



## Bringing the Black rhino back: Key factors for reintroduction success

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### ABSTRACT

Evaluating reintroduction success is fundamental to wildlife management and conservation. Movement affects animal fitness and survival and is the first response of reintroduced animals, making it an excellent indicator of reintroduction success. However, there is limited information on the early post-release movement of reintroduced animals. Here, we addressed this important issue by studying the post-release behaviour of the critically endangered black rhinoceros, *Diceros bicornis minor*, reintroduced to the Gonarezhou National Park, Zimbabwe, in 2021. We used daytime sighting data collected from 21 rhinoceros for 1.5 years to investigate survival and reproduction, movement patterns and habitat selection after release. We examine how sex, age and different release sites affect the short-term movement behaviour and habitat selection of black rhinos. Rhinos showed progressive and consistent changes in movement patterns and habitat selection, shifting from large-scale movements during the early stages of release to smaller-scale movements after home ranges were established. We found that rhinos released in the large area had larger activity areas with less overlap between individuals and moved further away from the release site (less fidelity to the release site) than the individuals released in the smaller area. These findings confirm the great capacity of black rhinos to adapt to the environment, occupying large ranges when given the opportunity, but populations with smaller ranges can also be viable. Based on our study and a literature review, we stress the importance of long-term monitoring and believe that reserve size, rhino density, fencing, food and water availability, familiarity between conspecifics and human disturbance are key factors in the successful establishment of a rhino population that should be considered in future reintroductions. Finally, the high survival and birth rates in the first 1.5 years after reintroduction, together with most rhinos having established their home range, suggest a successful reintroduction in the short term.

### 1. Introduction

Translocations and reintroductions are stressful and invasive experiences for animals, as they force them to acclimate and adapt to

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their new environment in a short period. Nevertheless, they can sometimes be the only chance for the survival of certain free-living species or populations (Stüwe and Nievergelt, 1991), making them crucial tools for species conservation (IUCN/SSC, 2013). In recent decades, the number of reintroduction programmes of endangered species for ecological conservation and restoration has increased, but information on their success or failure is often lacking (Resende et al., 2020). Yet an elaborate evaluation is essential to provide evidence for deciding whether to continue these efforts, and to improve the effectiveness of future reintroductions.

Successful reintroduction programmes require not only adequate pre-release planning (e.g. funding, habitat suitability, Ewen and Armstrong, 2007), but also effective post-release monitoring of reintroduced animals (Seddon, 1999). Monitoring survival and reproduction offers insights into the establishment of individuals and the potential for a stable long-term population (Tweed et al., 2003). For example, if a release fails to establish a population, it is crucial to find out why the animals did not survive to identify the mechanisms responsible for the failure of the release efforts (e.g. release methods). In this regard, movement behaviour is also an excellent indicator of reintroduction success (Berger-Tal and Saltz, 2014; Kemink and Kesler 2013). Immediately after release, individuals usually engage in an exploratory phase, moving long distances in search of suitable habitats, followed by a settlement phase, during which individuals are expected to establish their home range depending on factors such as resource availability, predation risk or reproductive success (Berger-Tal and Saltz, 2014; Saltz and Getz, 2021; Yiu et al., 2017). Home range characteristics (e.g. food availability and shelter), ranging behaviour (e.g. fidelity to release site, dispersal), and inter- and intra-specific interactions of released animals contribute to assessing individual responses after release and the overall success of reintroduction efforts (Berger-Tal and Saltz, 2014; Dunham, 2000; Flanagan et al., 2016; Yiu et al., 2017).

Rhinos have become keystone species for international conservation (Emslie and Brooks, 1999) and play an important role in regulating the structure and functioning of the ecosystem in which they live. Over the last century, the black rhino, *Diceros bicornis*, became extinct in most African countries, mainly due to poaching that intensified in the 1970s, so that by the end of the 20th century the species was confined to South Africa, Namibia, Kenya and Zimbabwe, and numbered fewer than 2500 individuals (Emslie and Brooks, 1999). Since then, numerous strategic translocations to more secure areas have been carried out regularly to establish new populations and maintain genetically healthy populations (Adcock et al., 1998; Fyumagwa and Nyahongo, 2010; Göttert et al., 2010; Knight and Kerley, 2009; Storfer, 1999). This is probably the only way to increase the species' range, as the species now exists in isolated populations in public and private reserves (sanctuaries). Successful reintroductions of black rhino into new areas certainly depend upon the anti-poaching efforts (e.g. fencing, patrols, Pfannerstill et al., 2022), but other factors may influence the ability of individuals to establish themselves and form viable populations in the long term. The size of the available area (i.e. fenced or unfenced), resource availability (food and water) and population density influence home range formation and use (Buk and Knight, 2010; le Roex et al., 2019; Linklater and Swaisgood, 2008). For example, in the unfenced Serengeti National Park (12,920 km<sup>2</sup>), Tanzania, rhino density was 0.05 individuals/km<sup>2</sup> and the home range size of established black rhinos was larger (43–133 km<sup>2</sup>, Frame, 1980) than in the fenced Ndumu Game Reserve (116 km<sup>2</sup>), Mozambique, where rhino density was 0.38 individuals/km<sup>2</sup> (7.6 fold increase) and home ranges were ~4–14 km<sup>2</sup> (Conway and Goodman, 1989). Black rhinos are sensitive to anthropogenic disturbance and tend to avoid areas of human activity (Muntifering et al., 2019; Odendaal-Holmes et al., 2014). Finally, the survival and capacity of released individuals to adapt may also depend on internal factors, such as their age and sex (Adcock et al., 1998; Plotz et al., 2016). Despite the increase in reintroduction efforts and growing knowledge accumulated by past translocations, post-release monitoring is lacking and studies on home range establishment (e.g. when reintroduced individuals stop searching and establish their home range) and utilization (e.g. in relation to available habitats or the release site) of reintroduced rhinos remain limited (Pfannerstill et al., 2022), or are based on small sample sizes (Göttert et al., 2010; Schwabe et al., 2015). Here we investigate the survival, reproduction, ranging behaviour (e.g. release site fidelity), home range establishment and habitat selection of black rhinos reintroduced in Gonarezhou National Park, south-eastern Zimbabwe.

In Gonarezhou National Park, the black rhino went locally extinct around the 1940s (Goza et al., 2019). To rebuild a viable population, 77 rhinos were reintroduced in the area between 1969 and 1971. The reintroduction programme was successful, but the subsequent protection failed as the rhino population was again eradicated by 1994 due to illegal hunting (du Toit et al., 2005). More than 25 years later, the Gonarezhou Conservation Trust, a co-management partnership between the Zimbabwe Parks and Wildlife Management Authority (ZPWMA) and the Frankfurt Zoological Society (FZS) implemented a second re-introduction programme. In 2021, 29 rhinos were re-introduced in the north-western part of Gonarezhou National Park, in a large fenced Intensive Protection Zone (IPZ) established for this purpose. To increase the chances of success, more investment in conservation activities, law enforcement and post-release monitoring was implemented. Here, we use sighting data from rhinos collected for 1.5 years after their release to: (1) document survival, reproduction and causes of mortality among released rhinos, (2) describe movements and interactions between reintroduced rhinos while they are trying to settle and (3) gain insight into how natural and anthropogenic factors influence ranging behaviour and home range establishment. As rhinos are not expected to have established home ranges soon after release, we used the term 'activity area' throughout, rather than home range, to describe the area used, which thus includes exploratory movements and dispersal events, until settlement. We tested the predictions that (1) rhinos engage in exploratory behaviour after release, resulting in an increase in activity areas and distance to the release site, which gradually stabilise once individuals have settled, (2) the activity area after settlement is a portion of the area explored after release, (3) available area affects rhino movement patterns and space use, where individuals released into a smaller area would occupy smaller activity areas and distances to the release site, and share more space with their conspecifics and (4) rhinos would select areas providing food and water, and avoid areas close to roads to minimise human disturbance. We use our findings, together with the available literature, to identify key factors for successful rhino reintroductions.

## 2. Material and methods

### 2.1. Study area

The study was carried out in a 500 km<sup>2</sup> fenced Intensive Protection Zone (IPZ) in the northern part of Gonarezhou National Park, located in the southeast lowveld Zimbabwe (21°15'S, 30°32'E). The study site is situated in the semi-arid climate zone, and most rain falls during the wet season (between November and March). The soils are shallow and siliceous, and the vegetation is mainly dry deciduous savanna of various types, dominated by *Colophospermum mopane* forests and riparian and alluvial forests (Cunliffe et al., 2012; Gandiwa et al., 2014). There is a high density of shrubs made up of *Colophospermum mopane*, *Combretaceae* and *Spirostachys*, which are known to be palatable and good quality browsing for black rhinos (Goza et al., 2019; Matipano, 2003). Altitude ranges between 300 and 500 m above sea level. The study area is divided by the natural and perennial Runde River, providing water for animals throughout the year, but the high water levels and steep, rocky nature are expected to be a physical barrier to the rhinos, preventing them from accessing all sides of the Runde River banks (Gandiwa and Zisadza-Gandiwa, 2015). The study area is thus stratified into two zones, i.e. on both sides of the Runde River, with the northern zone representing an area of 410 km<sup>2</sup> and the southern zone 95 km<sup>2</sup>, resulting in a very low rhino density of 0.05 and 0.09 rhinos per km<sup>2</sup>, respectively (no rhinos were present in the area before the reintroduction). Other herbivore species inhabit the area, the most common of which are African elephant (*Loxodonta africana*), Cape buffalo (*Syncerus caffer*), and blue wildebeest (*Connochaetes taurinus*). Carnivores such as lions (*Panthera leo*), leopards (*Panthera pardus*), brown (*Hyena brunnea*) and spotted hyenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) inhabit the study area as well.

### 2.2. Translocation procedures and animals

As part of the joint Zimbabwe Parks and Wildlife Management Authority (ZPWMA) and the Frankfurt Zoological Society rhino reintroduction project, 29 black rhinos were translocated to the IPZ in 2021 and released at two separate sites: in the southern (small) part of the IPZ ( $n = 9$ ), and in the (large) northern part ( $n = 20$ , Table 1). The translocated rhinos originated from three conservation areas in south-eastern Zimbabwe: the Buby Valley Conservancy (linear distance between capture and release site: ~100 km), the Malilangwe Conservation Trust (~20 km) and the Save Valley Conservancy (~50 km). Rhinos were immobilised by helicopter and transported to the IPZ by trucks. The black rhinos were released "softly", i.e. kept in pens at the release site for several days. The purpose of this period of confinement was to relax the rhinos after travel and ensure acceptance of local food in their diet (Morkel and Kennedy-Benson, 2007). Rhinos released in the south had access to an enclosure providing water for one week after release. The surrounding area was regularly checked for footprints, but no rhinos were found to have returned. Although the climate was drier during the releases in the north (June to August), the rhinos did not have access to water to avoid attracting curious elephants to the area and encounters between elephants and rhinos soon after the releases.

Age was determined based on their known dates of birth and individuals were classified into three categories based on age and sexual maturity. Rhinos were considered calves until 2 years of age or until the birth of the mother's next calf, subadults until 7 years of age or at first calving for females and 8 years of age for males, adults otherwise (Law and Linklater, 2014). All adult females were with a calf older than 16 months at the time of release (Table 1). Adults and subadults were fitted with VHF horn transmitters to support monitoring. Approval for the translocation projects was given by the Zimbabwe Parks and Wildlife Management Authority, and all animal handling was performed by experienced, qualified veterinarians, security rangers and authorized monitoring personnel.

### 2.3. Movement data collection

Between 30 May 2021 and 31 December 2022, the rhinos were located regularly (at least once a week) at irregular intervals during the day by VHF radio-telemetry, using a R-1000 receiver (Telonics, Inc., Mesa, AZ, USA), combined with tracking and sighting methods by foot, as well as aerial observations. Each rhino has its physical characteristics, such as ear notches, allowing the rangers to recognise the individual. When a rhino was located in the field, the rangers reported the GPS location (up to 20 m away from the rhino), the identity of the rhino and its activity to a central station where these data were recorded using the EarthRanger software program. Only one position was recorded when two or more rhinos were observed at close distance to each other (observed < 50 m apart).

Calves ( $n = 8$ ) were excluded from the analysis as they are dependent on their mothers and have the same movement patterns. Thus, we analysed 2138 observations of 21 reintroduced individuals (11 females and 10 males) tracked for ~1.5 years after release to assess

**Table 1**

Number of black rhinos ( $n = 29$ ), by sex and age, released in two sites in the Intensive Protection Zone in Gonarezhou National Park from May to August 2021.

Release dates	Area	Source population	Subadult females	Adult females	Subadult males	Adult males	Calves
May 2021	South	Malilangwe Conservation Trust	2	2	1	1	2
June-July 2021	North	Buby Valley Conservancy	1	4	4	2	4
		Save Valley Conservancy		2			2
August 2021	South	Malilangwe Conservation Trust				1	
August 2021	North	Malilangwe Conservation Trust				1	

their settlement behaviour. The number of locations per individual varied between 57 and 172 (mean  $\pm$  SD = 101.81  $\pm$  27.41) and the mean ( $\pm$  SD) interval between successive locations was 5.70  $\pm$  1.25 days.

#### 2.4. Exploratory movement, settlement and release-site fidelity

To determine the exploratory time, we calculated the activity area size against time in days for every rhino using the 95% bivariate kernel utilization distribution (KUD) with a smoothing parameter of 500 m and a cell size of 100 m (Plotz et al., 2016). We computed KUDs from the first five locations, and then re-estimated them by adding each newly acquired location. We considered the study area fence and the Runde river, both restricting rhino movement, using the method developed by Benhamou and Cornélias (2010) in the “adehabitatHR” package in R (Calenge, 2007). To meet the requirements of this approach, we simplified the boundaries by reducing vertices to one every 2.5 km. Exploratory time coincides with the time when the activity area size reached 90% of the total cumulative activity area size (i.e. approaching the asymptote), providing  $>$  15 locations to determine the asymptote and ensure a stabilization. Without this condition, individuals were considered as non-settled and their exploratory time corresponded to their tracking time.

We used the exploratory time for each individual to identify the exploratory and settlement phases. We quantify the movement range size during both phases by calculating full activity area (95% KUD) and core activity area (50% KUD) for each rhino and phase. During the exploratory phase, the full activity area reflects the initial exploration area, while during the settlement phase, it represents the initial home range. We also provide the 1.5-year activity area sizes calculated using two estimators, KUD and minimum convex polygons (MCP) in the Supporting Information to allow comparisons with translocated animals (e.g. Pfannerstill et al., 2022). Based on a minimum of 30 annual locations to accurately estimate the KUD activity area, all rhinos had sufficient data, but only 19 rhinos were used to estimate the MCP activity areas to meet the minimum requirement of  $\sim$ 50 annual locations (Plotz et al., 2016). We investigated release site fidelity by calculating the distance between the release site and all individual locations over time. We compared the location of the settlement full and core activity areas to the explored areas by calculating the proportion of the settlement full and core activity areas covered by the exploratory full and core activity areas, respectively.

We fitted multiple linear regression models to examine the effects of sex, age and release site (north vs. south) on the exploratory time, and of sex, age, release site and phase (exploratory vs. settlement) on full and core activity area sizes because data were normally distributed. We tested the effects of sex, age, release site, and days after release on the distance to the release site using a mixed linear regression model, with rhino identity as a random effect because of the different sample sizes and repeated observations among the individuals. Distance to the release site was square-root transformed prior to analysis to achieve a normal distribution of this response variable. We could not test the source population’s influence on the space use of the released rhinos because almost all individuals from the same source population were released at the same site (Table 1). Given our small sample size, we did not include any interaction between the explanatory variables.

#### 2.5. Sociality

To investigate how rhinos respond to other rhinos after release in terms of space use, we calculated the overlap of full and core activity areas between paired individuals (dyad) during exploratory phase and settlement phase. We estimated the overlap of the full and core activity areas between dyads as the proportion of one animal’s area covered by another animal’s area (Fieberg et al., 2005).

We tested the effects of sex (4 levels: F-F: ‘female-female’, F-M: ‘female-male’, M-F: ‘male-female’, M-M: ‘male-male’) and age (4 levels: A-A: ‘adult-adult’, SA-A: ‘subadult-adult’, A-SA: ‘adult-subadult’, SA-SA: ‘subadult-subadult’) of the dyad, release site, and phase on full and core activity area overlap using 2 mixed linear regression models with a binomial distribution of errors. Dyad identity was included as a random intercept because dyads were not independent (individuals can belong to several dyads).

#### 2.6. Habitat composition and use of activity areas

We classified habitat within our study area using an existing vegetation map from Cunliffe et al. (2012) at a scale of 1:100,000. Based on predominant habitats within the study area, we reclassified habitats into five basic types: mixed *Brachystegia tamarindoides* woodland, *Colophospermum mopane* woodland, open *Combretum apiculatum* woodland, *Androstachys johnsonii* woodland (dry forest and thickets) and wooded grassland. We obtained elevation data at 30 m resolution from the Copernicus Digital Elevation Model (DEM) produced by the European Space Agency (ESA) and acquired from the Digital Earth Africa platform (DEAfrica, 2021). We created shapefiles of roads, open water (rivers and dam), and fences from satellite images in Google Earth and in field ground mapping.

To explore how rhinos used the environment during the exploratory phase, we contrasted habitat between observed rhino locations during the exploratory phase and locations randomly generated in the available area (north or south) at a 1:10 ratio (i.e. 10 random points for each location used) (hereafter “landscape scale”, also called “second-order habitat selection”; Johnson, 1980). During the establishment phase, we assessed habitat selection at two spatial scales: (1) the location of the full activity area in the landscape (landscape scale) and (2) within the full activity area (hereafter “activity area scale”, also called “third-order habitat selection”; Johnson, 1980). For the landscape-scale analyses, we compared habitat between 100 random locations in each individual full activity area (95% KUD) in the establishment phase and 1000 random locations in the available area (north or south), ensuring a 1:10 ratio of used to available positions among individuals (Fieberg et al., 2021; Northrup et al., 2013). For the activity area-scale analyses, we compared habitat between observed rhino locations and randomly generated locations in their full activity area during the establishment phase at a 1:10 ratio. For each used and random location, we calculated the linear distance to the nearest water, road and fence, and extracted the values of elevation and vegetation class.

We used generalized linear mixed models (GLMM) to assess the relationships between covariates and the relative probability of rhino habitat use at the different scales (landscape and activity area) and phases (exploratory and settlement) at the population level. Since the response variable is binary (indicating habitat use or availability), we used a binomial error distribution and a logit link function. To account for the non-independence of data from the same individual, we included a random intercept for each individual in the models (Gillies et al., 2006). We also included random slopes for our continuous explanatory variables to account for individual-specific variation in habitat selection as recommended by Muff et al. (2020). To ensure the robustness of the results, we assigned a weight of 5000 to each available location and a weight of 1 to each used location and setting the variance of random intercepts to  $10^6$  (Fieberg et al., 2021; Muff et al., 2020). We scaled our continuous predictors by 1 standard deviation and centered them at zero to compare resource selection strength effect sizes. We chose the ‘mixed *Brachystegia tamarindoides* woodland’ as the reference level for the habitat category because it is the most abundant habitat category in the study area. The analysis represents daytime use because we used sighting data (collected during the day).

We used the R package ‘glmmTMB’ (Brooks et al., 2017) to estimate the GLMM parameters, which implements maximum likelihood estimation. All significance levels were set at 5%. All analyses were performed in the R statistical computing environment (R Core Team, 2020).

### 3. Results

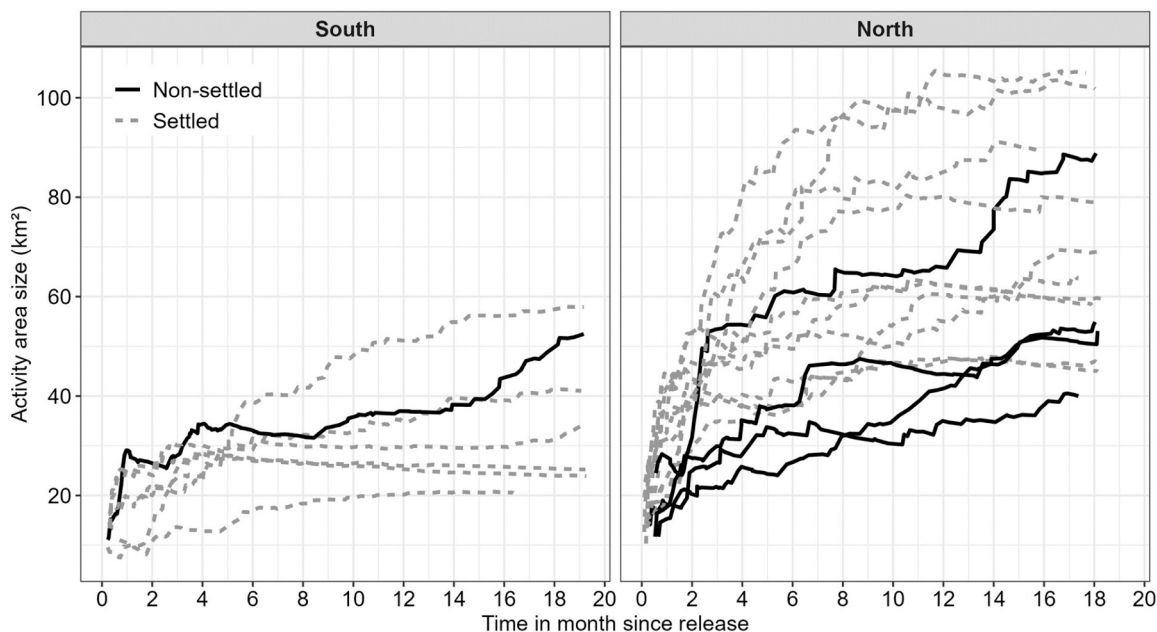
#### 3.1. Survival and breeding success

Of the 29 rhinos released, 27 individuals (93.10%) survived the entire monitoring period. Two individuals died before the end of the study, irrespective of the release site: a male in the southern area and a female in the northern area died 15 and 12 months after release, respectively. These two individuals were calves at the time of release and both died of natural causes shortly after weaning.

Over the same period, 6 out of 8 (75%) adult females gave birth to a new calf (including the mothers of the two dead calves): in the northern area, only four adult females out of six gave birth again, but one of these calves unfortunately died. This calf was the first born after the release (~ 5 months) and was probably predated by hyenas, while its mother hid it to go to the water.

#### 3.2. Exploratory movement, settlement and release-site fidelity

The cumulative area of 95% KUD of all rhinos increased rapidly after release, indicating an expansion of full activity area (Fig. 1). A stabilization in cumulative area was detected for most rhinos, suggesting settlement, but five individuals continued to expand their range throughout the study period (Fig. 1). Mean ( $\pm$  SD) exploratory time was  $313.9 \pm 160.0$  days (range = 66 – 575 days) and did not vary between individuals according to their sex ( $p = 0.54$ ), age ( $p = 0.33$ ) and release site ( $p = 0.48$ ). However, during the exploratory phase, both full and core activity areas were significantly larger ( $n = 21$ , mean  $\pm$  SD: 95% KUD<sub>exp</sub> =  $57.2 \pm 21.0$ , 50% KUD<sub>exp</sub> = 11.2



**Fig. 1.** Cumulative area of 95% utilization distribution of 21 rhinos during early post-release period in 2021–2022 in the Gonarezhou National Park, Zimbabwe, depending on release site (south vs. north). The grey and dotted curves represent individuals for which a long stabilisation was detected, suggesting settlement. Five individuals (solid curves in black) continued to extend their full activity area throughout the monitoring period.

$\pm 3.7$ ) than during the settlement phase ( $n = 16$ , 95%  $KUD_{set} = 34.3 \pm 14.9$ , 50%  $KUD_{set} = 8.5 \pm 3.4 \text{ km}^2$ ), but there was no difference in area size according to age and sex of the individual (Table 2). Activity areas of rhinos released in the southern area (mean  $\pm$  SD: 95%  $KUD = 31.0 \pm 12.6$ , 50%  $KUD = 7.3 \pm 2.7 \text{ km}^2$ ) were significantly smaller than those of individuals released in the northern area (mean  $\pm$  SD: 95%  $KUD = 56.1 \pm 20.5$ , 50%  $KUD = 11.5 \pm 3.4 \text{ km}^2$ , Table 2). Among settled individuals, the full activity areas during the establishment phase largely overlapped with those of the exploratory phase ( $69.24 \pm 7.46\%$ ), in contrast to the core areas ( $28.5 \pm 23.2\%$ ).

The distance rhinos travelled from the release site to the relocation sites increased with time since release and differed between release sites, with individuals released in the northern area moving further from the release site (lower site fidelity) than those released in the southern area (Fig. 2, Table 3). Subadults tended to travel less far than adults, especially in the northern area, and there was no difference between sexes (Table 3).

### 3.3. Sociality

In most cases, rhinos were observed alone or with their calves for adult females (87.2% of locations), but they occasionally formed groups of two (12.2%) and three animals (0.6%). Most groups consisted of an adult male and one or two subadult females (~30%), an adult and subadult female (~29%), and an adult female accompanied by either an adult male (15%) or a subadult male (12%). All-male groups represented only 6.77% of the groups observed, while all-female groups represented 33.08%.

The full and core activity areas overlapped to some extent between individuals. The proportion of spatial overlap was independent of the sex and age of the dyad, but varied significantly with release site; individuals released in the southern area showed higher overlap (mean  $\pm$  SD: 95%  $KUD = 41.8 \pm 30.1$ , 50%  $KUD = 17.1 \pm 25.0\%$ ) than those released in the larger northern area (mean  $\pm$  SD: 95%  $KUD = 16.8 \pm 20.0$ , 50%  $KUD = 4.2 \pm 10.7\%$ ; Table 4, Fig. 3A). In addition, during the settlement phase, there was less overlap between the full activity areas of individuals ( $16.2 \pm 27.4\%$ ) than during the exploratory phase ( $25.1 \pm 22.5\%$ ); no such difference was observed for the core activity areas, which are smaller than full activity areas in both phases (Table 4, Fig. 3B).

### 3.4. Habitat composition and use of activity areas

Vegetation type is the habitat that most influences how rhinos use the environment. During the exploratory phase, rhinos significantly avoided *A. johnsoni* and mopane woodlands, but preferred wooded grasslands, compared to mixed *Brachystegia tamarindoides* woodlands (Table 5). Though not significant, there was also a trend towards increased space use as elevation increased (Table 5). In the same way, rhinos established their initial home range within the study area according to vegetation, with a strong avoidance of *A. johnsoni* woodlands and *C. apiculatum* (Table 5, landscape scale). Mopane woodlands tend to be avoided, and wooded grasslands favoured compared to mixed *Brachystegia tamarindoides* woodlands, but the trends were slightly significant. None of the tested variables significantly influenced habitat selection within their initial home range (during establishment phase), but distance to the nearest road showed a slight positive effect, hardly significant (Table 5, activity area scale).

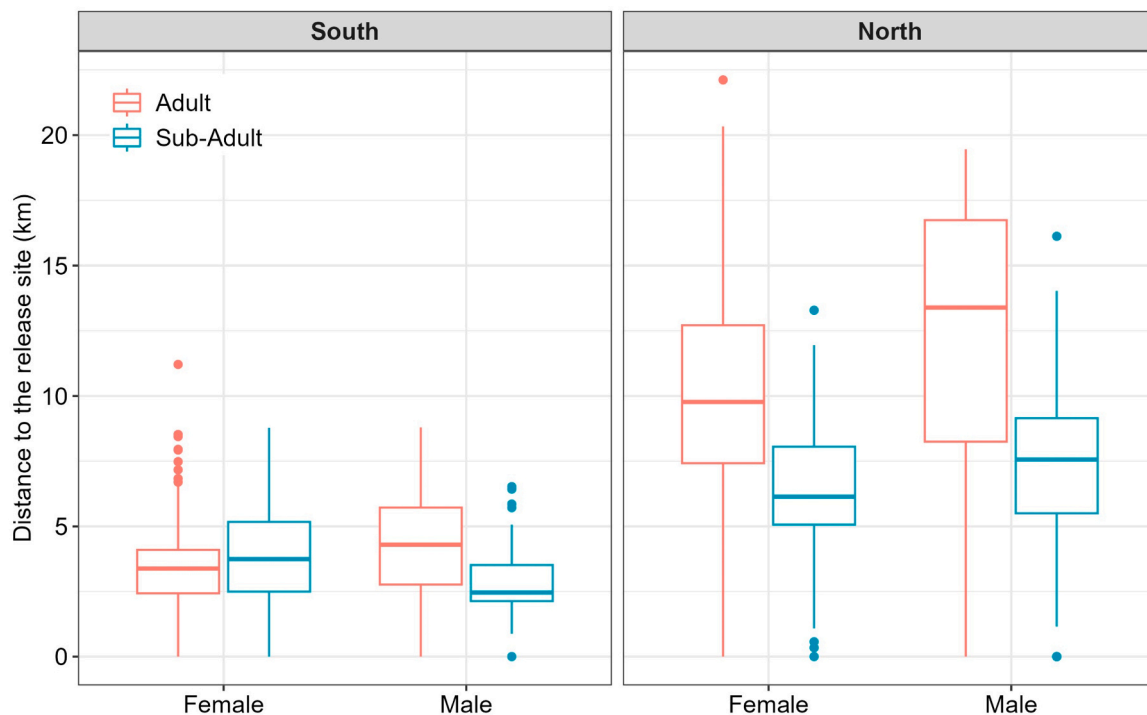
## 4. Discussion

Black rhinos showed progressive and consistent changes in movement patterns after introduction to a new area. The cumulative activity area size of rhinos increased substantially after release and the full and core activity areas during the exploratory phase were greater than during the establishment phase. These results suggest a shift in movement patterns from expanding movements during the early stages of release to more localized movements after initial home ranges were established and the animals became more familiar with the environment. The post-settlement full activity area largely overlapped the one used during exploration, whilst post- and pre-settlement core activity areas overlapped less, suggesting rhinos established their initial home range within the explored area but

**Table 2**

Effects of sex, age category (subadult/adult), phase (exploratory/settlement) and release site on activity area sizes ( $\text{km}^2$ ) of 21 reintroduced rhinos in IPZ in Gonarezhou National Park in 2021–2022. The rhinos were reintroduced in two sites (north/south) within the study area (Table 1). Rhino identity was included as a random effect.

Explanatory variables	$\beta$	SE	<i>t</i>	P
<b>Full activity area size (95% KUD)</b>				
Intercept	65.963	4.585	14.388	<0.001
Sex (male vs. female)	-0.673	5.034	-0.134	0.895
Age (Subadult vs. adult)	-1.199	5.364	-0.224	0.825
Release site (south vs. north)	-23.934	5.260	-4.551	<0.001
Phase (settlement vs. exploratory)	-21.973	5.000	-4.396	0.001
<b>Core activity area size (50% KUD)</b>				
Intercept	12.801	0.931	13.743	<0.001
Sex (male vs. female)	-0.465	1.024	-0.454	0.652
Age (Subadult vs. adult)	0.125	1.090	0.115	0.909
Release site (south vs. north)	-4.221	1.069	-3.950	<0.001
Phase (settlement vs. exploratory)	-2.565	1.015	-2.525	0.017



**Fig. 2.** Distance from the release site to the relocations of 21 rhinos in 2021–2022 that were reintroduced in two sites in Gonarezhou National Park, Zimbabwe.

**Table 3**

Effects of sex, age category (subadult/adult), release site and number of days after release on square root of the distance from the release site to 2138 relocations of 21 reintroduced rhinos in IPZ in 2021–2022. The rhinos were reintroduced in two sites within the study area (Table 1). Rhino identity was included as a random effect.

Explanatory variables	$\beta$	SE	$z$	P
Intercept	1.885	0.203	9.269	<0.001
Sex (male vs. female)	0.119	0.204	0.584	0.560
Age (Subadult vs. adult)	-0.388	0.210	-1.847	0.065
Release site (north vs. south)	1.008	0.211	4.786	<0.001
Days after release	0.001	0.000	7.172	<0.001

intensively use distinct zones. Although some rhinos stabilized in full activity area size, five individuals (23.8%) continued expanding throughout the study period, indicating that activity area expansion of reintroduced rhinos is a lengthy process that can last more than 1.5 years. Adcock et al. (1998) reported that translocated black rhinos can require up to 3 years to settle and establish suitable home ranges. This lengthy settlement period highlights the importance of monitoring reintroduced rhino over long periods (Gedir et al., 2018).

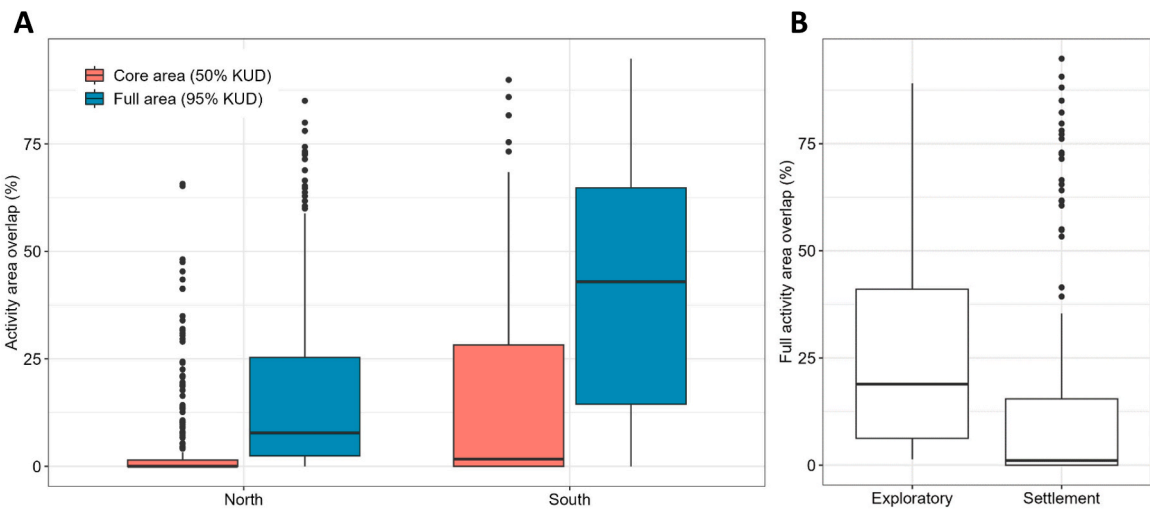
Rhinos released in the northern area had larger activity areas with less overlap between individuals and moved further away from the release site (less fidelity to the release site) than individuals living in the southern area. Although our release sites followed the guidelines proposed by Linklater and Swaisgood (2008) in terms of reserve size and conspecific density, the northern area was larger (400 km<sup>2</sup> vs. 95 km<sup>2</sup>) and had a lower rhino density (0.05 vs. 0.09 inds/km<sup>2</sup>) than the southern area. As observed in previous studies (le Roex et al., 2019; Linklater and Swaisgood, 2008; Tatman et al., 2000, Table S2), the available area (due to fencing and river) and population density in our study likely shaped black rhino movements and home range formation, with individuals living in a small area having less space to explore and disperse, forcing them to stay close to the release site and establish small home ranges with more overlap with their conspecifics. However, activity area sizes of all rhinos remained below half or a quarter the size of the available area in the south (< 50 km<sup>2</sup>) or north (< 100 km<sup>2</sup>, Appendix S1: Table S1), respectively, suggesting that rhinos were able to acquire essential resources for survival within small areas. Black rhinos show high adaptability (Linklater and Swaisgood, 2008), so they can explore and occupy large ranges when given the space to do so, but viable populations with smaller ranges (our study) demonstrate that a large area is not a prerequisite for successful rhino survival and reproduction. However, this is only true if the habitat can sustain the overall rhino population, and it is therefore crucial to accurately assess the appropriate number of individuals to be reintroduced in proportion to the size of the available area (Linklater and Swaisgood, 2008; Tatman et al., 2000).

**Table 4**

Effects of sex and age of the dyad, phase (exploratory/settlement) and release site (north/south) on spatial overlap of activity areas of 21 reintroduced rhinos in IPZ in Gonarezhou National Park in 2021–2022. We fitted response variables with binomial generalized linear mixed models with dyad identity as a random effect.

Explanatory variables	$\beta$	SE	z	P
<b>Full activity area overlap (95% KUD)</b>				
Intercept	-1.292	0.317	-34.081	<0.001
Sex (F-M vs. F-F)	0.119	0.379	0.314	0.753
Sex (M-F vs. F-F)	0.125	0.378	0.331	0.741
Sex (M-M vs. F-F)	-0.352	0.446	-0.790	0.430
Age (A-SA vs. A-A)	-0.223	0.364	-0.611	0.541
Age (SA-A vs. A-A)	-0.114	0.359	-0.319	0.750
Age (SA-SA vs. A-A)	-0.414	0.507	-0.815	0.415
Release site (south vs. north)	1.397	0.308	4.533	<0.001
Phase (settlement vs. exploratory)	-0.718	0.308	-2.334	<0.020
<b>Core activity area overlap (50% KUD)</b>				
Intercept	-3.417	0.590	-5.791	<0.001
Sex (F-M vs. F-F)	-0.312	0.606	0.515	0.607
Sex (M-F vs. F-F)	0.354	0.601	0.589	0.556
Sex (M-M vs. F-F)	-0.887	0.876	-1.012	0.311
Age (A-SA vs. A-A)	0.292	0.578	0.506	0.613
Age (SA-A vs. A-A)	0.377	0.567	0.665	0.506
Age (SA-SA vs. A-A)	-0.191	0.846	-0.226	0.821
Release site (south vs. north)	1.475	0.459	3.213	0.001
Phase (settlement vs. exploratory)	0.201	0.451	0.447	0.655

Note: Sex (4 levels: F-F: 'female-female', F-M: 'female-male', M-F: 'male-female', M-M: 'male-male'), Age (4 levels: A-A: 'adult-adult', A-SA: 'adult-subadult', SA-A: 'subadult-adult', SA-SA: 'subadult-subadult').



**Fig. 3.** Spatial overlap of (A) full and core activity areas depending on release site and (B) full activity areas depending on phase.

Black rhinos shared more space during the exploratory phase than during the settlement phase, suggesting a preference for establishing exclusive activity areas. Moreover, we observed our individuals mostly alone or with their young for adult females. Social interactions leading to spatial overlap generally occur around waterholes, which rhinos visit mainly at night (Kasiringua et al., 2017; Mukinya, 1977). We may have missed this behaviour, simply because we used data collected during the day. Previous studies have documented the existence of temporary groups and social interactions between individuals, especially outside the breeding season (Göttert et al., 2010; Tatman et al., 2000). Although based on a smaller sample, Göttert et al. (2010) observed rhinos forming groups of up to four individuals during the day for 21.7% of the time (compared to 12.8% of the time in our study) and Goddard (1967) reported a group of 13 rhinos, although the animals separated after 2 h. Due to our small sample size, we used spatial overlap as a proxy of social interactions (Robert et al., 2012), but we acknowledge that this estimator probably overestimates contact rates, especially as we observe high spatial overlap despite most individuals being observed alone. In the future, monitoring our population with technologies that allow regular tracking, particularly at night, would definitely improve our knowledge of the social behavior of black rhinos.

Familiarity among conspecifics likely influenced space sharing between individuals in our study. Rhinos released in the south originated from the same population, whereas rhinos in the north came from three different populations. Individuals in the south may have overlapped more, especially during the exploratory phase, because they were familiar with each other before the translocation.



**Table 5**

Summary table of the generalized linear mixed models for (1) the landscape-scale (second-order selection) resource selection function during exploratory phase and (2) the landscape (second-order selection) and activity area (third-order selection) scales resource selection function during the settlement phase after release of black rhinos in Gonarezhou National Park, Zimbabwe, 2021–2022. Population-level, fixed-effects coefficient estimates of relative selection strength on the natural logarithmic scale ( $\beta$ ) with standard errors (SE), z-values and p-values from the model are provided. Note that continuous variables (i.e. elevation, distance to the nearest road, water and fence) were scaled by 1 standard deviation and centered at their means prior to analysis for relative coefficient comparisons.

Explanatory variables	$\beta$	SE	z	P
1 – Exploratory phase (n = 21 rhinos)				
<b>Landscape scale (full activity areas within the landscape)</b>				
Elevation	0.302	0.155	1.944	0.052
Distance to the nearest road	-0.0168	0.124	-1.350	0.177
Distance to the nearest water	-0.057	0.383	0.148	0.882
Distance to the nearest fence	0.254	0.187	1.361	0.174
Vegetation class (C. <i>apiculatum</i> vs. mixed B. <i>tamarindoides</i> woodland)	-0.084	0.115	-0.727	0.468
Vegetation class (A. <i>johnsonii</i> vs. mixed B. <i>tamarindoides</i> woodland)	-1.531	0.324	-4.726	< 0.001
Vegetation class (Wooded grassland vs. mixed B. <i>tamarindoides</i> woodland)	0.306	0.104	2.940	0.003
Vegetation class (Mopane vs. mixed B. <i>tamarindoides</i> woodland)	-0.222	0.080	-2.757	0.006
2 – Settlement phase (n = 16 rhinos)				
<b>Landscape scale (full activity areas within the landscape)</b>				
Elevation	0.257	0.251	1.022	0.307
Distance to the nearest road	-0.027	0.205	-0.132	0.895
Distance to the nearest water	0.091	0.559	0.163	0.870
Distance to the nearest fence	0.128	0.208	0.614	0.539
Vegetation class (C. <i>apiculatum</i> vs. mixed B. <i>tamarindoides</i> woodland)	-0.281	0.122	-2.300	0.021
Vegetation class (A. <i>johnsonii</i> vs. mixed B. <i>tamarindoides</i> woodland)	-0.865	0.238	-3.632	< 0.001
Vegetation class (Wooded grassland vs. mixed B. <i>tamarindoides</i> woodland)	0.190	0.098	1.931	0.053
Vegetation class (Mopane vs. mixed B. <i>tamarindoides</i> woodland)	-0.149	0.079	-1.882	0.060
<b>Activity area scale</b>				
Elevation	0.091	0.145	0.631	0.528
Distance to the nearest road	0.271	0.144	1.884	0.060
Distance to the nearest water	0.172	0.208	0.830	0.406
Distance to the nearest fence	-0.009	0.096	-0.092	0.926
Vegetation class (C. <i>apiculatum</i> vs. mixed B. <i>tamarindoides</i> woodland)	0.222	0.161	1.381	0.167
Vegetation class (A. <i>johnsonii</i> vs. mixed B. <i>tamarindoides</i> woodland)	0.201	0.372	-0.540	0.589
Vegetation class (Wooded grassland vs. mixed B. <i>tamarindoides</i> woodland)	0.061	0.157	0.390	0.697
Vegetation class (Mopane vs. mixed B. <i>tamarindoides</i> woodland)	-0.016	0.164	-0.097	0.923

We propose that conflicts between reintroduced rhinos could be mitigated by selecting individuals carefully, favoring those from same populations, while ensuring genetic diversity and providing sufficient physical and social space.

Over a year post-reintroduction, high survival and birth rates suggest short-term success (Gedir et al., 2018). No cases of poaching were reported during the monitoring period, which is probably the result of careful site selection, complete fencing and regular patrols. Nevertheless, sustained long-term monitoring and protection of rhinos is crucial to prevent poaching, as observed in Botswana after the reintroduction of white and black rhinos (Pfannerstill et al., 2022). There were no significant differences in movement behavior between subadults and adults after release, suggesting that age has little effect on the adaptability of rhinos. Reintroducing adult female black rhinos, in particular older females, is encouraged to promote released population growth and long-term reintroduction success (Gedir et al., 2018), but translocating adult females is challenging as they are either pregnant or have a calf at foot. Young rhinos are generally more vulnerable to translocation, so translocations of mothers with calves younger than 16 months are discouraged (Brett, 1998; Emslie and Brooks, 1999; Gedir et al., 2018; Linklater and Swaisgood, 2008). All the calves reintroduced in our study area were > 16 months old. Unfortunately, two of them died a year later, shortly after the birth of another calf from their mother. Before giving birth to a new calf, rhino mothers wean their previous calf (generally aged between 25 and 29 months, Goddard, 1967; Hrabar and Toit, 2005). This phase is critical as weaned animals immediately lose maternal protection, facing various risks, such as lack of knowledge of resources, competition and conflicts for resources, disease, interspecific conflict, and misadventure. In established populations, calves join older siblings or familiar animals (Goddard, 1967), but in a new population such as ours, they are often on their own after the weaning phase. The first calf born post-translocation (approximately 5 months later) also died, likely due to predation by a hyena while the mother was fetching water in a distant area (Goddard, 1967; Hitchins and Anderson, 1983). The deaths of calves were therefore probably not linked to the reintroduction per se. Six calves were born during the monitoring period, with the latest birth occurring in July 2022, approximately 14 months after the first release. Given the gestation period of black rhinos (15–18 months, Goddard, 1967), the births recorded were from conceptions in the source population. The female black rhinos adapted sufficiently and obtained adequate resources to maintain gestation and not abort after translocation. This is promising for the survival and maintenance of this population. The next challenge will be to find out whether the females are able to mate and reproduce in their new habitat.

How rhinos used and selected patches seemed strongly linked to forage and cover availability (Mukinya, 1973; Reid et al., 2007). At the landscape scale, both during exploratory and establishment phases, rhinos avoided dry *A. johnsonii* woodland and mopane woodlands, but preferred wooded grasslands compared to mixed *B. tamarindoides* woodlands, the most abundant vegetation in our

study area. They additionally avoided *C. apiculatum* when establishing their initial home range. Wooded grasslands are dominated by *Spirostachys africana*, *Dichrostachys* spp. and *Acacia* spp. all of which are palatable to rhinos, unlike *Androstachys johnsonii* (Buk and Knight, 2010; Buk and Knight, 2012; Mukinya, 1977; Oloo et al., 1994). Surprisingly, we found no effect of distance to water on habitat selection at any scale and phase, despite water being a recognized limiting factor for black rhinos, as they need to drink around 40 liters a day (Bothma, 2002 in Kasiringua et al., 2017; le Roex et al., 2019). This is probably due to our data collection through direct observation, reflecting rhino daytime habitat use. Black rhinos are mainly nocturnal and drink water in the evening and at night (Goddard, 1967; Kasiringua et al., 2017; Mukinya, 1977). Additionally, rhinos used areas ~1.2 km away from water sources, on average, with a maximum distance to any water source being ~3 km, so the rhinos were always relatively close to water sources. Consistent with our observations, Buk and Knight (2012) found that distance to water was not among the top five factors influencing habitat suitability for black rhino, whilst Odendaal-Holmes et al. (2014) found that rhinos avoided water sources during the daytime. We found that rhinos tended to slightly, but not significantly, avoid areas near roads within their established home range. It is well known that human disturbance negatively affects black rhinos, which tend to avoid areas of human activity (Buk and Knight, 2012; Mukinya, 1973; Muntiferung et al., 2019; Odendaal-Holmes et al., 2014). While limiting human disturbance seems crucial for identifying suitable areas for rhino reintroductions, roads also aid in monitoring and protecting of animals, as well as supporting wildlife-based tourism, a valuable tool for conserving animal species (Muntiferung et al., 2019).

## 5. Conclusions

This study offers insights into the establishment behavior of a reintroduced black rhino population. Based on our findings and a literature review, we propose eight key factors for successful rhino reintroduction: (1) reserve size; (2) release density; (3) food and (4) water availability remain the most important criteria in determining whether the reserve can support a viable number of individuals. But our findings suggest (5) considering familiarity between conspecifics and (6) minimizing human disturbance in the release area, particularly around favourable areas, such as water sources. We also highlight the importance of (7) reserve security, including fencing, and (8) regular, long-term monitoring by patrols to ensure the long-term success of rhino settlement and their protection. The future of the species in the area appears favourable and the low short-term mortality rate gives hope for future rhino translocations. Still, continuous monitoring is necessary to prevent potential poaching events that could be disastrous for the population's survival.

## CRedit authorship contribution statement

**Heurich Marco:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing – review & editing. **Wieprecht Sashimi:** Formal analysis, Methodology, Writing - review & editing. **Mandinyenya Bob:** Conceptualization, Investigation, Resources, Writing - review & editing, Data curation. **Wielgus Elodie:** Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing, Software, Visualization.

## Declaration of Competing Interest

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

## Data Availability

The locations of the rhinos are sensitive data and are therefore not publicly available.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02756](https://doi.org/10.1016/j.gecco.2023.e02756).

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