methodological analyses and insight into rhino behaviour which might be applied and extended in future research.

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2. Effects of age and sex on site fidelity, movement ranges and home ranges of white and black rhinoceros translocated to the Okavango Delta, Botswana

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Abstract

Evaluating translocation success is essential for wildlife management and conservation; short-term success can be evaluated by analysing settlement behaviour after release. We analysed GPS collar data from 47 white *(Ceratotherimum simum simum,* Burchell, 1817*)* and 25 black *(Diceros bicornis minor,* Drummond, 1876*)* rhinoceros translocated to the Okavango Delta in Botswana between 2014 and 2018. We tested for effects of age and sex on site fidelity and compared movement ranges after translocations between different release sites and between newly released and established individuals. White rhinoceros adults displayed higher site fidelity than subadults and males higher than females. Adults may therefore be better translocation candidates. Site fidelity of black rhinoceros did not differ between sexes or ages. Established rhinoceros movement ranges were smaller than those of newly released ones, pointing towards extended post-translocation exploratory movements and later settlement in smaller home ranges. Movement ranges of white rhinoceros released on an island were significantly smaller than others, which shows together with annual home range sizes compared to the literature that reserve size and rhinoceros density affect home range size. All rhinoceros in this study survived for more than one year post translocation, so these translocations can be deemed successful in the short term.

Key words

conservation translocation, translocation success, settlement behaviour, mammal, exploratory movement, reintroduction

Introduction

Translocation is defined as the intentional movement of wild animals from one part of their range to another (IUCN/SSC Re-introduction Specialist Group, 1998), and is a valuable tool for management and conservation (Fischer & Lindenmayer, 2000). Translocations are commonly used to move individuals away from areas with high extinction risk (Andau, Hiong, & Sale, 1994), tackle overpopulation, restock endangered populations to ensure their long-term viability (Poirier & Festa-Bianchet, 2018) or reintroduce species into areas where they have been exterminated (IUCN Species Survival Commission, 2013; Stringer, Watts, Thornburrow, Chappell, & Price, 2014).

Translocations are expensive procedures that are stressful for animals, so it is essential to evaluate short- and long-term translocation success. In the short term, translocation success can be evaluated via the survival of the translocated individuals and their release-site fidelity (Berger-Tal & Saltz, 2014). Site fidelity is the tendency to stay at and return to a pre-occupied area (Switzer, 1993), in this case the area around the release site, which should be advantageous for the translocated animal because release sites are usually selected for optimal resource conditions (Batson, Gordon, Fletcher, & Manning, 2015). Individuals staying close to the release site also have higher chances of survival and reproductive success, because they do not waste energy on extended locomotion (Moehrenschlager & Macdonald, 2003) and stay in the vicinity of possible reproductive partners (Hardman & Moro, 2006). In addition, high release-site fidelity of translocated animals helps managers to monitor the released individuals (Hardman & Moro, 2006).

Long-term translocation success is defined as the establishment of self-sustaining populations (Griffith, Scott, Carpenter, & Reed, 1989), but measuring this requires long-term monitoring, so it is rarely assessed or reported by studies (Fischer & Lindenmayer, 2000; Massei, Quy, Gurney, & Cowan, 2010; Mésochina, Bedin, & Ostrowski, 2003). Both short- and long-term translocation success depend on several factors, including the translocation procedure, age, sex, and release method (e.g., “hard” release immediately after capture or “soft” release with an acclimatisation time in on-site enclosures; Bell, 2016). Translocations involve physical handling, transport and release of animals into an unknown environment, and animals stressed by these procedures can have a lower chance of survival (Dickens, Delehanty, & Michael Romero, 2010; Letty, Marchandeau, & Aubineau, 2007). Age and sex of the translocated animals affect their chances of survival because it can be easier for older or bolder animals to orientate themselves and find resources, shelter, and conspecifics in an unknown environment (Bacon, Hingrat, & Robert, 2017; Bright & Morris, 1994; Troy, Coates, Connelly, Gillette, & Delehanty, 2013). The size of the release area, number of released animals and the sex ratio in the released group can also affect translocation success, because these factors influence socialisation, reproduction, and intraspecific conflicts (Letty et al., 2007; Matějů et al., 2012). Furthermore, habitat quality, presence of predators and food availability due to seasonality must be considered when planning translocations (Baling, Stuart-Fox, Brunton, & Dale, 2016; Facka et al., 2016).

Animals usually engage in an exploratory phase directly after release when they move extended distances. In some species, the extended movement has been identified as homing behaviour, whereby the translocated animals attempt to return to their capture site (Miller & Ballard, 1982). Furthermore, translocated animals explore new areas to familiarise themselves with feeding and resting sites, a process known as acclimatisation (Göttert, 2011). Following this exploratory phase comes a settlement phase, when animals repeatedly return to known feeding points and spend a longer time at preferred resting sites, thus showing site-fidelity (Berger-Tal & Saltz, 2014). Such settlement behaviour also leads to the establishment of home ranges or territories (Berger-Tal & Saltz, 2014).

African rhinoceroses (hereafter referred to as “rhinos”, in this study southern white rhino, *Ceratotherium simum* s*imum* Burchell, 1817*,* and southern-central black rhino, *Diceros bicornis minor*, Drummond, 1876) exist in distinct populations in public and private game reserves. This helps to spread the risk of local extinctions through poaching (Emslie & Brooks, 1999), but also requires regular translocations to maintain genetically healthy populations or to establish new populations (Hastings & Harrison, 1994). Understanding rhino settlement behaviour is key to the success of these translocations (Sheil & Kirkby, 2018).

Previous studies found that translocation success of rhinos depended on age and sex. In both species, subadult males showed the highest mortality after release due to fighting with conspecifics or stress (Adcock, Hansen, & Lindemann, 1998; Pitlagano, 2007; Thompson, Avent, & Doughty, 2016). A long-term study for black rhinos showed that older females were more likely to become pregnant with a shorter delay after translocation than younger females (Gedir, Law, Du Preez, & Linklater, 2018), so translocating older females could contribute to the faster development of a self-sustaining population.

Few studies have investigated the settlement behaviour of rhinos after translocations, but black rhinos seemed to avoid other rhinos for at least 100 days after release (Linklater & Swaisgood, 2008). This points to a behavioural adaptation to avoid fights (and thus injuries or death) if the reserve is large enough and the rhinos are released at the same time at different sites (Patton, Mulama, Mutisya, & Campbell, 2010). In white rhinos, subsequent releases in different years at the same site have led to higher dispersal away from the release site (Støen, Pitlagano, & Moe, 2009). Homing behaviour has been observed for a group of six white rhinos translocated to Botswana (Rees, 2018). Other studies have reported that home range sizes of translocated rhinos are highly variable in size and – based on a very small sample size – suggested that this is independent of sex (Göttert, Schöne, Zinner, Hodges,

& Böer, 2010; Støen et al., 2009). In established populations, females usually have larger overlapping home ranges, whereas white rhino males have exclusive territories (Owen-Smith, 1975). Black rhino males and females have home ranges that can overlap to a larger extent compared to white rhinos, and subadults generally have larger home ranges than adults (Goddard, 1967). Annual home ranges of black rhino females are larger than those of males, but during the wet season, females can also have smaller home ranges than males (Plotz, Grecian, Kerley, & Linklater, 2016). For both species, the home range or territory sizes depend on resource availability and population density, which extends to reserve size and the area available for home range formation (Goddard, 1967; Thompson et al., 2016; White, Swaisgood, & Czekala, 2007). For example, black rhino home range sizes were larger (43 - 133 km², Frame, 1980) in the unfenced Serengeti (12,920 km²), Tanzania, where the rhino density was 0.02 individuals per km², than in the fenced Sweetwaters Rhino Sanctuary (93 km²), Kenya, with a rhino density of 0.2 individuals per km² and home ranges of 2.25 – 14.40 km² (Tatman, Stevens-Wood, & Smith, 2000).

In this study, we analysed movement patterns of African rhinos after translocation to the area of the Okavango Delta in Botswana using GPS tracking data. We use the term “movement range” for short-term activity ranges, in contrast to annual home ranges. We tested the hypotheses that (i) age and sex would affect site fidelity, with females and younger animals predicted to show lower site fidelity, (ii) initial exploratory behaviour would lead to larger movement range sizes in newly released individuals than in established, resident individuals, and (iii) animals released into a delimited area would occupy smaller movement ranges than unrestricted individuals. Finally, we provide annual home range estimates for African rhinos that give insight into the effect of reserve size on home range sizes.

Methods

Study area

The Okavango Delta is a floodplain ecosystem located in a semi-arid climate in northern Botswana between 22.0° - 24.0° E and 18.5°- 20.5° S (Heinl, Neuenschwander, Sliva, & Vanderpost, 2006) with an area of approximately 15 000 km². It encompasses the government-managed Moremi Game Reserve and adjacent private and community Wildlife Management Areas, between which animals can move freely. The only fence is a veterinary one in the south of the area that aims to keep wild animals and cattle from settlements separated. The vegetation consists of several savannah vegetation types: riparian woodland, mopane woodlands, mixed shrubland, acacia woodlands, grasslands and floodplains (Bennitt, Bonyongo, & Harris, 2015). These vegetation types provide good rhino habitat and support high levels of biodiversity, including all locally native large mammals

(Ramberg et al., 2006). The Delta is a flood-pulsed ecosystem fed by rainfalls in Angola, which arrive and advance between April and July and recede between August and November (Bennitt et al., 2015). December to March are usually the months with most rainfall, therefore surface water is abundant throughout the year but varies seasonally in its distribution (Bennitt et al., 2015). Rhinos were present in Botswana until a first extirpation in the 20th century through hunting for horn (Emslie & Brooks, 1999). White rhinos were reintroduced in 1967, but only a few individuals survived until the end of the 1980's. These were captured and translocated to protected sanctuaries (Tjibae, 2002). The first new attempt to reintroduce rhinos to the Okavango Delta and thus to the wild in Botswana was taken in the early 2000s with 32 individuals released (Støen et al., 2009). By the beginning of the translocations analysed in this study, about 80 rhinos existed in an area of 9000 km², resulting in a very low rhino density of 0.0089 rhinos per km².

Translocation procedure

We used data from rhinos translocated over several years as part of restocking projects, so we compiled and analysed existing data rather than collecting new data. We were granted permission for this study by the Ministry of Environment, Natural Resources Conservation and Tourism (MENT) of Botswana (Permit ENT8/36/4XXXXII 58). All rhino translocations in this study were coordinated through a group effort by Rhinos Without Borders, the Botswana Department of Wildlife and National Parks, and Rhino Conservation Botswana. Approval for the translocation projects was given by MENT and all animal handling was performed by experienced, qualified veterinarians registered in Botswana and authorised monitoring personnel. Details about the translocation procedure are available as reference for future translocations in the appendix, but generally, best practices as described in Emslie, Amin, & Kock, 2009; Morkel & Kennedy-Benson, 2007; Reuter & Adcock, 1998 were used. Details about individual rhinos are provided in the supplementary material. Releases took place between April and September, details about release batches are provided in Table 2.3 in the appendix. We were not able to account for effects of the season, month, or year because of small sample sizes. White rhino adults were 'semi-hard' released, i.e., walked out of the transport crate under immobilisation and control with ropes, and given reversal drugs at the release site, where they could walk free immediately. White rhino mother-calf combinations were kept for one night in holding pens with ample food and water to ensure hydration after travel and bonding of the calves with their mothers. Black rhinos were released 'softly', i.e., kept in holding pens at the release site for 14 days. Black rhinos relax in confined spaces quickly and have a more complex browse feed than white rhinos. The 14-day-period was to relax the rhinos after travel and ensure acceptance of local browse feed into their diet (Morkel & Kennedy-Benson, 2007). During cleaning of the holding pens, dung was collected into polypropylene bags for distribution in the release area to artificially mark home ranges and territories with a smell that was familiar to the rhinos, which was presumed to increase the likelihood of settlement in the area after release. The dung was distributed daily until release of the rhino.

Movement data

Adult and subadult rhinos were fitted with tracking devices prior to release. Juveniles were not collared to prevent injury from increasingly tight collars following natural growth. Adults were older than six years, subadults between two and six years (Law & Linklater, 2013). The tracking devices used were Iridium Satellite ankle collars (African Wildlife Tracking, Pretoria, South Africa), fitted around the front ankles by experienced personnel and double checked by other members of the team to ensure proper fit. The collars were programmed to obtain and send a GPS location via satellite every 3 hours; however, this was rarely achieved for prolonged periods due to collar software and hardware failure and environmental factors hampering signal strength and collars falling off animals. GPS points were timestamped and accessed via an encrypted computer application, and we subtracted the coordinates of the release site from the location data of each individual to prevent publicising real rhino locations. For the analysis, we deleted all GPS points taken before the release date in Botswana.

Settlement behaviour

To measure short-term settlement behaviour immediately after release, we calculated individual movement ranges with a 95 % Kernel Density Estimation (KDE) for two consecutive ten-day chunks, starting with the day of release, and calculated the overlap of the two movement ranges as a proxy for the rhino’s site fidelity. A high movement range overlap indicates a strong site fidelity, whereas a low movement range overlap indicates movements away from the release site. Collar failures led to low sample size, which limited the settlement period that could be considered; however, in their study with 39 black rhinos, Linklater and Swaisgood (2008) observed a stabilisation of post-release movement after 15 days and we can therefore expect our observations of site fidelity within the first 20 days to be representative for settlement behaviour. We excluded movement ranges with fewer than ten GPS location logs within either ten-day-fragment to be able to calculate representative movement ranges.

The release site for one cohort of white rhinos (cohort A, ten individuals) was on an island in the Okavango Delta surrounded by deep water channels and thus their movement was restricted. We excluded this cohort from the analysis of movement range overlaps, as we surmised that they would not be comparable to the settlement behaviour and movement ranges at other release sites. We used t-tests to analyse differences between sexes and between age classes (adult and subadult) and corrected the p values with false discovery rate adjustment (Benjamini & Hochberg, 1995). We did not test other possibly influencing variables because those were highly correlated in our dataset (e.g., all individuals from the same source population were released on the same day and thus in the same season) and because all release sites were chosen to provide a similar availability of water and high-quality forage.

Movement range sizes

For settlement behaviour in the medium term, we calculated three-month movement ranges of translocated white rhinos from the first 90 days after release. We used two estimators, Minimum Convex Polygons (MCP) and Kernel Density Estimations (KDE), for movement range calculation for better comparability with other rhino studies. MCPs are most frequently used for white rhinos (Conway & Goodman, 1989; Owen-Smith, 1973; Pienaar, Du Bothma, & Theron, 1993; Rachlow, Kie, & Berger, 1999; Sheil & Kirkby, 2018; White et al., 2007), but they can include large areas of non-utilised habitat and have been replaced by KDEs in newer studies (Shikuku, 2014; Thompson et al., 2016). We used 95 % movement ranges to exclude extreme outliers. We compared the movement ranges of the newly translocated individuals to three-month movement ranges of previously released individuals that had been living for three to five years in the Okavango Delta. We differentiate those groups hereafter with the terms “new” and “established”. We were not able to account for annual or seasonal variation because of temporal variation in data availability. However, Shrader and Perrin (2006) observed that seasonal variation in home range sizes of white rhinos is negligible at sites with low rhino densities, which is the case in our study area. Thus, we used a Wilcoxon rank sum test to test for the differences in home range sizes between new and established white rhinos.

We also used a Wilcoxon rank sum test to compare the three-month movement range sizes of the subadult females of Cohort A with those of subadult white rhino females released at other sites to determine whether the size of the release area had an effect on movement range sizes.

Annual home range sizes

We calculated annual home range sizes for white and black rhinos when the GPS collars worked for at least one year. Plotz et al. (2016) reported that rhino home range sizes depend on the method used and can be inflated if an insufficient number of GPS locations is used. All individuals had more than 400 locations during the year, which is sufficient for the calculation of annual home ranges with recommended minimum 30 locations (Plotz et al., 2016). We calculated 95 % MCP and 95 % KDE home ranges for the reasons explained in the section on movement range sizes, and because KDEs are more commonly used for black rhinos (Cain et al., 2014; Le Roex, Dreyer, Viljoen, Hofmeyr, & Ferreira, 2019; Reid, Slotow, Howison, & Balfour, 2007) or both estimators are reported (Plotz et al., 2016). Furthermore, we provide MCP 100 % home range sizes as used in Conway & Goodman, 1989;

Kretzschmar, 2002; Owen-Smith, 1973; Pienaar et al., 1993; Pienaar, 1994; Rachlow et al., 1999; Sheil & Kirkby, 2018 in Table 2.6 (appendix).

We performed all data analysis in R (v4.0.3 (2020-10-10), The R Foundation for Statistical Computing), using the packages tidyverse (Wickham et al., 2019) for workflow, ggplot2 (Wickham, 2016) and ggsignif (Ahlmann-Eltze & Patil, 2021) for visualisation, amt (Signer, Fieberg, & Avgar, 2019) and lubridate (Grolemund & Wickham, 2011) for movement analysis and home range estimation. We used an Alpha value of 0.05 and thus considered p-values below 0.05 as statistically significant.

Results

We analysed satellite GPS data from 47 white rhinos (34 females, 13 males) and 25 black rhinos (12 females, 7 males) translocated between April 2014 and July 2018 to assess their settlement behaviour after translocations. The final dataset for white rhinos consisted of 32,668 locations ranging from 15 to 1896 locations per individual. Individuals were tracked for 21 to 630 days after release, depending on the time of collar failure. For black rhinos, the dataset consisted of 11,088 locations with 63 to 796 locations per individual. The number of days with locations before failure of the collars varied between 60 and 475 days per individual (details are provided in the supplementary material).

Settlement behaviour

Excluding cohort A and individuals with fewer than five GPS locations within the ten-day fragments reduced the dataset for white rhinos from 47 to 34 individuals and for black rhinos from 25 to 19 individuals.

For white rhinos, overlap of individual movement ranges and thus site fidelity differed significantly between sexes and age classes (Figure 2.1, Table 2.1). Adult movement ranges overlapped more and thus they showed a higher site fidelity than subadults (overall adult – subadult t=2.28; adult female – subadult female t=2.55; adult male – subadult male t=3.88, for all comparisons p<0.05, Table 2.1, Figure 2.1). Adult female movement ranges overlapped significantly less than those of adult males (t=-4.38, p<0.05, Table 2.1, Figure 2.1). Range overlap was similar in subadult females and subadult males (t=-1.59, Table 2.1). In black rhinos, there was no effect of sex or age class on movement range overlap (overall adult – subadult t=1.24; overall male – female t=1.54; adult female – subadult female t=1.31; adult male – subadult male t=0.46, subadult female – subadult male t=0.41, for all comparisons p>0.1, adult female – adult male t=1.88, p=0.09), although there was a non-significant trend for movement ranges to overlap more in adults than subadults, and in females than males (Figure 2.1, Table 2.1).

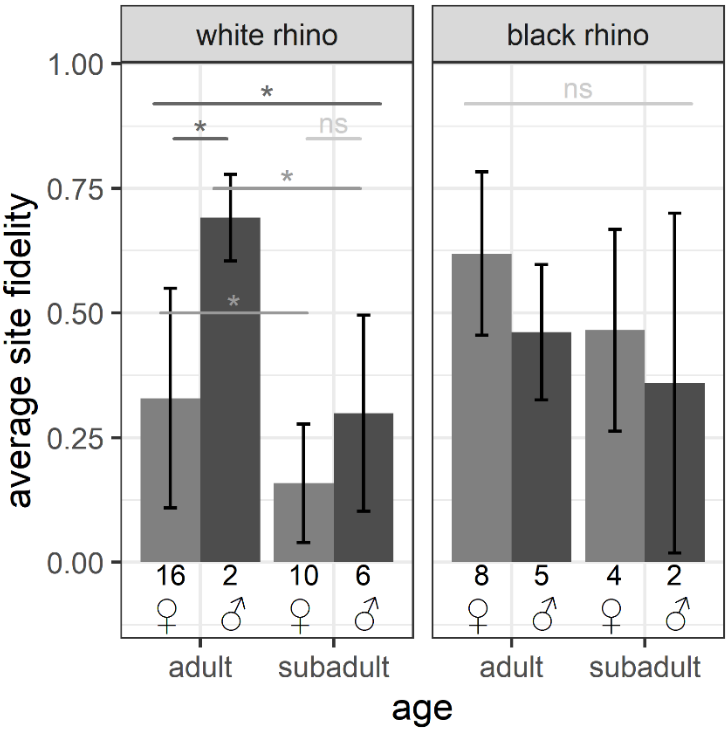

Figure 2.1 Site fidelity of 34 white rhinos and 19 black rhinos translocated to the Okavango Delta, Botswana. Site fidelity was calculated as the overlap between an individual's movement range in the first ten days with its movement range in the second ten days after release. The number of individuals is indicated below each bar, stars show significant differences, ns=not significant.

Table 2.1 Pairwise t-tests for site fidelity calculated in overlaps between a translocated rhino's movement range in the first ten days with its movement range in the second ten days after release into the Okavango Delta, Botswana. Values shown in bold are significant at p<0.05. Symbols: > higher range overlap than the following group, < lower range overlap than the following group, = no significant difference.

	Average overlap	Direction	Compared to	Average overlap	**Adjusted p value (false discovery rate adjustment)**
White rhino					
Adult	**0.37**	**>**	**Subadult**	**0.21**	**0.04**
Male	0.40	=	Female	0.26	0.19
Adult female	**0.33**	**>**	**Subadult female**	**0.16**	**0.04**
Adult male	**0.69**	**>**	**Subadult male**	**0.30**	**0.04**
Adult female	**0.33**	**<**	**Adult male**	**0.69**	**0.04**
Subadult female	0.16	=	Subadult male	0.30	0.18
Black rhino					
Adult	0.56	=	Subadult	0.43	0.38
Male	0.43	=	Female	0.57	0.38
Adult female	0.62	=	Subadult female	0.47	0.38
Adult male	0.46	=	Subadult male	0.36	0.75
Adult female	0.62	=	Adult male	0.46	0.38
Subadult female	0.47	=	Subadult male	0.36	0.75

Movement range sizes

Three months of data from new white rhinos were available for 25 individuals (excluding cohort A and two individuals that had dispersed out of the Delta and had to be recaptured). Data from established rhinos were available for 9 individuals in 2018.

Established white rhinos had significantly smaller three-month movement ranges than new ones, for both MCP and KDE estimations (Wilcoxon rank sum exact test, MCP: W=46, p=0.0046, KDE: W=46, p=0.0081, Figure 2.2, Table 2.4 in the appendix). Established individuals also showed a much smaller scattering in their movement range sizes than new ones (Figure 2.2, Table 2.4 in the appendix).

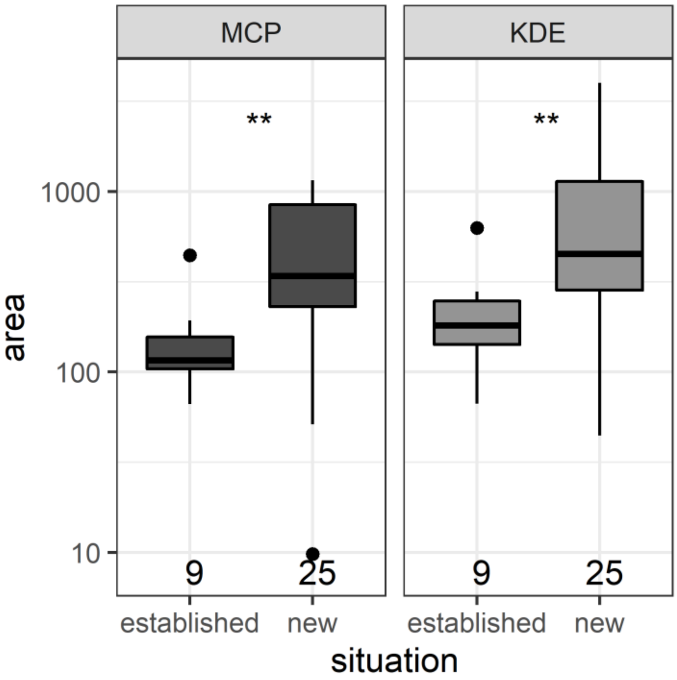

Figure 2.2 Three-month movement ranges for established and newly translocated white rhinos in the Okavango Delta, Botswana. MCP= Minimum Convex Polygon, KDE= Kernel Density Estimation, calculated at 95 % levels. Area size in km²; note the logarithmic scale. The number of individuals is indicated below each boxplot, stars show significant differences.

Subadult Cohort A females (6 individuals) had significantly smaller MCP and KDE three-month movement ranges than subadult white rhino females released at other sites (7 individuals) (Wilcoxon rank sum test, MCP: W=0, p=0.0012, KDE: W=0, p=0.0004, Figure 2.3, Table 2.5 in the appendix).

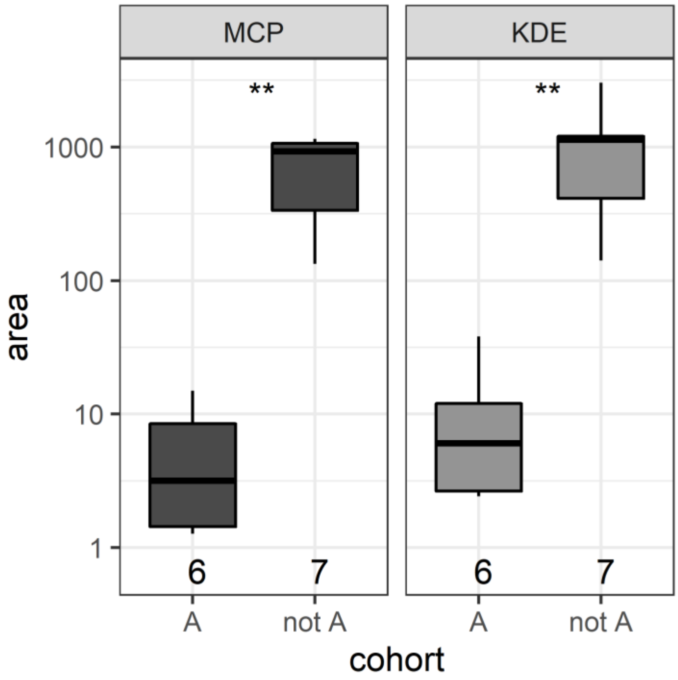

Figure 2.3 Three-month movement ranges of subadult white rhino females translocated to the Okavango Delta, Botswana, at a delimited release site (A) and at other release sites (not A). MCP = Minimum Convex Polygon, KDE = Kernel Density Estimation, calculated at 95 % levels. Area size in km²; note the logarithmic scale. The number of individuals is indicated below each boxplot, stars show significant differences.

Annual home range sizes

For white rhinos, annual data were only available for five females (one adult, four subadults) of cohort A. For black rhinos, data were available for 9 individuals (3 subadult females, 3 adult females, 3 adult males). Because of this small and female-biased dataset, we did not use statistical tests to compare the home range sizes between sexes and age classes but here we report the results to provide reference values for comparison to other studies. With limited data, both methods showed that subadults appeared to occupy larger home ranges than adults (Table 2.2). MCP estimates generally led to smaller home range sizes than KDE estimates.

Table 2.2 Annual home range sizes of white and black rhinos translocated to the Okavango Delta, Botswana. MCP = Minimum Convex Polygon, KDE = Kernel Density Estimation, calculated at 95 % levels.

Annual home ranges			**Female**		**Male**
		Age	**Adult**	**Subadult**	**Adult**
White rhino	Number of individuals		1	4	0
	MCP	Mean	13	29 ± 15	
		Min. to max.	-	17 – 50	
	KDE	Mean	16	31 ± 14	
		Min. to max.	-	18 – 50	
Black rhino	Number of individuals		3	3	3
	MCP	Mean	37 ± 6	64 ± 43	49 ± 17
		Min. to max.	30 – 43	27 – 110	32 – 67
	KDE	Mean	98 ± 38	155 ± 118	122 ± 39
		Min. to max.	80 – 141	48 – 281	78 – 153

Discussion

Understanding animal movement after translocation can increase translocation success. In this study, we investigated settlement behaviour, movement ranges and annual home ranges of translocated rhinos. For white rhinos, our results supported the hypothesis that adults would display a higher release-site fidelity than subadults and males a higher site fidelity than females, but black rhino site fidelity did not differ between age classes or sexes. As predicted, white rhino movement ranges in the first three months after release were significantly larger than those of white rhinos that had been established for three to five years post translocation. Furthermore, we found that three-month movement ranges of subadult females released on an island were significantly smaller than those of subadult females released at other sites, supporting our hypothesis that release into a delimited site would reduce movement range size.

Site fidelity after release avoids fitness loss and individuals staying close to the release site are thus better suited for translocations than individuals that show extended movement (Moehrenschlager

& Macdonald, 2003). The lower site fidelity in subadult white rhinos could be linked to the "natural dispersal behaviour" of subadults that move away from their maternal home ranges to form their own home ranges (Shrader & Owen-Smith, 2002). Dominant adults could also cause the subadults to move away from release sites (Metrione, Penfold, & Waring, 2007). Therefore, our results indicate that adult white rhinos are more likely to settle close to the release sites and thus might be better suited than subadults to translocation into reserves with low rhino density.

Adult male white rhinos showed a higher site fidelity than females, perhaps because adult males occupy and defend territories that are generally smaller than female home ranges (Owen-Smith, 1973). However, our sample size may have biased results, so further research is needed to confirm this finding. Previous translocations of adult males have resulted in occasionally fatal fights (Pitlagano, 2007), hence adult males should only be translocated when the release site provides sufficient space for the number of released territorial males and when adult males can be released at different sites (Støen et al., 2009).

There was little evidence for differences in the site fidelity for black rhinos, although we observed a tendency for females to show higher site fidelity than males and adults than subadults. One reason for this could be abundant surface water during black rhino releases, which took place during the early flood season. Le Roex et al. (2019) reported that surface water is the limiting resource for black rhino females, so when released at a site with abundant water, high site fidelity is likely. Similarly, black rhino females in Kruger National Park had smaller home ranges than males during the wet season, whereas female home ranges were larger than male home ranges during dry season (Plotz et al., 2016). Another reason for higher site fidelity in females than in males could be that they were accompanied by dependent calves, which also leads to smaller home range sizes (Alibhai, Jewell, & Towindo, 1996). Males, on the other hand, might have explored more possible territories or have dispersed away from previously released individuals (Linklater & Swaisgood, 2008). These findings are similar to previous studies, where males showed slightly larger home ranges after translocations, but overall, no significant differences in home ranges sizes between sexes were found (Göttert et al., 2010; Schwabe, Göttert, Starik, Levick, & Zeller, 2015; Tatman et al., 2000). Our results for the effect of age are different to a study by Göttert et al. (2010), who observed more exploratory behaviour in adults than subadults. Their study was conducted in a relatively small private reserve, so adults may have explored the area in the beginning to find and occupy the most favourable feeding sites. Our study was conducted in an open area, so all rhinos could access and settle in their preferred area.

In the long term, however, there are indications that black rhino adult females are better suited for establishing new populations: Gedir et al. (2018) found a higher offspring recruitment rate for adult females than for subadults. Linklater et al. (2012) reported a higher vulnerability to translocation failure of black rhino subadults during restocking. The individuals in our study were additionally monitored in ground and air patrols on daily or at least weekly basis and no injuries from fights were observed. This supports the speculation by Linklater and Shrader (2008) that in large reserves, black rhinos can avoid each other and thus prevent conflicts and injuries, allowing them to form stable social associations and home ranges.

Newly translocated white rhino individuals had larger three-month movement ranges than established ones, pointing to an initial exploratory behaviour after translocation, which declined with time. Exploratory behaviour after translocations has been observed for other ungulate species, followed by a settling phase (Berger-Tal & Saltz, 2014). A previous study reported that the range sizes of translocated rhinos decreased over several years post release (Støen et al., 2009). Further studies with equal sex ratio in the dataset could analyse the duration of the settling phase in white rhinos. Subadult females released on an island (cohort A) showed significantly smaller movement ranges during the first three months than subadult females released at other sites. Cohort A did not leave the island and the size of the island most likely also restricted their annual home range sizes. Thus, our results suggest that initial exploratory behaviour could be restricted by keeping the animals in a confined area, which might increase release-site fidelity, but the provision of temporary enclosures is not always supported financially or logistically (Berger-Tal, Blumstein, & Swaisgood, 2020). All but two translocated white rhinos settled successfully without an enclosure, demonstrating the efficiency of existing translocation procedures for white rhinos.

Comparing white rhino movement range sizes from our study to ranges described in the literature, initial movement ranges were very large (for KDE with 44 – 3992 km² up to 142 times the size of established movement ranges over 15 months in a fenced private game reserve, 7 – 28 km², Thompson et al., 2016). Those striking differences in the movement range sizes, even though calculated about differing periods of time, point to a high adaptability of white rhinos to the reserve size. Our results show that rhinos can walk several hundred kilometres within a few days or weeks and occupy large movement ranges when given the opportunity, but viable rhino populations with smaller home ranges illustrate that ample space is not a requirement for successful rhino reproduction, provided that the habitat can sustain the number of rhinos present (Tatman et al., 2000). The female white rhino annual 95 % MCP home range sizes of 13 – 50 km² were similar to those reported from Hluhluwe-iMfolozi Game Reserve, South Africa, of 6 – 66 km² (White et al., 2007). However, the annual white rhino ranges in our study were from rhinos on an island and therefore their movement was restricted in a similar manner to fenced reserves and their home range sizes were likely not representative of the home ranges of rhinos released in the unfenced area.

Annual home range size for black rhinos was similar sizes to those in the Serengeti National Park, Tanzania (43 – 133 km² MCP, Frame, 1980) and larger than home range sizes in smaller reserves (0.75 – 45 km² MCP, Pienaar et al., 1993). This supports previous observations (Göttert et al., 2010; White et al., 2007) that home range size depends on reserve size and rhino density. During early black rhino translocations, home ranges were still changing three years after release (Adcock et al., 1998). Longer-term movement datasets from translocated black rhinos would allow to study home range establishment, but these were not available from our dataset.

Although our data do not allow us to directly compare the two species, we observed that movement ranges of subadult females appeared to be much smaller for black than for white rhinos. Black rhino site fidelity also appeared to be generally higher than that of white rhinos. These differences between white and black rhinos may partly be due to the different social behaviour and ecology of the two species. While white rhinos often move in groups of up to eight individuals and are classified as “semi-social” (Owen-Smith, 1975), black rhinos are usually more solitary and aggressive towards conspecifics, and only subadults sometimes move in pairs (Goddard, 1967). This behaviour could also lead to a more pronounced territoriality in black rhinos, which could be a possible explanation for the observed higher site fidelity. However, territoriality has actually only been described for white rhinos (Owen-Smith, 1971), while black rhinos have been described as having overlapping home ranges (Goddard, 1967). Another possible explanation for strong site fidelity is the conservative movement behaviour of black rhinos, which results in a self-imposed limit of movement after release (Linklater & Swaisgood, 2008). Finally, differences in release protocols could also have contributed to divergent results for the two species. Longer time in an on-site enclosure, together with purposeful laying of dung to encourage site fidelity, could have led to black rhinos settling faster than whites.

In conclusion, our study reports a good practice example of rhino translocations where all rhinos settled in their new environment thanks to interventions enabled by long-term monitoring. The only two rhinos that did not settle immediately at the release site were recaptured and released at a different site, where they settled as well. All rhinos in this study survived for more than one year after translocation, which could qualify as short-term translocation success (Gedir et al., 2018). Future translocations might benefit from the collection of more long-term data appropriate for answering research questions relating to movement patterns and home range establishment following release, with the recognised caveat of financial sustainability. We did not have permission to analyse long-term survival data, which would give insight into long-term translocation success. Unfortunately, since data were collected for this study, Botswana has seen a dramatic increase in rhino poaching, so ultimately translocation success is contingent on long-term protection as well as best practice in translocation procedures.

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Data availability statement

Rhino GPS locations are sensitive data and thus not publicly available.

Conflict of interest statement

The authors declare no known conflicting interests.

Appendix

Translocation procedure

The timeous settlement of translocated animals can be supported by management measures. For example, “soft” or delayed release, when animals are first kept in on-site enclosures, can help them to acclimatise to their new environment and result in lower dispersal distances away from the release site (Roe et al., 2010). Conversely, “hard” or immediate release is preferable for species that suffer from high stress levels and condition loss through captivity (Richardson et al., 2015). “Hard release” at different places can also be the best method to avoid intraspecific conflicts (Støen et al., 2009). However, translocation success has not always been assessed or reported, so information relating to the evaluation of different methods is rarely accessible to managers (Batson et al., 2015; Linklater, 2003). As recommended in the Guidelines for reintroductions and other conservation translocations (IUCN Species Survival Commission, 2013), we provide here a more detailed description of the rhino translocations in this study.

Rhinos transported into Botswana must spend a minimum of 28 days in a quarantine area for veterinary clearance in their source country. This can be in the form of a confined pen or an open field, as long as they do not come into contact with other megafauna for the duration of quarantine. Exact capture procedures from these quarantine facilities varied slightly, but all encompassed the same core step and follow well established capture techniques which are documented elsewhere (Emslie, Amin, & Kock, 2009). Rhinos were immobilised and partially reversed to load by walking them into a transport crate, with mothers and calves adjacent to each other. Individual rhinos had individual crates. During transport, rhinos remained partially sedated through different drug management. All drug handling and administering was performed by qualified veterinarians.

Transport duration was dependent upon loading place and transport method. The longest travel time was 44 hours, all by road, with the shortest travel time being 18 hours by combination of road and aircraft.

Release types were dependent upon species and demographics. All white rhinos were released 'semi-hard', except for the cow and calf combinations that were released 'softly'. A 'semi-hard' release entailed the rhino being given immobilisation drugs while inside the crate. Just before the rhino was completely immobilised, the crate was opened, and the rhino was walked out under control with ropes. It was then dropped in a suitable position and given partial reversal to manage its state of immobilisation. Consequently, the rhino was given new identity ear notches (cut into the ears), microchips were checked, body measurements taken, and tracking devices fitted if the animal was over four years old. Once these activities were completed, all rhinos were given reversal drugs simultaneously so that they woke up together.

A 'soft' release is similar to the 'semi-hard' protocol; however, the rhinos were walked from their crates into holding pens which housed each mother and calf combination in a separate pen each with ample food and water. This was to ensure that the calves were hydrated after their travel and that they bonded with their mothers again after being in separate crates for an extended period. Once walked into the holding pens, rhino body sizes were measured, given microchips, ear notches and tracking devices as required. All younger calves, under 18 months old, received hydration drips as well. In this study, the mothers and calves had no issues within the holding pens, and so were kept for only one night, being released early morning the day after arrival. Dependent on arrival and unloading times, this was between six and twelve hours.

The black rhino transportation procedure was similar to that for white rhinos. However, black rhinos were kept in holding pens at the release site called "bomas" for 14 days. Black rhinos relax in confined spaces quickly and have a more complex browse feed than white rhinos. The 14-day-period was to relax the rhinos after travel and ensure acceptance of local browse feed into their diet. The bomas consisted of adjacent holding pens connected with sliding doors. Calves that were still dependent on their mothers shared holding pens with them, all other black rhinos had individual holding pens. Rhinos were fed twice per day with lucerne, an acacia-based feeding supplement for protein, and browse cuts from local bushes. The browse cuts were taken from three to six different species and fed from the walls of the enclosures to imitate natural food intake as much as possible (Morkel & Kennedy-Benson, 2007). Water was available throughout the day in a trough. The pens were cleaned daily; for this, the rhinos were moved to the next free pen either for the duration of cleaning or in a rotational manner. During cleaning, dung was collected into polypropylene bags for distribution in the release area to artificially mark home ranges and territories with a smell that was familiar to the rhinos, which was presumed to increase the likelihood of settlement in the area after release. The dung was distributed daily until release of the rhino. While in the boma, all rhinos were assessed against a scoring metric to grade their overall wellbeing (Reuter & Adcock, 1998). Ideally, rhinos were released in peak wellbeing by the end of their holding time.

Table 2.3 Release batches of rhinos translocated to Botswana. Note that all released individuals are listed here, but only adults and subadults were fitted GPS collars, so juveniles do not appear in the movement analysis.

Species	Introduction date	Female	Male	Total
White rhino	01/04/2017	8	4	12
	16/09/2017	12	4	16
	21/09/2017	11	4	15
	04/10/2017	2	2	4
	06/10/2017	2	2	4
	13/06/2018	0	2	2
	26/07/2018	4	1	5
	28/07/2018	1	4	5
	11/05/2014	2	1	3
Black rhino	11/05/2014	2	1	3
	23/05/2014	1	2	3
	30/06/2014	1	0	1
	04/07/2014	1	0	1
	05/07/2014	2	0	2
	11/07/2014	1	0	1
	16/07/2014	0	1	1
	17/07/2014	1	1	2
	18/07/2014	0	1	1
	21/07/2014	0	1	1
	07/06/2015	3	2	5
	24/06/2015	3	2	5
	30/06/2015	0	1	1
	06/07/2015	4	0	4

Table 2.4 Three-month movement range sizes of established and newly translocated white rhinos in the Okavango Delta, Botswana.

Three-month movement ranges		**Established rhinos**	**Newly translocated rhinos**
MCP	Mean	157 ± 114 km²	393 ± 456 km²
	Min. to max.	66 – 442 km²	10 – 1153 km²
KDE	Mean	222 ± 167 km²	894 ± 1087 km²
	Min. to max.	67 – 629 km²	44 – 3992 km²

Table 2.5 Three-month movement range sizes of subadult white rhino females translocated to the Okavango Delta, Botswana, at a delimited release site (A) and at other release sites (not A).

Three-month movement ranges		Subadult females of cohort A	Subadult females other cohorts
MCP	Mean	5 ± 5 km²	595 ± 442 km²
	Min. to max.	1 – 14 km²	133 – 1152 km²
KDE	Mean	12 ± 14 km²	885 ± 918
	Min. to max.	2 – 38 km²	141 – 3020 km²

Table 2.6 Annual home ranges of rhinos translocated to the Okavango Delta, Botswana, calculated with 100 % Minimum Convex Polygon (MCP).

Annual home ranges MCP 100		Female		Male
	Age	**Adult**	**Subadult**	**Adult**
White rhino	Number of individuals	1	4	0
	Mean	15	35 ± 17	
	Min. to max.	-	23 – 59	
Black rhino	Number of individuals	3	3	3
	Mean	59 ± 19	89 ± 57	80 ± 35
	Min. to max.	38 – 74	43 – 153	52 – 119

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Supplementary material: Details about rhinos translocated to Botswana

ID	Sex	Age	Introduction Date	Number of GPS collar days	Number of relocations	Settled?	Overlap of first two ten-day movement ranges	3-month 95% MCP movement range size	12-month 95% MCP movement range size
WF303	Female	subadult	01/04/2017	299	903	yes	Excluded from analysis	10	50
WF304	Female	subadult	01/04/2017	630	1896	yes		5	NA
WF305	Female	subadult	01/04/2017	299	854	yes		15	NA
WF306	Female	subadult	01/04/2017	427	1214	yes		1	21
WF335	Female	adult	01/04/2017	451	1680	yes		9	13
WF342	Female	subadult	01/04/2017	451	1049	yes		2	29
WF349	Female	subadult	01/04/2017	573	743	yes		1	17
WM311	Male	subadult	01/04/2017	311	863	yes		9	NA
WM312	Male	adult	01/04/2017	299	846	yes		19	NA
WM331	Male	subadult	01/04/2017	214	732	yes		10	NA
WF143	Female	subadult	16/09/2017	197	942	yes	0.29	341	NA
WF167	Female	adult	16/09/2017	199	1301	yes	0.36	397	NA
WF212	Female	subadult	16/09/2017	190	944	yes	0.01	1047	NA
WF230	Female	adult	16/09/2017	163	308	yes	0.09	911	NA
WF313	Female	adult	16/09/2017	160	538	relocated	0.01	1998	NA
WF317	Female	adult	16/09/2017	169	686	yes	0.43	395	NA
WF324	Female	subadult	16/09/2017	213	896	yes	0.14	930	NA
WF325	Female	adult	16/09/2017	185	316	yes	0.17	846	NA
WF332	Female	adult	16/09/2017	173	859	yes	0.24	805	NA
WF56	Female	subadult	16/09/2017	177	796	yes	0.16	329	NA
WM150	Male	adult	16/09/2017	109	59	yes	NA	NA	NA

WM215	Male	adult	16/09/2017	216	1070	yes	0.63	415	NA
WM242	Male	subadult	16/09/2017	205	1200	yes	0.12	308	NA
WF152	Female	adult	21/09/2017	236	1836	yes	0.6	248	NA
WF208	Female	subadult	21/09/2017	199	939	relocated	0.34	6485	NA
WF216	Female	adult	21/09/2017	212	1259	yes	0.19	175	NA
WF244	Female	subadult	21/09/2017	189	995	yes	0.04	1076	NA
WF341	Female	adult	21/09/2017	100	161	yes	0.52	10	NA
WF350	Female	adult	21/09/2017	157	785	yes	0.72	139	NA
WF41	Female	subadult	21/09/2017	185	958	yes	0.18	133	NA
WF45	Female	adult	21/09/2017	195	679	yes	0.1	51	NA
WM246	Male	subadult	21/09/2017	162	608	yes	0.33	441	NA
WM351	Male	subadult	21/09/2017	338	329	yes	0.05	863	NA
WF251	Female	adult	04/10/2017	144	574	yes	0.04	259	NA
WF89	Female	adult	04/10/2017	160	947	yes	0.4	309	NA
WF226	Female	subadult	06/10/2017	204	689	yes	0.3	1153	NA
WF344	Female	adult	06/10/2017	101	282	yes	0.33	81	NA
WM268	Male	subadult	13/06/2018	104	297	yes	0.39	230	NA
WF159	Female	adult	26/07/2018	61	139	yes	0.62	NA	NA
WF247	Female	adult	26/07/2018	27	57	yes	0.46	NA	NA
WF287	Female	subadult	26/07/2018	30	70	yes	0.08	NA	NA
WF339	Female	subadult	26/07/2018	61	136	yes	0.05	NA	NA
WF290	Female	subadult	28/07/2018	21	15	yes	NA	NA	NA
WM225	Male	adult	28/07/2018	40	86	yes	0.75	NA	NA
WM261	Male	subadult	28/07/2018	21	27	yes	NA	NA	NA
WM289	Male	subadult	28/07/2018	38	73	yes	0.6	NA	NA
WM295	Male	subadult	28/07/2018	28	32	yes	0.3	NA	NA

BF2	Female	adult	11/05/2014	412	676	yes	0.52	56	43
BF4	Female	adult	11/05/2014	199	683	yes	0.38	21	NA
BM30	Male	adult	11/05/2014	366	561	yes	0.61	43	32
BF1	Female	subadult	23/05/2014	366	796	yes	0.51	113	110
BM10	Male	adult	23/05/2014	269	543	yes	0.6	13	NA
BM20	Male	adult	23/05/2014	94	287	yes	0.42	30	NA
BF35	Female	adult	30/06/2014	362	702	yes	0.77	17	NA
BF10	Female	subadult	05/07/2014	351	488	yes	0.46	2	NA
BF22	Female	subadult	05/07/2014	475	596	yes	0.2	21	54
BF57	Female	adult	11/07/2014	366	565	yes	0.64	23	30
BM4	Male	subadult	16/07/2014	337	523	yes	0.12	7	NA
BF23	Female	subadult	17/07/2014	474	696	yes	0.69	16	27
BM76	Male	adult	18/07/2014	60	206	yes	0.37	NA	NA
BM24	Male	adult	21/07/2014	391	675	yes	0.31	10	67
BM60	Male	adult	23/05/2015	393	210	yes	NA	30	48
BF44	Female	adult	07/06/2015	307	334	yes	NA	21	NA
BF6	Female	adult	07/06/2015	389	402	yes	0.51	39	37
BF62	Female	adult	14/06/2015	93	124	yes	0.58	26	NA
BF70	Female	adult	14/06/2015	309	350	yes	0.9	3	NA
BM61	Male	subadult	14/06/2015	361	534	yes	0.6	8	NA
BM64	Male	adult	14/06/2015	313	315	yes	NA	44	NA
BM13	Male	adult	30/06/2015	73	63	yes	NA	NA	NA
BF21	Female	adult	06/07/2015	331	212	yes	NA	58	NA
BF70B	Female	adult	06/07/2015	97	124	yes	NA	69	NA
BF72	Female	adult	06/07/2015	325	423	yes	0.66	442	NA

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

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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 transportations, 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 towards 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 behavioural 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 behavioural 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.

Key words

bioacoustics, conservation behaviour, mammal, playback, socio-negative, socio-positive, vocalisation

Introduction

In species conservation, knowledge of animal behaviour is an important basis for management decisions (Bro-Jørgensen, Franks, & Meise, 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, P. S. [ed.], 2018). Translocation success relies on understanding species-specific movement patterns and social behaviours to avoid problems, e.g., long-distance dispersal (Knox & Monks, 2014; Le Gouar, Mihoub, & Sarrazin, 2012), homing behaviour (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 behaviour 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 habitat (Hayward et al., 2007), pingers are used to deter harbour porpoises from fishing nets (Larsen & Eigaard, 2014), and bee swarm playbacks to deter elephants from crop fields (Ngama, Korte, Bindelle, Vermeulen, & Poulsen, 2016). Conspecific playbacks have successfully been used to attract amphibians (James, Stockwell, Clulow, Clulow, & Mahony, 2015) and birds (Ahlering et al., 2010; Bradley, Ninnes, Valderrama, & Waas, 2011; Molles et al., 2008) by demonstrating the high quality of a habitat through the presence of conspecifics (Kiester, 1979) and mating partners (Szostek, Schaub, & Becker, 2014). Studies with mammals are rare but also indicate that animals can be attracted by conspecific playbacks (Bryant et al., 2016; Filatova, Fedutin, Burdin, & Hoyt, 2011; Knörnschild, Blüml, Steidl, Eckenweber, & Nagy, 2017). In contrast, alarm call playbacks can be used to train predator avoidance in predator-naïve species (Morris, Pitcher, & Chariton, 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, Amin, & Kock, 2009). These translocations are nowadays common practice and highly successful when rhinos are released into fenced reserves (Patton, Mulama, Mutisya, & Campbell, 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, Pitlagano, & Moe, 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, MacDonald, Flamand, & Czekala, 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, Keep, & Rochat, 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, Tomášová, Holečková, & Frynta, 2008) with eleven different vocal signals described in Owen-Smith (1973). Two of the most common calls are Pant and Hiss calls (Jenikejew, Chaignon, Linn, & Scheumann, 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 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 is 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 Pants calls; territorial males also responded with dung or urine marking, showing the possibility to stimulate territorial behaviour 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, Moss, Sayialel, & Baker, 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 hypothesised that (i) rhinos will display a higher intensity and longer response duration towards conspecific calls than to control sounds, including being attracted by Pants and deterred by Hisses; (ii) responses will be consistent between sexes; (iii) rhino behavioural 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, Fischer, &

Hammerschmidt, 2011) and social factors (behavioural state, presence of surrounding rhinos) affect rhino behavioural responses to playbacks.

Methods

Ethics statement

This article contains data derived from playback experiments influencing behaviour 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.

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, Knight, Jones, & Balfour, 2020). In reserve A, the vegetation consisted of grasslands and mixed savannah bushland. We tested eleven rhinos (8 females, 3 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 15 rhinos (8 females, 7 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.

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 3.3). 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 standardise loudness, the playback stimuli were levelled to the same sound pressure of 85 dB at 1 m distance (Brüel & Kjaer, Type 2233 with microphone type 4155). The behaviour of the animal was videotaped using a digital camera (Sony α 65, Germany, or Medion M86641, USA).

Experimental procedure of playback experiments

Experiments were performed in semi-randomised 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 five minutes (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 into 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 3.1). In the first block, we tested how eleven 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 eleven 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 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 the wind speed can influence sound propagation, we classified wind speed in the three categories *almost no wind, low wind* and *high wind* speed 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*.

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 analysed rhino responses for two minutes after stimulus onset, because preliminary video screening showed almost no further responses after that. We coded the following point behaviours: ear movement, ears turned to the speaker, head moved up, head turned more than 45° to the speaker, body moved at least 1 to max. 3 steps towards or away from the speaker, body moved more than 3 steps towards or away from the speaker, alert behaviour (head lifted and not chewing), vocalisations and urination as a sign of excitement (Table 3.2 in the supporting information). Further, we noted the response duration. We defined the start of a response when the rhino changed its behaviour or body position from that before the playback (e.g., ear or head movement) and the end when the rhino returned to its previous behaviour and body position. When the rhino did not return to its previous behaviour and body position within the two minutes of observation time, then the duration of the response was counted until the end of the observation (two minutes).

We scored the response intensity by giving a point for the occurrence of each response behaviour, 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 behaviour of grazing and moved away after three seconds 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 relaxed body position and behaviour, rhinos sometimes changed their behaviour shortly before the playback sequence started. Therefore, we also coded the following behavioural states before the playback: *alert, feeding, locomoting,* or *resting* and included the behaviour as another potentially confounding variable.

To ensure reliability of the behaviour 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).

Statistical analysis

We used three data sets (Table 3.1) to test the effects of three variables of interest (VOI): Stimulus, Familiarity, and Reserve (variables occurring in statistical models are capitalised for emphasis). 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 behavioural responses in reserve A and reserve B.

Table 3.1: Overview of datasets used for analyses of the variable of interest in bold and additional predictor variables, levels of each variable 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) * Call type (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) * Call type (Hiss (7), Pant (7))

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, Behaviour before playback), we ran a generalized linear mixed model (glmm) for each of the behavioural 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 standardise 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 behavioural 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 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 non-significant 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 visualisation, we used an index subtracting the number of avoidances from the number of approaches and divided 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 (2020-10-10), 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 *Supporting Information* Table 3.4 – 3.16. P-values<0.05 were considered as statistically significant.

Results

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 behavioural measurements. For Behaviour before playback, an effect was found on Duration (Chi^2=26.49, df=3, p<0.001), but no interaction with the Stimulus. Rhinos showed a shorter Duration for playbacks when they were feeding compared to alert or resting behaviour (*alert vs. feeding* estimate=28.48±10.1, CI=0.91–56.05, t(55)=2.83, p=0.020; *feeding vs. resting* estimate:=-25.00±7.40, CI=-45.26 to -4.75, t(55)=-3.38. p=0.008, Table 3.5). For Wind condition, we found a significant interaction between Stimulus and Wind for both behavioural measurements (Score: Chi^2≥10.95, df=4, p=0.027; Duration: Chi^2=10.23, df=4, p=0.037) suggesting that Wind condition affected the perception of the stimuli (Figure 3.1). Therefore, for the further analyses of Score and Duration, we analysed the dataset for the three Wind conditions separately.

Nevertheless, in all eight models, the Stimulus had a significant effect on the behavioural measurements (Score: Chi2≥9.57, p≤0.008; Duration: Chi2≥7.77, p≤0.020; Table 3.5).

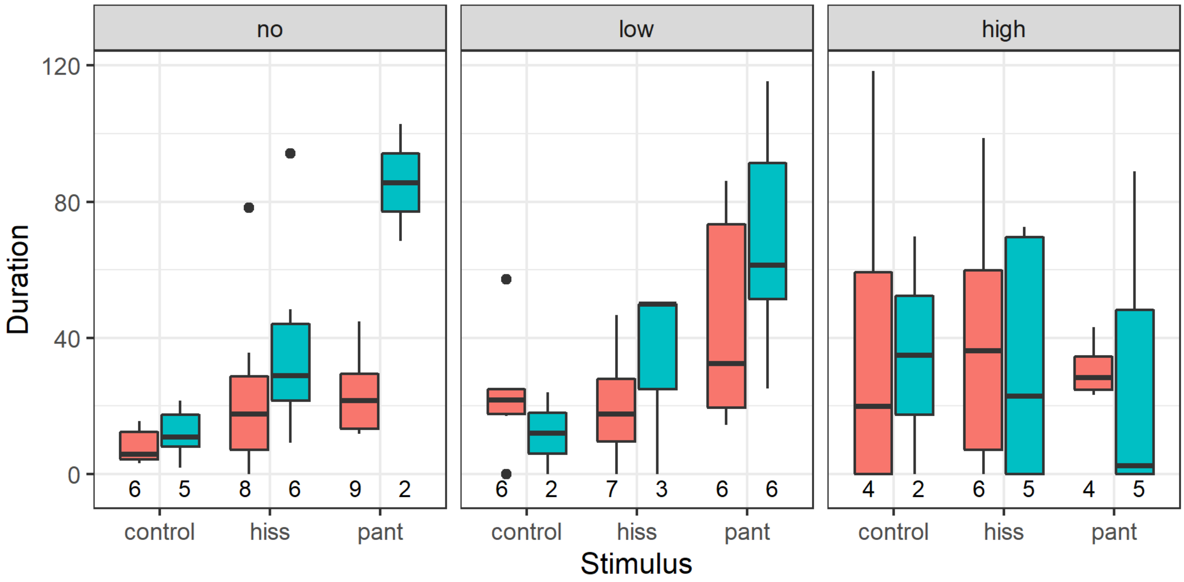

Figure 3.1 Effect of Stimulus on response duration of eleven rhinos (eight females, three males) for the three wind conditions no=almost no wind, low=low wind, high=high wind speed in 92 experiments. The number of experiments per condition is indicated below the boxplots. Boxplots represent lower and upper quartile; thick black line is the median. Red=females, blue=males.

For the *almost no wind* condition, we found a significant interaction between Stimulus and Sex on both behavioural measurements (Score: Chi^2=6.68, df=2, p=0.036; Duration: Chi^2=12.45, df=2, p=0.002; Figure 3.1, Table 3.6). Males showed higher scores towards Pants and Hisses than towards control playbacks (*control vs. pant*: estimate=-3.50±0.57, CI=-6.28 to -0.72, t(3)=-6.108, p=0.016; *control vs. hiss*: estimate=-2.41±0.42, CI=-4.47 to -0.35, t(3)=-5.675, p=0.016, Table 3.7) and a tendency for a longer duration toward Pants compared to controls (estimate=-75.5±19.2, CI=-168.9–17.9, t(3)=-3.93, p=0.088) whereas females showed no significant effect of Stimulus. For the *low wind* condition, a significant effect of Stimulus was found for both behavioural measurements (Score: Chi^2=21.72, df=2, p<0.001; Duration Chi^2=11.56, df=2, p=0.003). 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=0.001, *hiss vs. pant:* estimate=-2.36±0.67, CI=-4.33 to -0.39, t(9)=-3.52, p=0.001; Duration: *control vs. pant:* estimate=-32.7±12.1, CI=-68.2–2.81, t(9)=-2.70, p=0.038, *hiss vs. pant:* estimate=-30.29±11.3, CI=-63.4–2.82, t(9)=-2.68, p=0.038, Table 3.7). For the *high wind* condition, no effect of Stimulus or Sex was found either for the Score nor for the Duration.

In 47 playback experiments rhinos responded with body movement (towards (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 3.8). However, there were significant differences between males and females for the two conspecific rhino call types (Hiss: $Chi^2=5.92$, df=1, p=0.015; Pant: $Chi^2=4.92$, df=1, p=0.027) but not for the control ($index_{female}=0$, $index_{male}=0.20$). In response to Hisses, females moved away ($index_{female}=-0.60$, Figure 3.2), 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 ($index_{female}=0.17$).

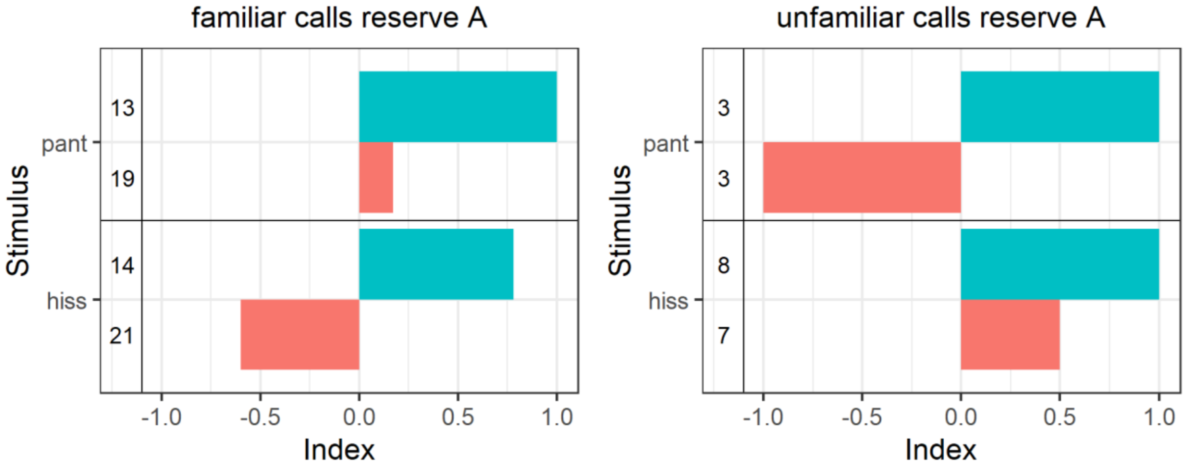

Figure 3.2 Index of body movement direction of eleven rhinos (eight females, three males) in response to familiar and unfamiliar calls in 88 experiments. The number of experiments per condition is indicated on the left side of the graphs. -1=away from the loudspeaker, 1=towards the loudspeaker. Red=females, blue=males.

Familiar *versus* unfamiliar conspecific calls

Investigating methodological variables, we found no effect for Wind and Other rhinos present on the two behavioural measurements. For Behaviour before playback, there was an effect for both behavioural measurements (Score: $Chi^2=8.52$, df=3, p=0.036; Duration: $Chi^2=26.47$, df=3, p<0.001), 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=0.020; *alert vs. locomoting* estimate=-39.93±16.8, CI=-6.00–85.86, t(53)=2.38, p=0.031; *feeding vs. resting* estimate=-47.86±17.1, CI=-94.73 to -1.00, t(53)=-2.80, p=0.021; *locomoting vs. resting* estimate=-54.58±21.3, CI=-112.99–3.84, t(53)=-2.56, p=0.027, Table 3.10). The effect of Behaviour 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 interaction between Familiarity and Distance ($Chi^2=12.16$, df=1, p<0.001) suggesting that the Distance affected the response duration. Nevertheless, in almost all models, the effect of Familiarity on the behavioural response measurements was significant (Score: $Chi^2\geq3.99$, $p\leq0.046$; Duration: $Chi^2\geq5.52$, $p\leq0.019$; Table 3.9), 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=0.020, estimate=0.99±0.44, CI=0.14–1.84, Table 3.11), but no strong effect of Sex and Stimulus.

For the Duration, we analysed 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<0.001, estimate=73.68±12.72, CI=47.28–100.08, Figure 3.3, Table 3.11) 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<0.001, estimate=-30.93±9.27, t(12)=-3.34, p=0.006, CI=-50.21 to -11.64).

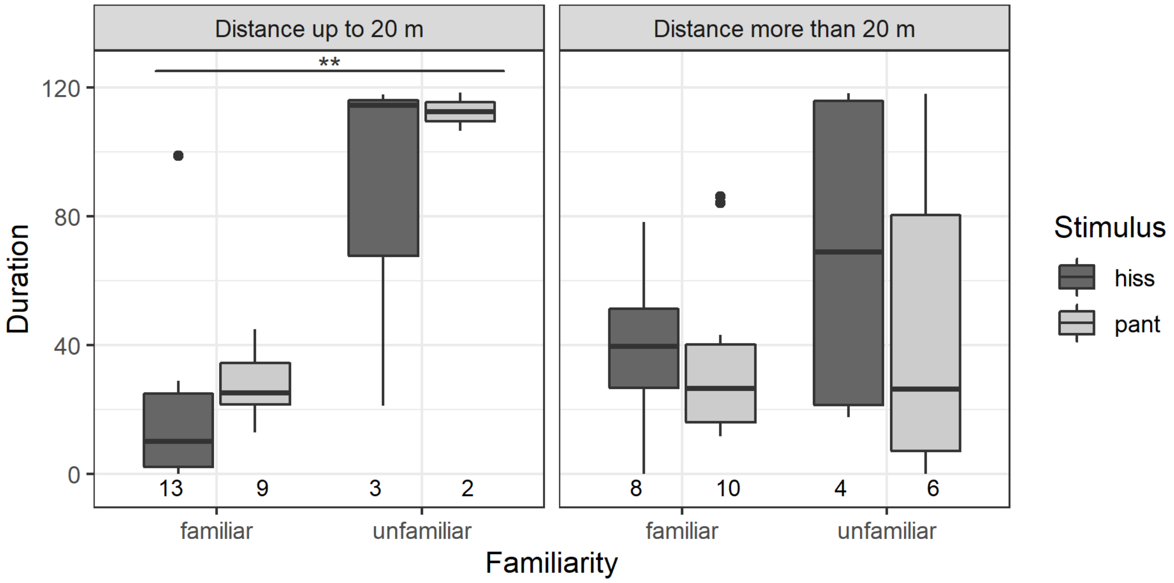

Figure 3.3 Effect of Familiarity on response duration of eight female rhinos for the two distance categories in 55 experiments. The number of experiments per condition is indicated below the boxplots. Boxplots represent lower and upper quartile; thick black line is the median.

Comparing the total number of playback trials with body movements, no significant effect of Familiarity was revealed (Table 3.12). However, in response to unfamiliar Pants, females avoided the loudspeaker ($index_{female}$=-1) significantly more often compared to familiar Pants where they were more likely to approach the loudspeaker ($index_{female}$=0.17; Chi^2=4.96, df=1, p=0.026, Figure 3.2). Males, on the other hand, approached the loudspeaker in response to unfamiliar Pants ($index_{male}$=1.00; Chi^2=7, df=1, p=0.008, Figure 3.2).

Effect of reserve: Reserve A *versus* reserve B

Investigating methodological variables, we found no effect of Wind on the two behavioural measurements. For Behaviour before playback, an effect was found on Duration (Chi^2=16.85, df=3, p<0.001), 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=0.013, Table 3.14). For Other rhinos present, there was an effect on the Score (Chi^2=6.57, df=1, p=0.010), 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=0.016) suggesting that the Distance affected the response Duration. Nevertheless, in all eight models, the Reserve had a significant effect on the behavioural measurements (Score: Chi^2≥13.44, p≤0.001; Duration: Chi^2≥3.85, p≤0.050; Table 3.13).

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<0.001, estimate=-1.77±0.49, CI=-2.73 to -0.81), but no effect of Stimulus and Sex.

For the Duration, we analysed the dataset for the two Distance categories separately due to the above-mentioned interaction. Again, only females were analysed 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=0.005, estimate=-71.24±28.91, CI=-152.81–10.33, Figure 3.4, Table 3.15) but no effect of Stimulus. For *more than 20 m,* there was no significant effect of Reserve or Stimulus on Duration.

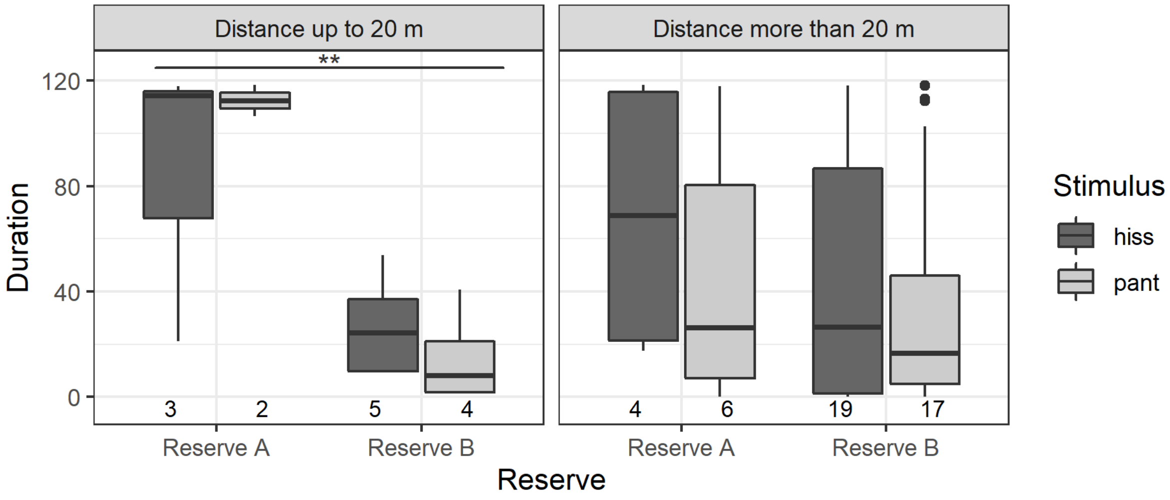

Figure 3.4 Effect of Reserve on response duration of 16 female rhinos for the two distance categories in 60 experiments. The number of experiments per condition is indicated below the boxplots. Boxplots represent lower and upper quartile; thick black line is the median.

Comparing the total number of playback experiments where rhinos approached *versus* avoided the loudspeaker, no differences between the two reserves were revealed (Table 3.16) even if separated for call type and sex. A summary of the most important results is given in Table 3.2.

Table 3.2 Summary of predictor and confounding variables that significantly impacted rhino behavioural responses to playbacks of conspecific calls based on the output of generalised 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	Behaviour 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	Behaviour before playback	Rhinos show shorter responses when feeding or locomoting.
		Distance	Rhinos show at close distances longer responses to unfamiliar than to familiar calls.
Reserve	Score		Habituated rhinos show stronger responses than non-habituated rhinos.
	Duration	Behaviour before playback	Rhinos show longer responses when alert.
		Distance	Habituated rhinos show at close distances longer responses than non-habituated rhinos.
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.

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 behavioural responses with a higher intensity and duration towards unfamiliar callers. Responses differed between reserves in intensity, but not in body movement responses. Some methodological factors influenced the behavioural responses and should be considered when developing playbacks of conspecific calls as a management tool. Our study is therefore exemplifying the relevance of behaviour 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 e.g., 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, Papworth, Boesch, & Zuberbühler, 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, signalling 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 a 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 socialised 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 behavioural 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 behavioural 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, behavioural 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, which can be explained with the acoustic characteristics of the calls: Pants have a higher harmonic to noise ratio and higher frequencies, thus more energy than Hisses (Linn et al. 2018). 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 behavioural responses depended on the behaviour before the playback. The most intense and longest responses were observed when the rhino was already alert or standing, scanning the surrounding and ready to change its behaviour. We also observed that the time to response 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 behavioural responses of rhinos to playbacks of conspecific calls, but also distance, wind, and behaviour before the playback. Sound dispersion can also be affected by temperature (Bradbury & Vehrencamp, 2011;

Garstang, Larom, Raspet, & Lindeque, 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 that rhinos pass at a close distance.

Our results indicate that rhinos showed specific responses to conspecific calls, but these responses rarely lasted longer than two minutes, often only consisted of a lifting of the head for several seconds, and body movements towards 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 behavioural responses and a to test a design that would be successful after translocations

Drone and siren sounds (Penny et al., 2019) are promising possibilities to manage the behaviour of rhinos but could also result in habituation and stress (Fàbregas, Fosgate, Ganswindt, Bertschinger, & Meyer, 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 behavioural 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 behavioural 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 towards 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.

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Data availability

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.

Conflict of interest

The authors declare no known conflict of interest.

Supporting information

Method S1: Detailed description of recording, preparation, and presentation of playback stimuli

Recordings were done from March to May 2020 in reserve A using a Sennheiser omni-directional microphone (MKH 8020; Sennheiser, Wedemark, Germany; flat frequency response from 10 to 20000 Hz ± 5db) covered with a wind shield and fitted on a boom pole. The microphone was connected to a Zoom F4 Field recorder (setting 44.1 kHz sampling rate, uncompressed .wav format). Rhino calls were extracted from the audio file of 30-minute focal observations. Bird calls were recorded with the same recorder and microphone in reserve A to only use stimuli from the natural surroundings of the subjects. Bird species were Cape turtle dove (*Streptopelia capicola*), blacksmith lapwing (*Vanellus armatus*), crowned lapwing (*Vanellus coronatus*), red-billed spurfowl (*Pternistis adspersus*), and dark-capped bulbul (*Pycnonotus tricolor*). Further recordings of rhino calls were realised in a pilot study in 2018 by using five Swift Recorders (Cornell University, USA; POW-1644L-B-LW100-R omnidirectional microphone, PUI Audio, Fairborn, USA; frequency response: 50 to 16000 Hz, setting 8 kHz sampling rate, uncompressed .wav format) together with camera traps (Bushnell and Moultrie D-55IRXT). Camera trap photos were scanned for rhino sightings and subsequently rhino calls were extracted from the audio file for processing into playback chains. We decided to use these recordings despite of the low sampling frequency, because recording from zoos showed that the main energy of rhino calls lies below 4 kHz (Linn, Boeer, & Scheumann, 2018; Policht et al., 2008) and these recordings would provide calls from rhinos in similar surrounding as our study subjects, but from unfamiliar individuals.

We extracted rhino and bird calls using the software Raven (Center for Conservation Bioacoustics, 2019) from the audio file and selected vocalisations with good signal to noise ratio and no overlaying calls for playback stimuli. We selected single vocalisations and cut them to a length between 3.5 and 5.5 s. We cut the vocalisation at nearest zero crossing and added a linear ramp (10 ms, both sides at zero crossing) using Praat (Boersma & Weenink, 1992-2021) to avoid any clicking sounds at the onset of the playback. Then, we placed the vocalisations three times in a row with three seconds silence in between in playback chains. To account for the same loudness, the playback stimuli were levelled to the same sound pressure of 85 dB at 1 m distance using an integrated precisions impulse sound level meter (Brüel & Kjaer, Type 2233 with microphone type 4155) in a sound-damped chamber. Playbacks were played from a JBL Xtreme 2 loudspeaker connected via Bluetooth with a laptop (HP 250 G7 Notebook PC) in uncompressed .wav format using the software Praat. Because the Bluetooth connection had a short delay in activating the loudspeaker, we added 3 ms of an ultrasonic sinus tone of 22 kHz, which is not audible for rhinos, in the beginning of the playback chain to ensure a clear start of the playback without a delay from the loudspeaker.

Table 3.3 Details on rhino call stimuli and their distribution over 175 experiments performed with 26 white rhinos between March and December 2020 in Botswana.

Reserve	Call	Call context	Number of tested females	Number of tested males	Number of experiments
A	hiss1	hiss female to male	3	3	6
	hiss2	hiss female to male	3	2	5
	hiss3	hiss male to male	3	2	5
	hiss4	hiss male to male	5	3	8
	hiss5	hiss female to female	4	2	6
	hiss6	hiss male to female	3	2	5
	pant1	pant calf to playback	3	2	5
	pant2	pant male to playback	4	2	6
	pant3	pant female to male	3	5	8
	pant4	pant male to female	4	1	5
	pant6	pant female to female	5	3	8
	hiss k1	unknown	7	2	9
	hiss k2	unknown	0	1	1
	pant k1	unknown	6	2	8
	pant k2	unknown	2	1	3
B	hiss1	hiss female to male	7	5	12
	hiss2	hiss female to male	5	6	11
	hiss7	hiss male to male	4	2	6
	hiss8	hiss female to male	4	4	8
	hiss9	hiss female to female	3	6	9
	pant1	pant calf to playback	4	2	6
	pant2	pant male to playback	7	4	11
	pant7	pant female to female	3	4	7
	pant8	pant female to calf	6	4	10
	pant9	pant female to calf	2	5	7

Table 3.4 Rhino behavioural responses to playbacks that were scored for the response intensity score. One point was given for the first occurrence of each behaviour. The response score was defined as sum of all points.

Behavioural response	**Definition**
ear movement	Rhino moved its ears back and forward.
ears turned to the speaker	Rhino turned both ears towards the loudspeaker.
head is moved up	Rhino moved its head up.
head is turned more than 45° to the speaker	Rhino turned its head towards the loudspeaker.
body is moved 1 to 3 steps to the speaker	Rhino moved at least one maximum three steps towards the loudspeaker.

body is moved 1 to 3 steps away from the speaker	Rhino moved at least one maximum three steps away from the loudspeaker.
body is moved more than 3 steps to the speaker	Rhino moved more than three steps towards the loudspeaker.
body is moved more than 3 steps away from the speaker	Rhino moved more than three steps away from the loudspeaker.
alert	Rhino stands with its head lifted above front ankle height without chewing.
vocalisations	Rhino vocalised in response to the playback.
urination	Rhino urinated.

Table 3.5 Results of generalised linear mixed models testing effects of the stimulus (Control, Hiss, Pant) on the intensity of behavioural responses represented by a score and response duration of 11 white rhinos in 92 playback experiments in Botswana. Models investigated the interaction between potential confounding methodological variables and stimulus. Bold: p<0.05.

	Score			**Duration**		
	Chi^2	df	p	Chi^2	df	p
Stimulus	**12.41**	**2**	**0.002**	**8.86**	**2**	**0.012**
Wind	3.57	2	0.168	2.42	2	0.298
Stimulus : Wind	**10.95**	**4**	**0.027**	**10.23**	**4**	**0.037**
Stimulus	**9.97**	**2**	**0.007**	**8.69**	**2**	**0.013**
Distance	0.01	1	0.924	2.52	1	0.112
Stimulus : Distance	2.07	2	0.355	4.72	2	0.094
Stimulus	**9.57**	**2**	**0.008**	**7.78**	**2**	**0.020**
Other rhinos present	0.05	1	0.823	0.78	1	0.379
Stimulus : Other rhinos present	1.12	2	0.571	1.28	2	0.527
Stimulus	**12.80**	**2**	**0.002**	**11.94**	**2**	**0.002**
Behaviour before playback	5.51	3	0.138	**26.49**	**3**	**<0.001**
Stimulus : Behaviour before playback	8.99	6	0.174	11.69	6	0.069

Table 3.6 Results for the final generalised linear mixed models testing effects of stimulus (Control, Hiss, Pant) and sex on the intensity of behavioural responses represented by a score and response duration of 11 white rhinos in playback experiments in Botswana in a break-down analysis separated by wind condition; bold: p<0.05.

	Score			**Duration**		
	Chi^2	df	p	Chi^2	df	p
Subset: Almost no wind						
Stimulus	**21.97**	**2**	**<0.001**	**17.01**	**2**	**<0.001**
Sex	1.69	1	0.193	**10.61**	**1**	**0.001**
Stimulus : Sex	**6.68**	**2**	**0.036**	**12.45**	**2**	**0.002**
Subset Male: Stimulus	**64.97**	**2**	**<0.001**	**20.23**	**2**	**<0.001**
Subset Female: Stimulus	1.71	2	0.426	4.38	2	0.112

Subset: Low wind						
Stimulus	**21.72**	**2**	**<0.001**	**11.56**	**2**	**0.003**
Sex	0.34	1	0.559	1.77	1	0.183
Subset: High wind						
Stimulus	0.19	2	0.910	0.46	2	0.794
Sex	0.32	1	0.569	0.00	1	0.980

Table 3.7 Pairwise comparisons of the intensity of behavioural responses represented by a score and response duration between stimuli (Control, Hiss, Pant) for significant main effects of the final models for stimulus and sex (Table 3.6); ES=estimate, SE=standard error, df=degrees of freedom, p=p-value; bold: p<0.05.

	Score					**Duration**				
Pairwise comparison	ES	SE	df	t	p	ES	SE	df	t	p
Subset: Almost no wind condition - Males										
Control - Hiss	**-2.41**	**0.42**	**3**	**-5.68**	**0.016**	-26,10	13,80	3	-1.89	0,155
Control - Pant	**-3.50**	**0.57**	**3**	**-6.11**	**0.016**	-75,50	19,20	3	-3.93	0,088
Hiss - Pant	-1.09	0.56	3	-1.93	0.149	-49,40	18,70	3	-2.64	0,117
Subset: Low wind condition										
Control - Hiss	-0.39	0.74	9	-0.53	0.608	-2.41	12.30	9	-0.20	0.849
Control - Pant	**-2.75**	**0.72**	**9**	**-3.83**	**0.001**	**-32.70**	**12.10**	**9**	**-2.70**	**0.038**
Hiss - Pant	**-2.36**	**0.67**	**9**	**-3.52**	**0.001**	**-30.29**	**11.30**	**9**	**-2.68**	**0.038**

Table 3.8 Results of Chi^2-Tests comparing body movement responses of 11 white rhinos in experiments in Botswana across Pant, Hiss and control playback stimuli and comparing sexes between playback stimuli; m=male, f=female; bold: p<0.05

Comparison	Chi^2	df	p-value
Control - Hiss - Pant	1.94	2	0.379
Control m - Control f	0.12	1	0.725
Hiss m - Hiss f	**5.92**	**1**	**0.015**
Pant m - Pant f	**4.92**	**1**	**0.027**

Table 3.9 Results of generalised linear mixed models testing effects of familiarity (familiar, unfamiliar) on the intensity of behavioural responses represented by a score and response duration of 11 white rhinos in playback experiments in Botswana. Models investigated the interaction between potential confounding methodological variables and familiarity; bold: p<0.05.

	Score			**Duration**		
	Chi	df	p	Chi	df	p
Familiarity	3.56	1	0.059	**6.99**	**1**	**0.008**
Wind	4.94	2	0.084	0.97	2	0.616
Familiarity : Wind	1.47	2	0.481	0.43	2	0.808
Familiarity	**3.99**	**1**	**0.046**	**5.52**	**1**	**0.019**

Distance	0.61	1	0.437	1.00	1	0.307
Familiarity : Distance	0.78	1	0.377	**12.16**	**1**	**0.001**
Familiarity	**4.80**	**1**	**0.028**	**6.34**	**1**	**0.012**
Other rhinos present	0.44	1	0.508	0.61	1	0.434
Familiarity : Other rhinos present	0.32	1	0.569	0.15	1	0.696
Familiarity	**6.78**	**1**	**0.009**	**7,31**	**1**	**0.007**
Behaviour before playback	**8.52**	**3**	**0.036**	**26.47**	**3**	**<0.001**
Familiarity : Behaviour before playback	0.22	3	0.975	1.52	3	0.678

Table 3.10 Pairwise comparisons of the intensity of behavioural responses represented by a score and response duration between different behaviours before the playback (alert, feeding, locomoting, resting) for the final model with familiarity (Table 3.9); ES=estimate, SE=standard error, df=degrees of freedom, p=p-value; bold: p<0.05.

	Score					Duration				
Pairwise comparison	ES	SE	df	t	p	ES	SE	df	t	p
alert - feeding	0.11	0.60	53	0.19	0.852	**33.22**	**10.80**	**53**	**3.07**	**0.020**
alert - locomoting	-0.68	0.93	53	-0.74	0.698	**39.93**	**16.80**	**53**	**2.38**	**0.031**
alert - resting	-1.15	1.05	53	-1.10	0.663	-14.65	18.90	53	-0.77	0.531
feeding - locomoting	-0.79	0.81	53	-0.98	0.663	6.71	14.60	53	0.46	0.648
feeding - resting	-1.26	0.94	53	-1.34	0.663	**-47.86**	**17.10**	**53**	**-2.80**	**0.021**
locomoting - resting	-0.47	1.18	53	-0.40	0.828	**-54.58**	**21.30**	**53**	**-2.56**	**0.027**

Table 3.11 Results for the final generalised linear mixed models testing effects of familiarity, sex, and stimulus on the intensity of behavioural responses represented by a score and response duration of 11 white rhinos in Botswana tested in 88 experiments. The table shows results for the full data set (8 females, 3 males) for the score and a break-down analysis per distance categories for the duration for females (8 individuals in 55 experiments). Bold: p<0.05.

	Score			Duration		
Final model	Chi^2	df	p	Chi^2	df	p
Full data set						
Familiarity	**5.43**	**1**	**0.020**			
Stimulus	3.18	1	0.075			
Sex	1.16	1	0.282			
Subset: Distance up to 20 m – Females						
Familiarity				**37.73**	**1**	**<0.001**
Stimulus				1.63	1	0.200
Subset: Distance more than 20 m – Females						
Familiarity				2.06	1	0.151
Stimulus				**12.46**	**1**	**<0.001**

Table 3.12 Results of Chi²-Tests comparing body movement responses of 11 white rhinos in 88 playback experiments in Botswana across unfamiliar and familiar Pants and Hisses and comparing sexes between call types. m=male, f=female; bold: p<0.05.

Comparison	Chi²	df	p-value
familiar Hiss - unfamiliar Hiss	0.31	1	0.580
familiar Pant - unfamiliar Pant	5.19	1	0.023
familiar Hiss f – unfamiliar Hiss f	2.72	1	0.099
familiar Pant f – unfamiliar Pant f	4.96	1	0.026
unfamiliar Hiss m - unfamiliar Hiss f	0.60	1	0.439
unfamiliar Pant m - unfamiliar Pant f	7.00	1	0.008

Table 3.13 Results of generalised linear mixed models testing effects of reserve (reserve A, reserve B) on the intensity of behavioural responses represented by a score and response duration of 26 white rhinos in 108 playback experiments with calls from unfamiliar senders in Botswana. Models investigated the interaction between potential methodological confounding variables and reserve. Bold: p<0.05.

	Score			Duration		
	Chi²	df	p	Chi²	df	p
Reserve	**14.50**	**1**	**<0.001**	**3.85**	**1**	**0,050**
Wind	0.84	2	0.656	0.61	2	0,739
Reserve : Wind	1.34	2	0.512	0.51	2	0,774
Reserve	**13.44**	**1**	**<0.001**	**4.76**	**1**	**0,029**
Distance	2.14	1	0.144	0.38	1	0,539
Reserve : Distance	0.19	1	0.665	**5.76**	**1**	**0,016**
Reserve	**14.86**	**1**	**<0.001**	**4.39**	**1**	**0,0362**
Other rhinos present	**6.57**	**1**	**0.010**	1.45	1	0,228
Reserve : Other rhinos present	0.33	1	0.566	0.28	1	0,595
Reserve	**14.18**	**1**	**<0.001**	**5.01**	**1**	**0,025**
Behaviour before playback	0.82	3	0.844	**16.85**	**3**	**<0,001**
Reserve : Behaviour before playback	0.30	3	0.960	4.68	3	0,197

Table 3.14 Pairwise comparisons of the intensity of behavioural responses represented by a score and response duration between different behaviours before the playback (alert, feeding, locomoting, resting) for the final model with reserve (Table 3.13); ES=estimate, SE=standard error, df=degrees of freedom, p=p-value; bold: p<0.05

contrast	ES	SE	df	t	p
alert - feeding	**36.34**	**11.30**	**49**	**3.23**	**0.013**
alert - locomoting	23.71	17.90	49	1.32	0.383
alert - resting	-1.94	22.30	49	-0.09	0.931
feeding - locomoting	-12.63	16.50	49	-0.77	0.537
feeding - resting	-38.27	21.20	49	-1.81	0.231
locomoting - resting	-25.65	25.30	49	-1.01	0.475

Table 3.15 Results for the final generalised linear mixed models for the effects of reserve, sex and stimulus on behavioural responses of 26 white rhinos in playback experiments in Botswana for the full data set for score and the break-down analysis for duration separated by distance categories for females; bold: p<0.05

	Score			**Duration**		
Final model	Chi^2	df	p	Chi^2	df	p
Full data set						
Reserve	**13.80**	**1**	**<0.001**			
Stimulus	0.22	1	0.636			
Sex	0.00	1	0.999			
Subset: Distance up to 20m – Females						
Reserve				**7.73**	**1**	**0.005**
Stimulus				0.29	1	0.588
Subset: Distance more than 20m – Females						
Reserve				0.47	1	0.493
Stimulus				0.27	1	0.603

Table 3.16 Results of Chi^2-Tests comparing body movement responses of 26 white rhinos in 108 playback experiments with calls from unfamiliar senders in Botswana between reserves and comparing sexes between call types; m=male, f=female; bold: p<0.05.

Comparison	Chi^2	df	p-value
reserve A Hiss - reserve B Hiss	1.90	1	0.168
reserve A Pant - reserve B Pant	1.89	1	0.170
reserve B Hiss m - reserve B Hiss f	0.03	1	0.855
reserve B Pant m - reserve B Pant f	0.00	1	1.000

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4. Dehorning impacts white rhinoceros behaviour less than social events: evidence from Botswana

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Abstract

Dehorning is a conservation measure used to protect rhinoceroses ("rhinos") from being poached by removing most of the visible horn and thus reducing the monetary value of the animal to poachers. The effects of dehorning on stress levels and reproduction rates of rhinos have been analysed, but to our knowledge, behaviour studies so far focussed on single behaviours such as fighting and horn rubbing. We aimed to add a study that examines general activities of rhinos in a before-after comparison. We observed nine (six females and three males) wild white rhinos (*Ceratotherium simum simum*) in Botswana for one month before and one month after dehorning to evaluate changes in their behaviour. Rhinos use their horns in comfort and aggressive behaviour, and the dehorning operation induces stress responses and solitary movement. Therefore, we expected decreases in aggressive and affiliative behaviours and increases in avoidance behaviours after dehorning. The proportions of feeding, resting, comfort, aggressive, avoidance, and affiliative behaviours did not change significantly within one month after dehorning. We observed sex-specific changes in proportions of locomotion and in vocalisation rates, which we linked to the social events of a fight and two births in the study population. Our results suggest that dehorning has no major impact on rhino behaviour and can thus be justified from an animal ethics point of view. However, there is a key need to investigate the effectiveness of dehorning in reducing poaching events.

Key words

aggressive interaction, calving, *Ceratotherium*, conservation, mammal, movement rate, poaching, vocalisation

Introduction

One of the drivers of the ongoing biodiversity crisis is the illegal harvesting of animals, i.e., poaching (IPBES, 2019; Morton et al., 2021). Rhinoceroses (hereafter called "rhinos") are some of the most targeted species in wildlife poaching, and their numbers have decreased from 29,085 in 2012 to 26,261 individuals at the end of 2021 (Emslie et al. 2016; Ferreira et al., 2022; Save The Rhino International, 2022a). This dramatic decrease is due to poaching and illegal trafficking that fuels a market for rhino horn in south-east Asia, especially Vietnam, where increasing wealth forms a growing group of customers who can afford rhino horn medicine (Dang Vu & Nielsen, 2018; Cheung et al., 2021; Dang Vu, 2021), ceremonial drinks to improve business relations, or carvings and jewellery made out of rhino horn (Dang Vu, Nielsen & Jacobsen, 2022; Milliken & Shaw, 2012; Rademeyer, 2016; Truong, Dang & Hall, 2016).

The populations of Asian rhinos have decreased to a few tens (Javan *Rhinoceros sondaicus* and Sumatran rhino *Dicerorhinus sumatrensis*) or a few thousand individuals (greater one-horned rhino *Rhinoceros unicornis*; Save The Rhino International, 2022b). African rhinos had been extensively overharvested between 1970 and 1990 but recovered through conservation efforts (Ferreira et al., 2022). The demand for rhino horn increased in 2008 and poaching developed into a war-like conflict between conservationists and organised international criminals (Rademeyer, 2016). African black rhinos are listed as critically endangered because of the poaching-related population decline (Emslie, 2020b), and white rhinos, although only listed as near threatened (Emslie, 2020a), have the largest total losses in individuals to poaching (Ferreira et al., 2022; International Rhino Foundation, 2022). Campaigns aiming to reduce the demand for rhino horn have so far been unsuccessful (Dang Vu and Nielsen, 2018; Dang Vu, Nielsen & Jacobsen, 2020) and corruption supports a transnational organised crime network (Milliken and Shaw, 2012; Rademeyer, 2016). To protect their rhinos, managers invest in anti-poaching patrols and technological equipment to catch poachers in reserves (Reuter & Bisschop; Kamminga et al., 2018; Moore et al., 2018). Another approach is to guard every individual around the clock with armed rangers (Patton, Campbell & Genade, 2018), but for large populations in inaccessible areas this is very expensive and requires unsustainable logistical efforts (Haas & Ferreira, 2018).

The incentive for poaching can be reduced through dehorning rhinos, whereby most of the horn is removed in a veterinary procedure (Kock & Atkinson, 1993; du Toit & Anderson, 2013; Badenhorst et al., 2016). To prevent injury to the animal, the horn growth plate together with 9–11 cm horn is left intact (Badenhorst et al., 2016; Ververs, 2018). Rhino horn regrows at an approximate rate of 10% annually (Patton, 2021), therefore, dehorning should be repeated every 12–24 months (Rachlow & Berger, 1997; Lindsey & Taylor, 2011). The first dehorning operations in 1989 in Namibia and 1991 in

Zimbabwe were undertaken as emergency measures to respond to sudden increases in poaching when ranger patrols and prosecution of poachers did not suffice to halt the poaching (Lindeque, 1990; Kock and Atkinson, 1993). Extensive research about the possible effects of dehorning on rhinos was thus not possible beforehand. Dehorning is now applied widely with 2217 reported dehorning incidences in African range states from 2018 to 2021 (Ferreira et al., 2022) and not only used as a poaching deterrent but also to prevent injury between rhinos in high-density populations, or to harvest and stockpile horn for financial gain (Taylor et al., 2014; Trendler, 2014). Previous studies found no effects of dehorning on rhino survival and reproduction rates (Kock and Atkinson, 1993; Lindeque & Erb, 1995; du Toit and Anderson, 2013; Penny et al., 2020a; Chimes et al., 2022) and hormonal stress responses to dehorning are only short-term (Badenhorst et al., 2016; Penny et al., 2020b). Behaviour studies mostly focussed on specific behaviours such as fighting (Patton et al., 2018) and horn rubbing (Penny et al., 2021). With this study, we aim to add an immediate before-after comparison analysing all occurring rhino daytime behaviours, thereby responding to calls for such research, especially for white rhinos (Lindsey and Taylor, 2011; du Toit and Anderson, 2013; Badenhorst et al., 2016; Patton et al., 2018).

White rhinos are megaherbivores that spend the largest parts of the day feeding and resting (Owen-Smith, 1973; Rees, 2018). Dominant white rhino males defend territories, whereas females and subordinate males occupy overlapping home ranges (Owen-Smith, 1975). Through this dynamic spatial organisation, white rhinos often move in groups (Owen-Smith, 1975) and display a large repertoire of social interactions, such as naso-nasal sniffing, social flehming, and vocalisations (Jenikejew et al., 2020). Vocalisations play an important role in intra-sexual communication and can give insight in rhino social networks (Jenikejew et al., 2020). Females are usually accompanied by their youngest calf and sometimes by other females and subadults, but, when giving birth, the female isolates herself for several weeks (Owen-Smith 1974). Socio-negative interactions are often shown by females that deter approaching males or other females and calves from their feeding places, and fights between two males can take place at territory boundaries or with subordinate males that challenge the territory owner (Owen-Smith, 1975).

The horn of an adult rhino weighs around 7 kg (Pienaar, Hall-Martin & Hitchins, 1991). Removing such a heavy part of the head will change the centre of gravity and the rhino's perception of weight on the head. There is no evidence that white rhinos use their horns during general activities such as feeding and resting, in contrast to black rhinos that use their horns to break branches to access browse (Joubert & Eloff, 1971). White rhinos rub their horns against objects (Pienaar et al., 1991; Rachlow, 2001) and use them during comfort behaviour such as wallowing to test the consistency of the mud (Owen-Smith, 1973). Rhinos also use their horns in fights or in playful horn wrestling (Owen-Smith

1974; Owen-Smith, 1975). Horn growth is faster in males than in females (Rachlow and Berger, 1997), and although horn size is not the deciding factor for female mate choice (Kretzschmar et al., 2020), it can affect the rhino's dominance status (Penny et al., 2022). Therefore, it seems likely that dehorning would affect white rhino comfort behaviour and social interactions. However, Penny et al. (2021) found no effects of dehorning on rubbing and wallowing and Penny (2019) noted no differences in affiliative and aggressive behaviours between horned and dehorned populations. On the other hand, in a study where rhinos were dehorned because of high aggression and observed before and after dehorning, the number of fights between males was reduced by 68% after dehorning (Patton et al., 2018). Furthermore, fights were not a cause of death in populations of dehorned rhinos, compared to 17% of deaths caused by fights in a population of horned rhinos (Chimes et al., 2022). Since rhinos lack their weapons for fights after dehorning, a decrease in aggressive and an increase in avoidance behaviour would be expected. This might be more prevalent in males than in females, because only males defend territories, and because in black rhinos, horn size influences social dominance among males but not females (Berger & Cunningham, 1998).

The dehorning operation includes chasing and immobilisation and is thus a stressful procedure for rhinos, resulting in short-time stress responses (Badenhorst et al., 2016) and the separation of groups (Pfannerstill & Maboga, 2021). Group size affects the number of social interactions and the vocalisation rate, because rhinos are prone to communicate more when they have more neighbours standing by at short distances (Jenikejew et al., 2020). Therefore, less affiliative behaviour and reduced vocalisation rates could be indirect effects of dehorning.

The aim of this study was to investigate effects of dehorning on rhino behaviour, including general activities, comfort behaviour and social interactions in a before-after comparison. We hypothesised that there would be (i) no effects of dehorning on general rhino activities such as resting, feeding and locomoting; (ii) no effects of dehorning on comfort behaviour; (iii) less aggressive behaviour after dehorning than before, especially in male rhinos; (iv) more avoidance behaviour after dehorning than before; (v) less affiliative behaviour after dehorning; and (vi) lower vocalisation rates after dehorning.

Methods

Ethics statement

This article contains observations of natural behaviour from wild white rhinoceros (*Ceratotherium simum simum*). A research permit (ENT 8/36/4 XXXXII 58) was issued by the Ministry of Environment, Natural Resources Conservation and Tourism of Botswana. The dehorning was carried out by experienced and qualified veterinarians from the Department of Wildlife and National Parks as part of the country-wide rhino dehorning operation (Mguni, 2020; Senyatso 2021). No animal was injured and no adverse effects were observed immediately following the dehorning.

Study area and subjects

The study was conducted from March to May 2020 with free-roaming white rhinos in a private reserve of approximately 33,000 ha in Botswana. We refer to this timeframe of approximately two months as "medium-term" in differentiation to short-term stress responses within a day or long-term effects over the lifetime of an individual. The name and exact location of the reserve are not stated for security reasons (Clements et al., 2020). The vegetation consisted of grasslands and mixed savannah bushland. Lions (*Panthera leo*) were present at the study site, which may prey on rhino calves (Le Roex & Ferreira, 2020). The study population consisted of one subadult female and eight adult rhinos (five females, three males) that were identified through their individual ear notches (Rhino ID in Table 1). The rhinos were habituated to vehicles as monitoring personnel visited them daily. All females except one subadult had dependent calves during the observation period. The rhinos formed flexible groups of two to eight individuals. Dehorning took place on the 11th or 12th of April 2020. The observations after dehorning began four days after the event because regular monitoring patrols were given higher priority than the research observation and the researcher therefore did not have access to the study area earlier.

Table 4.1: Details about nine white rhino study subjects observed between March and May 2020 in Botswana before and after a dehorning event. Rhino ID refers to the identifying ear notches. F=female, M=male.

Rhino ID	Year of birth	Age at time of observation (approximately, in years)	Sex	Observation duration before dehorning (hh:mm:ss)	Observation duration after dehorning (hh:mm:ss)	ID and age of calf at beginning of observation
WF344	2017	3 (subadult)	F	02:24:48	03:34:52	-
WF306	2014	6	F	02:46:29	03:07:36	WF11 – 9 months
WF304	2013	7	F	02:52:45	03:00:23	WM19 – 9 months
WF305	2013	7	F	03:02:27	03:09:47	WF14 – 6 months
WF349	2013	17	F	02:10:59	03:00:27	WF6 – New-born end of March 2020
WF335	2000	20	F	02:53:37	02:59:12	WF21 – 4 months
WM311	2012	8	M	02:45:14	03:01:21	-
WM331	2012	8	M	02:30:32	03:00:11	-
WM312	2010	20	M	03:00:21	02:58:52	-

Video and audio recording

We performed focal animal observations (Altmann, 1974) between 6:30 am and 11:30 am and between 4:30 pm and 6:45 pm. These times were selected as the most active hours for rhinos to increase the chance to observe a wide range of social behaviours (Owen-Smith, 1973). As the rhinos moved freely in the reserve, we had to search for them every day. Each rhino was observed a maximum of once per day and for logistical reasons, we were able to observe 1-3 individuals per day. To account for effects of time of day and temperature on rhino activity (Owen-Smith, 1973), we semi-randomised recording times to balance morning and afternoon observations for each individual. After sighting a rhino or a group of rhinos, we approached them in a vehicle up to a distance of 10 to 30 m, depending on visibility, loudness of background noises such as wind, and the behavioural state of the rhino. Recordings were started when the engine of the vehicle was switched off and when the rhino had returned to its previous behaviour before possible disturbance by the approaching vehicle. Rhinos were videotaped for approximately 30 min using a Sony α 65 camera (Sony Corporation, Thailand) and a Medion video camera (Medion AG, Essen, Germany). Audio recordings were made using a Sennheiser omni-directional microphone (MKH 8020; Sennheiser, Wedemark, Germany; flat frequency response from 10 to 20 000 Hz ± 5db) covered with a wind shield and fitted on a boom pole. The microphone was connected to a Zoom F4 Field recorder (set at 44.1 kHz sampling rate, uncompressed .wav format). When the focal animal moved out of recording range during the observation, as indicated by listening to the live recording with headphones, or out of sight behind vegetation, we stopped the recording, changed the position of the vehicle, and continued recording from the new position. After 30 minutes, we either started a new searching process or switched focal observations to another individual in the same group. Although we aimed to observe each animal six times before and six times after dehorning with three morning and three afternoon observations each, we could not choose the dehorning date and observations sometimes had to be stopped early, e.g., due to rain that would mask rhino vocalisations. Therefore, total observation durations differed among individuals (Table 4.1).

Video analysis

All behaviour videos were synchronised with respective audio recordings and analysed using the software Observer XT (version 12, Noldus Information Technology, Netherlands, Noldus, 1991). After a pre-survey of 25 videos, we re-examined, extended, and adapted the ethogram by Jenikejew et al. (2020) to our observations of free-roaming rhinos and used the modified ethogram (Table S1). According to our hypotheses, we focussed on the following categories: general activity, comfort, aggressive, avoidance, and affiliative behaviours. Although vocalisations were classified according to the literature (Policht et al., 2008; Linn, Boeer & Scheumann, 2018; Jenikejew et al., 2020; Linn, Schmidt & Scheumann, 2021; Table S1) we grouped for them for analyses because none of them occurred at sufficiently high frequencies for separate analyses. We calculated the frequency of the point events by dividing the number of point events by the observation duration in minutes. We noted the nearest neighbour to the focal animal, its proximity in adult rhino body lengths (2.5-3 m, Owen-Smith, 1973), and for all social behaviours the interaction partner using the same method as Jenikejew et al. (2020).

To ensure reliability of the behaviour coding, 25% of the observations were compared with the coding of a second observer. Inter-observer reliability was high with 85% agreement for durations and 78% agreement for point events. Lower agreement in point events was caused by the rarity of the events and by different reaction times of the observers.

Statistical analysis

We had a total of 110 observations from all nine focal individuals (six females, three males) before and after dehorning (female before: 36, female after: 39, male before: 17, male after: 18). For each behaviour, we created a model in which we added the proportion of time of the respective behaviour as the dependent variable using the cbind function in R, which defined the time when the behaviour was observed (success) versus the time when the behaviour was not observed (failure) (Zach, 2021). Fixed effects were dehorning status and sex and their interaction, and we included Rhino ID as random intercept in each model to account for repeated measurements of the same individual. We ran generalised linear mixed models with the beta-binomial family (logit-link-function) and zero-inflation structure to account for the high number of zeros (glmmTMB package, Brooks et al., 2017). We performed model diagnostics with the DHARMa package (Hartig, 2022). We used the corrected Akaike's Information Criterion (AICc) to identify the most parsimonious models using the aictab function from the package AICcmodavg (Mazerolle, 2020). The model with the fewest predictors that was within two AICc of the model with the lowest total AICc was chosen. If a model other than the null model (intercept+random effect only) was the most parsimonious, we performed post hoc tests with the emmeans function (Lenth, 2021), whereby estimates were compared pairwise between explanatory factor levels on a log-odds ratio scale due to the link function applied in the model. For graphical presentation, we divided the duration of the behaviour by the observation time to obtain behaviour proportions.

To analyse vocalisation rates, we divided the sum of vocalisations of the focal animal by the respective observation duration to get a standardised vocalisation rate per minute. The vocalisation rate was left-skewed, and we therefore transformed the data to square root values. We ran generalised linear mixed models (lmer function from the lme4 package, Bates et al., 2015) on the transformed data, with the fixed factors dehorning status, number of neighbours, sex, and the three-way interaction among them, and focal animal as the random factor. We used the dredge function from the package MuMIn (Barton, 2022) to identify the most parsimonious model. Any competitive models with ΔAIC<2 were averaged using the model.avg function to estimate model-averaged parameter values.

All statistical analyses were performed in R (v4.0.3 (2020-10-10), The R Foundation for Statistical Computing), using the packages tidyverse (Wickham et al., 2019) for workflow, and ggplot2 (Wickham, 2016) for visualisation. We considered p-values below 0.05 as statistically significant.

Results

The most prominent rhino behaviours throughout the observations were resting and feeding (Fig. 1). A high proportion of aggressive behaviour was observed in two observations on the same day through a fight between two males (WM312 and WM331). The female WF349 calved during the observation period and showed a higher proportion of feeding and comfort behaviour before calving (up to observation four) and more resting and affiliative behaviour after calving. The female WF306 showed a higher proportion of affiliative behaviour than other rhinos, which was in this case playing with calves in observation six and nine and playing with calves and other adults in observation 11. In comfort behaviours, we did not observe wallowing and rubbing was only observed after dehorning.

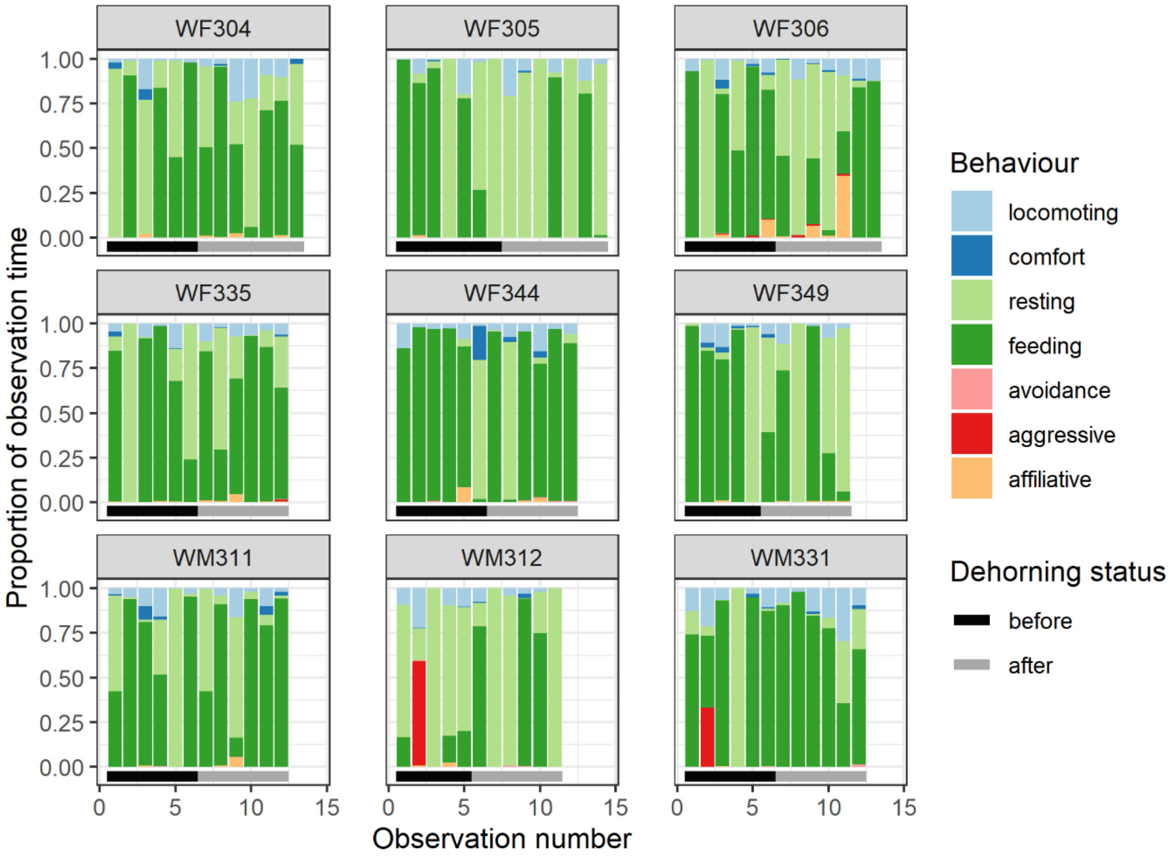

Figure 4.1 Proportion of observation time of behaviours per observation before and after a dehorning event for nine focal rhinos (six females, three males) observed between March and May 2020 in Botswana.

For resting and feeding, the null model was the most parsimonious (resting: AICc=1377.03, AICcω=0.42; feeding: AICc=1409.39, AICcω=0.22, Figure 4.2), so dehorning status, sex or their interaction did not have any significant effect on these behaviours.

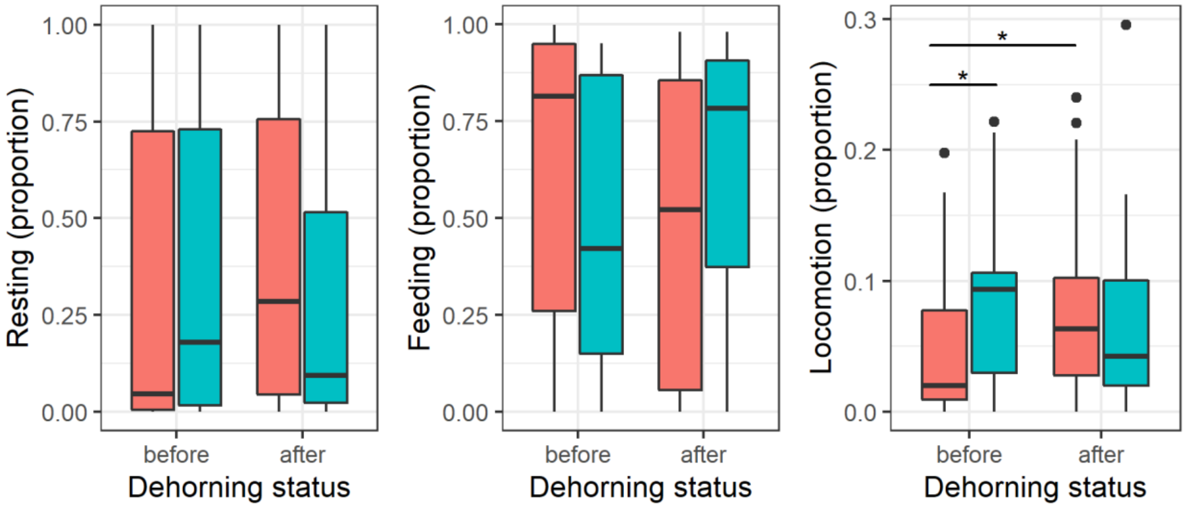

Figure 4.2 Boxplots of behaviour proportions for the general activities resting, feeding and locomotion in dependence of dehorning status and sex based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before 17, male after 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. Note different scales for y-axes, red=females, blue=males, stars indicate significant differences.

For locomotion, the model with the interaction between dehorning status and sex was the most parsimonious; no other models were competitive (ΔAIC=2.56, AICcω=0.64). Before dehorning, males showed significantly more locomotion than females (log-odds ratio=0.51±0.13, df=103, t=-2.56, p=0.04). After dehorning, females showed more locomotion than before (log-odds ratio=1.87±0.38, df=103, t=3.06, p=0.02); males appeared to locomote less after dehorning than before, but this result was not significant (Figure 4.2).

For comfort, aggressive and affiliative behaviour, the null model was the most parsimonious (comfort: AICc=522.18, AICcω=0.21; aggressive: AICc=171.14, AICcω=0.46; affiliative: AICc=477.23, AICcω=0.25; Table 4.4, Figure 4.4 in the supplementary material). Dehorning status, sex or their interaction did not have a significant effect on these behaviours.

For avoidance behaviour, there were not enough data points to include the interaction in the model, and we only ran the additive models. The null model was the most parsimonious (AICc=179.35, AICcω=0.24, Table 4.4, Figure 4.4 in the supplementary material), thus, dehorning status and sex did not have a significant effect on avoidance behaviour.

For the vocalisation rate, the model with the interaction between dehorning status and sex plus the interaction between number of neighbours and sex was the most parsimonious (AICc=-86.8, AICcω=0.50), but the model with the three-way interactions was competitive (ΔAICc=1.01, AICcω=0.30) and we averaged both models (Table 4.2).

Table 4.2 Model averaged parameter values explaining variation in white rhino vocalisation rates according to dehorning status, sex and number of neighbours based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before 17, male after 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. Significant effects are highlighted in bold.

Parameter	**Estimate**	**Adjusted Std. Error**	***z* value**	***p* value**
(Intercept)	0.160	0.041	3.911	0.000
Dehorning.status_before	0.046	0.056	0.821	0.412
Sex_male	0.148	0.080	1.828	0.068
Number of neighbours	**0.084**	**0.017**	**4.890**	**0.000**
Dehorning.status_before:Sex_male	0.129	0.115	1.118	0.264
Number of neighbours:Sex_male	**-0.101**	**0.037**	**2.723**	**0.006**
Dehorning.status_before:Number of neighbours	-0.015	0.026	0.568	0.570
Dehorning.status_before:Number of neighbours:Sex_male	0.035	0.054	0.648	0.517

The vocalisation rate increased with the number of neighbours, but this effect was smaller for males than for females (Table 4.2, Figure 4.3a). The interaction between the number of neighbours and sex was stronger than the interaction between dehorning status and sex, but the best model included both interactions, which was caused by fewer male vocalisations after dehorning than before (Figure 4.3b). However, the standard error for the interaction between dehorning status and sex was larger than for the interaction between number of neighbours and sex, and the effect was therefore not significant in the model output.

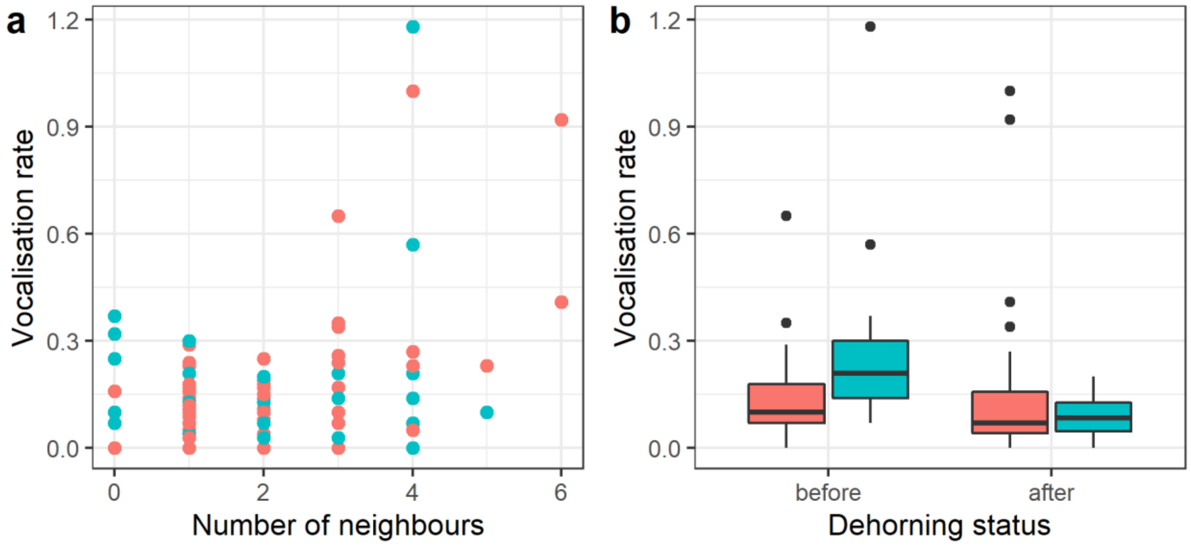

Figure 4.3 Vocalisation rate (number of vocalisations per minute) in dependence of (a) number of neighbours and sex and (b) dehorning status and sex based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. Red=females, blue=males.

Discussion

Studying the effects of dehorning on rhino behaviour, our results did not show evidence for changes in proportions of resting, feeding, comfort, aggressive, avoidance, and affiliative behaviours during the more active morning or afternoon hours caused by dehorning. This supports our hypothesis that dehorning did not affect feeding, resting, and comfort behaviour, but rejects our hypothesis that aggressive, avoidance, and affiliative behaviours are affected by dehorning. Furthermore, we detected sex-specific changes in the proportions of locomotion and of vocalisation rates before and after dehorning, in contrast to our expectations.

Our first hypothesis that general activities would not change after dehorning was partly supported, as we did not find effects of dehorning on resting and feeding behaviour. This is in line with previous studies on short-term stress responses (Badenhorst et al., 2016; Penny et al., 2020b) and suggests that dehorning also did not cause medium-term stress. In some observations, we did not record feeding behaviour, coincidentally several times in the same focal animal, but this is related to our limited focal observation time, as we encountered the rhino on these days when it was resting. Interestingly, we found effects of dehorning on locomotion. Males showed more locomotion than females before dehorning, which aligns with a study by Seidel et al. (2019) that observed larger distances moved by male than female black rhinos. This might be caused by the territorial behaviour of males, who may patrol their territory daily to place scent marks (Owen-Smith, 1971), whereas females usually only move from one feeding patch to the next. In contrast, females might have moved more after dehorning than before potentially avoiding the vehicle in anticipation of a new immobilisation operation (Pfannerstill and Maboga, 2021). Weather could have affected behaviour because rhinos usually tend to move more on cooler, cloudy days (Owen-Smith, 1973), but the weather changed from cool and rainy in March to hotter and sunnier in May and it is therefore an unlikely explanation for the observed increase in locomotion. The sex-specific change in locomotion could also be linked to the birth we observed in our study population instead of the dehorning. The female WF349 gave birth less than two weeks (March 31st) before dehorning and only one focal observation was collected from her between the birth and the dehorning event. In addition, a second female that was not included in the observations gave birth in the first week of April. The births changed the behaviour of the females from mainly feeding to mainly resting and more comfort behaviour, but also affected the male WM312, who locomoted more, possibly while searching for the females that had isolated themselves for giving birth. Therefore, we conclude that dehorning can temporarily increase proportions of rhino locomotion but social events in the population can have stronger effects.

Our hypothesis that comfort behaviour would not change after dehorning was supported, but we observed that rubbing, a behaviour which involved the horn, occurred only after dehorning and not before. This is similar to observations by Penny et al. (2021) of only two horn rubbing events by horned rhinos in contrast to 31 horn rubbing events by dehorned rhinos. Thus, the effects of dehorning might not be detectable through the rare occurrence of the specific behaviours that involve the horn. However, rhinos are able to adapt to the strong change in their facial structure as horns occasionally break off and wear down naturally; such adaptation has been shown in previous dehorning studies (Kock and Atkinson, 1993; Patton, 2021; Penny et al., 2022).

We found no effects of dehorning on aggressive, avoidance, and affiliative social behaviours, but several of these occurred rarely and for short durations. Our observations of rare events were limited due to time constraints. We observed only one fight, which occurred before dehorning. Thus, our results neither confirm a decrease (Patton et al., 2018) nor an increase (Penny et al., 2022) of agonistic social interactions after dehorning, but the low number of aggressive interactions observed supports the classification of white rhinos as the most social rhino species. Since the dehorning in the study by Patton et al. (2018) was undertaken to reduce the number of fights, effects of dehorning on aggressive behaviour might have only been observable due to an atypically high rate of aggressive interactions before dehorning.

We had expected an increase in avoidance behaviour after dehorning as rhinos would have lost their weapon for aggressive encounters and therefore should avoid social confrontations, resulting in more escaping behaviour. However, in a previous study on the same population we observed that rhinos were solitary for about one week after dehorning (Pfannerstill and Maboga, 2021), which already decreased social interactions. Thus, during this time, rhinos showed less direct avoidance behaviour because they were not displaced by other rhinos. The solitary movement lasted only a week, and our observations began four days post-dehorning and continued for one month, so the effect of the solitary movement was very short-lived. Our results therefore indicated that dehorning had no strong effect on avoidance behaviour in the medium term.

We expected less affiliative behaviour after dehorning caused by stress related to the dehorning operation. However, most affiliative behaviours occurred between females and their calves that stayed together throughout the observation time and the proportions of affiliative behaviour therefore did not change. In the case of the female that gave birth shortly before dehorning, the proportions of affiliative behaviour presumably increased as a response to the presence of the new-born calf and not to the dehorning. Overall, finding no changes in affiliative behaviour aligns with the study by Penny (2019), who found similar frequencies of cohesive behaviour in a dehorned and a horned population.

Vocalisation rates generally increased with the number of neighbours. This confirms that rhinos use vocal communication mainly at short distances and more neighbours mean more potential communication partners, resulting in more frequent vocalisations (Jenikejew et al., 2020). Males showed lower vocalisation rates after dehorning than before, but this was most likely related to the births and the fight in an observation before dehorning. When a male searched for females shortly before they gave birth, he called them with contact and courtship calls, contributing to higher vocalisation rates before dehorning. Even more pronounced was the influence of the fight, when the two males were vocalising continuously. This was exceptional and not recorded in other observations. The decrease in male vocalisations rates after dehorning might therefore either be a biased result because we observed only one fight or an indirect effect of reduced aggressive interactions after dehorning, thereby supporting the findings by Patton et al. (2018) and Chimes et al. (2022). Future research could examine affiliative and aggressive call types separately to identify changes in vocalisation rates depending on the social context.

There are limited opportunities to observe wild rhinos around dehorning events, therefore, our results are based on a small number of individuals. However, with nine individuals, our sample size is comparable to other studies (Patton et al. 2018: n=6, Penny et al. 2022: n=6). For logistical reasons, our observation times were relatively short and rare events such as a fight after dehorning might therefore not have been observed due to a sampling effect. Nevertheless, our method of focal animal sampling that includes following an individual provides the opportunity to observe it at different locations and in different social groupings, which might not be possible using stationary camera traps at water holes (Penny et al. 2021). Furthermore, rare behaviours such as rubbing remained rare events with occurrence sampling on a larger number of individuals over longer observation periods (Penny et al. 2021) and our result are therefore likely an adequate representation of rhino behaviour. All but one observed female had a calf and one gave birth during data collection, so this could have affected our results concerning affiliative behaviour, and our findings may not be applicable to other populations; further investigations with larger sample sizes should therefore be undertaken. Still, our study adds valuable observations to the existing literature from adults of both sexes in a population where all individuals were dehorned at the same time.

To conclude, we found very limited evidence for effects of dehorning on rhino behaviour within one month. When compared to social events – two births and a fight – that occurred in the same timeframe and induced visible behavioural changes, our results suggest that dehorning has no strong effect on rhino behaviour. In the light of our findings, dehorning can thus be seen as a reasonable method from an animal ethics point of view. However, the benefits of dehorning as a management measure should be weighed against possible disadvantages. There are risks to animal welfare associated to the immobilisation that is necessary prior to dehorning (Lindsey and Taylor, 2011; Trendler, 2011; du Toit and Anderson, 2013) and dehorned rhinos might be less able to defend themselves against predators, leading to higher calf mortality (Le Roex and Ferreira, 2020). If dehorning is efficient in reducing poaching, then immobilisation and the possible loss of a calf would be the smaller risk compared to the possible loss of an adult female through poaching, which also has compound effects of losing future calves (Nhleko et al., 2022). Our research permit did not include the analysis of poaching data, but previous studies showed that the proportion of poached rhinos was not different between horned and dehorned populations (Chimes et al., 2022) and suggested that also dehorned rhinos need continuous protection (Kock and Atkinson, 1993; Lindsey and Taylor, 2011; Dang Vu et al., 2022). Further research is therefore necessary to evaluate the effectiveness of dehorning in reducing poaching events in comparison to other conservation measures, including leadership training and the development of income-generating activities for local communities around rhino reserves or value creation of living rhinos (Ball et al. 2019; Ferreira et al., 2022), so that resources for rhino conservation can be allocated most efficiently.

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Data availability

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. Behaviour data tables can be accessed at DOI 10.5281/zenodo.7286117.

Conflict of interest

The authors declare no known conflict of interest.

Author contributions

VP, EB, and MS designed the study. VP and OM collected the data. VP and RH analysed the data. VP drafted the article and EB, MS, RH and NB revised the article for intellectual content. All authors approved the final version for submission.

Supplementary material

Table 4.3 Ethogram for focal animal observations of free-roaming rhinos in Botswana.

Functional behavioural system	Behaviour	Definition	Condition	Measure
Acoustical behaviour	Vocalisation	Every kind of noise generated by the vocal tract of the focal animal or another conspecific. Classified into pant, hiss, whine, snort, snarl, squeal and grunt		Point event
General activity	Resting	Focal animal stays, sits or lays in relaxed body posture and does not show any other activity.	Latency: at least 3 sec.	Duration
	Feeding	Focal animal takes food (grass/water) into its mouth, chews visibly and walks no more than four steps without taking a new bite.	Latency: at least 3 sec.	Duration
	Locomotion	Focal animal moves away from the previous location.	Distance: at least four steps without taking a new bite of grass	Duration

	Playing	Focal animal performs any behaviour that contains parts of aggressive interactions (horn clashing, staring, chasing, pushing etc.) in a non-aggressive context or receives parts of sexual behaviour (mounting, head placing) performed by calves.		Duration
Comfort behaviour	Wallowing	Focal animal lays or sits in mud hole while covering its body with mud, sometimes changing the position within 2-3 sec.	Latency: at least 3 sec.	Duration
	Rubbing	Focal animal scrubs any part of its body against objects.	Latency: at least 3 sec.	Duration
	Manipulation	Focal animal scratches with its horn/forelegs on the ground or pushes/lifts/scrapes objects with it.	Latency: at least 3 sec.	Duration
	Defecation & Urination	Focal animal excretes faeces or urine.		Duration
	Marking	Focal animal urinates intermittently or spreads its defecation with its hind legs.		Duration
	Sniffing	Focal animal explores ground/objects or urine/faeces by inclining towards it, "sliding" along the surface with the snout, visibly moving the nostrils at least 3 times while it does not show any locomotion.	Latency: at least 5 sec.; Distance to snout: max. 10 cm	Duration
	Flehming	Focal animal opens its mouth and curls back its upper lip exposing its teeth while inhaling with nostrils usually closed.	Latency: for at least 3 sec.	Duration

Affiliative behaviour	Approaching	Focal animal moves directly towards another conspecific and shortens the distance.	Only recorded if no social behaviour follows the "Approaching" directly; Distance to relevant conspecific: at least 1 body length or less and is encoded when it undercuts 1 body length to relevant conspecific	Point event
	Following	Focal animal moves after a conspecific while it changes the location.	Distance to relevant conspecific: max. 2 body lengths	Duration
	Snout contact	Focal animal explores the body of another conspecific (except the snout) with its snout.	Latency: at least 3 sec; Distance to snout: max. 10 cm	Duration
	Social Flehming	Focal animal opens its mouth and curls back its upper lip exposing its teeth while scenting a defecating/urinating conspecific is standing close by.	Latency: for at least 3 sec.; Distance to relevant conspecific: less than 1 body length	Duration
	Naso-nasal sniffing	Focal animal contacts the nasal region of another conspecific with its own snout.	Latency: at least 3 sec.; Distance to relevant conspecific: less than one snout-length	Duration
	Ano-genital sniffing	Focal animal contacts the ano-genital region of another conspecific with its own snout.	Latency: at least 3 sec.; Distance to relevant conspecific: less than one snout-length	Duration
	Head placing	Focal animal lays it's head on the back of another conspecific.	Latency: at least 3 sec.	Duration
	Body contact	Focal animal touches or brushes another conspecific while moving with any part of its body (except snout) or rubs itself against a conspecific in waving movements.	Distance before: at least one snout-length; Latency: at least 3 sec.	Duration
Aggressive behaviour	Displacing	A conspecific animal changes its position or location after being approached by or agonistic interaction with the focal animal.	Latency: within 3 sec. after interaction; Distance: at least 1 body length	Duration
	Nodding	Focal animal swings its head back and forth.		Point event

	Lifting	Focal animal lifts another conspecific's head or leg with its head/horn.		Duration
	Staring	Focal animal is standing horn to horn in front of another conspecific with an uplifted head.	Latency: at least 3 sec.	Duration
	Pushing	Focal animal presses any part of its body against another conspecific making him change the position or location.	Latency: at least 3 sec.	Duration
	Chasing	Focal animal follows another conspecific, which tries to keep the focal animal at a distance, in a trotting manner	Distance: min. 1 body length	Duration
	Feigned attacking	Focal animal is moving with a lowered horn directly towards another conspecific and stops suddenly without causing body contact.		Duration
	Attacking	Focal animal hits its horn against another conspecific.		Duration
	Horn clashing	Escalated confrontation following Attacking involving both animals hitting their horns against each other.	Latency: at least 3 sec.	Duration
Avoidance behaviour	Avoiding	Focal animal changes its position or location after being approached by, agonistic interaction with or agonistic vocalisation (threat/grunt/snarl) from a conspecific.	Latency: within 3 sec. after interaction; Distance: at least 1 body length	Duration
	Escaping	Focal animal moves away from a conspecific in a trotting manner after an agonistic interaction.	Distance: at least 1 body length	Duration

*Table 4.4 Overview of corrected Akaike's Information Criterion (AICc) values of models testing effects of dehorning status and sex on rhino behaviours based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. 0=null model; +=additive model dehorning status+sex; *=model including dehorning status, sex, and the interaction between dehorning status and sex; DeltaAICc=difference in AIC value to the best model; AICcWt=Akaike weights or model probabilities; Cum.Wt=Cumulative Akaike weights; LL=Log-likelihood of the model. All models included the rhino ID as a random factor to account for repeated observations of the same individual.*

Behaviour	Model fixed factors	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Resting	0	4	1377.03	0	0.42	0.42	-684.33
	dehorning status	5	1378	0.96	0.26	0.69	-683.71
	sex	5	1379.01	1.98	0.16	0.84	-684.22
	+	6	1380.02	2.98	0.1	0.94	-683.6
	*	7	1380.94	3.9	0.06	1	-682.92
Feeding	dehorning status	5	1408.63	0	0.32	0.32	-699.03
	*	7	1408.8	0.17	0.29	0.61	-696.85
	0	4	1409.39	0.76	0.22	0.82	-700.5
	+	6	1410.86	2.22	0.1	0.93	-699.02
	sex	5	1411.58	2.95	0.07	1	-700.5
Locomotion	*	7	1198.28	0	0.64	0.64	-591.59
	dehorning status	5	1200.84	2.56	0.18	0.82	-595.13
	+	6	1202.12	3.84	0.09	0.91	-594.65
	0	4	1203.3	5.02	0.05	0.96	-597.46
	sex	5	1203.84	5.55	0.04	1	-596.63
Comfort	*	7	520.78	0	0.42	0.42	-252.84
	0	4	522.18	1.41	0.21	0.64	-256.9
	dehorning status	5	522.48	1.7	0.18	0.82	-255.95
	sex	5	523.74	2.96	0.1	0.91	-256.58
	+	6	523.95	3.17	0.09	1	-255.57
Aggressive	0	4	171.14	0	0.46	0.46	-81.38
	dehorning status	5	172.61	1.47	0.22	0.68	-81.02
	sex	5	173.26	2.12	0.16	0.84	-81.34
	*	7	174.46	3.32	0.09	0.93	-79.68
	+	6	174.78	3.65	0.07	1	-80.98
Defensive	dehorning status	5	178.6	0	0.35	0.35	-84.01
	+	6	179.12	0.52	0.27	0.62	-83.15
	0	4	179.35	0.75	0.24	0.86	-85.48
	sex	5	180.36	1.76	0.14	1	-84.89
Affiliative	sex	5	476.64	0	0.34	0.34	-233.03
	0	4	477.23	0.59	0.25	0.59	-234.42
	+	6	478.24	1.6	0.15	0.74	-232.71
	*	7	478.5	1.87	0.13	0.87	-231.7
	dehorning status	5	478.57	1.93	0.13	1	-233.99

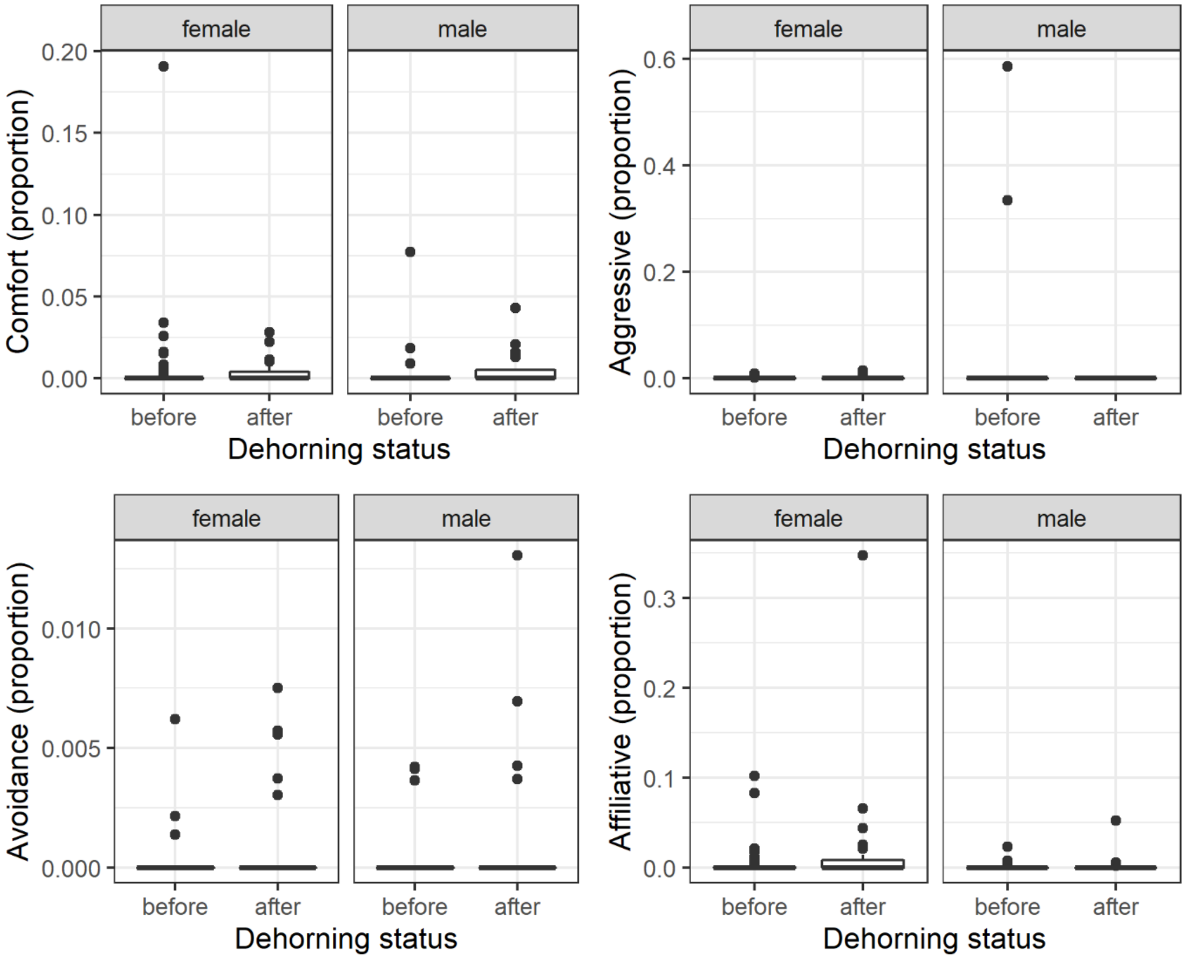

Figure 4.4 Boxplots of behaviour proportions for comfort, aggressive, avoidance and affiliative behaviour in dependence of dehorning status and sex based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. Note different scales for y-axes.

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5. General Discussion

The aim of this thesis was to improve our understanding of effects of management interventions on rhino behaviour, with the ultimate goal of contributing to ameliorated rhino conservation actions. Best practices are nowadays shared among rhino managers, and handbooks suggesting optimal procedures have been published (Emslie et al. 2009; Morkel & Kennedy-Benson 2007). However, some crucial elements are still unknown, particularly concerning rhino spatial behaviour following translocation and how to handle long-distance dispersal in the context of a conservation programme where animals must remain in a given protected area. I used both descriptive and experimental approaches and analysed movement data and behaviour observations to address these gaps. My results give novel insights into rhino movement after translocations and report the potential for using an innovative management tool to address long-distance dispersal. Furthermore, I evaluated the impact of dehorning as a common conservation practice on natural rhino behaviour, which is important to inform management decisions.

Recommendations for rhino management derived from this study

Considering site fidelity in rhino translocations

In **Supplementary study 1**, I tested several indicators for home range establishment to identify the best possible method to analyse rhino movement patterns with the available data. In the data were multiple gaps, and the timeframes of continuous GPS relocations were short. Therefore, I selected site fidelity as the short-term indicator for rhino settlement at the release site. In **Chapter 1**, I showed that site fidelity of white rhinos after translocation was higher for adults than subadults, making adults the better translocation candidates. I did not find this difference for black rhinos. Higher site fidelity in black rhinos might be related to their more restricted movement behaviour (Linklater & Swaisgood 2008) and the abundance of surface water in my study area, as this is the limiting resource for black rhino females (Le Roex et al. 2019). In addition, black rhinos were held in on-site enclosures before release, whilst white rhinos were released from the transport crate. Thus, the release type might also have affected the movement patterns, although my data did not allow to compare the two species. White rhino subadult females released at a confined site had smaller movement ranges within three months than subadult females released at other sites. Fencing the release site could therefore reduce dispersal movement. The movement ranges over three months of newly released rhinos were larger than movement ranges of rhinos that had been living in the same area for 3-5 years, which points to an exploratory phase. This is consistent with studies on other ungulates (Berger-Tal & Saltz 2014) and with other studies on rhino movement after release, which show that rhino movement range sizes are very variable and depend on the reserve size (Göttert et al. 2010; Thompson et al. 2016).

Although my results pointed towards adults as the better translocation candidates than subadults, more factors than site fidelity must be considered when selecting individuals for translocations. The main reason for post-release mortality in translocated black rhinos are fights (Adcock et al. 1998; Linklater et al. 2012; Linklater & Swaisgood 2008). Thus, the release of several adult males at the same site must be avoided (Adcock et al. 1998; Linklater et al. 2012; Linklater & Swaisgood 2008). Heavily pregnant females or those with small calves should not be translocated as this would likely result in the death of the calf (Morkel & Kennedy-Benson 2007). In healthy populations, adult females always either have a dependent calf or are pregnant, which would leave only subadults or females in early stages of pregnancy as possible translocation candidates. Furthermore, adult individuals have a stable neighbourhood system where they defend territories against rivals but may share them with subadults (Owen-Smith 1971). So, translocating adults would disrupt the territorial system in the source area and leave empty areas of suitable rhino habitat, as rhinos are slow to colonise areas that had been occupied before (Linklater & Hutcheson 2010). Furthermore, disrupting the neighbourhood favours conflicts among translocated individuals (Shier & Swaisgood 2012). Regarding the above-mentioned factors, subadults seem to be more suitable for translocations than adults. On the other hand, subadults are also slower to start reproducing after translocation (Gedir et al. 2018) and are more prone to show long-distance dispersal. Translocation strategies must therefore consider all these factors: individuals must be selected based on the age and sex-class of potential candidates but also on the spatial pattern of territories of the source population to avoid negative changes in the social system.

There are several management strategies and interventions that can help to improve post-release site fidelity (Tetzlaff et al. 2019). My results suggested that fencing the release area or penning translocated rhinos would hinder long-distance movements and help rhinos to establish their new home ranges faster. Furthermore, fences can be essential to avoid human-wildlife conflicts by keeping animals away from human settlements and agricultural sites (African Parks 2022). However, fencing might be problematic, particularly in the Okavango Delta. In contrast to most other reserves that hold rhinos, the Okavango Delta is very large (app. 15,000 km^2), consists of many concessions with different managers and without physical borders between them, and large parts are hardly accessible other than by aircraft. Building fences around the release area would require the construction of roads, and fence maintenance would be extremely laboursome and expensive. In addition to the logistical efforts that would be necessary, one goal of reserves is to keep environmental disturbance to a minimum (Allan et al. 2018). Fences would disrupt movements and gene flow of other species, having thus non-negligible effects on biodiversity (Woodroffe et al. 2014). Fences around large parts of the release area should therefore be temporary and permeable for other species. This was for example applied successfully in a reintroduction of bison (*Bison bison*) in Canada, where bison fences allowed free movement of elk (*Cervus canadensis*) and wolves (*Canis lupus*) (Laskin et al. 2020). In restocking events, where individuals are translocated into existing populations of the same species, the effects of fences in hindering social interactions should be considered (McEvoy et al. 2022). Smaller on-site enclosures for a delayed release of translocated individuals as the alternative to fencing the release area were in the Okavango Delta applied successfully for black rhinos (see appendix of chapter 1). This could be extended to individuals that are the most susceptible to start long-distance dispersal movement, e.g., white rhino subadult females.

Applying playbacks for rhino management

In **Chapter 2**, I evaluated the potential of using playbacks of conspecific calls to attract or deter rhinos. I performed experiments with socio-positive and socio-negative calls, which extends the existing literature where contact and mating calls were used (Cinková & Policht 2016; Cinková & Shrader 2020, 2022) with aggressive calls. White rhinos responded with head and body movements and calling to playbacks of conspecific calls. Responses with directed body movement were rare and the durations of responses were mostly shorter than two minutes. Males approached the loudspeaker more often than females, and females ran away from calls of unfamiliar senders. This supports the possibility of using playbacks to guide rhino movement, although the intensity and duration of the responses depended not only on the call type, but also on several factors such as wind speed, familiarity with the sender, and behaviour before the playback. In Reserve B, experienced strong sound attenuation by the vegetation, which probably decreased the strength of behavioural responses to the playbacks.

In **Supplementary study 2**, I also tested juvenile calls in playback experiments, but the experiments with this call type were stopped after an explorative study and were therefore not analysed in Chapter 2. In addition, there was most likely an observer effect in reserve B. Here, groups of rhinos often ran away from the loudspeaker, presumably because they detected the experimenters when the playback was started. Although I noticed during the experiments that hiding the loudspeaker in vegetation and recording responses from a farther distance or with camera traps might reveal more conclusive results, I could not change the methodology because of the outbreak of the Covid-19 pandemic, which limited my movements and purchases. However, keeping a standardised experimental design allowed me to obtain comparable data from different locations.

In **Supplementary study 3**, I compared durations of vigilance behaviour and distances moved during one hour before and after the playback. I had expected that rhinos would show increased vigilance and more movement after the playbacks because they would be disturbed or searching for the caller, but I did not find evidence for this effect. This might have been related to the habituation of the rhinos to the observation vehicle in the study area.

For a successful application of playbacks with conspecific calls to guide rhino movement, I recommend further research with a different study design. Playbacks should be ideally broadcast from automated behavioural response systems (Palmer et al. 2022; Suraci et al. 2017) and under the same wind conditions. The effects of the vegetation could be tested in different vegetation zones. Due to the sex-specific responses, playbacks should be adapted to the targeted individual, and to elicit stronger and longer lasting responses, interactive playbacks with different stimuli, including olfactory and visual, should be tested (King 2015; Madliger 2012).

Apart from the idea of directing movement of free-roaming rhinos to reduce dispersal after translocations, playbacks might be applied to improve breeding success of captive rhinos (Cinková & Policht 2014, 2016). Male vocalisations are important for successful mating rituals and therefore for reproduction (Jenikejew et al. 2021a). To avoid sibling-like relations in a breeding pair, playbacks could be used to simulate the presence of a second male and thus competition, which might help to induce female sexual behaviour (Jenikejew et al. 2021b).

Dehorning as a conservation measure

In **Chapter 3**, I showed that dehorning did not significantly change the proportions of daytime behaviours of white rhinos, except for locomotion. Rhinos might have locomoted more after dehorning because they avoided the vehicle in anticipation of a new immobilisation procedure, but the increase in locomotion was not conspicuous in day-to-day observations, in contrast to behaviour changes following a rhino birth. Thus, social events seemed to impact the behaviour of the rhinos in the study population more than dehorning. My results therefore support previous studies (Penny et al. 2021; Penny, White, MacTavish, Scott, & Pernetta 2020) and provide more evidence for the safety of dehorning as a conservation practice from an animal welfare point of view. I observed only one fight and can therefore not conclude on effects of dehorning on aggressive behaviour. However, male vocalisation rate was linked to the fight and lower after dehorning than before. This might be an indirect indicator of reduced aggressive interactions after dehorning, supporting Patton et al. (2018).

One goal of dehorning is to reduce the incentive for poachers to kill rhinos as they would receive less income through less available horn (du Toit & Anderson 2013). The method is only effective when poachers know that rhinos are dehorned and if there is a risk that poachers will be caught and penalised, so they can weigh the risk they take by poaching and possibly being caught against the potential revenue from selling the horn to dealers (du Toit & Anderson 2013; Haas & Ferreira 2018a). Therefore, it is now less the impact of dehorning on rhino behaviour than the difference that dehorning makes for rhino survival, which must be evaluated when considering dehorning a rhino population. In the most recent study by Chimes et al. (2022) the proportion of poached rhinos did not differ between horned and dehorned individuals in the same populations. This highlights the importance of other conservation measures in addition to dehorning and I recommend further research on the effectiveness of dehorning compared to other interventions to encourage the most efficient resource use for the protection of rhinos. For example, the reserve Malilangwe in Zimbabwe reports leadership training and involvement of the local communities as the most important and successful way to halt rhino poaching (Ball et al. 2019).

History of free roaming rhino in Botswana

My study was developed in 2018, when rhino translocations from different source populations in Zimbabwe and South Africa to Botswana were completed successfully. The research questions relating to improving rhino translocation protocols were therefore relevant and timely. Unfortunately, the situation of the rhino population in Botswana changed dramatically during the time of my study.

Rhinos have been exterminated in Botswana in the wild already three times. First during colonial times (1800s) when European settlers brought firearms to southern Africa and no consideration of the conservation of wild animals existed yet (Player & Feely 1960). Between 1967 and 1980, there were 95 individuals reintroduced to Botswana by the Natal Parks Board (Tjibae 2002). However, poaching for horn had reversed these efforts quickly and the second extermination is dated to the end of the 1980's and beginning of 1990's, when seven remaining individuals were captured and transported to a protected reserve, namely Khama Rhino Sanctuary (Tjibae 2002). To regrow the population of rhinos in Botswana, Khama Rhino Sanctuary was restocked with individuals from South Africa and two more rhino conservancies were created (Tjibae 2002). The conservancies were essential to protect rhinos and regrow their populations. In the early 2000s, five individuals from the sanctuaries in Botswana and 31 rhinos from South Africa were reintroduced to the Okavango Delta (Tjibae 2002). The Department of Wildlife and National Parks specifically stated that the safety of these rhinos was of major concern and measures for their protection in form of ground-, aerial- and water-borne patrols were taken (Tjibae 2002). Since this protection was successful and rhino poaching in South Africa began to significantly increase from 2009 onwards, further collaborations between the private sector and government were created to translocate 100 more individuals from South Africa to Botswana (Great Plains Foundation 2014). The non-governmental organisation Rhino Conservation Botswana was founded in 2014 to support rhino monitoring and observed good reproduction rates of both rhino species (Rhino Conservation Botswana, personal communication). The population grew to approximately 220 white and 45 black rhinos in the Okavango Delta in 2018 (Rhino Conservation Botswana, personal communication).

Media coverage can be extremely powerful for conservation translocations (Seddon et al. 2007) and was greatly used as a marketing and fundraising tool for the rhino translocations to Botswana. In the "operation rhino" in the 1960-80s led by Ian Player and Toni Haarthoorn, radio reports and newspaper articles were key elements for the success as they created public awareness and interest of landowners and governments to take rhinos, which was needed to create meta-populations and this way save white rhinos from extinction (Player 2013). Unfortunately, the circumstances nowadays are very different, and the publication of rhino locations can place the animals in immediate threat of being poached (Ferreira et al. 2022). In South Africa, rhino protection has developed into a heavily armed conflict between rangers and poachers (Rademeyer 2016). The reserves are mostly fenced and the area can be covered by strategical placement of ranger patrols (Mulero-Pázmány et al. 2014). An exception is the Kruger National Park, which therefore also faces severe difficulties in protecting rhinos (Haas & Ferreira 2018b). Botswana, in contrast, has extremely strict gun laws which make it very difficult for non-state security agencies to procure and license guns (Alpers & Picard 2022). Therefore, monitoring rangers in Botswana do not carry guns and rely upon state security agencies to provide protection and anti-poaching efforts. The vastness of the Okavango Delta and the fact that many areas within it are inaccessible by vehicles makes daily visits of every rhino individual impossible. In addition, poachers can enter the Delta on foot unhindered and finding them is very difficult. Consequently, by the end of 2020, 99 rhinos had been poached (Senyatso 2021). These official poaching numbers are based on carcasses found and confirmed to have been poached. However, there are several rhinos that are unaccounted for either alive or by a carcass, and it is suspected that these have also been poached but their carcasses were not found. The 'missing' rhinos would significantly increase the total poached number. By the end of 2021, the few remaining alive individuals in the Delta were captured and brought to secured reserves (Senyatso 2021).

Interdisciplinarity of conservation behaviour

Conservation behaviour is a cross-section domain that is based on interdisciplinarity as it not only includes behavioural research but also aims to bridge the gap between research and management (Durant et al. 2019; Salafsky et al. 2002). With the growing literature on conservation behaviour, an increasing number of frameworks, flow charts and decision trees exist, which explain the value of behavioural observations for conservation and aim to help managers and researchers to improve the conservation outcome of their work (Berger-Tal et al. 2011; Bro-Jørgensen et al. 2019; Durant et al. 2019; Tadesse 2018; Tobias & Pigot 2019; Tuomainen & Candolin 2011). Long-distance dispersal after translocation, which I addressed in my first study, has been identified as one of the most important issues in conservation (Berger-Tal et al. 2020; Greggor et al. 2016) and is one of the most studied behaviours in combination with conservation (Berger-Tal et al. 2016). This stands in contrast to many other behaviours that can be of conservation concern but where cross-disciplinary work between behavioural ecology and conservation biology is missing (Berger-Tal et al. 2016). The gap between behavioural research and conservation has been analysed and criticised by several authors, because the two disciplines can profit from each other and should work together for efficient management interventions that help to halt biodiversity loss (Angeloni et al. 2008; Berger-Tal et al. 2016; Buchholz 2007; Linklater 2004). One of the reasons for poor contribution of behavioural research to conservation is that the origin of behavioural biology is in examination of individuals whereas conservation is focussed on populations (Rabin et al. 2003; Tobias & Pigot 2019). However, individual behaviour affects an individual's fitness, which in turn affects survival, reproduction, dispersal, and population growth (Bro-Jørgensen et al. 2019; Rabin et al. 2003; Tadesse 2018; Tuomainen & Candolin 2011; Figure 5.1). Understanding individual behaviours can thus contribute to solving specific conservation problems (Buchholz 2007; Hasanah 2010).

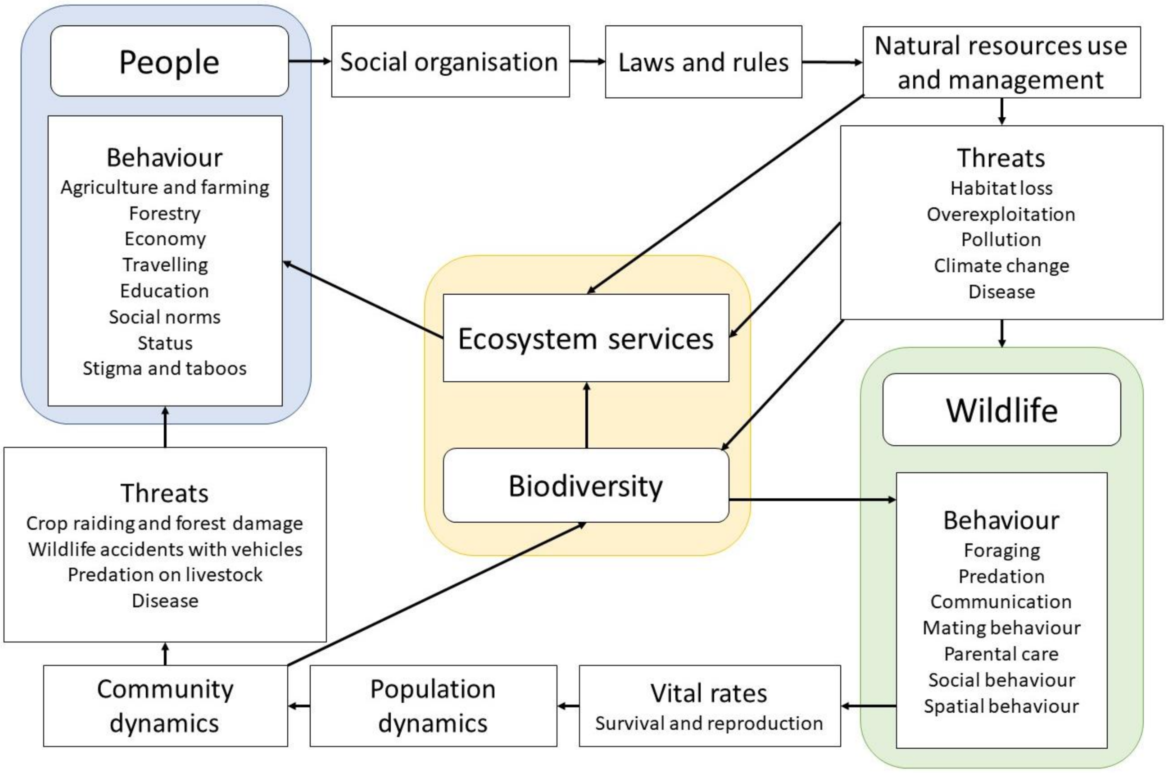

Figure 5.1 Framework of the interrelationships between human and wildlife behaviour with biodiversity and ecosystem services as the central elements. Adapted from Bro-Jørgensen et al. 2019.

Especially promising to provide effective solutions for conservation problems is comparative physiology or the application of knowledge about animal senses (Dominoni et al. 2020; Elmer et al. 2021). For example, understanding the visual spectrum of animals and applying deterring cues can help to avoid collisions with vehicles and airplanes, or stop aquatic insects from laying eggs on solar panels which would otherwise represent an ecological trap (Blumstein & Berger-Tal 2015). Acoustic stimuli are especially suited in environments with low visibility or over larger distances than visual cues. Furthermore, they can easily be recorded, analysed, synthesised, and played back as management tools (Laiolo 2010). Thus, playbacks are used to attract animals to breeding sites (Ahlering et al. 2010; Buxton & Jones 2012; Friesen et al. 2017), to facilitate population census and capture of animals by attracting them to desired locations (Massawe et al. 2022; Robbins & McCreery 2003; Western et al. 2022), and to deter animals from anthropogenic structures to avoid human-wildlife conflicts (King et al. 2018; Larsen & Eigaard 2014; Ngama et al. 2016; Widén et al. 2022). Playbacks of human vocalisations can also be used to create a landscape of fear and thus to guide animal landscape use, e.g., deter rhinos from high-risk poaching areas or deer from sensitive forest areas to avoid ecological damage (Nhleko et al. 2022; Widén et al. 2022). There is enormous potential for such applications of comparative physiology in conservation, which thus depends on interdisciplinary projects (Rabin et al. 2003; Rosa & Koper 2018).

Other than directing animal behaviour through purposefully placed cues, behavioural conservation research can also focus on effects of anthropogenic disturbances on natural animal behaviour (Adams et al. 2019; Delhey & Peters 2017; Dyndo et al. 2015). For example, anthropogenic noise can mask natural communication signals, leading to impaired sexual selection, reduced fitness and the hybridisation of species (Laiolo 2010) or mask predator arrival and alarm calls, resulting in reduced survival (Tuomainen & Candolin 2011). Chemical pollution can affect health, learning and behaviour and thus reduce population growth (Laiolo 2010). Some conservation interventions, such as dehorning, are also invasive and practitioners try to keep the effect of the intervention on natural animal behaviour minimal. Rhino dehorning is quite unique, as the special structure of rhino horn makes rhinos the only species where the removal of the upper part of the horn is possible without inflicting pain and while allowing regrowth (Rachlow & Berger 1997). Another example of an invasive conservation intervention is the application of contraception in elephants for population management (Kerley & Shrader 2007), but the effects these treatments are visible only after five to ten years (Delsink et al. 2013). Likewise, analysing the effects of dehorning on calf survival and inter-calf intervals needed data of 23 years and still might not be representative for all rhino populations (Penny, White, MacTavish, MacTavish, et al. 2020). This highlights the difficulty of using research to improve wildlife management: most conservation problems are urgent and need instant intervention (Salafsky et al. 2002), while science requires representative data collection and large sample sizes that most often take a long time to collect, especially in animals with long life histories and low reproduction rates. There is therefore a growing group of advocates for publishing evaluations of management actions on conservationevidence.com, including unsuccessful interventions, to avoid duplicated efforts and to improve exchange between geographically distant management entities that face the same conservation problems (Blumstein & Berger-Tal 2015).

Applying conservation behaviour in animal translocations

The number of animal translocations is increasing worldwide because translocations are a valuable tool to halt biodiversity loss, especially with the increasingly fragmented habitats and populations (Berger-Tal et al. 2020; Breed et al. 2019). Translocations were and are used to reverse defaunation and re-establish almost extinct species from zoos or from very small, isolated populations, for example the scimitar-horned oryx (*Oryx dammah*) (Mertes et al. 2019) and the takhi (*Equus ferus przewalskii*) (van Dierendonck & Wallis de Vries 1996). Translocations are used for assisted migration as climate change mitigation (Breed et al. 2019; Tobias & Pigot 2019) and for genetic exchange between captive populations or to re-wild animals that have been confiscated from illegal trade, e.g., orang-utans (*Pongo abelii*) (Zoologische Gesellschaft Frankfurt 2021).

Unsurprisingly, releasing omnivorous, generalist species in large groups has been identified as the way to successful translocations (Griffith et al. 1989; Wolf et al. 1996, but see van Houtan et al. 2009) but translocations as a conservation tool also deal with rare, endangered species. Therefore, using knowledge about the behaviour of the species can be key for translocation success. For example, training in captivity can avoid predator naivety in prey species and thus increase the survival of released individuals (Tetzlaff et al. 2019). In birds, hand-raising chicks with puppets instead of directly from human hands can inform correct mate choice and thus be key for population establishment (Letty et al. 2007). Often, translocated individuals have difficulties in finding resources and sometimes select unsuitable habitat, but it is possible to facilitate adaptation to the new environment through conditioning in captivity (Letty et al. 2007). The same food as available at the release site can be fed before release and animals can be trained to neutral cues in captivity (e.g., a smell or artificial objects) that can be applied at the release site as well, this way making the animal “feel at home” (natal habitat preference induction, Stamps & Swaisgood 2007).

Although from a conservation biology perspective, the establishment of a viable population matters more than the survival of every individual, it is important to also consider an animal welfare perspective in translocations because high mortality decreases the effectiveness of the operation and the public credibility of the project or the implementing organisation (Harrington et al. 2013). Furthermore, it is crucial to monitor translocated animals and to continue their protection after release (Fischer & Lindenmayer 2000; IUCN Species Survival Commission 2013; Mertes et al. 2019), otherwise, the time and money spent on the translocation were squandered. In the case of rhinos in Botswana, the translocations were very successful initially. However, because external conditions changed and poaching increased, it would have been unwise to introduce more rhinos to the Okavango Delta. Instead, rhino management was adapted by moving the animals into areas where they could be protected. Thus, management decisions must be informed by monitoring and be evaluated on a regular basis. Furthermore, the lessons learned must be reported and shared so that other practitioners can profit from them before implementing future conservation actions (Sanchirico et al. 2014). Adaptive management is a systematic approach to projects that uses experience from previous actions to inform and improve the next steps, this way increasing the probability of achieving the desired project outcome (Redford et al. 2018). Management is here not seen as a linear start – goal process, but as a circular process. This adaptive management circle is promoted by the conservation biology community with the Open Standards framework and the free accessible software MIRADI (Redford et al. 2018; Sanchirico et al. 2014). When developing project plans with the Open Standards method, it becomes clear that conservation biology and thus conservation behaviour are intertwined with social sciences and depend on several stakeholders.

Applying conservation behaviour to combat illegal wildlife trafficking

Legal rhino horn trade is still a matter of debate (Dang Vu et al. 2020, 2022; Jakins 2018). There is evidence that consumers would be willing to pay more for legal rhino horn and would prefer it over the illegal product, which could help to protect rhinos as it would allow rhino owners to re-invest the income into conservation (Dang Vu et al. 2022). However, there are several conditions that must be met before this positive outcome of legal rhino horn trade could be realised (Biggs et al. 2013; Dang Vu et al. 2022). Employment for possible poachers around rhino habitats must be created (Haas & Ferreira 2018a; Fischer et al. 2021) and international criminal networks must be disrupted (Haas & Ferreira 2016). Most importantly, the laundering of illegal horn into the legal market must be prevented, which requires expert knowledge and technology. It is possible to genetically identify or to microchip rhino horn and confirm its legality on an index system (RhODIS), but this can only prevent rhino horn laundering when law enforcement officers have the ability and the necessary equipment to crosscheck the data (Dang Vu et al. 2022; Ferreira et al. 2022). Furthermore, arguments for legal rhino horn trade mostly imply that the price of rhino horn is static, but the amount consumers are willing to pay depends on their income (Dang Vu et al. 2022). The availability of cheaper rhino horn is thus likely to increase demand. Prices on the legal market could be kept high based on the availability of sustainably harvested rhino horn, but if these prices are undercut by black market products, then poaching will persist to supply the illegal market because many consumers are not concerned about rhino conservation status (Dang Vu et al. 2022). Rhino poaching will only stop when the demand is reduced, which means that it depends on the behaviour of consumers. Social studies are therefore needed to understand the drivers of demand for rhino horn and thus to develop successful demand-reducing campaigns (Dang Vu et al. 2022). Behavioural studies are therefore the starting points at both ends of the chain of illegal wildlife trafficking: understanding consumer behaviour to reduce demand and understanding wildlife behaviour to improve conservation measures.

Conservation science is extremely complex because it deals with natural ecosystems and human societies (Salafsky et al. 2002; Figure 5.1). Conservation goals are often compromised by goals of improving human welfare, but both can be part of sustainable development goals (Salafsky et al. 2002). Ecosystem services influenced by biodiversity affect human societies, who, in turn, manage natural resources and thus influence biodiversity (Bro-Jørgensen et al. 2019; Figure 1).

Thus, to reach conservation targets, ecosystems can never be seen by themselves but must always be understood together with the people who live in or use them (Salafsky et al. 2002). Stakeholder engagement in planning and implementation of conservation actions is therefore one of the key elements for success. Illegal wildlife trade is fuelled by different drivers that must be treated with different approaches. The driver that quickly causes the extinction of species is the trade of animals as pets or luxury products (Keskin et al. 2023). In this case, there is no basic need fulfilled by purchasing wildlife products and consumer behaviour driven by the perception of social status affects the survival of wild animals (Figure 5.1). Other drivers are harvesting of wild animals as the only source of (valuable) economic income (Douglas & Alie 2014; Jones et al. 2008; Keskin et al. 2023). Here, creating alternative income possibilities is part of the tasks of conservation agencies (Ball et al. 2019; Haas & Ferreira 2018a). In addition, providing access to basic and higher education can make enormous differences to local communities, as it enables them to find and implement their own solutions (Fischer et al. 2021; Macharia et al. 2010).

Importantly, traditional ecological knowledge can also help to preserve biodiversity (Drew & Henne 2006). Taboos on the consumption of specific species have protected rare animals (Jones et al. 2008; Muchaal & Ngandjui 1999) and the respect for sacred natural places has conserved important islands of habitat (Bhagwat & Rutte 2006; Woods et al. 2017). These traditional rules are opportunities to build upon and must not be undermined by new conservation laws prescribed by external entities (Byers et al. 2001; Jones et al. 2008). Although international conservation agencies usually act upon best intentions and sound ecological knowledge, cultural differences and communication difficulties can lead to misunderstandings and aversions against the conservation actions (Dang Vu et al. 2020; Dang Vu & Nielsen 2018; Dickman 2010). This is a further reason why campaigns and conservation projects need to be constructed through a dialogue among different stakeholders and be re-evaluated on a regular basis (Caro & Berger 2019). What seems simple in theory can be exceedingly challenging in practice due to barriers to effective communication, trust, funding, and other factors (Dickman 2010; Reed 2008; Taylor et al. 2017).

Behavioural ecologists can be perfect advocates for conservation because they have unique insights into the lives of individual animals, which often results in love for the study species (Caro & Sherman 2011). As a side effect, they often become experts in the ecology of their species and of the situation around the study site (Sutherland 1998). Using this passion and knowledge for conservation has in the past successfully been used to generate interest and political will, to create nature reserves, and to maintain protection once the reserves were recognized (Caro & Berger 2019). Caro and Sherman (2011) formulate specific recommendations for behavioural ecologists to contribute to postponing species extinctions with the hope that the current human population with the extreme resource demand is a bottleneck and pressures on wildlife will decline. One of them is to give classroom presentations about the behavioural biology and protection of the study species (Caro & Sherman 2011). My doctoral project therefore included four public outreach events where I showed parts of the behaviour videos collected for this study in a rhino movie, which hopefully increased awareness and interest in rhino conservation among the audience.

Overall, the results of this study highlight important research gaps in rhino management methods, provide behaviour-based evaluations of common management practices, and show the potential of using natural rhino communication signals as management tools. This can contribute to improving rhino conservation and can be extended to other species, biodiversity conservation and reaching sustainable development goals.

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6. Supplementary studies

S1: Time to home range establishment after translocations

Rhino translocations are the management method to establish meta-populations and to ensure genetic exchange between them (Emslie & Brooks 1999). The translocations of rhinos into the Okavango Delta in Botswana were a novelty in the sense that rhinos were released into a large, mainly unfenced area. Rhino movement after translocations is known to be very variable and dispersal off the release site had been reported before (Støen et al. 2009). Furthermore, homing behaviour has been observed in six rhinos released into the Okavango Delta (Rees 2018). Therefore, investigations of movement patterns after translocations were important to provide information that could inform future translocations. For the establishment of a new population, it is especially important to know how fast rhinos settle after their translocation, i.e., the time to home range establishment. In preparation of Chapter 2, I tried different approaches and indices to analyse the time to home range establishment and settlement behaviour. These approaches will be presented here.

Methods

I used the data as described in Chapter 2, but only data of 36 white rhinos (27 females and 9 males). I created movement tracks using the package amt (Signer et al. 2019) in R (v4.0.3 (2020-10-10), using one GPS location per day to avoid autocorrelation. From these movement tracks, I calculated several indices:

- Step lengths, i.e., distances between successive GPS locations. The step lengths thus represent daily movement distances.
- Net squared distance to the release site. If this distance reached an asymptote, the animal did not move further away from the release site, which might indicate home range establishment. On the contrary, if this distance increased, then the rhino showed dispersal behaviour.
- Net squared distance to the release site to the reserve of origin. If this distance decreases, this would be a sign for homing behaviour.
- Movement ranges within successive ten-day periods. It was expected that movement ranges would be larger in the beginning, showing the exploratory phase after release, and then stabilise at a smaller size, indicating that the rhino had settled in a home range.
- Home range asymptotes, i.e., accumulative movement area size over time. It was expected that the movement range size would stop to increase when the rhino had established a home range.

- Time to home range establishment as shown in variograms. Variograms visualise the autocorrelation structure of movement data, which shows changes from ongoing dispersal to range residence behaviour. Thus, it is possible to extract the day of change from dispersal to residence behaviour from the variograms, i.e., the time to home range establishment. I used the package ctmm (Calabrese et al. 2016) to calculate variograms.
- Cumulative distance moved until the day of home range establishment. The sum of consecutive movements from day to day is added up. The larger the distance, the more the rhino moved away from the release site.
- Distance of the rhino to its release site on the day of home range establishment. If this distance was large, then the rhino moved far from the release site, showing unwanted long-distance dispersal. Individuals with shorter distances settled closer to the release site and were thus better translocation candidates.

I analysed all indices visually (representative graphs built with ggplot2 (Wickham 2016) see below; graphs for all individuals can be provided by the author upon request). For the number of days to home range establishment, cumulative distance moved and distance to the release site, I also ran linear mixed models with age and sex as fixed effects and the source population as the random effect. Age was classified as subadult (younger than six years) and adult (older than six years). However, the results of these models were inconclusive, and I performed a power analysis to test whether the sample size was sufficient.

Results

Step lengths varied between a few hundred metres and more than 40 km moved per day. All rhinos showed a relatively high variability in the step lengths, suggesting that they tended to spend some days mainly resting and other days mainly locomoting, instead of constantly moving the same distances per day. For some rhinos, the step lengths were indicators for settlement behaviour, for example in the adult female WF350 (Figure 6.1). The female showed initially longer step lengths, pointing towards exploratory movement, and a tendency for reduced step lengths with time, indicating settlement. On the opposite, the subadult WF208 showed generally longer step lengths, which also increased over time, pointing towards dispersal behaviour.

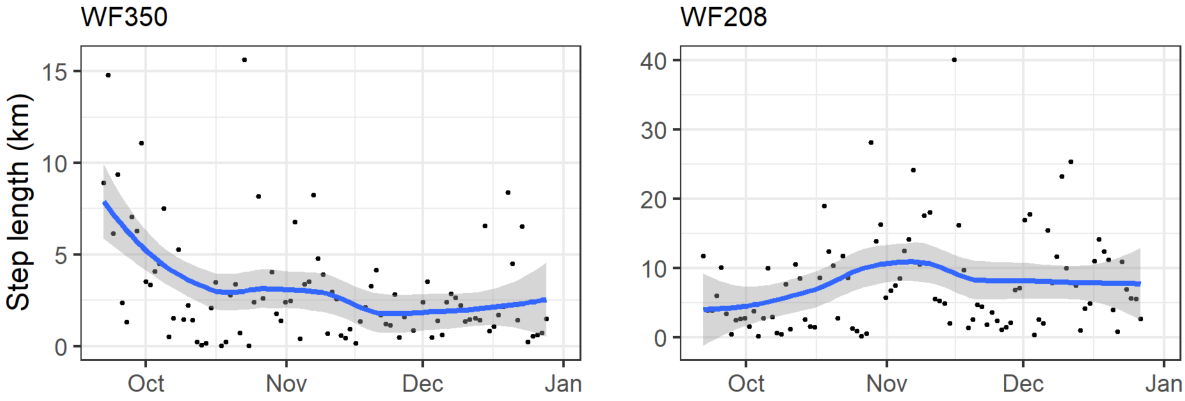

Figure 6.1 Step lengths, i.e., distances between successive relocations, over time for two white rhino females over a total of 90 days after release in Botswana. Note different scales on y axes.

The **net squared distances to the release site** seemed to be a good indicator for home range establishment for some individuals, where it reached a plateau and then stayed relatively stable over time, for example for the adult female WF350 (Figure 6.2). However, for other individuals there were large fluctuations in the net squared distance to the release site and two subadult females, WF208 and WF244, showed long-distance dispersal reflected in increasing net-squared distances (Figure 6.2).

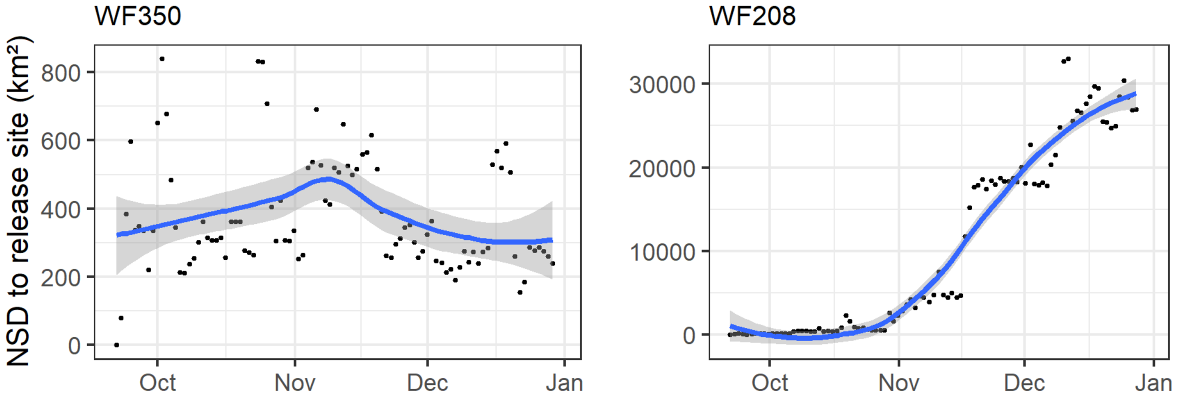

Figure 6.2 Net squared distance (NSD) to the release site over time for two white rhino females over a total of 90 days after release in Botswana. Note different scales on y axes.

Changes in the **net squared distance to the source population** were negligible for most rhinos (Figure 6.3.). Homing behaviour was observed in only one female that was recaptured and relocated to a different part of the Okavango Delta, where she settled (WF313). This individual was taken out from the following analysis because the relocation took place within the timeframe of the observation and the movement range sizes would otherwise be extremely large, although the rhino did not walk these distances itself. In the case of the two subadults that had shown an increase in the net squared distance to the release site, the distance to the source population also increased (Figure 6.3).

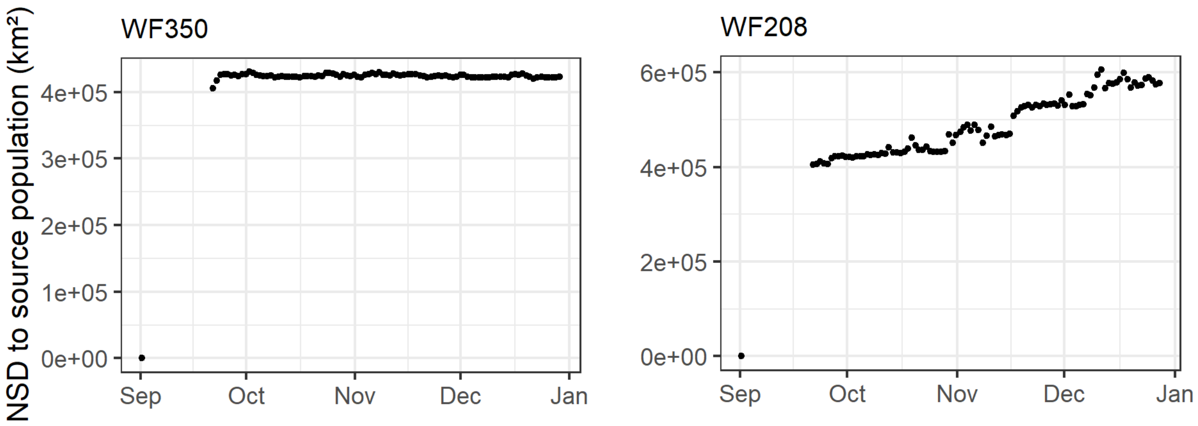

Figure 6.3 Net squared distance (NSD) to the source population for two white rhino females over a total of 90 days after release in Botswana. The first point is the capture location before translocation. Note different scales on y axes.

Movement range sizes were similarly to the net squared distance to the release site a good indicator for some individuals, where the ranges were larger in the beginning, reflecting the exploratory phase, and stabilized at a plateau, representing the home range establishment (e.g., WF350, Figure 6.4). However, for several individuals, the number or GPS locations was not sufficient for range calculations; or the movement range sizes fluctuated, so that no plateau could not be interpreted as home range establishment; or the movement range size stayed stable over the entire observation period. The movement ranges of the dispersing subadult females were generally much larger than for adult females, for example, the average movement range size for WF208 was 156 km², almost ten times larger than for WF350, which had an average movement range size of 16.4 km² (Figure 6.4).

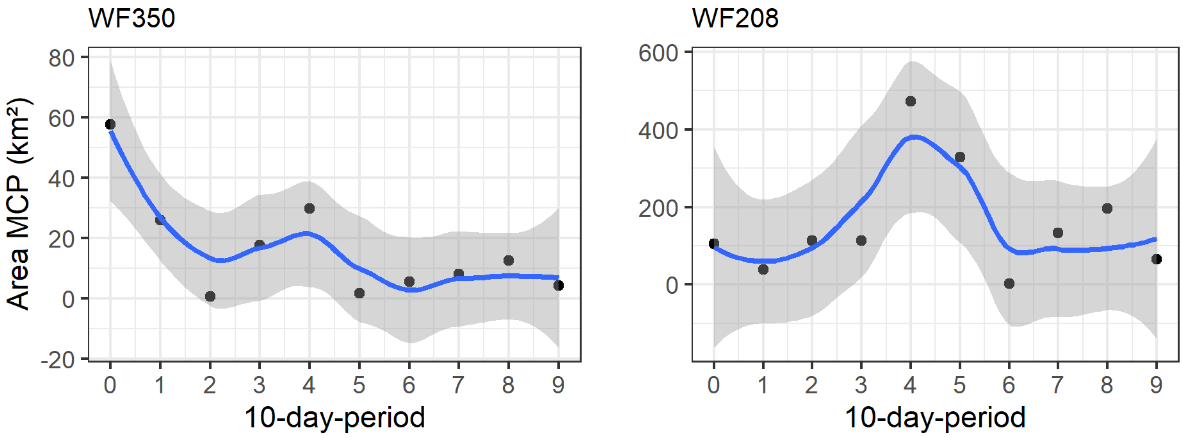

Figure 6.4 Movement range sizes estimated with minimum convex polygon (MCP) over time for two white rhino females over a total of 90 days after translocation to Botswana. Note different scales on the y axes.

To summarise these indices per age and sex class, I calculated averages of step lengths, net squared distances to the release site and movement range sizes per individual. The visual inspection of these averages showed that the subadult WF208 was an outlier and differences between age classes in averages of the indices were little, except for the movement range sizes, which seemed to be larger in subadult females than in adults (Figure 6.5).

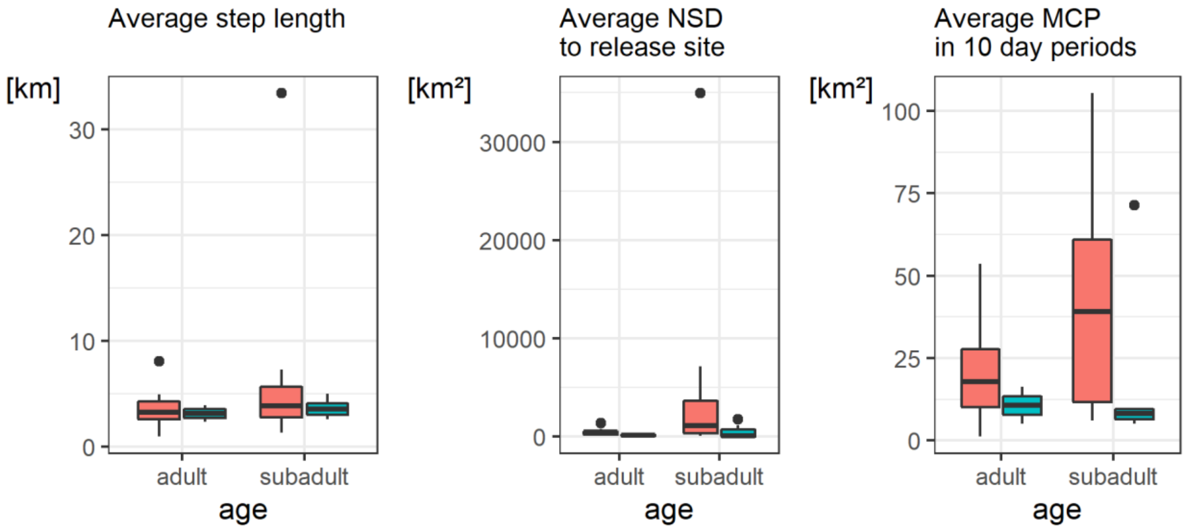

Figure 6.5 Boxplots of averages of variables describing movement behaviour of 35 rhinos (adult female=12, subadult female=14, adult male=2, subadult male=7) after translocation to Botswana. Adults are rhinos aged 6 years and older. Step length=distance travelled per day between satellite collar locations; NSD to release site=Net squared distance to the release site; Average MCP in 10-day-periods=Minimum convex polygon of the movement range of the rhino calculated separately for every ten days after release. Boxplots represent lower and upper quartile; thick black lines indicate the median. Red=females, blue=males. Note different scales on y axes.

Home range asymptotes proved to be very variable between individuals and did not stay stable over the sampling period, thus it would have been difficult to select the time frame from how many days on of the same range area size one would speak of a home range. Only a few individuals had stable home range asymptotes like the adult female WF350, that showed a plateau after 48 days (Figure 6.6). For the dispersing subadult WF208, no plateau was observed for longer than 20 days and the area size kept increasing (Figure 6.6).

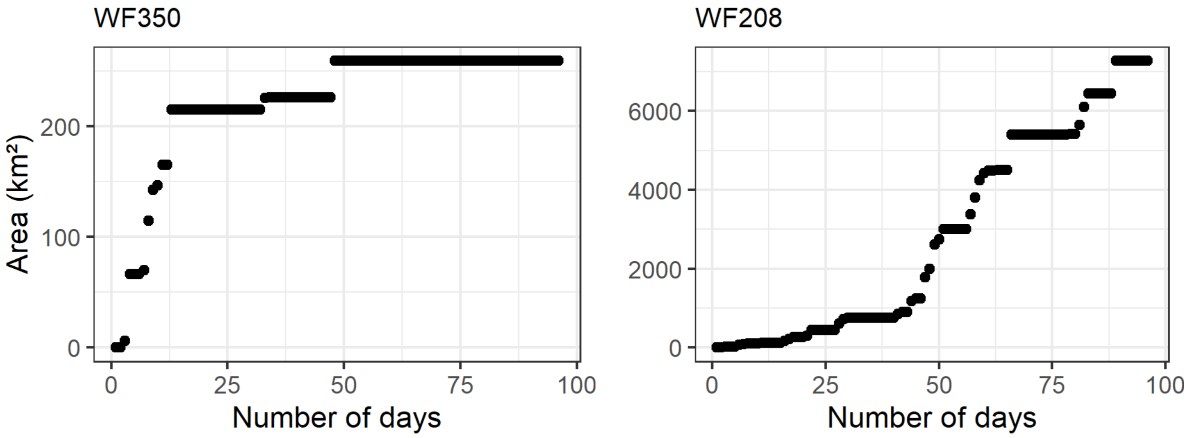

Figure 6.6 Home range asymptotes for two white rhino females translocated to Botswana observed over 99 days after release. Note different scales on y axes.

Based on the variograms, the **time to home range establishment** of the 35 translocated rhinos varied between 2 and 49 days. The semi-variance of WF350 reached a plateau after only four days, pointing towards range-residency behaviour after this short time (Figure 6.7). The semi-variance in the variogram from WF208 increased constantly over two months, showing dispersal behaviour (Figure 6.7). However, there were many individuals that according to the visual inspection of the semi-variance did not establish a home range, although the other indicators and observations of the animal in the field showed settlement behaviour. Thus, the model apparently needs quite accurate data which was not available in this study due to gaps in the GPS relocations.

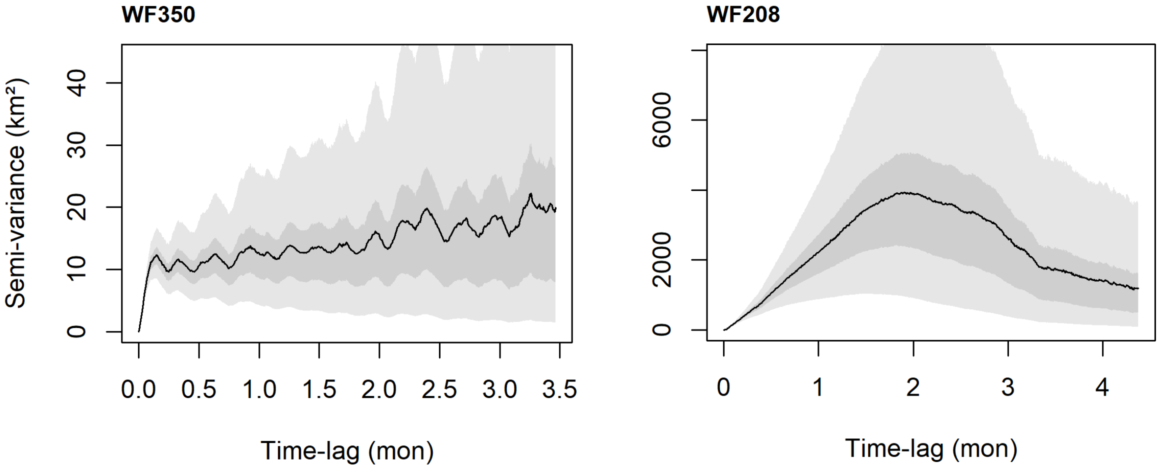

Figure 6.7 Variograms representing the semi-variance in the average square distance travelled over time (mon=months) for two white rhino females translocated to Botswana. Note different scales on x and y axes.

The visual inspection of the **time to home range establishment** according to the variograms, **cumulative distance** walked on the day of home range establishment and the **distance to the release site on the day of home range establishment** for age and sex classes showed that subadult females tended to take longer and walk farther until they established a home range compared to adults and to males (Figure 6.8). However, in our data the number of subadult females (14) exceeded the number of individuals in the other categories (adult females: 13; adult males: 2; subadult males: 7). Therefore, the variability in male movement behaviour after translocation might be larger than represented in the data of this study.

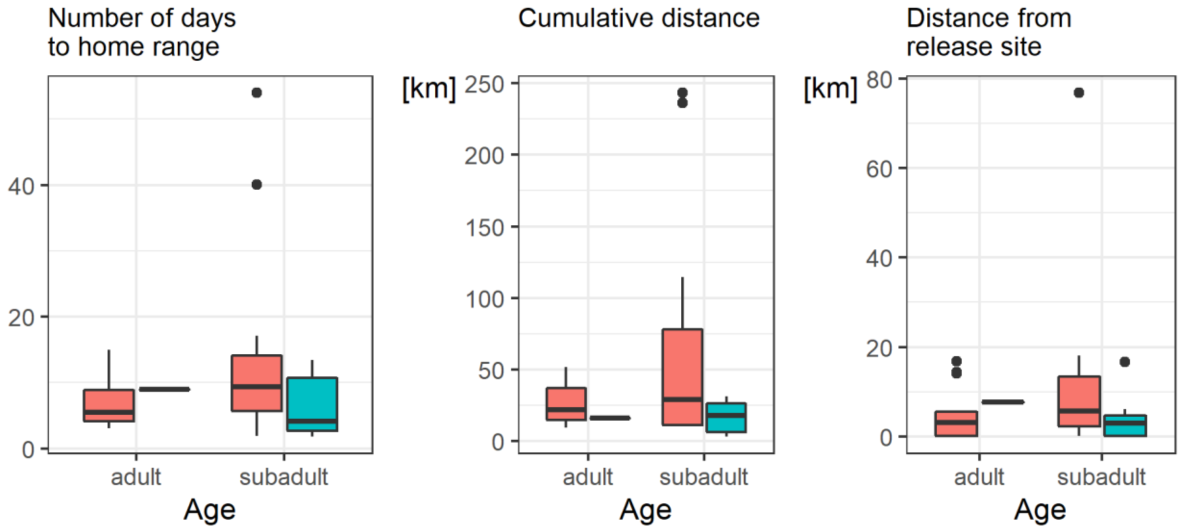

Figure 6.8 Boxplots of number of days to home range establishment, cumulative distance walked on the day of home range establishment and distance to the release site on the day of home range establishment for 35 rhinos (adult female=12, subadult female=14, adult male=2, subadult male=7) translocated to Botswana. Boxplots represent lower and upper quartile; thick black lines indicate the median. Red=females, blue=males. Note different scales on y axes.

For the statistical analysis, I had to exclude two more individuals where the data was not sufficient to calculate the time to home range establishment, resulting in a reduced sample size of 33 individuals. The linear mixed models showed only weak evidence for effects of age and sex on the response variables (Table 6.1), but the power analysis also suggested that the sample size in this study was very likely too small to detect significant effects if there were some. As an example, Figure 6.9 shows the simulation of the sample size needed to detect effects of age and sex on the time to home range establishment, which was similar for cumulative distance and distance to the release site. Therefore, larger sample sizes and more accurate GPS relocation data would be necessary to detect significant effects.

Table 6.1 Results of linear mixed models testing effects of age and sex on indicators for settlement behaviour of white rhinos translocated to Botswana. Random effect was the source population. DF=degrees of freedom.

Response variable	Fixed effect	Value	DF	t-value	p-value
Time to home range	Age (subadult)	6.3±3.8	27	1.7	0.11
	Sex (male)	-6.4±4.6	27	-1.4	0.17
Cumulative distance	Age (subadult)	39276.0±19554.7	27	2.0	0.05
	Sex (male)	-45964.4±23594.7	27	-1.9	0.06
Distance to the release site	Age (subadult)	7116.3±4984.2	27	1.4	0.16
	Sex (male)	-6013.9±6001.4	27	-1.0	0.33

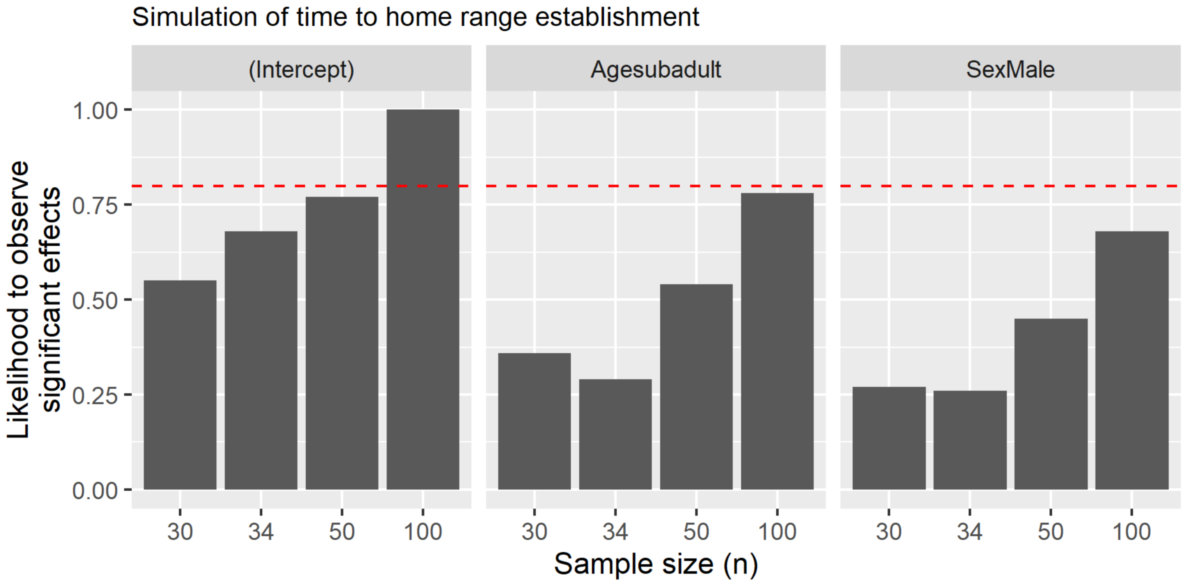

Figure 6.9 Power analysis simulating the sample size (n=number of individuals) that would be necessary to detect significant effects in the time to home range establishment based on data of 33 rhinos translocated to Botswana.

Discussion of indicators for home range establishment

There are several ways to describe home range establishment from GPS relocation data. All indicators tested in this section relied on complete data sets, which was not available in our study, and we therefore used different approaches in Chapter 2. The range of identified time frames of home range establishment between indicators was surprisingly large. For example, the adult female WF350 established her home range according to the reduced step lengths and MCP area approximately after one month; according to the home range asymptote after 48 days; and according to the variogram after only four days. Thus, general trends might be identifiable with one of the indicators but an exact time to home range establishment seems to be difficult to analyse. Nevertheless, also with these indicators I observed the general trend that subadults were more likely to take longer until establishing a home range compared to adults, even if this was not a statistically significant effect. The power analysis showed that I might not have detected effects due to the small sample size.

S2: Playback experiments with whine calls

In pilot experiments, we observed that especially females seemed to respond strongly to playbacks of juvenile calls ("whines"). Therefore, we tested whines as a third call type in our playback experiments. I expected females to approach the loudspeaker as a response to whine calls, and bulls not. However, during the experiments and during video analysis it became clear that rhinos did not respond strongly to whines. In reserve B, there even seemed to be a habituation effect where the rhinos ran away from whine playbacks, presumably because they had detected the experimenters in a first trial and then avoided human contact in all following trials. Therefore, the experiments with whines were excluded from the publication. I could not test the effect of familiarity for whines as I had only played back calls from unfamiliar senders. However, I report the findings to inform other researchers and to avoid duplicated efforts.

We played back whine calls using the same method as described in Chapter 3. The calls had been recorded during a pilot study in Khama Rhino Sanctuary and in reserve A. Calls from the pilot study were played to 10 individuals (7 females, 3 males) in reserve A and calls from reserve A were played to 15 individuals (8 females, 7 males) in reserve B. After the experiments, I performed first a preliminary analysis of all 414 experiments with all stimuli based on direct observations during the experiments. Here, I counted the number of body position changes, vocalisations, and conspicuous behaviours such as lip smacking and social interactions that happened immediately after the playback. In visual inspection of this data, I found that the number of responses to whines was slightly lower than for hiss and pant calls, but higher than for controls (Figure 6.10).

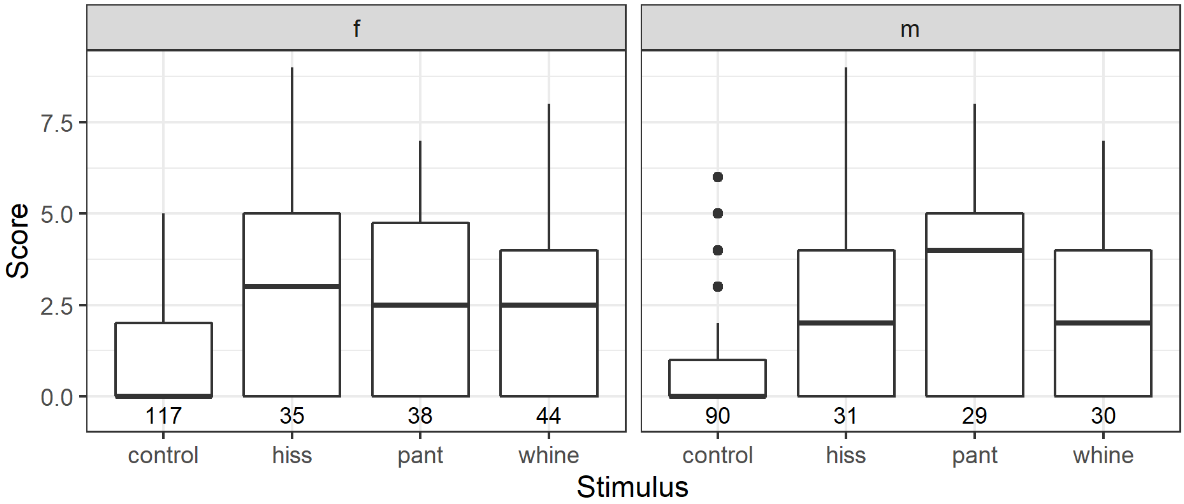

Figure 6.10 Boxplots of the number of rhino behavioural responses (e.g., body movement, vocalisation, social interaction) to playbacks of either control sounds (bird calls) or rhino calls from 414 experiments with 25 (15 females, 10 males) rhinos in Botswana in 2020. The number of experiments per stimulus is indicated below the boxplots. Boxplots represent lower and upper quartile; thick black lines indicate the median.

To analyse effects of stimulus and sex and their interaction on the number of responses, I used linear mixed models with the rhino ID as random effect to account for repeated experiments with the same individual. I used corrected AIC values (AICc) to identify the most parsimonious model with the aictab function from the AICcmodavg package (Mazerolle 2020). The model with only the stimulus had the lowest AICc value (ΔAICc to the next best model=2.07). It showed that the number of responses to all rhino calls was significantly higher than to controls (value>1.2±0.3, DF=386, t>4.8, p<0.001), but not significantly different between call types. Out of 74 experiments with whines, I observed only **three** times rhinos approaching the speaker as a response, **two** times by females and **once** by a male. Rhinos ran away from the loudspeaker **17** times as a response to whine calls, **ten** times observed in females and **seven** times in males. However, sixteen of these observations were from the abovementioned groups that presumably ran away from the experimenters.

For the detailed video analysis, we excluded from the total of 414 all experiments with control sounds and experiments where the focal rhino had already been alerted by external factors before the playback, for example, when a male was following a female or when an individual was standing in the same group with other focal subjects but had already been tested on the same day. This resulted in a reduced sample size of 60 experiments. The visual inspection of this data showed that the duration of the response, i.e., the time until the rhino returned to its previous behaviour, was longer for whine calls than for the other call types, especially for females (Figure 6.11). However, when analysed with linear mixed models in the same way as above, the null model was the most parsimonious (ΔAICc to the next best model=2.26) and differences were not statistically significant.

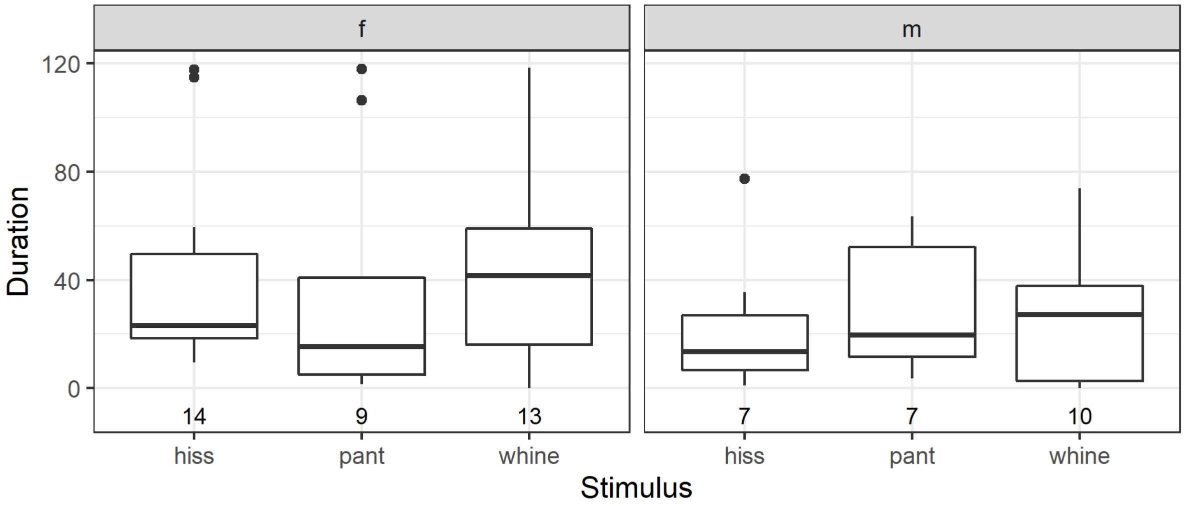

Figure 6.11 Boxplots of the duration of rhino behavioural responses to playbacks of rhino calls from 60 experiments with 21 (12 females, 9 males) rhinos in Botswana in 2020. The number of experiments per stimulus is indicated below the boxplots. Boxplots represent lower and upper quartile; thick black lines indicate the median.

S3: Vigilance behaviour and daily movement of rhinos after playbacks

As described in Chapter 3, I performed playback experiments in three blocks. In the first block, I added behaviour occurrence observations (Altmann 1974) for vigilance behaviour during one hour before and one hour after the playback. I undertook these behaviour observations for one experiment per call type (control, hiss and pant) per rhino, in total 30 experiments. I noted the duration of vigilance, defined as “rhino stands with head lifted above front ankle height and does not chew”. Additionally, I had a GPS tracker (Open Street Map for Android mobile phone with route recording plugin, Open Street Map Foundation 2020) running that took a GPS points every minute. I calculated step lengths, i.e., distances between successive GPS points to analyse the distances moved before and after the experiment. I hypothesised that a) rhinos would show longer vigilance durations after the playback than before because the playback would have disturbed them; and b) that step lengths would be longer after the playback than before because the rhinos might move away from the location where they heard the playback or walk around and search for the caller.

Statistical analysis

I tested the impact of the fixed effects playback experiment (before and after), stimulus (control, pant, or hiss) and their interaction on the duration of vigilance behaviour and on step lengths with linear mixed models. Rhino ID and the date were included as random effects to account for repeated measurements with the same individual and on the same day. For step lengths, I created movement tracks from the GPS location data with the package amt (Signer et al. 2019) in R (v4.0.3 (2020-10-10), The R Foundation for Statistical Computing 2020) and added the step lengths up for ten-minute-intervals because the displacement from one minute to the next was very small. The following analyses assumed a normal distribution of the residuals, hence I log-transformed the data for both vigilance and step lengths. The most parsimonious model was selected based on the AICc value (aictab function of the AICcmodavg package, Mazerolle 2020). When models were competitive (ΔAICc<2), they were averaged with the model.avg function of the MuMIn package (Barton 2022) and the averaged effects were reported. To identify effect sizes, I used the emmeans function with the type “response”, which back-transforms the log data.

Results

Vigilance behaviour duration

The duration of a single "vigilance event" lasted from 1 to 603 s, with an average of 21 s. During the two hours of observation, rhinos were on average 691 s alert. Single events with more than 400 s (n=2) were occasions when other rhinos approached the focal subject and were taken out from the following analysis. In visual inspection, the durations of vigilance behaviour seemed to be shorter after the playback than before for all call types, although there were many outliers (Figure 6.12). The vigilance duration seemed to be slightly longer for playbacks of pant calls than for control and hiss (Figure 6.12, Table 6.2).

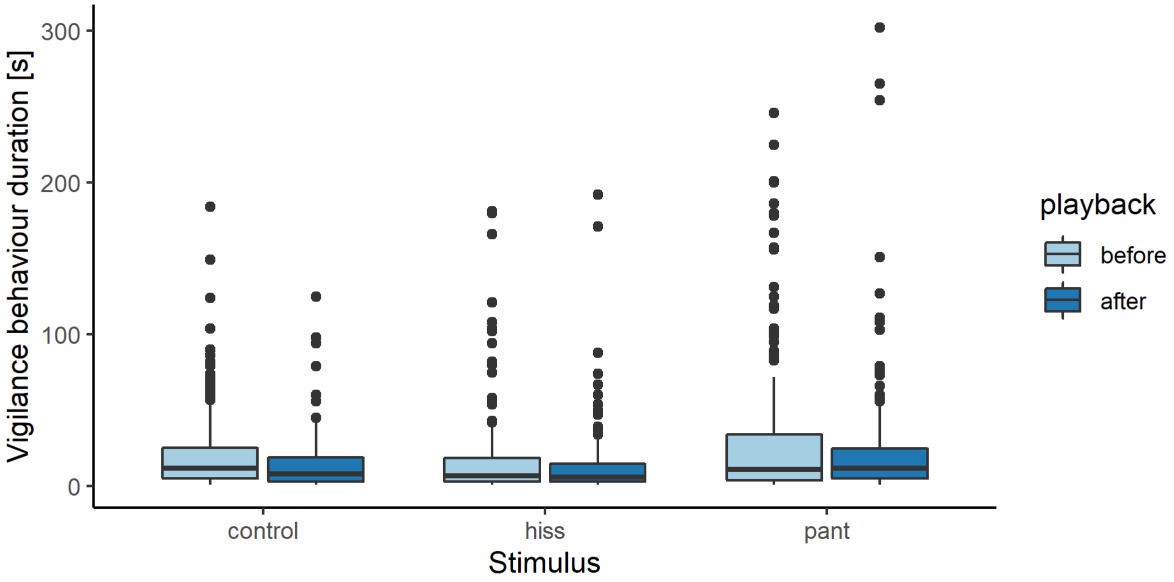

Figure 6.12 Boxplots of vigilance behaviour durations of 10 (7 females, 3 males) white rhinos during two hours of observation before and after a playback experiment in Botswana in 2020. Boxplots represent lower and upper quartile; thick black lines indicate the median.

The models with the interaction, the additive model, and the model with only the playback were competitive. After model averaging, the effect of the playback was significant with shorter vigilance duration after the playback (estimate=0.25±0.12, z=2.02, p=0.04). The comparison of the means showed a difference of 0.86 s between after and before the playback.

Step lengths

Step lengths within the ten-minute-intervals ranged between 0.03 and 1354 m and were on average 72 m. Within the two hours of observation, the rhinos moved on average 876 m. The step lengths appeared to be shorter after the playback than before, although there were many outliers (Table 6.2, Figure 6.13).

Table 6.2 Average vigilance behaviour durations and step lengths, i.e., GPS relocations within ten-minute intervals, of 10 (7 females, 3 males) white rhinos during two hours of observation before and after a playback experiment in Botswana in 2020.

Stimulus	**Control**		**Hiss**		**Pant**	
Playback	**Before**	**After**	**Before**	**After**	**Before**	**After**
Vigilance	21.41	15.19	18.36	13.75	33.68	26.07
Step length	82.03	82.25	84.72	60.88	63.86	49.44

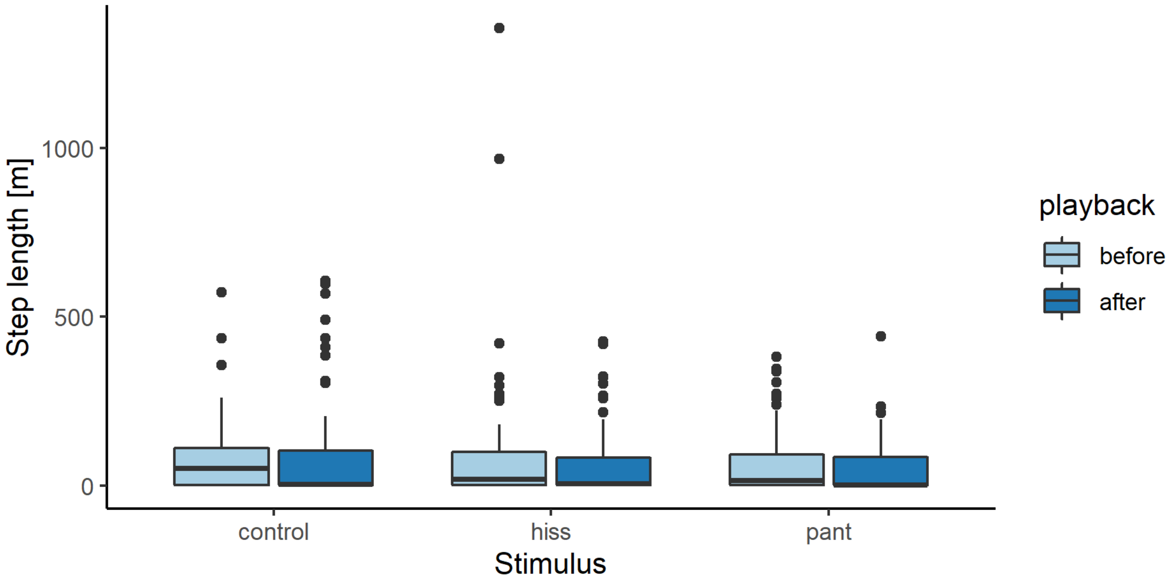

Figure 6.13 Boxplots of step lengths, i.e., GPS relocations within ten-minute intervals of 10 (7 females, 3 males) white rhinos during two hours of observation before and after a playback experiment in Botswana in 2020. Boxplots represent lower and upper quartile; thick black lines indicate the median.

The additive model and the model with only the playback were competitive. After averaging, the models showed evidence for an effect of the playback with longer step lengths before the playback experiment than after (estimate=0.70±0.22, z=3.14, p<0.01). The comparison of the means showed a difference of 1.26 m between after and before the playback.

Discussion of vigilance behaviour and step lengths

The observation that vigilance behaviour duration and step lengths were shorter after the playback than before stands in contrast to my expectation. However, two seconds difference in vigilance behaviour duration and one metre difference in step lengths between before and after the playback are very small differences in an observation of two hours. Thus, the identified effects of playbacks on rhino vigilance behaviour duration and step lengths are questionable.

It is possible that the arriving vehicle in the beginning of the observation had a greater disturbing effect than the playback experiment. When we approached the rhinos for the first time of the day, they almost always showed increased vigilance, but the longer we stayed with them and followed them, the more they got used to the presence of the vehicle and did not look up as often anymore. Likewise, the rhinos may have moved more initially to avoid the vehicle, but ultimately, they stopped caring to move. Although the rhinos in this reserve were habituated to vehicles from daily monitoring patrols, vehicles are intruders in the natural system. Sometimes, the rhinos must be anesthetised for management purposes, and the anaesthesia is injected through a dart gun from the vehicle. In the beginning of any observation, the rhinos therefore responded with avoidance to the approaching vehicle and were attentive to any sudden, loud, or unusual sounds. When no action followed the unusual sound and when the engine was turned off, then they went back to grazing or resting quite quickly.

However, it might also be possible that the rhinos were attracted to the loudspeaker after the playback and tended to stay in its vicinity to find out whether there was a conspecific. Rhino calls, on the contrary to vehicles, are not a direct threat to rhinos. Although the rhinos were sometimes disturbed and responded to playbacks as described in Chapter 3, these responses seldom lasted for longer than a few minutes. The vigilance behaviour in the responses was always interrupted by locomotion, feeding, or resting. Our observations made evident that rhinos rely on more than the acoustic stimuli to check whether a conspecific is present. After the playback, some focal subjects searched for additional olfactory and visual information, shown by blowing the nostrils and walking around the vehicle towards the direction where they perceived the call. Since they could not smell or see any rhino that might have produced the sound, they did not follow the stimulus and returned to grazing or their other behaviour before the playback. Playbacks combined with olfactory or visual stimuli would probably attract greater attention of the rhinos than acoustic stimuli alone. Furthermore, rhinos mainly use acoustic communication at close distance. When rhinos did not find the conspecific that might have produced the sound, they might have concluded that they were not the receiver of the vocalisation.

The experiments in this first block of experiments were all performed with calls from familiar senders and held short with only one playback of approximately 30 seconds. As such, the experiments were designed not to disturb the rhinos too much, because we did not want to impact the existing, functioning home ranges and social structures. During the last two blocks of experiments, where we used calls from unfamiliar callers, there were several cases where the rhinos ran away from the loudspeaker for several hundred metres. Therefore, it might still be possible to influence the movement of rhinos with playbacks of calls from unfamiliar senders. However, our observations suggest that it would probably not be possible to set the direction of the movement when rhinos run away from playbacks as they chose the direction in which the vegetation allowed unhindered movement.

Vigilance behaviour duration

There were several disturbances that made rhinos lift their head up. For example, when elephants or lions walked past, when birds flew up suddenly or when antelopes were running. Before drinking, the rhinos always scanned the surrounding and only then lowered their head to the water. The car in which the experimenters moved towards the rhinos also disturbed them. Depending on the character and the daily mood of the rhino, this disturbance lasted longer or shorter. The longest time that rhinos showed vigilance was when other rhinos approached. In some cases, it was not clear if the rhino was vigilant or resting, because it showed a relaxed body posture, but the head was a little bit higher than front ankle height. In very few cases, the head position was not clear because the rhino was hiding in the bushes and was only partly visible. Additionally, the rhinos often scanned the surrounding with the head up and pointed their ears while chewing, which was not recorded as vigilance. These occurrences of vigilance might have been missed in the analysis, but since the same definition was used before and after the playback, this should not have influenced the result.

Longer vigilance durations for pants compared to other stimuli were visible already before the playback experiment (Figure 6.12) and were therefore unlikely caused by the playback experiment itself. Other disturbances as mentioned above (elephants, lions, birds, rhino interactions…) might have coincidentally occurred more often on days with pant call experiments, or there might have been an experimenter effect. Since pant calls are softer than hiss calls and controls, I might have accidentally disturbed the rhinos before the playback of pant calls more than with other stimuli because I wanted to get extra close to the focal animal; or I expected a stronger response to playbacks of pant calls and the rhinos sensed my excitement already before the playback.

Step lengths

There were a few cases where the focal rhino searched for conspecifics in other parts of the reserve and therefore moved during most of the observation time. Even then, the playback did not seem to affect the movement speed and thus the step lengths or direction. In these cases, the rhino responded to the playback by stopping for a few seconds and looking at the loudspeaker, but then went on its previous movement path. Hence, a temporary behaviour change did not result in strong effects of playback experiments on step lengths.

The GPS device was with the experimenters in the vehicle and the distance from the device to the rhino differed between 10 and 100 metres. The locations and step lengths are thus not the exact position of the rhino and might result in a large error margin. Directional displacement of the rhinos was nevertheless reflected in the movement of the vehicle as we stayed at the same location as long as the rhino was grazing and moved the vehicle when the rhino started locomoting for longer distances than a few meters. However, in future research, GPS collars that are attached directly to the animal might be a better alternative to analyse the effect of playback experiments on fine-scale rhino movement. GPS collars would also allow to study the movement over longer periods of time without the need of the experimenter to be present.

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List of publications

Conference contribution: Pfannerstill V., Bennitt E., Scheumann M. (2020). Behavioural responses of white rhinoceros to species-specific playbacks. *African Bioacoustics Conference 2020.*

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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* 60:344-346.

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Submitted to the *Journal of Zoology*: Pfannerstill V., Härdtner R., Maboga O., Balkenhol N., Bennitt E., Scheumann M. Dehorning impacts white rhinoceros behaviour less than social events: evidence from Botswana.

Thesis declaration

I hereby confirm that I have written this doctoral thesis independently, that I have not used other sources or facilities other than the ones mentioned, that I have not used unauthorized assistance and that I have not submitted this thesis previously in any form for another degree at any university or institution.

Vera Pfannerstill
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