

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 (*Ceratotherium 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 with the literature that reserve size and rhinoceros density affect home range size. All rhinoceros in this study survived for more than 1-year post-translocation, so these translocations can be deemed successful in the short term.

KEY WORDS

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

Résumé

L'évaluation du succès d'une translocation est essentielle pour la gestion et la conservation de la faune sauvage. Le succès à court terme peut être évalué en analysant le comportement de l'établissement sur site après la libération. Nous avons analysé les données des colliers GPS de 47 rhinocéros blancs (*Ceratotherium simum simum*, Burchell, 1817) et 25 rhinocéros noirs (*Diceros bicornis minor*, Drummond,

1876) transloqués dans le delta de l'Okavango au Botswana entre 2014 et 2018. Nous avons testé les effets de l'âge et du sexe sur la fidélité au site et comparé les domaines de mouvement après les translocations entre différents sites de relâchement et entre les individus nouvellement relâchés et les individus établis. Les rhinocéros blancs adultes ont affiché une fidélité au site plus élevée que les subadultes et les mâles plus élevée que les femelles. Les adultes pourraient donc être de meilleurs candidats à la translocation. La fidélité au site des rhinocéros noirs ne différait pas entre les sexes ou les âges. Les domaines de mouvement des rhinocéros établis étaient plus petits que ceux des rhinocéros nouvellement relâchés, ce qui indique des mouvements exploratoires prolongés après les translocations et un établissement ultérieur dans des domaines vitaux plus petits. Les domaines de déplacement des rhinocéros blancs relâchés sur une île étaient significativement plus petits que les autres, ce qui montre, avec la taille des domaines vitaux annuels, en comparaison avec la littérature, que la taille des réserves et la densité des rhinocéros affectent la taille des domaines vitaux. Tous les rhinocéros de cette étude ont survécu pendant plus d'un an après leur translocation, de sorte que ces translocations peuvent être considérés comme un succès à court terme.

1 | 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 et al., 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 et al., 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 et al., 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 et al., 1989), but measuring this requires long-term monitoring, so it is rarely assessed or reported by

studies (Fischer & Lindenmayer, 2000; Massei et al., 2010; Mésochina et al., 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 et al., 2010; Letty et al., 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 et al., 2017; Bright & Morris, 1994; Troy et al., 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 et al., 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 rhinoceros (hereafter referred to as 'rhinos', in this study southern white rhino, *Ceratotherium simum simum* Burchell, 1817, and southern-central black rhino, *Diceros bicornis minor*, Drummond, 1876), exist in distinct populations in public and private game reserves. This not only 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 et al., 1998; Pitlagano, 2007; Thompson et al., 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 et al., 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 et al., 2010). In white rhinos, subsequent releases in different years at the same site have led to higher dispersal away from the release site (Støen et al., 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 et al., 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 with 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 et al., 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 et al., 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 et al., 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.

2 | METHODS

2.1 | 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 et al., 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 (Bennett et al., 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 (Bennett 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 (Bennett et al., 2015). Rhinos were present in Botswana until the 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 1980s. 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.

2.2 | 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 1](#), but generally, best practices as described in Emslie et al. (2009); Morkel & Kennedy-Benson (2007); Reuter & Adcock (1998), were used. Details about individual rhinos are provided in the [Appendix S1](#). Releases took place between April and September, and details about release batches are provided in [Table A1](#) in the [Appendix 1](#). 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, that is 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', that is 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.

2.3 | 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 6 years, subadults between 2 and 6 years (Law & Linklater, 2014). 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 h; 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.

2.4 | 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 10-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 10 GPS location logs within 10-day fragment to be able to calculate representative movement ranges.

The release site for one cohort of white rhinos (cohort A, 10 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.

2.5 | Movement range sizes

For settlement behaviour in the medium term, we calculated 3-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 et al., 1993; Rachlow et al., 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 3-month movement ranges of previously released individuals that had been living for 3 to 5 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 3-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.

2.6 | Annual home range sizes

We calculated annual home range sizes for white and black rhinos when the GPS collars worked for at least 1 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 et al., 2019; Reid et al., 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 A4 (Appendix 1).

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 et al., 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.

3 | RESULTS

We analysed satellite GPS data from 47 white rhinos (34 females and 13 males) and 25 black rhinos (12 females and 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 Appendix S1).

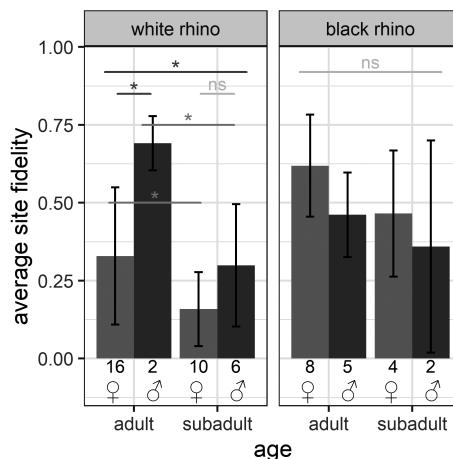


FIGURE 1 Site fidelity of 34 white rhinos and 19 black rhinos translocated to the Okavango Delta, Botswana. Site fidelity was calculated as the overlap between an individual's movement range in the first 10 days with its movement range in the second 10 days after release. The number of individuals is indicated below each bar, and stars show significant differences

3.1 | Settlement behaviour

Excluding cohort A and individuals with fewer than five GPS locations within the 10-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 1, Table 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 1, Figure 1). Adult female movement ranges overlapped significantly less than those of adult males ($t = -4.38$, $p < 0.05$, Table 1, Figure 1). Range overlap was similar in subadult females and subadult males ($t = -1.59$, Table 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 1, Table 1).

3.2 | 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.

TABLE 1 Pairwise t-tests for site fidelity calculated in overlaps between a translocated rhino's movement range in the first 10 days with its movement range in the second 10 days after release into the Okavango Delta, Botswana

	Average overlap	Direction	Compared with	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

Note: 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.

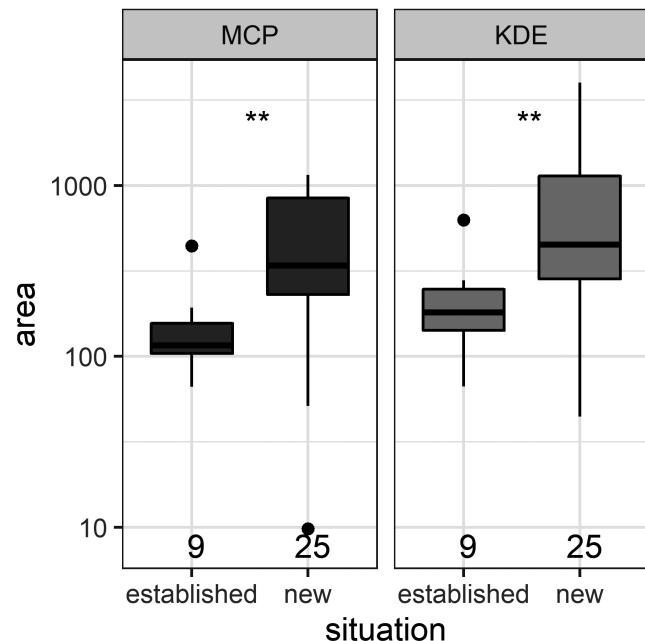


FIGURE 2 Three-month movement ranges for established and newly translocated white rhinos in the Okavango Delta, Botswana. MCP, minimum convex polygon; KDE, kernel density estimation, calculated at 95% levels. Area size in km^2 ; note the logarithmic scale. The number of individuals is indicated below each boxplot, stars show significant differences

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, Table A2 in the Appendix 1](#)).

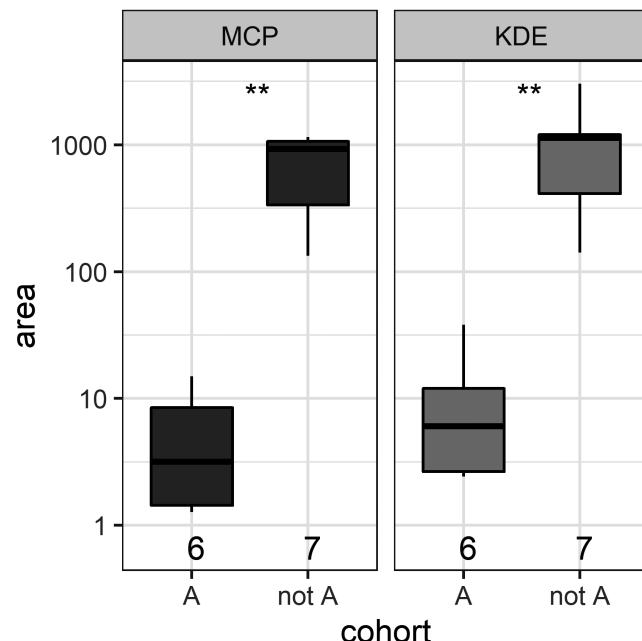


FIGURE 3 Three-month movement ranges of subadult white rhino females translocated to the Okavango Delta, Botswana, at a delimited release site (a) and at other release sites (not a). MCP = minimum convex polygon, KDE = kernel density estimation, calculated at 95% levels. Area size in km^2 ; note the logarithmic scale. The number of individuals is indicated below each boxplot, and stars show significant differences

Established individuals also showed a much smaller scattering in their movement range sizes than new ones ([Figure 2, Table A2 in the Appendix 1](#)).

Subadult Cohort A females (6 individuals) had significantly smaller MCP and KDE 3-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 3, Table A3 in the Appendix 1).

3.3 | Annual home range sizes

For white rhinos, annual data were only available for five females (one adult and four subadults) of cohort A. For black rhinos, data were available for 9 individuals (3 subadult females, 3 adult females and 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). MCP estimates generally led to smaller home range sizes than KDE estimates.

4 | 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 3 months after release were significantly larger than those of white rhinos that had been established for 3–5-year post-translocation. Furthermore, we found that 3-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 et al., 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 et al., 1996). Males, on the contrary, 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 et al., 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 Swaisgood (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 3-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

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
Black rhino		Min. to max.	-	18–50
	Number of individuals	3	3	3
	MCP	Mean	37 ± 6	64 ± 43
		Min. to max.	30–43	27–110
KDE	Mean	98 ± 38	155 ± 118	122 ± 39
	Min. to max.	80–141	48–281	78–153

Abbreviations: KDE, kernel density estimation; MCP, minimum convex polygon, calculated at 95% levels.

females released on an island (cohort A) showed significantly smaller movement ranges during the first 3 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 logically (Berger-Tal et al., 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 $44\text{--}3992\text{ km}^2$ up to 142 times the size of established movement ranges over 15 months in a fenced private game reserve, $7\text{--}28\text{ km}^2$, 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 100 km 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 $13\text{--}50\text{ km}^2$ were similar to those reported from Hluhluwe-iMfolozi Game Reserve, South Africa, of $6\text{--}66\text{ km}^2$ (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 in this study that were released at other sites.

Annual home range size for black rhinos was similar sizes to those in the Serengeti National Park, Tanzania ($43\text{--}133\text{ km}^2$ MCP, Frame, 1980) and larger than home range sizes in smaller reserves ($0.75\text{--}45\text{ km}^2$ MCP, Pienaar et al., 1993). This supports previous observations (Göttert et al., 2010; White et al., 2007) that home range

TABLE 2 Annual home range sizes of white and black rhinos translocated to the Okavango Delta, Botswana

size depends on reserve size and rhino density. During early black rhino translocations, home ranges were still changing 3 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 and best practice in translocation procedures.

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CONFLICT OF INTEREST

The authors declare no known conflicting interests.

DATA AVAILABILITY STATEMENT

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

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APPENDIX 1

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 et al., 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 h, all by road, with the shortest travel time being 18 h 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

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 A1 Release batches of rhinos translocated to Botswana

Note: 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.

TABLE A2 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	$157 \pm 114 \text{ km}^2$	$393 \pm 456 \text{ km}^2$
	Min. to max.	66–442 km ²	10–1153 km ²
KDE	Mean	$222 \pm 167 \text{ km}^2$	$894 \pm 1087 \text{ km}^2$
	Min. to max.	67–629 km ²	44–3992 km ²

TABLE A3 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	$5 \pm 5 \text{ km}^2$	$595 \pm 442 \text{ km}^2$
	Min. to max.	1–14 km ²	133–1152 km ²
KDE	Mean	$12 \pm 14 \text{ km}^2$	885 ± 918
	Min. to max.	2–38 km ²	141–3020 km ²

TABLE A4 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

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 4 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 6 and 12 h.

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 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 well-being (Reuter & Adcock, 1998). Ideally, rhinos were released in peak well-being by the end of their holding time.